



UNIVERSITÀ
DEGLI STUDI
DI PADOVA



UNIVERSITÉ
DE MONTPELLIER

Administrative units: **University of Padova, University of Montpellier**

Departments: **Land, Environment, Agriculture and Forestry (TESAF)**

Institut des Sciences de l'Evolution de Montpellier (ISEM)

PhD Programs: **Land, Environment, Resources and Health (LERH)**

Écologie, Evolution, Ressources Génétique, Paléobiologie (EERGP)

Batch: XXXIV

Effect of fires, human impact, and climate change on long-term forest dynamics in mountain areas: the case of the central Dinaric Alps

PhD Program Coordinator: Prof. Marco Borga

Supervisors: Prof. Emanuele Lingua and Prof. Ilham Bentaleb

Co-Supervisors: Dr. Walter Finsinger

PhD candidate: Eleonora Cagliero



UNIVERSITÀ
DEGLI STUDI
DI PADOVA



UNIVERSITÉ
DE MONTPELLIER

Sedi Amministrative: **Università degli Studi di Padova, Università di Montpellier**

Dipartimento Territorio e Sistemi Agro-Forestali (TESAF)

Institut des Sciences de l'Evolution de Montpellier (ISEM)

CORSI DI DOTTORATO DI RICERCA: **Land, Environment, Resources, Health (LERH)**
Écologie, Evolution, Ressources Génétique, Paléobiologie (EERGP)

Ciclo: XXXIV

**Effetto degli incendi, dell'impatto antropico e del cambiamento climatico
sulle dinamiche forestali a lungo termine nelle aree montane: il caso
studio delle Alpi Dinariche centrali**

Coordinatore: Prof. Marco Borga

Supervisori: Prof. Emanuele Lingua and Prof. Ilham Bentaleb

Co-Supervisori: Dr. Walter Finsinger

Dottorando: Eleonora Cagliero

THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En EERGP - Écologie, Evolution, Ressources Génétique, Paléobiologie

École doctorale GAIA - Biodiversité, Agriculture, Alimentation, Environnement, Terre, Eau

Unité de recherche Institut des Sciences de l'Evolution de Montpellier - UMR 5554

En partenariat international avec l'Université de Padoue, Italie

**L'effet des incendies, de l'impact humain et du changement
climatique sur la dynamique forestière à long terme dans les
zones de montagne : le cas des Alpes Dinariques centrales**

Présentée par Eleonora CAGLIERO

Le 24 juin 2022

**Sous la direction de Ilham BENTALEB, Emanuele LINGUA,
Walter FINSINGER**

Dr. Enikő Magyari, Professeur, Université Eötvös Loránd, Budapest, Hongrie

Dr. Antonio Saracino, Professeur, Université de Naples Federico II, Italie

Rapporteuse

Rapporteur

Devant le jury composé de

Dr. Marco Carrer, Professeur, Université de Padoue, Italie

Dr. Marie-Pierre Ledru, Directeur de Recherche, Université de Montpellier, France

Dr. Christoph Schwörer, Senior research assistant, Université de Berne, Suisse

Dr. Petr Kuneš, Maître de conférence, Université Charles, Prague, République Tchèque

Président du jury

Membre du jury

Membre du jury

Membre du jury



**UNIVERSITÉ
DE MONTPELLIER**

Index

Abstract	9
Riassunto	11
Résumé	13
List of papers.....	15
Glossary	17
Introduction	19
Motivation.....	19
Mountain forest ecosystems: value and threats	19
The need for integrative methodological approaches.....	20
European primary and old-growth forests: definition, dynamics, and threats	22
The Dinaric Alps: a presumed high naturalness mountain region with a poorly constrained vegetation history	26
Aims	29
Main results.....	30
Land-cover mapping with very-high-resolution satellite images.....	30
Legacies of past human activities on old-growth forests and the value of long-term history for the restoration and protection of old-growth forests	30
The role of fire disturbances, human activities and climate change on long-term mountain forest dynamics	31
References	33
<i>PAPER 1: Land-cover mapping in the Biogradska Gora National Park with very-high-resolution Pléiades images</i>	<i>41</i>
Abstract	42
Introduction.....	43
Methodology	44
Study site	44
Field surveys.....	45
Image pre-processing.....	45
Image segmentation and classification.....	45
Results.....	46
Discussion	47
Conclusion	49
Figures	50
References	54
<i>PAPER 2: Legacies of past human activities on one of the largest old-growth forests in south-east European mountains</i>	<i>57</i>
Abstract.....	58
Introduction.....	59

Materials and Methods	60
Study area	60
Current forest composition and structure	61
Long-term vegetation and fire disturbance histories	62
Results and interpretation	64
Present vegetation composition and forest structure	64
Long-term environmental changes	65
Discussion	67
Current forest structure within the old-growth stands and the surrounding forest	67
Stand-scale long-term vegetation dynamics, land-use changes and disturbances by fire	69
Legacies of past human activities	70
Conclusions	72
Acknowledgement	73
Figures	74
References	81
Electronic Supplementary Material	89
Materials and Methods	89
Results	94
References	108
<i>PAPER 3: The value of long-term history of small and fragmented old-growth forests for restoration ecology</i>	<i>111</i>
The value of old-growth forests	112
Old-growth forests remnants in the Balkans	113
Legacies of past land uses at an old-growth forest's fragment edge	113
Outlook	114
Figures	115
References	116
<i>PAPER 4: The role of fire disturbances, human activities and climate change on long-term mountain forest dynamics in the central Dinaric Alps</i>	<i>117</i>
Abstract	118
Introduction	119
Material and methods	121
Study area and study site	121
Field work and sediment-core correlation	122
Sediment composition and chronology	122
Pollen, non-pollen palynomorphs, and plant macrofossils analyses	123
Charcoal analyses	124
Fire-events detection, change point analysis, and ECA	124
Climate data	125
Generalized additive models	126
Results and interpretation	126

Lithology and chronology.....	126
Long-term vegetation dynamics	127
Charcoal-inferred fire history.....	129
Response of fire to variations in climate and human impact	130
Response of dominant forest canopy species to variations in climate, fire and human impact	130
Discussion	130
Long-term vegetation dynamics in a regional setting.....	131
Regional vs local land-use	132
Regional vs local fires.....	134
Response of dominant forest canopy species to variations in climate, fire and human impact	135
Conclusions.....	136
Acknowledgements.....	138
Figures.....	139
References.....	149
Electronic Supplementary Material.....	158
References	160
<i>Discussion and Conclusion</i>	<i>161</i>
General findings.....	161
Species responses	162
Silver fir	163
European beech	164
Norway spruce	165
References.....	167
<i>APPENDIX 1: Introduction, Discussion, and Conclusion in French</i>	<i>173</i>
<i>Thank you</i>	<i>209</i>

Abstract

Mixed mountain forests of silver fir (*Abies alba* Miller), beech (*Fagus sylvatica* L.), and spruce (*Picea abies* (L.) Karst.) are widespread in Europe and have a high ecological and socio-economic value. In the upcoming decades, these forests will likely undergo substantial restructuration due to climate change and altered disturbance regimes. In this context, knowledge of species responses to variations in climate and disturbance regimes (e.g. fire and human impact) may offer critical information to infer the vulnerability of a large part of European mountain forest ecosystems. Since environmental changes generally occur on multiple spatial scales and their effects on forests operate on long-time scales, integrative methodological approaches are required. A high naturalness of forests is key prerequisite to study natural species-environmental interactions. While many European forests were deeply transformed since the Neolithic (around 6500 years ago), the Dinaric Alps still host some of the last remnants of primary and old-growth forests.

This study combined the assessments of contemporary forests structure and composition, remote sensing analyses and multi-proxy palaeoecological records in two forests located in the central Dinaric Alps (Montenegro) to provide insights on the long-term vegetation dynamics. The results supported the high naturalness of some mountain forest ecosystems located in the central Dinaric Alps. However, land-use pressure (agriculture and grazing) as well as fires (probably mainly human-induced) likely played an important role in reducing the area of fir-spruce-beech old-growth forests during the Middle Ages. Legacies of past land-use activities are still visible both in tree species composition and structure of current forest stands. Fire was confirmed to be an important disturbance agent during the Holocene. Although further research from European mixed forests is necessary to validate the responses of spruce, beech, and fir to fire, climate, and human impacts, our results suggest that *A. alba* may be well adapted to warmer-than-present summers and could be resistant to low frequency and low severity fires or even rare high-severity fires. However, it is a species highly sensitive to human impact. *F. sylvatica* may be sensitive to increasing summer temperatures and could be favored by low biomass burning whereas it is insensitive to human impact. *P. abies* may be insensitive to variations in summer temperature, human impact, and biomass burning and can persist under fire-return intervals of c. 200-300 years or even after rare high-severity fires. Our study shows that combining integrative methodological approaches can generate valuable insights able to support the definition of protection, restoration, and management strategies of European mixed spruce-beech-fir mountain forests.

Keywords

Mountain ecosystems, primary forests, old-growth forests, palaeoecology, human impact, land-use legacy, forest structure, very-high resolution satellite imagery, gap dynamic, fire history

Riassunto

Le foreste miste di montagna di abete bianco (*Abies alba* Miller), faggio (*Fagus sylvatica* L.) e abete rosso (*Picea abies* (L.) Karst.) sono molto diffuse in Europa e hanno un alto valore ecologico e socio-economico. Nei prossimi decenni, queste foreste subiranno probabilmente un'alterazione sostanziale a causa dei cambiamenti climatici e dell'alterazione dei regimi di disturbo. In questo contesto, comprendere le risposte delle diverse specie alle variazioni del clima e all'impatto dei diversi disturbi (ad esempio il fuoco e l'impatto umano) può offrire informazioni critiche per dedurre la vulnerabilità di gran parte degli ecosistemi forestali montani europei. Poiché i cambiamenti ambientali si verificano generalmente su scale spaziali multiple e i loro effetti sulle foreste sono visibili su scale temporali lunghe, sono necessari approcci metodologici integrati. Un'elevata naturalità delle foreste è prerequisito essenziale per studiare le interazioni naturali specie-ambiente. Mentre molte foreste europee sono state profondamente trasformate fin dal Neolitico (circa 6500 anni fa), le Alpi Dinariche ospitano ancora alcuni degli ultimi residui di foreste primarie e vetuste.

Questo studio ha combinato le valutazioni dell'attuale struttura e composizione delle foreste, le analisi di telerilevamento e dati paleoecologici multi-proxy in due foreste situate nelle Alpi Dinariche centrali (Montenegro) per fornire informazioni sulle dinamiche della vegetazione a lungo termine in questa regione chiave. I dati confermano l'elevata naturalità di alcuni ecosistemi forestali montani situati nelle Alpi Dinariche centrali. Tuttavia, la pressione dell'uso del suolo (agricoltura e pascolo) così come gli incendi (probabilmente indotti dall'uomo) hanno probabilmente giocato un ruolo importante nel ridurre l'area delle foreste vetuste di abete bianco-abete rosso-faggio durante il Medioevo. L'eredità dell'uso del suolo passato sono ancora visibili nella composizione e nella struttura delle foreste attuali. Il fuoco è stato un importante agente di disturbo durante l'Olocene. Anche se sono necessarie ulteriori ricerche nelle foreste miste europee per convalidare le risposte di abete rosso, faggio e abete bianco al fuoco, al clima e all'impatto umano, i nostri risultati suggeriscono che *A. alba* potrebbe ben adattarsi a estati più calde di quelle attuali e potrebbe essere resistente a incendi di bassa frequenza e bassa severità o anche a rari incendi di alta severità. Tuttavia, è una specie altamente sensibile all'impatto antropico. *F. sylvatica* può essere sensibile all'aumento delle temperature estive e potrebbe essere favorita da una bassa intensità degli incendi, mentre risulta essere meno sensibile all'impatto antropico. *P. abies* è risultata insensibile alle variazioni della temperatura estiva, all'impatto antropico e agli incendi e può persistere a tempi di ritorno degli incendi di circa 200-300 anni o anche dopo rari incendi ad alta severità. Questo studio dimostra che la combinazione di approcci metodologici integrati può fornire utili indicazioni per definire le strategie di protezione, ripristino e gestione delle foreste montane europee miste di abete rosso-faggio-abete bianco.

Parole chiave

Ecosistemi di montagna, foreste primarie, foreste vetuste, paleoecologia, impatto umano, eredità dell'uso del suolo, struttura forestale, immagini satellitari ad altissima risoluzione, dinamica dei *gaps*, storia degli incendi

Résumé

Les forêts mixtes de montagne, composées de sapin (*Abies alba* Miller), de hêtre (*Fagus sylvatica* L.) et d'épicéa (*Picea abies* (L.) Karst.) sont répandues en Europe et ont une grande valeur écologique et socio-économique. Au cours des prochaines décennies, ces forêts subiront probablement une restructuration importante en raison du changement climatique et de la modification des régimes de perturbation. Dans ce contexte, connaître les réponses des espèces aux variations du climat et aux perturbations (par exemple, les incendies et l'impact de l'homme) peut offrir des informations essentielles, qui permettront de mieux appréhender la vulnérabilité d'une grande partie des écosystèmes forestiers de montagne européens. Étant donné que les changements environnementaux se produisent généralement à de multiples échelles spatiales et que leurs effets sur les forêts se manifestent sur le long terme, des approches méthodologiques intégratives sont nécessaires. La haute naturalité des forêts est une condition essentielle pour étudier les interactions naturelles entre les espèces et l'environnement. Alors que de nombreuses forêts européennes de montagne ont été profondément transformées depuis le néolithique (il y a environ 6500 ans), les Alpes Dinariques abritent encore certains des derniers vestiges de forêts primaires et subnaturelles.

Cette étude combine des évaluations de la structure et de la composition des forêts actuelles, des analyses de télédétection et des données paléoécologiques multi-proxy de deux forêts situées dans les Alpes Dinariques centrales (Monténégro), afin de fournir des informations sur la dynamique de la végétation sur le long terme dans cette région clé. Les données confirment le caractère hautement naturel de certains écosystèmes forestiers de montagne situés dans les Alpes Dinariques centrales. Cependant, la pression exercée par l'utilisation du sol (agriculture et pâturage) ainsi que les incendies (probablement d'origine humaine) ont certainement joué un rôle important dans la réduction de la superficie des forêts subnaturelles de sapins, d'épicéas et de hêtres au cours du Moyen Âge. L'héritage des activités passées de l'utilisation du sol sont encore visibles dans la composition et la structure des forêts actuelles. Le feu a été un agent de perturbation important au cours de l'Holocène. Bien que d'autres recherches sur les forêts mixtes européennes soient nécessaires pour valider les réponses de l'épicéa, du hêtre et du sapin au feu, au climat et à l'impact de l'homme, nos résultats suggèrent que *A. alba* pourrait bien s'adapter à des étés plus chauds qu'actuellement et pourrait être résistant à des feux de faible fréquence et de faible sévérité ou même à de rares feux de haute sévérité. Cependant, c'est une espèce très sensible à l'impact humain. *F. sylvatica* pourrait être sensible à l'augmentation des températures estivales et pourrait être favorisé par une faible intensité de feu, alors qu'il est insensible à l'impact humain. *P. abies* pourrait être insensible aux variations de la température estivale, à l'impact de l'homme et aux incendies et peut persister à des intervalles de retour du feu d'environ 200-300 ans ou même après de rares incendies de haute sévérité. Cette étude montre que la combinaison d'approches

méthodologiques intégratives peut générer des informations précieuses pour définir des stratégies de protection, de restauration et de gestion des forêts de montagne européennes mixtes épicéa-hêtre-sapin.

Mots clés

Écosystèmes de montagne, forêts primaires, forêts subnaturelles, paléoécologie, impact humain, héritage de l'utilisation du sol, structure forestière, imagerie satellitaire à très haute résolution, dynamique des *gaps*, histoire des feux

List of papers

Cagliero E., Morresi D., Marchi N., Paradis L., Finsinger W., Garbarino M., Lingua E. (2022) *Land-cover mapping in the Biogradska Gora National Park with very-high-resolution Pléiades images*. In: Borgogno-Mondino E., Zamperlin P. (eds) *Geomatics and Geospatial Technologies*. ASITA 2021. Communications in Computer and Information Science, vol 1507. Springer, Cham. https://doi.org/10.1007/978-3-030-94426-1_2

Cagliero E., Morresi D., Paradis L., Čurović M., Spalević V., Marchi N., Meloni F., Bentaleb I., Motta R., Garbarino M., Lingua E., Finsinger W. (2021) *Legacies of past human activities on one of the largest old-growth forests in south-east European mountains*. *Vegetation History and Archaeobotany*. <https://doi.org/10.1007/s00334-021-00862-x>

Finsinger, W., **Cagliero, E.**, Morresi, D., Paradis, L., Curović, M., Garbarino, M., Marchi, N., Meloni, F., Spalević, V., Lingua, E., Motta, R. (2022) *The value of long-term history of small and fragmented old-growth forests for restoration ecology*. *Past Global Changes Magazine*, 30, vol 1, 8-9 doi.org/10.22498/pages.30.1.8

Cagliero, E., Paradis, L., Marchi, N., Lisztes-Szabó, Z., Braun, M., Bentaleb, I., Hubay, K., Motta, Spalević V., R., Lingua, E., Finsinger, W. (*Manuscript*). The role of fire disturbances, human activities and climate change on long-term mountain forest dynamics in the central Dinaric Alps.

Glossary

Forest canopy gap – a “hole” in the forest through all levels down to an average height of 2 m above ground (Brokaw 1982a, b; Runkle 1982) caused by the death of single or groups of dominant forest canopy trees as consequence of small and intermediate natural disturbances (e.g., wind, ice, snow, insects, and pathogens) (Muscolo et al. 2014)

Gap abundance or density – number of gaps intersected from a transect (#/m) (Fajardo and de Graaf 2004) or number of gaps detected per hectare (#/ha) (Schliemann and Bockheim 2011)

Gap closure – death of a gap, disagreement on the definition. Runkle (1982) contend that regrowth in the gap must be 10-20 m above ground for a gap to be considered closed, while Brokaw (1982 a, b) argue that a regrowth height of 2 m is sufficient. Tyrrell and Crow (1994) present three criteria to assess whether a gap could be considered closed: trees in a gap are one half to two thirds the height of the surrounding canopy trees, trees in the gap have a diameter > 25 cm, or the tree canopy is so dense that the original gap is no longer easily distinguishable.

Gap fraction – the proportion of a tract of forest that is in gaps (%) (Runkle, 1982)

Natural forests – Forest stands predominantly composed of self-sown native trees. Naturalness levels from n1 (low degree of naturalness, *Plantation-like natural forests*) to n10 (ultimate degree of naturalness, *Primeval Forests*), (Buchwald 2005).

Primary forest – Relatively intact forest areas that have been always or at least for the past 60 to 80 years essentially unmodified by human activity. Human impacts in such forest areas have normally been limited to low levels of hunting, fishing and harvesting of forest products, and, in some cases (levels of naturalness from n5 to n8), to historical or pre-historical low intensity agriculture (Buchwald 2005). According to Buchwald (2005), this category includes forests with high levels of naturalness (from n5 to n10): *Long untouched forests*, *Old-growth forests*, *Near-virgin forests*, *Frontier forests*, *Virgin forests* and *Primeval forest*. These forests differ in magnitude and time since the last human impact. From relatively intact forests that have been essentially unmodified by human activity for the past 60 to 80 years or for an unknown, but relatively long, time (*Long untouched forests*) to forest ecosystems never modified by modern man/civilization even indirectly, where the degree of impact on the ecosystem by indigenous people has not been significantly higher than the impacts of natural wildfire and of large wild animals (*Primeval forest*).

Secondary forest – Forest stands of native species regenerated largely through natural processes after significant human and/or natural disturbance of the original forest vegetation at a single point in time or over an extended period, and displaying a major difference in forest structure and/or canopy species composition with respect to primary forests on similar sites (Buchwald 2005). According to Buchwald (2005), this category includes forests with naturalness levels from n1 to n4: *Plantation-like natural forests*, *Exploited natural forests*, *Specially managed forests* characterized by low-intensity use, and *Newly untouched forests* (for less than 60 to 80).

Old-growth forests – According to Buchwald (2005) they are ecosystems (stand scale) with a high degree of naturalness (n6) distinguished by old trees and related structural attributes. Old growth encompasses the later stages of stand development that typically differ from earlier stages in a variety of characteristics which may include tree size, accumulations of large dead woody material, number of canopy layers, species composition, and ecosystem function. The age at which old-growth develops and the specific structural attributes that characterize old-growth will vary widely according to forest type, climate, site conditions, and disturbance regime. [...] However, old-growth is typically distinguished from younger growth by several of the following attributes: 1) large trees for species and site, 2) wide variation in tree sizes and spacing, 3) accumulations of large-size dead standing and fallen trees that are high relative to earlier stages, 4) decadence in the form of broken or deformed tops or bole and root decay, 5) multiple canopy layers, and 6) canopy gaps and understory patchiness (Buchwald 2005). According to FAO (2015), old-growth forests can be either primary or secondary depending on their origin. **Primary old-growth** forests are naturally regenerated forests of native species where there are no clearly visible signs of past human activities and ecological processes have not been significantly disturbed (FAO 2015). **Secondary old-growth** forests originate from the regrowth of woody vegetation after significant human and/or natural disturbances of the original forest vegetation (FAO 2015). The French translation of *old-growth forests* is *forêts subnaturelles* (Cateau et al. 2015).

Old-growthness – different degree to which forest stands express the structural and functional features associated with old conditions (Bauhus et al., 2009).

Introduction

Motivation

Mountain forest ecosystems: value and threats

Mountain forests occupy 23% of the Earth's forest cover, are home to an eighth of the world's population and supply goods and services essential to the livelihood of both highland and lowland communities (FAO 2011). They provide a variety of products (e.g., freshwater, timber, fuel, medicinal and aromatic plants, fodder and foods), and are praised due to their protective functions against natural hazards (such landslides, avalanches, and floods), as well as to their cultural values (i.e., spiritual and recreational values). In addition, acting as a major carbon sink, they contribute to mitigate climate change (Mina et al. 2017). The high heterogeneity of niches and of altitudinal climatic gradients make mountain forests home to a large number of endemic and threatened plant and animal species (FAO 2011). Overall, a third of the world's protected areas are located in the mountains and some of them currently host primary and old-growth forests (FAO 2011). Primary and old-growth forests are valuable as reference systems for the study of natural disturbances and successional dynamics in the different forested biomes (Burrascano et al. 2013; Sabatini et al. 2018) and are hotspots of biodiversity for species sensitive to human disturbance (Paillet et al. 2015).

However, in the upcoming decades, the ability of mountain forests to provide ecosystem services could be severely challenged. Mountain ecosystems are expected to be particularly at risk due to human-induced climatic changes (IPCC 2014, 2021). Mountain forests will experience more rapid changes compared to ecosystems at lower altitudes because the rate of warming is amplified with elevation (Mountain Research Initiative EDW Working Group 2015). Moreover, there is a strong evidence that climate change will markedly modify forest disturbance regimes with an increase in frequency and severity of disturbances (e.g., fire, insects outbreaks and droughts; Seidl et al. 2017). Direct effects of climate on vegetation include altered rates of tree mortality, growth and regeneration success, which interact and ultimately affect species distributions (Hansen et al. 2001). In a warming world, the response of mountain ecosystems to rapidly changing conditions will depend on the capacity of mountain species to adapt to the new conditions (European Environment Agency 2016) and on the adoption of appropriate management strategies. In keeping with this, the Agenda 2030 for Sustainable Development (UN General Assembly 2015) states that the implementation of concrete and sustainable measures is highly needed to strengthen the resilience of mountain areas to future changes (Gratzer and Keeton 2017; Wymann Von Dach et al. 2018). Increased resilience of mountain forests will probably minimize the loss of ecosystem services and preserve biodiversity (Millar and Stephenson 2015).

Recent research has shown that forests from a medium to a high degree of naturalness (*sensu* Buchwald 2005) are expected to be more resistant and resilient to environmental changes due to their high diversity of structural and functional traits (Messier et al. 2013; Sabatini et al. 2020). In this context, studying patterns and processes of primary and old-growth forests could contribute to guide the development of effective silvicultural methods able to increase or restore the stability and the long-term continuity of managed mountain forests in future (close-to-nature silviculture; Bauhus et al. 2009; Schütz et al. 2016). Moreover, assessing the responses of mountain species to warming temperatures and altered disturbance regimes could be useful to forecast potential ecosystem changes and to adopt preventive measures (e.g., promotion of more drought-tolerant species, assisted migration, thinning) that may preserve ecosystem services. However, investigating plants' responses is challenging because processes (such as changes in temperature or in disturbance regimes) generally operate on multiple spatial scales and their effects are discernible on long-time scales, particularly when long-lived species such as trees are involved.

The need for integrative methodological approaches

Forest structures, species composition and spatial patterns arise by the complex and long-term interactions among natural disturbances, human impact and climate (Frelich 2016, Fig. 1). Several methodological approaches can be employed to study forest dynamics, each with its own temporal and spatial scale.

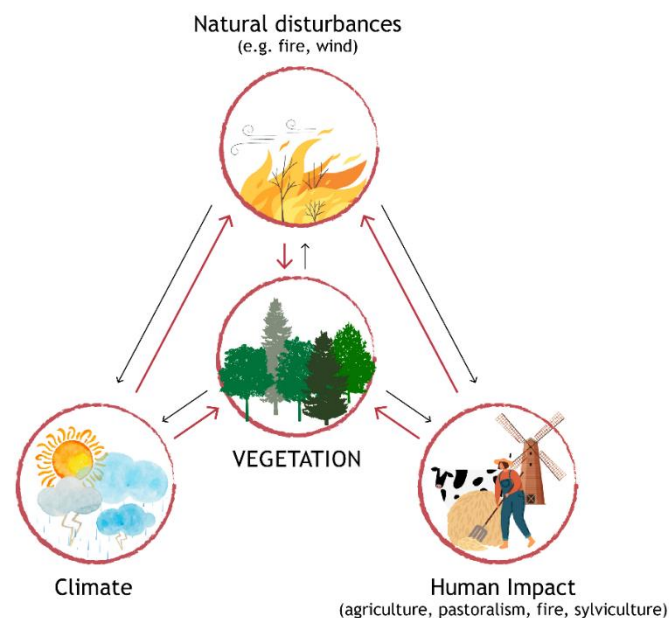


Fig. 1 Simplified diagram of the interactions among climate, natural disturbances, human impact and vegetation. Red arrows: interactions investigated in this study.

The fine scale of field surveys allows the description of species composition and structure (e.g., basal area, structural diversity indexes, amount of coarse woody debris) at stand level, as well as the detection of current growth stage of the stand (Bauhus et al. 2009). These features, together with the maximum age reached by trees, indirectly trace the length of time a site has been continuously wooded without major human impact (e.g., forest harvest, land-use changes) and without stand-replacing disturbances such as windthrows and fire. Field observations can provide evidence on the type of disturbances that could have affected a forest stand (e.g., human impact: cut stumps, charcoal kilns; fires: fire scars; wind: uprooted or snapped trees). However, to capture the structural and compositional variability of a forest, an adequate number of randomly distributed observations is necessary, which is time and energy consuming, and costly (Carrer et al. 2018; Mikoláš et al. 2019). Often, remote-sensing analyses are combined with field surveys to up-scale the observations made at the stand level over a large area (landscape or regional level). Analyses of multispectral satellite images with a high or very-high spatial resolution (c. < 5m) allow the mapping of land-cover types with a high precision. In addition, satellite imagery can show patterns of species' distribution, and the detection and quantification of forest cover changes due to natural or anthropogenic disturbances (Brandt et al. 2012; Knorn et al. 2013). However, the identification of species beyond broad categories (e.g., conifer trees, broadleaf trees) and the attribution to disturbance agents is often a difficult task (Wagner et al. 2018; Huo et al. 2019). Moreover, information on forest structures are lacking and the time horizon for multi-temporal analyses is limited by the availability of images (up to 20-40 years, depending on the spatial resolution).

Despite the relevance of both field surveys and remote sensing in describing the current conditions and dynamics of forest ecosystems, their short-time interval of observation (from decades up to a few centuries) is unable to capture vegetation responses that play out over longer time scales (centuries, millennia). These include, for instance, responses to infrequent disturbance events, changes in fire frequency or fire severity, as well as responses of forest ecosystems to environmental changes due to climate or human impact (Swetnam et al. 1999). In this regard, the extended temporal view (several millennia) provided by palaeoecological records from natural archives (e.g., lacustrine sediments, peat bogs, forest hollows) is particularly useful (Birks 2019). While the time interval covered by palaeoecological records depends on the maximum age reached by sediments, their temporal resolution varies depending on the deposition time and on the number of samples analyzed (Foster et al. 1990). Despite palaeoecological records generally come from single study sites, the spatial scale of their reconstructions varies based on whether sediments are collected from forest hollows or lakes (Foster et al. 1990) and on the type of proxy considered (e.g., plant-macrofossils vs pollen, Birks 2002; macroscopic charcoal vs microscopic charcoal, Whitlock and Larsen 2001). Sediments extracted from forest hollows, which are small wet sites within forests of c. 5 m in diameter, reflect the local vegetation in a radius of a few hundred meters (Calcote 1995, 1998). Lakes, depending on their size, are able to reflect landscape to regional-scale vegetation up to some kilometers at most (Sugita 1994; Hofstetter et al. 2006; Seppä 2013). Plant macrofossils and stomata provide realistic reconstruction of the local

vegetation within some decameters around a site (Ammann et al. 2014; Birks 2017). Microscopic-charcoals (10 -100 μm) mostly reflect regional fire history in a radius of 20-120 km (Whitlock and Larsen 2001) while macroscopic-charcoals ($> 150 \mu\text{m}$) are suitable to infer landscape-scale biomass burning at c. 50 km from the study site together with local fire episodes (c. $< 3 \text{ km}$) (Higuera et al. 2007, 2010; Carter et al. 2018). The use of multiple independent palaeoecological proxies (such as pollen, non-pollen palynomorphs, microscopic and macroscopic charcoal, plant macrofossils, chironomids, and stomata) has the advantage of reconstructing the long-term history of vegetation, disturbance by fire, climate and human impact at different spatial scales and of investigating possible interactions between them (e.g., plants' responses to climate change, land-use, or fire). The level of human impact is usually reconstructed from the relative abundances of pollen of primary anthropogenic indicators (PI), secondary indicators (SI), cultural indicators (CI), *Olea*, *Juglans*, and *Castanea* (OJC index), and from the AP/NAP ratio (arboreal pollen/non-arboreal pollen; Deza-Araujo et al. 2020). Dung fungi spores (*Sporormiella*-type) can be used as a proxy for grazing (Davis 1987; Baker et al. 2013). The long-term history of vegetation combined with that of human impact allows to evaluate the degree of alteration of forest ecosystems and the extent to which they retain natural components (Whitlock et al. 2018).

European primary and old-growth forests: definition, dynamics, and threats

Naturalness is one of the most important criteria in natural conservation and many attempts have been made to assign a degree of naturalness to ecosystems (Reif and Walentowski 2008).

The degree of naturalness is often assessed by the similarity of a biocenosis to the presumed natural state before humans obstructed natural successions (Reif and Walentowski 2008). According to Peterken (1996), the concept of naturalness mainly depends on whether humans are considered or not part of nature. However, it is not simple to discern what level of impact classifies humans as being part of nature. Buchwald (2005) suggests to consider the antonyms *nature* vs *culture* and *natural* vs *artificial*. The words are derived from the Latin *natura*, nature ($< natus$, born); *cultura*, cultivation of plants ($< colere$, to till) and *arte factum*, art work. From the meaning of these words, we may establish that humans set themselves apart from nature when they started to cultivate plants (tilling, sowing, and planting) and to produce art and crafts. In fact, the direct and indirect consequence of cultural development has been an increased impact on fauna and landscape (Buchwald 2005). From archeological evidence, the departure from nature can be established in the time period after the first artworks and before Neolithic farming started (Buchwald 2005), from c. 10,000 cal yr BP onwards in Europe (Roberts 2014). However, humans have been present for hundreds of thousands of years and possibly had impacted forest ecosystems at least since they started to use fire, more than 200,000 years ago (Sabatini 2014), indicating that humans had impacts on nature before ceasing to be part of it (Buchwald 2005). In this view, the idea that forests were totally unimpacted by humans until a few centuries ago is a misconception (Sabatini 2014).

Buchwald (2005) defines 14 ordinal classes of naturalness: almost no degree of naturalness (forest plantations p1-p4 and plantation-like or exploited natural forests n1-n2), medium-moderate degree of naturalness (specially managed forests with low intensity use and forests untouched for less than 60 to 80 years n3-n4) and high degree of naturalness (n5-n10). According to Buchwald's (2005) the category *primary forests* groups forests belonging to the five highest degree of naturalness (n5-n10), including the so-called *old-growth forests* (see glossary). However, as stated by FAO (2015), old-growth forests can be either primary or secondary depending on their origin. Primary old-growth are naturally regenerated forests of native species where there are no clearly visible signs of past human activities and ecological processes have not been significantly disturbed (FAO 2015). Instead, secondary old-growth forests originate from the regrowth of woody vegetation after significant human and/or natural disturbances of the original forest vegetation (FAO 2015). Old-growth forests are therefore primary or secondary forests that have achieved an age at which structures and species normally associated with old primary forests of that particular type have sufficiently developed (UNEP/CBD/SBSTTA 2001). The ageing without significant human impact is the necessary condition to allow a forest stand to reach an old-growth status in terms of structure, living biomass, deadwood traits and biological diversity (Spies 2004; Badalamenti et al. 2019). The different degree to which forest stands express the structural and functional features associated with old conditions is called old-growthness (Bauhus et al. 2009). In view of this, in this dissertation we opted for the term "primary and old-growth forest" in order to encompass all the categories included in primary forests (*sensu* Buchwald, 2005) and in old-growth forests (*sensu* FAO, 2015).

Moreover, for Buchwald (2005), is of interest the evaluation of forest continuity, defined as the length of time an area has been continuously wooded. Following the definition of Peterken (1996) forests with long-term continuity, the so-called *ancient woodlands*, are forest sites that have been continuously wooded for several hundreds of years or millennia. Continuity is not broken by felling, coppicing, planting nor any other forestry operation, as long as woodland of some kind regenerates immediately, but it is broken by an alternative land use, such as unwooded grazing or cultivation. Ancient woodlands, despite their medium or fairly low degree of naturalness (*sensu* Buchwald, 2005), have a high conservation value: the longer a piece of land has been forested, the more time there has been for species to colonize it and for many habitats to form (McMullin and Wiersma 2019).

In Europe, where millennia of intensive land-use deeply transformed both lowland and mountain forested landscapes (Kaplan et al. 2009; Birks and Tinner 2016; Bebi et al. 2017) and altered natural species-environment relationships since the Neolithic (European Environment Agency 2007), primary and old-growth forests are rare (< 3% of the total forested area; Barredo et al. 2021) and small (median size of 24 ha and only 4.3% of the forests larger than 1,000 ha; Sabatini et al. 2018). Remnants of primary and old-growth forests are mainly located in the remote mountain ranges of Central and Eastern

Europe (eastern Alps, Carpathians, and Dinaric Mountains; Parviainen 2005; Sabatini et al. 2018) and largely composed by different proportions of fir (*Abies alba* Miller), beech (*Fagus sylvatica* L.), and spruce (*Picea abies* (L.) Karst.) depending on elevation and site conditions (Burrascano et al. 2013).

In European primary and old-growth forests, stand-replacing disturbances are rare. The natural forest dynamic is mainly driven by small and intermediate natural disturbances (e.g., wind, ice, snow, and fungi) and by mortality of single or groups of dominant forest canopy trees (gap dynamic, Spies et al. 1990; Frankovič et al. 2021). This dynamic is reflected by a multi-layered and complex horizontal forest structure consisting on a fine-scale mosaic of stands in different growth stages (from groups of regeneration to old trees approaching their maximum longevity) and on a high amount of coarse woody debris in various decay stages (Wirth et al. 2009). Most of the gaps are generally small (c. < 100-250 m²; Nagel and Svoboda 2008; Garbarino et al. 2012; Motta et al. 2015). However, episodic intermediate-severity disturbances associated with windstorm events can cause openings of several thousand square meters in size (Drößler and von Lüpke 2005; Nagel et al. 2007; Frankovič et al. 2021). Differences in sizes and frequencies of gaps play a key role to maintain species diversity. Light-demanding species, such as maple (*Acer* sp.) and, to a lesser extent spruce, regenerate in large-medium gaps (Stancioiu and O'Hara 2006; Nagel et al. 2010). Infrequent and low intensity disturbances favor the suppressed advanced regeneration of fir, whereas periods with higher rates of small-medium disturbances favor the advanced regeneration of beech due to its ability to outperform fir when light conditions improve (Nagel et al. 2010; Motta et al. 2015).

Fire is traditionally considered a negligible disturbance agent in fir-spruce-beech primary and old-growth forest dynamics of Central and Eastern Europe (Adámek et al. 2015). In these ecosystems, natural wildfires (e.g., lightning-caused fires) are extremely sporadic (Niklasson et al. 2010; Nagel et al. 2017). However, emerging scientific literature has demonstrated that fires have occurred for millennia in mixed forests ecosystems of Central and Eastern Europe driven by both top-down (e.g., climate) and bottom-up drivers (e.g., human impact and vegetation changes) (Bobek et al., 2018b, 2018a; Carter et al., 2018, 2020; Feurdean et al., 2017, 2019). Moreover, future environmental changes will probably alter the role of fire in these ecosystems. Warming temperatures, more frequent extreme events, such as heat-waves and droughts (Seneviratne et al. 2012; Rajczak et al. 2013) coupled with no significant changes in precipitation (Auer et al. 2007; Bircher et al. 2016) will possibly increase the fire risk. In keeping with this, an increase in fire season length and in burned areas has been already observed over the past decades (San-Miguel-Ayán et al., 2021; Schmuck et al., 2015). Moreover, Eastern European mountains are expected to become a new fire-prone area due to the additional effect of fuel build-up and less fragmented landscapes as result of land abandonment due to rural depopulation (Krawchuk et al., 2009; Wu et al., 2015). In recent decades, the rise of tourism in National Parks of Eastern Europe may have increased the opportunities of fire ignition (Buckley 1991; Hall 2004). The

increased risk of fire may especially endanger smaller primary and old-growth forests, but it is not the only threat affecting these forests.

Although generally protected, smaller primary and old-growth forests are also vulnerable to a direct (e.g., cuts, salvage logging, poaching, grazing) and indirect (e.g., altered fire disturbance regime and land-use changes in the surrounding unprotected areas) human impact that may hinder the development of attributes associated with the old-growth stage. Even in regions where forests are expanding, primary and old-growth forests continue to disappear (Watson et al. 2016, 2018; Potapov et al. 2017; Song et al. 2018) due to the lack of an adequate protection, especially in Eastern Europe (Knorn et al. 2013; Grindean et al. 2019). Their loss and their surface reduction are cause for concern since primary and old-growth forests are particularly important for biodiversity conservation and promotion being source of propagules for rare or endangered forest species sensitive to human disturbance (Paillet et al. 2015).

Primary and old-growth mountain forests, will be also threatened by ongoing climate change. Some mountain species (e.g., beech, spruce) have already experienced growth declines associated with warming temperatures and drought events (Castagneri et al. 2014) and initial species' range shifts are already visible (Hanewinkel et al. 2013). In this regard, primary and old-growth mountain forests provide a unique setting for studying the natural response of plants to climatic changes, as trees growing at high altitudes are often close to their thermal limits and changes in the length of growing season together with winter cold or summer heat extremes can rapidly and strongly alter species distributions and productivity (Henne et al. 2011).

In this context, predicting the responses of dominant tree species of primary and old-growth forests (fir, beech, and spruce) to variations in climate, fire, and human impact is important, also because these species are widespread components of European mountain ecosystems (> 10 million ha, c. 600-1400 m asl; Hilmers et al. 2020) and have a high socio-economic value (Vacek et al. 2021). Moreover, highlighting the legacies of past and present human impact in primary and old-growth forests and their surroundings can be useful to detect possible losses or surface reductions and for guiding protection (e.g., buffer zones) and forest restoration measures (Foster et al. 1996; Swetnam et al. 1999; Mazziotta et al. 2016; Barredo et al. 2021). Additionally, the detection of historical legacies is also particularly important because they shape forest's vulnerability to projected climate change and related disturbance regimes (Conedera et al. 2017). For example, a reduction in tree species diversity (from a mixed beech-fir-spruce forest to one dominated by spruce or beech) or a change in forest structures (from an uneven-aged to an even-aged forest) due to past human impact could reduce the resilience of forest ecosystems to disturbances.

The Dinaric Alps: a presumed high naturalness mountain region with a poorly constrained vegetation history

The Dinaric Alps are situated in the western part of the Balkan Peninsula (southeastern Europe). They are one of the largest mountain regions in Europe extending from the southern edge of the Eastern Alps in Slovenia to the Šar-Korab massif in Albania. They are bounded by the Adriatic Sea along their western border and by the Pannonian Basin toward the east (Fig. 2) (Nagel et al. 2017). The Dinaric Alps encompass parts of Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Kosovo, Montenegro and Albania (Boncina 2011). The range is formed by Mesozoic rocks, which mainly consists of limestone and partly of dolomite and results in abundant presence of karst phenomena (Kranjc 2009). The predominant soils are cambisols and leptosols of different depths (Sirotkovic 1987). Most of the range lies over 500 m asl, with peaks typically reaching 1500 m asl and higher summits (around 2500 m asl) occurring in Bosnia-Herzegovina, Montenegro and Albania (Nagel et al. 2017). The range is located within the temperate climate zone with an average annual temperature of 6-8 °C, dropping at c. 3 °C at high elevations, and a high amount of precipitations (c. 1500-2500 mm per year).



Fig. 2 Map of the Dinaric Mountain range. Red dashed lines: approximate northern and southern range limits; black dashed lines: delimitation of the central Dinaric Alps; red squares: location of study sites in this research.

Precipitations are particularly high along the western side of the range due to the large amounts of humidity carried by the Westerly winds flowing over the Adriatic Sea (Mihevc et al. 2010).

From the Adriatic coast to the Dinaric plateau the pronounced vegetation gradient (Fig. 3) can be summarized as follows: Mediterranean type evergreen shrublands – sub-Mediterranean mixed thermophilus forests – beech dominated forests – mountain forests of beech, fir, and spruce in different proportions (Jovanovic et al. 1986; Nagel et al. 2017). Very steep and rocky sites often support stands of *Pinus nigra* Arnold while spruce-dominated stands mostly occur in karst depressions and sink holes where temperature inversions cause cold microclimates (Nagel et al. 2017). At higher altitudes, pure beech forests sometimes form the upper tree line and above them dwarf pine (*Pinus mugo* Turra) occurs (Boncina 2011). This forested region provides habitats for many endemic (e.g., Serbian spruce, *Picea omorika* (Pancic) Purk.) and endangered plant species including Arcto-tertiary relicts (Boncina 2011).

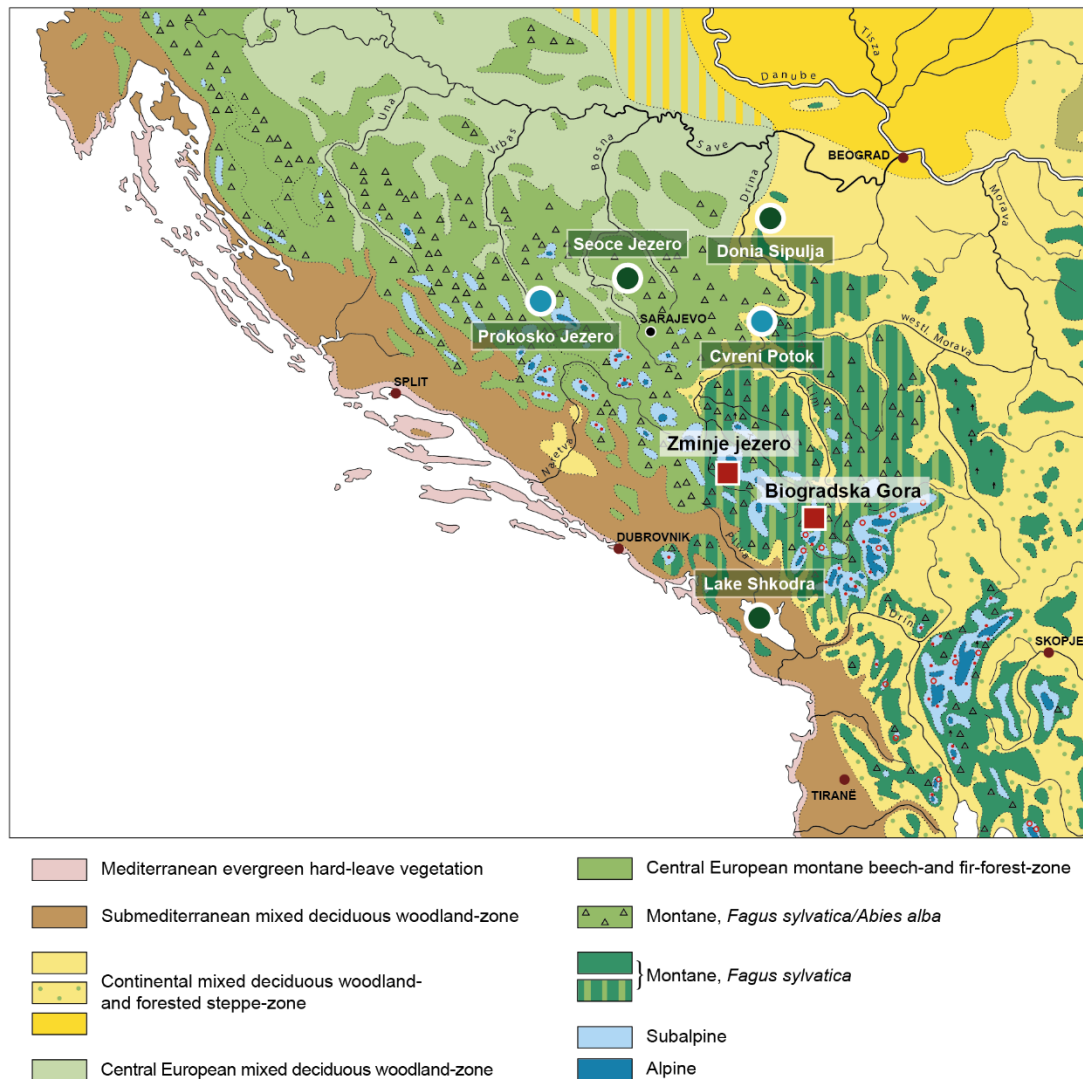


Fig. 3 Potential vegetation map from Horvat et al. (1974) with the location of the study sites of the palaeoecological records in the Dinaric Alps mentioned in the text: Prokoško Jezero (Dörfler 2013), Seoce Jezero (Wolters et al. 2010), Donja Sipulja (Kulkarni et al. 2016), and Lake Shkodra (Sadori et al. 2015). Blue circles: study sites in mountain areas; red squares: location of sites in this study.

A modelled retrospective study spanning the past three millennia suggests that forests of southeastern Europe (including Slovenia, Croatia, Bosnia and Herzegovina, Montenegro, Serbia, Macedonia) was not heavily exploited or cleared until the Middle Ages due to rugged terrain lands, low agricultural productivity, and a low population density (Kaplan et al. 2009). The model's result matches to the idea that some forests located in the remote interior of mountain ranges, such as in the central Dinaric Alps, have been possibly left relatively intact or have been managed with low intensity silvicultural systems until the present (Boncina 2011; Nagel et al. 2017). In keeping with this, the region of the Dinaric Mountain range has shown a high likelihood to host primary and old-growth forests (Sabatini et al. 2018) and currently hosts larger primary and old-growth mixed fir-spruce-beech forests (> 1000 ha) compared to other mountain ranges, such as the Alps and the Carpathians (Diaci 1999; Nagel et al. 2017; Sabatini et al. 2018). The long-term vegetation history of mountain forest ecosystems in the Dinaric Alps is of particular interest because the dominant tree species of these mountain forests (spruce, fir, and beech) are among the most widespread and the most socio-economically valuable species in European forest ecosystems (Euforgen 2009; Vacek et al. 2021). Moreover, the presumed high naturalness of the forests possibly allows to study natural species-environment interactions and to better disentangle possible effects of past human impacts on mountain ecosystems. However, the vegetation history of the Dinaric Alps is poorly constrained due to poor data coverage (Finsinger et al. 2017). Available palaeoecological records are generally located far from the mountain areas to allow the reconstruction of mountain forest's dynamics (Seoce Jezero, Wolters et al. 2010; Donja Sipulja, Kulkarni et al. 2016; Lake Shkodra, Sadori et al. 2015; Fig. 3), with few exceptions (Prokoško Jezero, central Dinaric Alps, Dörfler 2013; Crveni potok, internal Dinaric Alps, Finsinger et al. 2017; Fig. 3).

For the reasons outlined above, we selected two study sites located in the montane zone of the central Dinaric Alps, on the Bjelasica (Papers 1, 2, and 3) and Durmitor (Paper 4) massifs, in the northeastern and northwestern part of Montenegro, respectively (Fig. 2). Their early protection as royal reserves since 1907 and 1878, respectively and as National Parks since 1952 (the Durmitor National Park and the Biogradska Gora National Park) has possibly allowed the maintenance or the recovery of a high degree of naturalness until today. The Biogradska Gora National Park currently includes one of the largest central-southern European old-growth stands, whose large surface is suitable to develop a natural forest dynamic (gap dynamic) with the resulting mosaic of a large variety of developmental phases of forest stands (Motta et al. 2015; Barredo et al. 2021). Old-growth stands have not yet been reported in the Durmitor National Park, but scattered old monumental trees are present. A detailed description of the study sites is found in Paper 1, 2, and 4.

Aims

The research project aims to investigate the effects of climate, fire history, human impact, and their possible interactions on the long-term vegetation dynamics of mixed spruce-fir-beech mountain forest ecosystems of the Dinaric Alps. The four papers included in this dissertation, each with its own specific aims, contribute in different but complementary ways to address the main objective.

The individual aims of the study are as follows:

- To assess the suitability of employing very-high-resolution satellite imagery to map land-cover classes including forest-canopy gaps in old-growth forests. **Paper 1** addresses this aim by coupling an object-based image analysis (OBIA) and a Random Forest classifier on very-high-resolution Pléiades images of the Biogradska Gora forest.
- To identify the present-day extent of the primary and old-growth forest of Biogradska Gora, unfold the possible influence of fires and human impact that may have reduced or fragmented the primary and old-growth forest areas, and clarify the legacies of past disturbances on current forest ecosystems. **Paper 2** addresses these aims by combining field surveys of contemporary forest structure with remote sensing analyses and palaeoecological records from the primary and old-growth forest of Biogradska Gora and its surroundings (Bjelasica massif, Montenegro). **Paper 3** focuses on the value of long-term history of primary and old-growth forests and of their surrounding landscapes for nature protection and for the development of restoration measures.
- To assess the Holocene vegetation, fire dynamics and land-use history of mixed mountain forest ecosystems and to track the responses of the dominant montane trees (fir, beech, and spruce) to variation in climate, fire, and human impact. **Paper 4** addresses these aims by presenting a detailed and new multi-proxy palaeoecological study (including pollen, plant macrofossils, microscopic and macroscopic charcoal analyses) on well-dated sediments from the upper-montane zone (Zminje jezero, Durmitor massif, Montenegro) and by using Generalized Additive Models to assess the response of the dominant canopy taxa to variations in climate, fire, and human impact.

Main results

Land-cover mapping with very-high-resolution satellite images

The coupling of an object-based image analysis (OBIA) and a Random Forest classifier, trained with samples partially derived from field data, on very-high-resolution satellite images (Pléiades satellite imagery with a 0.5-m panchromatic band, PAN; 2-m resolution multispectral bands, RGB and NIR), revealed an overall good performance in mapping land-cover classes (overall accuracy > 95.6% and Cohen's Kappa accuracy > 92.5%). According to the image classification, the central part of the Biogradska Gora National Park consists mainly of forests (92.5%). Specifically, the inner part is dominated by conifers whereas the surrounding areas are dominated by pure beech stands. Although a high accuracy was obtained for the main land-cover classes (conifers, broadleaved trees, grasslands, bare ground, and water), the forest canopy gaps class was classified with a low accuracy. The classification of conifers and broadleaved tree classes showed a minimum producer's and user's accuracies of 92.9% and 95.6%, respectively, whereas forest canopy gaps were classified with a minimum producer's and user's accuracies of 75% and 54.5%, respectively. The use of textural metrics during the image segmentation and classification phases probably enhanced gap circumscription and the distinction between the dominant and the lower canopy layers. However, the lack of remote sensing data providing information on the vertical structure of the forest was probably the main reason of low accuracies in this category. In keeping with this, a gap fraction (< 2%), which is consistently lower than values derived from terrestrial methods (always > 15% from literature) suggests that the classification method underestimated the number of gaps, probably not being able to detect old-formed gaps (i.e. gaps almost closed by regeneration) and small-size gaps (i.e. formed by single tree death). The difficulty in detecting the gaps was accentuated by the presence of broadleaf trees (beech), which tend to close or reduce the size of gaps with lateral crown growth. Consequently, only 1% of all observed gaps were detected in the beech-dominated stands. However, the find of 99% of gaps in conifer-dominated stands could also suggest that these stands have a higher old-growthness. In the light of this, the coupling of an OBIA and a Random Forest classifier on very-high-resolution Pléiades satellite imagery was suitable to detect only recently formed and large gaps in which the regeneration has not yet reached great heights or has not completely colonized the gap's surface.

Legacies of past human activities on old-growth forests and the value of long-term history for the restoration and protection of old-growth forests

Field surveys and a detailed land-cover type map show that the mixed conifer-dominated (*Abies-Picea-Fagus*) primary and old-growth forest is surrounded by almost pure *Fagus* stands at Biogradska Gora. The high-resolution and stand-scale palaeoecological records (median sediment deposition time = 4

years cm^{-1}) from a forest hollow located in the beech forest at the current edge of the old-growth forest, show that crop cultivation, cattle herding, as well as human-driven fires to create open areas for agriculture and grazing, caused a reduction of *Abies* and *Picea* during the Middle Ages. These practices are attested by a low tree cover (arboreal pollen abundances around 40%), high values of primary anthropogenic pollen indicators and of *Sporormiella*-type spores between 1150-1350 CE. After a land abandonment around the Black Death pandemic (mid-14th century) and a weaker land-use phase (1500-1600 CE), which caused the collapse of the local conifer populations, human pressure declined. Markedly in contrast to decreasing forest cover elsewhere in the region due to intensifying land use since the 15th-16th century, forest cover gradually increased and a *Fagus*-dominated forest established from 1850, at the transition to the cooler Little Ice Age. The legacies of past land uses are still visible in the small and mostly multi-stemmed beech trees (diameters generally < 40 cm from single stools). Low values of coarse woody debris, dead to live wood ratio and structural diversity reflect a homogenous structure and even-age cohorts. By contrast, the fir-spruce-beech old-growth forest has a mixed and multi-layered structure shaped by gaps, a large amount of coarse woody debris and a dead to live wood ratio indicating that this part of forest has developed dynamically for a long period of time without human and natural stand-replacing disturbances. The conifer-dominated stands have probably been preserved from human disturbances due to their more remote location and difficult access, as supported by the results of the path analysis, at least since 1500 CE. This hypothesis is in line with the age of the older trees (> 500 years).

The presence of stomata and plant macrofossils of *Picea* and *Abies* in the currently *Fagus*-dominated forest since 950 CE supports the hypothesis that the area of these two conifers was reduced during the Middle Ages. These results attest that, at least from the Middle Ages, a consistent historical land-use pressure occurred even in the remote hinterland areas of the central Dinaric Alps and played an important role in reducing the area of the existing primary and old-growth forests, leading to small size and high fragmented forests surfaces.

Paleoecology, along with structural and dendrochronological research, can unfold the history of European primary and old-growth forests and assess their responses to past environmental changes as well as legacy effects of past land use. Information on the long-term history of forest ecosystems may be useful for defining conservation or restoration measures and for guiding management strategies to maintain resistant and resilient forests in future, considering climate change and associated changing in disturbance regimes.

The role of fire disturbances, human activities and climate change on long-term mountain forest dynamics

The Zminje jezero record (Durmitor massif) covers part of the Younger Dryas and the entire Holocene, from c. 12,450 cal yr BP to present (median sediment deposition time = 21.6 years cm^{-1}). During the

Younger Dryas and until 10,000 cal yr BP, vegetation was dominated by *Pinus* sp. and *Betula* sp. Between 10,000 and 9000 cal yr BP, a mixed *Picea-Abies* forest established in the upper-montane zone and from 5000 cal yr BP *Fagus* became co-dominant with the two conifers.

Climate was likely the main driver of fire dynamics in the mountain area. Biomass burning gradually decreased during the past 8500 years and the majority of the local fire episodes were of low severity. However, high-severity fires became more frequent since 5000 cal yr BP. Regional fire activity rose since the late Bronze Age (3000 cal yr BP) as consequence of higher land-use pressure in the wider region. Nevertheless, in the montane zone, anthropogenic pollen indicators only rose since 2000 cal yr BP, suggesting a remarkably low land-use pressure until the Roman period. After 2000 cal yr BP, *Abies* pollen sharply decreased and from 1200 cal yr BP *Fagus* expanded locally. From 480 cal yr BP, a higher human pressure in the mountain areas was probably responsible of the shift from a *Picea-Abies-Fagus* mixed forest to one dominated by *Picea* in the surrounding of Zminje jezero. The high human pressure was supported by a further rise of anthropogenic pollen indicators and by the presence of archeological settlements in the Durmitor. However, the continuous presence of plant macrofossils and stomata of trees (*Picea*, *Abies*, and *Fagus*), together with arboreal pollen abundances generally > 80% and AP/NAP ratio generally > 4 during the past 9000 years, could suggest that a high forest cover persisted in the surroundings of Zminje Jezero throughout the whole Holocene. Moreover, agriculture and forest clearances probably did not reach the surroundings of the lake. Response curves of the dominant montane trees to environmental variations show that *Picea* was relatively insensitive to long-term variation in summer temperatures, biomass burning and human impact. Thus, spruce forests may be not significantly impacted by fire and by warmer-than-present temperatures in the future. *Abies* was promoted by warmer-than-present summer temperatures while shown a significant negative relationship with increasing human impact. Finally, *Fagus* emerged as a species sensitive to summer temperatures and to high biomass burning but promoted by low biomass burning rates.

References

- Adámek M, Bobek P, Hadincová V, et al (2015) Forest fires within a temperate landscape: A decadal and millennial perspective from a sandstone region in Central Europe. *Forest Ecology and Management* 336:81–90
- Ammann B, van der Knaap WO, Lang G, et al (2014) The potential of stomata analysis in conifers to estimate presence of conifer trees: examples from the Alps. *Veget Hist Archaeobot* 23:249–264. <https://doi.org/10.1007/s00334-014-0431-9>
- Auer I, Böhm R, Jurkovic A, et al (2007) HISTALP—historical instrumental climatological surface time series of the Greater Alpine Region. *Int J Climatol* 27:17–46. <https://doi.org/10.1002/joc.1377>
- Badalamenti E, Battipaglia G, Gristina L, et al (2019) Carbon stock increases up to old growth forest along a secondary succession in Mediterranean island ecosystems. *PLoS ONE* 14:e0220194. <https://doi.org/10.1371/journal.pone.0220194>
- Baker AG, Bhagwat SA, Willis KJ (2013) Do dung fungal spores make a good proxy for past distribution of large herbivores? *Quaternary Science Reviews* 62:21–31. <https://doi.org/10.1016/j.quascirev.2012.11.018>
- Barredo JI, Brailescu C, Teller A, et al (2021) Mapping and assessment of primary and old-growth forests in Europe. Publications Office of the European Union, Luxembourg
- Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. *Forest Ecology and Management* 258:525–537. <https://doi.org/10.1016/j.foreco.2009.01.053>
- Bebi P, Seidl R, Motta R, et al (2017) Changes of forest cover and disturbance regimes in the mountain forests of the Alps. *Forest Ecology and Management* 388:43–56. <https://doi.org/10.1016/j.foreco.2016.10.028>
- Bircher N, Cailleret M, Zingg A, Bugmann H (2016) Potenzielle Grundflächenveränderungen auf Bestandesebene im Klimawandel. In: Pluess AR, Augustin S, Brang P (eds) *Wald im Klimawandel - Grundlagen für Adaptionsstrategien*. Haupt, pp 157–171
- Birks HH (2017) Plant macrofossil introduction. In: *Reference Module in Earth Systems and Environmental Sciences*. Elsevier
- Birks HH (2002) Plant Macrofossils. In: Smol JP, Birks HJB, Last WM, et al. (eds) *Tracking Environmental Change Using Lake Sediments*. Springer Netherlands, Dordrecht, pp 49–74
- Birks HJB (2019) Contributions of Quaternary botany to modern ecology and biogeography. *Plant Ecology & Diversity* 12:189–385. <https://doi.org/10.1080/17550874.2019.1646831>
- Birks HJB, Tinner W (2016) Past forests of Europe. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, et al. (eds) *Past forests of Europe*. European Atlas of Forest Tree Species. Publication Office of the European Union, Luxembourg, pp 36–39
- Boncina A (2011) History, current status and future prospects of uneven-aged forest management in the Dinaric region: an overview. *Forestry* 84:467–478. <https://doi.org/10.1093/forestry/cpr023>
- Brandt JS, Kuemmerle T, Li H, et al (2012) Using Landsat imagery to map forest change in southwest China in response to the national logging ban and ecotourism development. *Remote Sensing of Environment* 121:358–369. <https://doi.org/10.1016/j.rse.2012.02.010>
- Brokaw NVL (1982a) Treefalls: frequency, timing, and consequences. In: Leigh EG, Rand AS, Windsor DM (eds) *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*. Smithsonian Institution Press, Washington, D.C., pp 101–108

- Brokaw NVL (1982b) The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14:158–160
- Buchwald E (2005) A hierarchical terminology for more or less natural forests in relation to sustainable management and biodiversity conservation. In: Third expert meeting on harmonizing forest-related definitions for use by various stakeholders Food and Agriculture Organization of the United Nations. Rome, pp 111–127
- Buckley R (1991) Environmental impacts of recreation in parks and reserves. In: *Perspectives in Environmental Management*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 243–258
- Burrascano S, Keeton WS, Sabatini FM, Blasi C (2013) Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. *Forest Ecology and Management* 291:458–479. <https://doi.org/10.1016/j.foreco.2012.11.020>
- Calcote R (1995) Pollen Source Area and Pollen Productivity: Evidence from Forest Hollows. *The Journal of Ecology* 83:591. <https://doi.org/10.2307/2261627>
- Calcote R (1998) Identifying forest stand types using pollen from forest hollows. *The Holocene* 8:423–432. <https://doi.org/10.1191/095968398670894847>
- Carrer M, Castagneri D, Popa I, et al (2018) Tree spatial patterns and stand attributes in temperate forests: The importance of plot size, sampling design, and null model. *Forest Ecology and Management* 407:125–134. <https://doi.org/10.1016/j.foreco.2017.10.041>
- Carter VA, Moravcová A, Chiverrell RC, et al (2018) Holocene-scale fire dynamics of central European temperate spruce-beech forests. *Quaternary Science Reviews* 191:15–30. <https://doi.org/10.1016/j.quascirev.2018.05.001>
- Castagneri D, Nola P, Motta R, Carrer M (2014) Summer climate variability over the last 250 years differently affected tree species radial growth in a mesic *Fagus–Abies–Picea* old-growth forest. *Forest Ecology and Management* 320:21–29. <https://doi.org/10.1016/j.foreco.2014.02.023>
- Cateau E, Larrieu L, Vallauri D, et al (2015) Ancienneté et maturité : deux qualités complémentaires d'un écosystème forestier. *Comptes Rendus Biologies* 338:58–73. <https://doi.org/10.1016/j.crv.2014.10.004>
- Conedera M, Colombaroli D, Tinner W, et al (2017) Insights about past forest dynamics as a tool for present and future forest management in Switzerland. *Forest Ecology and Management* 388:100–112
- Davis OK (1987) Spores of the dung fungus *Sporormiella*: Increased abundance in historic sediments and before Pleistocene megafaunal extinction. *Quaternary Research* 28:290–294. [https://doi.org/10.1016/0033-5894\(87\)90067-6](https://doi.org/10.1016/0033-5894(87)90067-6)
- Deza-Araujo M, Morales-Molino C, Tinner W, et al (2020) A critical assessment of human-impact indices based on anthropogenic pollen indicators. *Quaternary Science Reviews* 236:106291. <https://doi.org/10.1016/j.quascirev.2020.106291>
- Diaci J (ed) (1999) Virgin forests and forest reserves in Central and East European countries: history, present status and future development. Proceedings of the invited lecturers' reports presented at the COST E4 management committee and working groups meeting in Ljubljana, Slovenia, 25–28 April, 1998. Dept. of Forestry and Renewable Forest Resources, Ljubljana, Slovenia
- Dörfler W (2013) Prokoško Jezero: An environmental record from a subalpine lake in Bosnia-Herzegovina. In: Müller J, Rassmann K, Hofmann R (eds) *Okolište 1 – Untersuchungen Einer Spätneolithischen Siedlungskammer in Zentralbosnien*, Universitätsforschungen Zur Prähistorischen Archäologie. Habelt Verlag, Bonn, pp 311–340
- Drößler L, von Lüpke B (2005) Canopy gaps in two virgin beech forest reserves in Slovakia. *J For Sci* 51:446–457. <https://doi.org/10.17221/4578-JFS>

- Euforgen (2009) Distribution map of European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*), and Silver fir (*Abies alba*). <http://www.euforgen.org>
- European Environment Agency (2016) European forest ecosystems: state and trends. Publications Office, Luxembourg
- European Environment Agency L (2007) European Forest Types. Categories and types for sustainable forest management reporting and policy. Copenhagen
- Fajardo A, de Graaf R (2004) Tree dynamics in canopy gaps in old-growth forests of *Nothofagus pumilio* in Southern Chile. *Plant Ecology* 173:95–105. <https://doi.org/10.1023/B:VEGE.0000026333.54741.97>
- FAO (2015) Forest resources Assessment Working Paper 180. In: Global Forest Resources Assessment 2015. Terms and definitions. Rome, p 36
- FAO (2011) Mountain forests in a changing world: realizing values, addressing challenges. FAO, Rome
- Finsinger W, Morales-Molino C, Galka M, et al (2017) Holocene vegetation and fire dynamics at Crveni Potok, a small mire in the Dinaric Alps (Tara National Park, Serbia). *Quaternary Science Reviews* 167:63–77. <https://doi.org/10.1016/j.quascirev.2017.04.032>
- Foster DR, Orwig DA, McLachlan JS (1996) Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Trends in Ecology & Evolution* 11:419–424
- Foster DR, Schoonmaker PK, Pickett STA (1990) Insights from Paleoecology to Community Ecology. *TREE* 5:119–122
- Frankovič M, Janda P, Mikoláš M, et al (2021) Natural dynamics of temperate mountain beech-dominated primary forests in Central Europe. *Forest Ecology and Management* 479:118522. <https://doi.org/10.1016/j.foreco.2020.118522>
- Frelich L (2016) Forest dynamics. *F1000Res* 5:183. <https://doi.org/10.12688/f1000research.7412.1>
- Garbarino M, Borgogno Mondino E, Lingua E, et al (2012) Gap disturbances and regeneration patterns in a Bosnian old-growth forest: a multispectral remote sensing and ground-based approach. *Annals of Forest Science* 69:617–625. <https://doi.org/10.1007/s13595-011-0177-9>
- Gratzer G, Keeton WS (2017) Mountain Forests and Sustainable Development: The Potential for Achieving the United Nations' 2030 Agenda. *Mountain Research and Development* 37:246–253. <https://doi.org/10.1659/MRD-JOURNAL-D-17-00093.1>
- Grindean R, Tanțău I, Feurdean A (2019) Linking vegetation dynamics and stability in the old-growth forests of Central Eastern Europe: Implications for forest conservation and management. *Biological Conservation* 229:160–169. <https://doi.org/10.1016/j.biocon.2018.11.019>
- Hall D (2004) Rural tourism development in southeastern Europe: transition and the search for sustainability. *Int J Tourism Res* 6:165–176. <https://doi.org/10.1002/jtr.482>
- Hanewinkel M, Cullmann DA, Schelhaas M-J, et al (2013) Climate change may cause severe loss in the economic value of European forest land. *Nature Clim Change* 3:203–207. <https://doi.org/10.1038/nclimate1687>
- Hansen AJ, Neilson RP, Dale VH, et al (2001) Global Change in Forests: Responses of Species, Communities, and Biomes. *BioScience* 51:765. [https://doi.org/10.1641/0006-3568\(2001\)051\[0765:GCIFRO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0765:GCIFRO]2.0.CO;2)
- Henne PD, Elkin CM, Reineking B, et al (2011) Did soil development limit spruce (*Picea abies*) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape

- model: Soil depth limits spruce expansion in the Alps. *Journal of Biogeography* 38:933–949. <https://doi.org/10.1111/j.1365-2699.2010.02460.x>
- Higuera P, Peters M, Brubaker L, Gavin D (2007) Understanding the origin and analysis of sediment-charcoal records with a simulation model. *Quaternary Science Reviews* 26:1790–1809. <https://doi.org/10.1016/j.quascirev.2007.03.010>
- Higuera PE, Gavin DG, Bartlein PJ, Hallett DJ (2010) Peak detection in sediment - charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *Int J Wildland Fire* 19:996–1014. <https://doi.org/10.1071/WF09134>
- Hilmers T, Biber P, Knoke T, Pretzsch H (2020) Assessing transformation scenarios from pure Norway spruce to mixed uneven-aged forests in mountain areas. *Eur J Forest Res* 139:567–584. <https://doi.org/10.1007/s10342-020-01270-y>
- Hofstetter S, Tinner W, Valsecchi V, et al (2006) Lateglacial and Holocene vegetation history in the Insubrian Southern Alps—New indications from a small-scale site. *Veget Hist Archaeobot* 15:87–98. <https://doi.org/10.1007/s00334-005-0005-y>
- Horvat I, Glavač V, Ellenberg H (1974) *Vegetation of Southeast Europe*. Gustav Fischer Verlag, Stuttgart
- Huo L-Z, Boschetti L, Sparks A (2019) Object-based classification of forest disturbance types in the Conterminous United States. *Remote Sensing* 11:477. <https://doi.org/10.3390/rs11050477>
- IPCC (2014) *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland
- IPCC (2021) *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press
- Jovanovic B, Jovanovic R, Zupancic M (1986) *Natural Potential Vegetation of Yugoslavia*. Scientific Council of Vegetation Map of Yugoslavia, Ljubljana
- Kaplan JO, Krumhardt KM, Zimmermann N (2009) The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews* 28:3016–3034. <https://doi.org/10.1016/j.quascirev.2009.09.028>
- Knorn J, Kuemmerle T, Radeloff VC, et al (2013) Continued loss of temperate old-growth forests in the Romanian Carpathians despite an increasing protected area network. *Envir Conserv* 40:182–193. <https://doi.org/10.1017/S0376892912000355>
- Kranjc A (2009) History of deforestation and reforestation in the Dinaric karst. *Geographical Research* 47:15–23. <https://doi.org/10.1111/j.1745-5871.2008.00552.x>
- Kulkarni C, Peteet D, Boger R, Heusser L (2016) Exploring the role of humans and climate over the Balkan landscape: 500 years of vegetational history of Serbia. *Quaternary Science Reviews* 144:83–94. <https://doi.org/10.1016/j.quascirev.2016.05.021>
- Mazziotta A, Heilmann-Clausen J, Bruun HH, et al (2016) Restoring hydrology and old-growth structures in a former production forest: Modelling the long-term effects on biodiversity. *Forest Ecology and Management* 381:125–133
- McMullin RT, Wiersma YF (2019) Out with OLD growth, in with ecological continEWity: new perspectives on forest conservation. *Front Ecol Environ* 17:176–181. <https://doi.org/10.1002/fee.2016>
- Messier C, Puettmann K, Coates D (2013) *Managing forests as complex adaptive systems: Building resilience to the challenge of global change*. NY: Routledge, New York
- Mihevc A, Prelovšek M, Hajna NZ (eds) (2010) *Introduction to the Dinaric karst*. Inštitut za raziskovanje krasa ZRC SAZU

- Mikoláš M, Ujházy K, Jasík M, et al (2019) Primary forest distribution and representation in a Central European landscape: Results of a large-scale field-based census. *Forest Ecology and Management* 449:117466. <https://doi.org/10.1016/j.foreco.2019.117466>
- Millar CI, Stephenson NL (2015) Temperate forest health in an era of emerging megadisturbance. *Science* 349:823–826. <https://doi.org/10.1126/science.aaa9933>
- Mina M, Bugmann H, Cordonnier T, et al (2017) Future ecosystem services from European mountain forests under climate change. *J Appl Ecol* 54:389–401. <https://doi.org/10.1111/1365-2664.12772>
- Motta R, Garbarino M, Berretti R, et al (2015) Structure, spatio-temporal dynamics and disturbance regime of the mixed beech–silver fir–Norway spruce old-growth forest of Biogradska Gora (Montenegro). *Plant Biosystems* 149:966–975. <https://doi.org/10.1080/11263504.2014.945978>
- Mountain Research Initiative EDW Working Group (2015) Elevation-dependent warming in mountain regions of the world. *Nature Clim Change* 5:424–430. <https://doi.org/10.1038/nclimate2563>
- Muscolo A, Bagnato S, Sidari M, Mercurio R (2014) A review of the roles of forest canopy gaps. *Journal of Forestry Research* 25:725–736. <https://doi.org/10.1007/s11676-014-0521-7>
- Nagel TA, Levanić T, Diaci J (2007) A dendroecological reconstruction of disturbance in an old-growth *Fagus-Abies* forest in Slovenia. *Ann For Sci* 64:891–897. <https://doi.org/10.1051/forest:2007067>
- Nagel TA, Mikac S, Dolinar M, et al (2017) The natural disturbance regime in forests of the Dinaric Mountains: A synthesis of evidence. *Forest Ecology and Management* 388:29–42. <https://doi.org/10.1016/j.foreco.2016.07.047>
- Nagel TA, Svoboda M (2008) Gap disturbance regime in an old-growth *Fagus – Abies* forest in the Dinaric Mountains, Bosnia-Herzegovina. *Canadian Journal of Forest Research* 38:2728–2737. <https://doi.org/10.1139/X08-110>
- Nagel TA, Svoboda M, Rugani T, Diaci J (2010) Gap regeneration and replacement patterns in an old-growth *Fagus – Abies* forest of Bosnia–Herzegovina. *Plant Ecol* 208:307–318. <https://doi.org/10.1007/s11258-009-9707-z>
- Niklasson M, Zin E, Zielonka T, et al (2010) A 350-year tree-ring fire record from Białowieża Primeval Forest, Poland: implications for Central European lowland fire history. *Journal of Ecology* 98:1319–1329. <https://doi.org/10.1111/j.1365-2745.2010.01710.x>
- Paillet Y, Pernot C, Boulanger V, et al (2015) Quantifying the recovery of old-growth attributes in forest reserves: A first reference for France. *Forest Ecology and Management* 346:51–64. <https://doi.org/10.1016/j.foreco.2015.02.037>
- Parviainen J (2005) Virgin and natural forests in the temperate zone of Europe. *For Snow Landsc Res* 79:9–18
- Peterken GF (1996) *Natural woodland: ecology and conservation in northern temperate regions*. Cambridge University Press, Cambridge UK
- Potapov P, Hansen MC, Laestadius L, et al (2017) The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. *Sci Adv* 3:e1600821. <https://doi.org/10.1126/sciadv.1600821>
- Rajczak J, Pall P, Schär C (2013) Projections of extreme precipitation events in regional climate simulations for Europe and the Alpine Region: Projection of extreme precipitation. *J Geophys Res Atmos* 118:3610–3626. <https://doi.org/10.1002/jgrd.50297>
- Reif A, Walentowski H (2008) The assessment of naturalness and its role for nature conservation and forestry in Europe. *Waldökologie, Landschaftsforschung u 64 nd Naturschutz* 6:63–76
- Roberts N (2014) The first farmers. In: *The Holocene: An Environmental History*. John Wiley & Sons, Ltd.

- Runkle JR (1982) Patterns of Disturbance in Some Old-Growth Mesic Forests of Eastern North America. *Ecology* 63:1533–1546. <https://doi.org/10.2307/1938878>
- Sabatini FM (2014) Causes and determinants of plant biodiversity in Southern European old-growth forests. Structural heterogeneity, dispersal limitation and abiotic resources. Sapienza Università di Roma. Facoltà di Scienze Matematiche, Fisiche e Naturali Dottorato in Sc. Ecologiche
- Sabatini FM, Burrascano S, Keeton WS, et al (2018) Where are Europe's last primary forests? Diversity and Distributions 24:1426–1439. <https://doi.org/10.1111/ddi.12778>
- Sabatini FM, Keeton WS, Lindner M, et al (2020) Protection gaps and restoration opportunities for primary forests in Europe. *Divers Distrib* 26:1646–1662. <https://doi.org/10.1111/ddi.13158>
- Sadori L, Giardini M, Gliozzi E, et al (2015) Vegetation, climate and environmental history of the last 4500 years at lake Shkodra (Albania/Montenegro). *The Holocene* 25:435–444. <https://doi.org/10.1177/0959683614561891>
- Schliemann SA, Bockheim JG (2011) Methods for studying treefall gaps: A review. *Forest Ecology and Management* 261:1143–1151. <https://doi.org/10.1016/j.foreco.2011.01.011>
- Schütz J-P, Saniga M, Diaci J, Vrška T (2016) Comparing close-to-nature silviculture with processes in pristine forests: lessons from Central Europe. *Annals of Forest Science* 73:911–921. <https://doi.org/10.1007/s13595-016-0579-9>
- Seidl R, Thom D, Kautz M, et al (2017) Forest disturbances under climate change. *Nature Clim Change* 7:395–402. <https://doi.org/10.1038/nclimate3303>
- Seneviratne SI, Nicholls N, Easterling D, et al (2012) Changes in Climate Extremes and their Impacts on the Natural Physical Environment. In: Field CB, Barros V, Stocker TF, Dahe Q (eds) *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation*. Cambridge University Press, Cambridge, pp 109–230
- Seppä H (2013) Pollen Analysis, Principles. In: Elias SA (ed) *The Encyclopedia of Quaternary Science*. Elsevier, Amsterdam, pp 794–804
- Sirotkovic J (1987) *Enciklopedija Jugoslavije*. Jugoslovenski leksikografski zavod Miroslav Krleža, Zagreb, Croatia,
- Song X-P, Hansen MC, Stehman SV, et al (2018) Global land change from 1982 to 2016. *Nature* 560:639–643. <https://doi.org/10.1038/s41586-018-0411-9>
- Spies TA (2004) Ecological concepts and diversity of old-growth forests. *Journal of Forestry* 102:14–20
- Spies TA, Franklin JF, Klopsch M (1990) Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can J For Res* 20:649–658. <https://doi.org/10.1139/x90-087>
- Stancioiu PT, O'Hara KL (2006) Morphological plasticity of regeneration subject to different levels of canopy cover in mixed-species, multiaged forests of the Romanian Carpathians. *Trees* 20:196–209. <https://doi.org/10.1007/s00468-005-0026-2>
- Sugita S (1994) Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *The Journal of Ecology* 82:881–897. <https://doi.org/10.2307/2261452>
- Swetnam TW, Allen CD, Betancourt JL (1999) Applied historical ecology: using the past to manage for the future. *Ecological Applications* 9:1189–1206. [https://doi.org/10.1890/1051-0761\(1999\)009\[1189:AHEUTP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[1189:AHEUTP]2.0.CO;2)
- Tyrrell LE, Crow TR (1994) Structural Characteristics of Old-Growth Hemlock-Hardwood Forests in Relation to Age. *Ecology* 75:370–386. <https://doi.org/10.2307/1939541>

- UN General Assembly (2015) Transforming our world : the 2030 Agenda for Sustainable Development
- UNEP/CBD/SBSTTA (2001) Main Theme: Forest Biological Diversity. Report of the Ad Hoc Technical Expert Group on Forest Biological Diversity. Seventh Meeting Montreal
- Vacek Z, Prokúpková A, Vacek S, et al (2021) Mixed vs. monospecific mountain forests in response to climate change: structural and growth perspectives of Norway spruce and European beech. *Forest Ecology and Management* 488:119019. <https://doi.org/10.1016/j.foreco.2021.119019>
- Wagner FH, Ferreira MP, Sanchez A, et al (2018) Individual tree crown delineation in a highly diverse tropical forest using very high resolution satellite images. *ISPRS Journal of Photogrammetry and Remote Sensing* 145:362–377. <https://doi.org/10.1016/j.isprsjprs.2018.09.013>
- Watson JEM, Evans T, Venter O, et al (2018) The exceptional value of intact forest ecosystems. *Nat Ecol Evol* 2:599–610. <https://doi.org/10.1038/s41559-018-0490-x>
- Watson JEM, Shanahan DF, Di Marco M, et al (2016) Catastrophic Declines in Wilderness Areas Undermine Global Environment Targets. *Current Biology* 26:2929–2934. <https://doi.org/10.1016/j.cub.2016.08.049>
- Whitlock C, Colombaroli D, Conedera M, Tinner W (2018) Land-use history as a guide for forest conservation and management. *Conservation Biology* 32:84–97. <https://doi.org/10.1111/cobi.12960>
- Whitlock C, Larsen C (2001) Charcoal as a fire proxy. In: Smol JP, Birks HJB, Last WM, et al. (eds) *Tracking Environmental Change Using Lake Sediments*. Springer Netherlands, Dordrecht, pp 75–97
- Wirth C, Gleixner G, Heimann M (eds) (2009) *Old-growth forests: function, fate, and value*. Springer, Berlin
- Wolters S, Enters D, Bittmann F (2010) Landscape history and land-use dependent soil erosion in central Bosnia from the Bronze Age to Medieval Times. In: *EGU General Assembly Conference Abstracts*. p 11200
- Wymann Von Dach S, Bracher CP, Peralvo M, et al (2018) Leaving no one in mountains behind: Localizing the SDGs for resilience of mountain people and ecosystems. <https://doi.org/10.7892/BORIS.120130>

PAPER 1: Land-cover mapping in the Biogradska Gora National Park with very-high-resolution Pléiades images

Eleonora Cagliero^{1,2}, Donato Morresi³, Niccolò Marchi¹, Laure Paradis², Walter Finsinger², Matteo Garbarino³, Emanuele Lingua¹,

¹ Department of Land, Environment, Agriculture and Forestry (TESAF), University of Padova, 35020 Legnaro (PD), Italy

² University of Montpellier, ISEM, CNRS, IRD, EPHE, Montpellier, France

³ Department of Agricultural, Forest and Food Sciences (DISAFA), University of Torino, 10095 Grugliasco (TO), Italy

Based on the manuscript published in: Borgogno-Mondino E., Zamperlin P. (eds) Geomatics and Geospatial Technologies. ASITA 2021. Communications in Computer and Information Science, vol 1507. Springer, Cham, 2022

https://doi.org/10.1007/978-3-030-94426-1_2

Abstract

Old-growth forests (OGFs) are extremely valuable relict ecosystems for studying natural disturbance dynamics. Small-scale disturbances caused by tree crown mortality of one or few individuals, i.e. gap dynamics, are the most frequent events occurring in OGFs. Understanding these processes requires information on the spatial arrangement of forest patches dominated by different tree species and forest canopy gaps at a fine spatial scale. Here, we aimed at mapping different land-cover classes including conifers, broad-leaved trees, and forest canopy gaps using two very-high-resolution satellite images, i.e. Pléiades images, in the mixed fir-spruce-beech OGF reserve of Biogradska Gora (Montenegro). Specifically, we coupled an Object-Based Image Analysis (OBIA) approach and a Random Forest classifier, trained with samples partly derived from field data. The adopted approach showed high accuracy for the main land-cover classes (conifers, broadleaved trees, grasslands, bare ground, and water), e.g. producer's and user's accuracy higher than 92% and 95%, respectively. Conversely, forest canopy gaps were classified with lower accuracy, e.g. minimum producer's and user's accuracies of 75% and 54%, respectively. Despite the exploitation of textural metrics during both image segmentation and classification, the lack of remote sensing data providing information on the vertical structure of the forest stand prevented us from accurately map forest canopy gaps.

Keywords: very-high-resolution satellite imagery, old-growth forest, land-cover map, object-based image analysis, forest canopy gaps

Introduction

Old-growth forests (OGFs) are ecosystems that have developed in the absence of anthropogenic influence and of stand-replacing natural disturbances for a period of time long enough (centuries-millennia) to develop peculiar structures and functions (Wirth et al. 2009). OGFs provide a wide range of ecosystem services, contributing to global biodiversity conservation and to mitigate climate change by carbon sequestration (Wirth et al. 2009). Moreover, OGFs act as reference systems for restoration and close-to-nature silviculture (Bauhus et al. 2009) because vegetation dynamics take place without direct human influence.

Depending on the predominant dynamics, OGFs have structural characteristics that vary among geographic areas. In temperate forests, large-scale natural disturbances are rare, and the stand dynamics are mainly characterized by small- to intermediate-scale forest canopy openings (gap dynamics) following the natural- or disturbances-caused mortality of single or small groups of dominant forest canopy trees (Garbarino et al. 2012). The temporal and spatial interplay of type, size and frequency of disturbance events influences the species composition of the canopy layer and determines the creation of a heterogeneous mosaic of structural types (Feldmann et al. 2018) that is particularly developed in large OGFs (>1000 ha). However, presumably due to widespread millennial-long and increasing rates of land-use change (Motta et al. 2015; Sabatini et al. 2018), large OGFs are rare today in Europe and mainly located in protected areas (Sabatini et al. 2018).

In the last decades, forest stand dynamics have been investigated mostly with terrestrial methods, such as representative sample plots (permanent or not), extensive field surveys, belt transects, and systematic grids (Nagel and Svoboda 2008; Bottero et al. 2011; Drößler and von Lüpke 2012; Petritan et al. 2013; Feldmann et al. 2018). However, the structural heterogeneity of OGFs requires a finer scale of analysis than terrestrial methods, which are expensive (Vepakomma et al. 2008) and time-consuming, especially in OGFs, as these often are in remote places and difficult to access.

In this context, coupling remote sensing methods with field data as ground-control (Garbarino et al. 2012) is particularly valuable since it allows analyzing patterns (e.g. land-cover maps) and processes (e.g. gap dynamics) at the landscape scale in a shorter amount of time (Rich et al. 2010; Garbarino et al. 2012; Hobi et al. 2015). Moreover, remote sensing allows performing multi-temporal analyses to assess forest cover changes through time (Torimaru et al. 2012). For instance, the extent and number of gaps continuously change due to (i) the formation of new ones and (ii) infilling by young trees and (iii) the expansion of older gaps. Even if the temporal dynamics can be deduced from field-based methods (by dendrochronology or repeated inventory in permanent plots), remote sensing analyses based on satellite imagery would be more cost-effective and could provide spatial information over broad areas. However, the detection of fine-scale forest components, such as tree crowns and small forest canopy gaps, is constrained by the availability of very-high-resolution (c. <5m) multispectral satellite imagery (e.g. Ikonos, Pléiades, QuickBird, Kompsat-2, WorldView-2) (Garbarino et al. 2012; Yang et al. 2015).

To our knowledge, only few studies employed single very-high-spatial-resolution satellite images for mapping forest canopy gaps (Garbarino et al. 2012) while others took advantage of stereo aerial imagery (Zielewska-Büttner et al. 2016) or integrated multispectral and LiDAR data (Yang et al. 2015). Given the smaller pixel dimension with respect to the image objects of interest, a common approach adopted with high-spatial-resolution imagery is to perform Object-Based Image Analysis (OBIA) (Hossain and Chen 2019). This technique aims at grouping neighboring image pixels with similar spectral and textural characteristics into objects, thus reducing their internal variability. OBIA avoids the “salt and pepper” noise commonly resulting from traditional pixel-based classification methods and aims at delineating image objects that closely correspond to the size and the shape of real features (Nyamgeroh et al. 2018). OBIA is usually composed of two main phases: (i) image segmentation, and (ii) feature extraction and classification (Hossain and Chen 2019).

Here we focused on the Biogradska Gora mixed beech-fir-spruce OGF (Montenegro), a forest landscape large enough to develop the whole natural temporal and spatial variability of forest dynamics (Motta et al. 2015). Specifically, we aimed at mapping different land-cover classes including conifers, broad-leaved trees, and forest canopy gaps, using two very-high-resolution Pléiades images and coupling OBIA and a Random Forest classifier.

Methodology

Study site

The Biogradska Gora National Park (Fig. 1) is located in the Dinaric Alps. The reserve area of the park (c. 6000 ha) includes a core area of strict protection of c. 2830 ha surrounded by a buffer zone (Fig. 1). In the core area, all land-use activities are prohibited except for scientific research and controlled tourism. Instead, pastoral farming is allowed in the buffer zone, as meadows and shepherds’ huts testimony. The reserve area is protected since 1885 CE, as royal hunting reserve and since 1950, when the National Park was established. The climate is characterized by a mean annual temperature of c. 7°C, and an annual average precipitation of 1962 mm with maximum values in November-December and minimum values in July-August. In the reserve area the overstorey is dominated by European beech, silver fir, and Norway spruce with lesser amounts of other tree species such as maples, common ash, and elms (Motta et al. 2015).

Field surveys

To characterize the forest structure and the tree-species composition and to obtain ground control points for remote sensing analyses, we carried out field campaigns in May and September 2019. We defined the location of the 51 survey plots (Fig. 1) using a forest map produced by Motta et al. (2015) obtained by the classification of a SPOT5 image (acquired in May 2007) adopting an unsupervised classification algorithm (ISODATA) on three multispectral bands (G, R, and NIR). In each circular plot (area = 615.5 m²; radius = 14 m) for all the living trees with a diameter at 1.30 m (DBH) $\geq$ 7.5 cm we recorded the species and DBH and for a sub-sample of individuals belonging to different species and diametrical classes we measured the height. We then measured the minimum and the maximum diameter and the length of the coarse woody debris (CWD) to assess the volume of dead biomass. We pooled the data of our 51 plots with the data of 30 plots surveyed by Motta et al. (2015) in a 120-m grid network adopting the same field protocol. For each of the resulting 81 plots we derived typical forest stand parameters, such as mean and standard deviation of DBH, total tree density (De), and basal area (BA). We inferred the unmeasured tree heights using specie-specific hypsometric curves that we built based on the field data and computed the volume of living trees (V) using a local volume table.

Image pre-processing

To map the distribution of six land-cover classes (conifer trees, broadleaved trees, grasslands-meadows, forest canopy gaps, bare ground, and water), we did an Object-Based Image Analysis (OBIA) on two very-high-resolution satellite images. Specifically, we used two Pléiades images (1A and 1B) acquired during the growing season of two subsequent years: on the 30th of August 2015 and on the 1st of August 2016, respectively. The images are spatially complementary, as the footprint of the 2015 image misses the upper part of the basin while the 2016 one was partly covered by clouds and cloud shadows over the forested area. The Pléiades images were provided already orthorectified and included a 0.5-m panchromatic band (PAN) and four 2-m resolution multispectral bands (RGB and NIR). We used the nearest neighbour diffusion (NNDiffuse) algorithm (Sun et al. 2014) to pan-sharpen the multispectral bands. The images were then co-registered in ENVI version 5.3.1 (Exelis Visual Information Solutions, Boulder, Colorado), using the Bing satellite image as reference. Subsequently, we masked invalid pixels, i.e. clouds and cloud shadows, through on-screen digitization.

Image segmentation and classification

We obtained image objects representing small groups of crowns using the Large-Scale Mean-Shift (LSMS) segmentation algorithm (Michel et al. 2015) implemented in Orfeo ToolBox version 7.0

(Grizonnet et al. 2017) (Fig. 4). In particular, we set the following parameters in the LSMS algorithm: a spatial radius of 20 pixels, a range radius of 0.015 (as all rasters in the input stack assumed values ranging from 0 to 1) and a minimum region size of 200 pixels. We employed the Normalized Difference Vegetation Index (NDVI), the near-infrared band (NIR), and textural data derived from the mathematical morphology technique called opening as input rasters in the LSMS segmentation procedure. The opening procedure involves an erosion operation followed by dilation using a 2-dimensional structuring element (SE) (Soille 2004), and it is applied to grey values of an image to eliminate objects smaller than the SE. Specifically, we used a 7-pixel diameter disc (corresponding to 3.5 m) as SE because this shape and size performed well to the smallest tree crowns recognizable in the Pléiades images. We performed the opening operation using grey values relative to the Value component of the Hue-Saturation-Value (HSV) transformation, which we applied to the red, green and blue bands of the Pleiades images. Since the Value component corresponds to the brightness of a surface, the opening procedure allowed us to maximize the contrast between sunlit crowns, generally located at the top of the forest stand, and darker portions in the background, corresponding to shorter trees and canopy gaps. We employed the Random Forest (RF) algorithm (Breiman 2001) implemented in the ‘ranger’ (Wright and Ziegler 2017) R package (R Core Team 2019) to perform a supervised classification of the image objects. We created a set of 1457 training samples evenly distributed over the study area and stratified by land-cover class (Table 1) through on-screen photointerpretation of image objects intersecting the ground forest plots (groups of broadleaved trees, groups of conifer trees, forest canopy gaps) and of objects we did not survey (grasslands-meadows, bare ground and water). Predictor variables used in the RF classifier included several textural metrics together with reflectance values and selected spectral vegetation indices (Table 2).

We assessed the classification accuracy through a 5-fold cross-validation procedure and we analyzed each Pléiades image separately, merging classification results to obtain a unique land-cover map for the whole study area.

Since forest canopy gaps are areas temporary without a tree canopy cover (due to natural disturbances, gap dynamics), all the gaps permanently without tree vegetation due to limiting factors to tree growth (e.g. edaphic conditions, shallow water table) or human activities (e.g. pastures) that were erroneously classified as forest canopy gaps were filtered out in QGIS by a topological query before computing the number of gaps, size statistics and the gap fraction (Schliemann and Bockheim 2011).

Results

The Biogradska Gora mixed fir-spruce-beech forest is characterized by the presence of large trees (DBH up to 150 cm, average DBH = 33.89 cm), and high volume of both living (907.3 m³/ha) and dead

biomass (251.57 m³/ha). The forest stands show a complex horizontal and vertical structure, a high tree size diversification (DBH standard deviation of 22.74 cm), and a rotated sigmoidal DBH distribution. The land-cover map derived from the Pléiades images (Fig. 2) confirmed on a small scale the spatial heterogeneity of the forest canopy. The overall good performance of the classifier is shown by high values of K and OA (Table 3). However, the classification accuracy differed greatly among classes. The Random Forest classifier performed better (in terms of both PA and UA) for conifers, broadleaved trees, grasslands, bare ground, and water classes while its accuracy was substantially lower for forest canopy gaps (Table 3).

According to the image classification (Fig. 2), the majority of the reserve area (61.09%) is covered by forest, followed by 33.56% of grasslands, 3.94% of bare ground, 1.15% of forest canopy gaps, and 0.25% of water. More in details, the core area consists mainly of forests (92.49%) while grasslands dominate (59.92%) in the buffer zone (Fig. 2). The inner part of the core area is dominated by coniferous trees while the surrounding area is dominated by mixed forest of beech-fir-spruce and by pure beech stands (Fig. 2). Forest canopy gaps were mainly found in conifer-dominated areas (99%).

Within the reserve area, 2638 forest canopy gaps were detected that cover a total of 67.95 ha, resulting in a gap fraction of 0.93% and a gap density of 0.45 #/ha (Table 4). The average size of gaps is 208.03 m² while the median value is 116.79 m² indicating that the majority of gaps are small, as confirmed by the negative exponential shape of the gaps size distribution (Fig. 3). In particular, 41% of gaps have a surface <100 m², 35% between 100 and 200 m², 18% between 200 and 500 m², and the remaining 6% are >500 m², whose 2% consists of gaps >1000 m² and only 0.15% are gaps >5000 m².

The core area and the buffer zones did not differ in terms of size (area), shape (perimeter), and frequency distribution of gaps (Table 4). On the other hand, the abundance of gaps was two times higher in the core area than in the buffer zone. However, since the buffer zone is characterized by a high proportion of grasslands (60%), the gap fraction relative to the forest area is higher in the buffer zone (Table 4).

Discussion

The Biogradska Gora mixed fir-spruce-beech forest clearly shows old-growthness characteristics. The forest structure and the occurring gap dynamic place the forest among the largest old-growth forest remnants in South-Eastern Europe.

The combination of textural metrics with spectral data during the segmentation process is not a common practice as they are mostly employed in the classification phase (Kupidura 2019), even if it has been shown to improve the classification accuracy of the land-cover classes in OBIA (Hossain and Chen 2019). In our case, the use of textural metrics during the segmentation phase (Fig. 4) enhanced the identification of individual tree crowns and forest canopy gaps as they provided proxy information on the vertical forest structure. In fact, the opening procedure allowed us to distinguish between the

circular-shaped and well-illuminated crowns of the dominant tree layer and the small trees and shrubs occurring in forest canopy gaps, characterized by lower brightness due to the shadow casted by the surrounding tree crowns.

Forest canopy gaps are more heterogeneous and with a rougher texture than the surrounding tree canopy cover (Rich et al. 2010; Nyamgeroh et al. 2018). However, the classification shows lower accuracy in detecting forest canopy gaps compared to the other land-cover classes, as highlighted by a minimum producer's accuracy of 75% and a minimum user's accuracy of 54% (Table 3). The low producer's accuracy associated with forest canopy gaps can be affected by shadows, which we limited by employing the NDVI and the textural metrics in the segmentation and classification phases. Specifically, as a normalized index, NDVI is less affected by the proportion of canopy shadows than single reflectance bands and enhances the distinction between vegetation and bare ground (Xu et al. 2019).

The category of forest canopy gaps includes openings in the dominant tree canopy cover that can be already occupied by regeneration in various stages of growth. Conventionally, when the infilling trees reach heights equal to half of the height of the surrounding mature trees in the upper canopy (Tyrrell and Crow 1994), the area is assigned to the dominant tree-canopy cover. If the gap is small, the opening can be closed by the lateral growth of the edging tree crowns. This process is particularly evident when broadleaved species are involved, especially beech, since they have higher crown plasticity than conifers (Muth and Bazzaz 2002). Of all observed gaps, only 1% were detected in broadleaved-dominated stands. This can be partially explained by the capacity of crowns to quickly close the gaps or reduce their size (Muth and Bazzaz 2002; Bottero et al. 2011). The majority of gaps (99%) were found in coniferous stands, not only for the absence of lateral crown expansion of spruce and fir, but also since those stands showed the highest OGF characteristics. In OGFs, mortality is mainly occurring at the canopy layer, involving large and old, sometimes even individual, trees (Wirth et al. 2009).

In the Biogradska Gora forest, canopy gaps are most often small (50-200 m²), and large gaps (> 1000 m²) are rare (Fig. 3). The large gaps could have been generated by intense windstorm events or most probably by the expansion and fusion of neighboring gaps. This is supported by the shape analysis, which shows that large gaps are characterized by complex and heterogeneous shapes with a large perimeter.

Our analysis suggests that the gap fraction is small (< 2%). Such small gap fraction values were also obtained in similar OGFs with remote sensing approaches using very-high-resolution images (Komsat-2 and WorldView-2) (Garbarino et al. 2012; Hobi et al. 2015). Such values are consistently lower compared to values derived from terrestrial methods (always > 15%) (Nagel and Svoboda 2008; Bottero et al. 2011; Drößler and von Lüpke 2012). It thus seems that the classification method substantially underestimates the fraction of the total forest canopy gaps. However, one should bear in mind that a broader range of gap ages and sizes are identified with field surveys (Garbarino et al. 2012). With their finer detail of analysis, field surveys can better detect very small gaps, including those caused by a

single tree-death. Moreover, field surveys can better detect old-formed gaps, including those that are almost closed or where regeneration is very high. Instead, the discrimination of gaps with remote sensing methods is hindered by the similar spectral response between the dominant tree canopy cover and the forest canopy gaps (Kupidura 2019). Conversely, remote sensing methods are suitable to detect recently formed gaps and large gaps in which the regeneration has not yet reached great heights or has not completely colonized the gap's surface. Moreover, remote sensing approaches are suitable to estimate the range of variability of disturbances over large areas. By contrast, terrestrial methods are often limited by the small size of the sampled area (Drößler and von Lüpke 2012) and by expensive and time-consuming field inventories, especially in OGFs, which are usually located on steep slopes or in remote areas.

Our study reveals that the analysis of very-high-spatial-resolution satellite imagery alone is not sufficient to map forest canopy gaps and the complex forest structure of mixed OGFs with high accuracy. Better results could be achieved using stereo-pair images or LiDAR data as they provide canopy heights, thereby allowing a better delineation of gaps (Vepakomma et al. 2008; Hobi et al. 2015). However, these approaches are more expensive due to image acquisition costs, especially in remote areas. Conversely, they achieve substantially higher accuracies (up to 96%) in gap detection (Vepakomma et al. 2008). Moreover, recent studies have shown the potential of combining optical and LiDAR data: LiDAR-derived Canopy Height Model allows to better isolate gaps during the segmentation phase. Simultaneously, the synergistic use of the two datasets can result in a more accurate classification map (Yang et al. 2015).

Conclusion

Coupling OBIA and a Random Forest classifier using two very-high-resolution Pléiades images provided high accuracy in mapping most land-cover classes with the exception of the forest canopy gap category. Even if the use of textural metrics during both the segmentation and classification phase enhanced gaps circumscription and the distinction between the dominant and the lower canopy layers, it was however not sufficient to obtain a good accuracy for this class. One reason for the low accuracy could be that the spectral indices (Table 2) derived from Pléiades MS bands (RGB and NIR) tend to saturate in dense vegetation conditions preventing an adequate distinction between young and mature crowns. Another possible reason could be the low number of training samples in the forest canopy gap category, since we used only the objects intersecting our field plot.

A reliable assessment of forest canopy gaps is extremely important to describe the complex forest structure and dynamics of mixed OGFs. Analyses based on single satellite imagery will lack the information on the vertical structure of the forests. Thus, to gain better results in terms of accuracy stereo-pair images, LiDAR data or a combination of optical and LiDAR data may be envisaged as better alternatives.

Figures

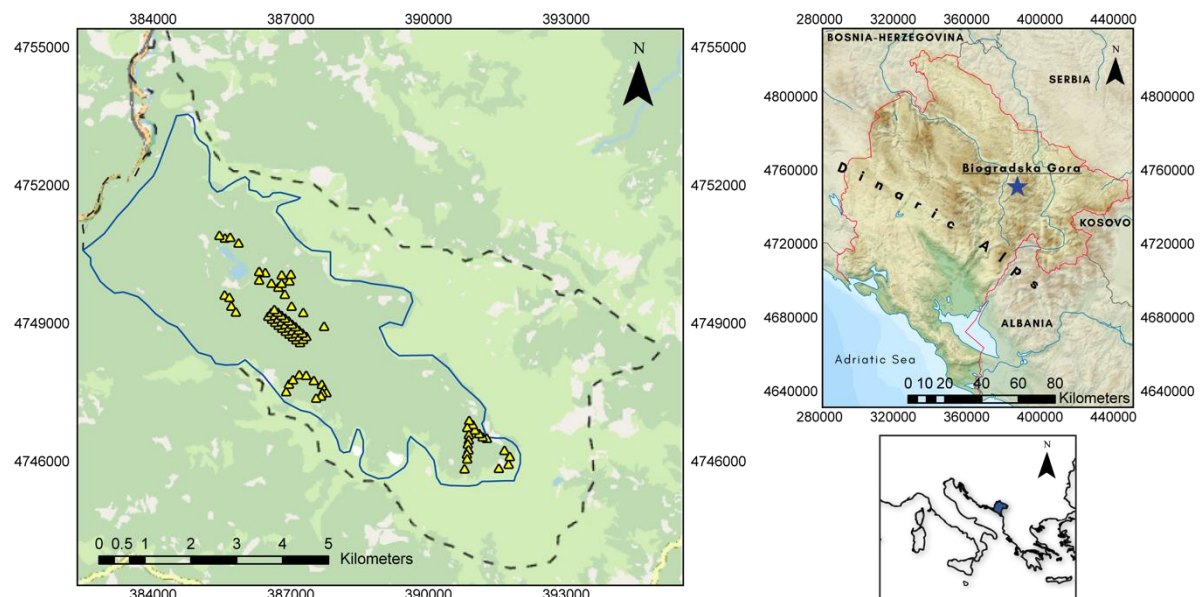


Fig. 1 Maps of the location of the study site at decreasing spatial scales and of the 81 forest plots (yellow triangles). Delimitation of the administrative boundary of Montenegro (red continuous line), of the reserve area (black dashed line) and of the core area of the Biogradska Gora National Park (blue continuous line). Reference system EPSG:32634 (WGS 84 / UTM zone 34N).

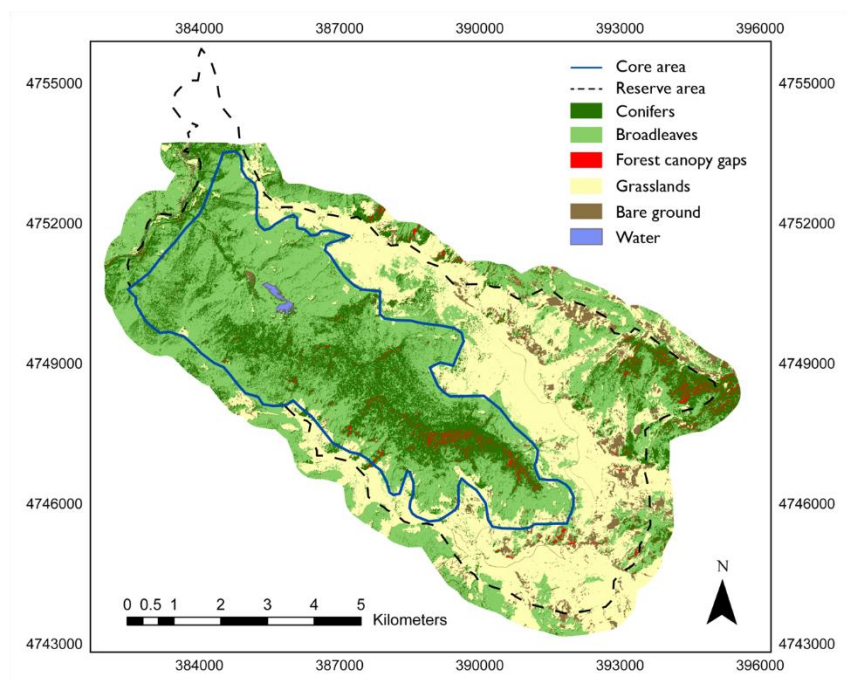


Fig. 2 Classification map of the land-cover classes of the Biogradska Gora National Park. Reference system EPSG:32634 (WGS 84 / UTM zone 34N).

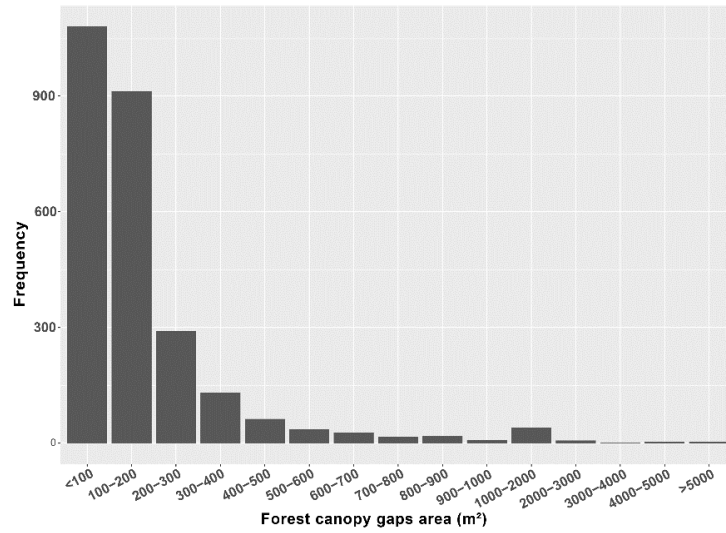


Fig. 3 Distribution of forest canopy gaps according to their size.

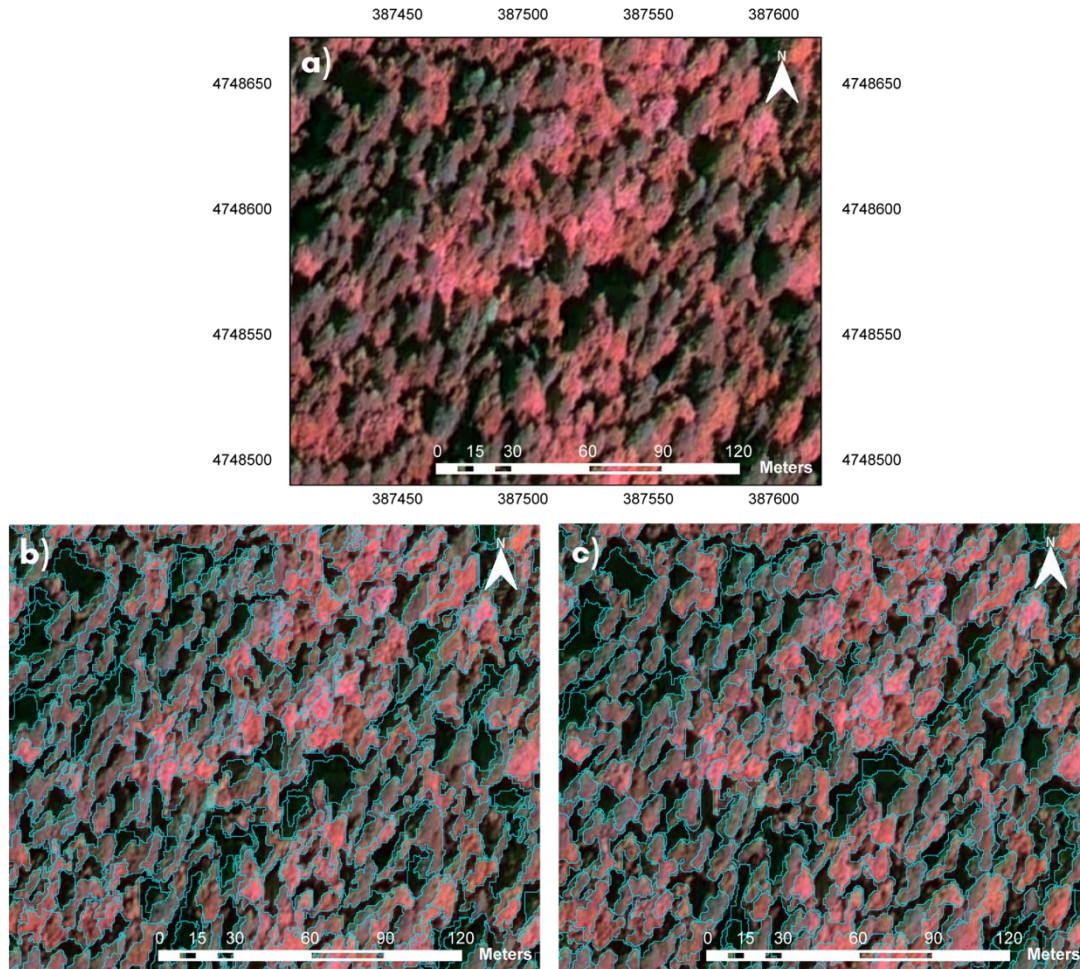


Fig. 4 Detail of the 2015 Pléiades-1B image displayed with false-color composite (R=NIR, G=Red, B=Green): original (a) and segmented either without (b) or with (c) the inclusion of textural information derived using the opening procedure. The parameters used in the Large-Scale Mean-Shift (LSMS) segmentation algorithm were held constant. Reference system EPSG:32634 (WGS 84 / UTM zone 34N).

Table 1 Number of training samples in each land-cover class.

	Training samples		
	Image acquisition		TOT
Class	30 th of August 2015	1 st of August 2016	
Conifer trees	611	93	704
Broadleaved trees	435	137	572
Forest canopy gaps	18	11	29
Grasslands	66	19	85
Bare ground	32	27	59
Water	8	-	8

Table 2 Details concerning the spectral and textural layers used to compute multiple summary statistics employed as predictor variables in the Random Forest (RF) model. NDVI=Normalized Difference Vegetation Index; EVI=Enhanced Vegetation Index; GNDVI=Green Normalized Difference Vegetation Index; MSAVI=Modified Soil Adjusted Vegetation Index; NDWI=Normalized Difference Water Index; SAVI=Soil Adjusted Vegetation Index; SR=Simple Ratio.

Spectral and textural layers	Summary statistics
Pléiades reflectance bands (PAN and MS)	Min; max; range;
Spectral vegetation indices (NDVI; EVI; GNDVI; MSAVI; NDWI; SAVI; SR)	sum; mean; variance; Gini coefficient;
Morphological opening (kernels widths: 3; 5; 7; 9; 11; 13)	standard deviation;
Simple Haralick textures (Energy; Entropy; Correlation; Inverse Difference Moment; Inertia; Cluster Shade; Cluster Prominence; Haralick Correlation)	percentiles (5 th , 25 th , 50 th , 75 th , 95 th)

Table 3 RF classification accuracy as assessed by means of overall (OA) and Cohen's Kappa (K) accuracies. Producer's (PA) and User's (UA) accuracies are grouped by land-cover classes.

	Image acquisition			
	30 th of August 2015		1 st of August 2016	
Class	PA	UA	PA	UA
Conifer trees	95.8	96.1	92.9	97.8
Broadleaved trees	95.2	95.6	98.5	97.8
Forest canopy gaps	75.0	66.7	100.0	54.5
Grasslands	100.0	97.0	100.0	100.0
Bare ground	100.0	100.0	96.4	100.0
Water	100.0	100.0	-	-
OA	95.6		96.5	
K	92.5		94.6	

Table 4 Landscape metrics and summary of gap attributes in the OGF of Biogradska Gora.

Variables	Core area	Buffer zone	Reserve area
Total area (ha)	2834.27	3052.66	5886.94
Number of gaps (#)	1674	964	2638
Density of gaps (#/ha)	0.59	0.32	0.45
Mean gap area (m²)	210.54	203.69	208.03
Median gap area (m²)	119.78	111.85	116.79
Mean gap perimeter (m)	86.34	84.36	85.62
Median gap perimeter (m)	60.91	57.93	59.87
Gap fraction (%)	1.24	0.64	0.93
Gap fraction in forest area (%)	1.34	2.01	1.53

References

- Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. *Forest Ecology and Management* 258:525–537. <https://doi.org/10.1016/j.foreco.2009.01.053>
- Bottero A, Garbarino M, Dukic V, et al (2011) Gap-phase dynamics in the old-growth forest of Lom, Bosnia and Herzegovina. *Silva Fennica* 45:<https://doi.org/10.14214/sf.76>
- Breiman L (2001) Random forests. 45:5–32
- Drößler L, von Lüpke B (2012) Canopy gaps in two virgin beech forest reserves in Slovakia. *Journal of Forest Science* 51:446–457. <https://doi.org/10.17221/4578-JFS>
- Feldmann E, Drößler L, Hauck M, et al (2018) Canopy gap dynamics and tree understory release in a virgin beech forest, Slovakian Carpathians. *Forest Ecology and Management* 415–416:38–46. <https://doi.org/10.1016/j.foreco.2018.02.022>
- Garbarino M, Borgogno Mondino E, Lingua E, et al (2012) Gap disturbances and regeneration patterns in a Bosnian old-growth forest: a multispectral remote sensing and ground-based approach. *Annals of Forest Science* 69:617–625. <https://doi.org/10.1007/s13595-011-0177-9>
- Grizonnet M, Michel J, Poughon V, et al (2017) Orfeo ToolBox: open source processing of remote sensing images. *Open Geospatial Data, Software and Standards* 2:15. <https://doi.org/10.1186/s40965-017-0031-6>
- Hobi ML, Ginzler C, Commarmot B, Bugmann H (2015) Gap pattern of the largest primeval beech forest of Europe revealed by remote sensing. *Ecosphere* 6: art76. <https://doi.org/10.1890/ES14-00390.1>
- Hossain MD, Chen D (2019) Segmentation for Object-Based Image Analysis (OBIA): A review of algorithms and challenges from remote sensing perspective. *ISPRS Journal of Photogrammetry and Remote Sensing* 150:115–134. <https://doi.org/10.1016/j.isprsjprs.2019.02.009>
- Kupidura P (2019) The Comparison of Different Methods of Texture Analysis for Their Efficacy for Land Use Classification in Satellite Imagery. *Remote Sensing* 11:<https://doi.org/10.3390/rs11101233>
- Michel J, Youssefi D, Grizonnet M (2015) Stable Mean-Shift Algorithm and Its Application to the Segmentation of Arbitrarily Large Remote Sensing Images. *IEEE Transactions on Geoscience and Remote Sensing* 53:952–964. <https://doi.org/10.1109/TGRS.2014.2330857>
- Motta R, Garbarino M, Berretti R, et al (2015) Structure, spatio-temporal dynamics and disturbance regime of the mixed beech–silver fir–Norway spruce old-growth forest of Biogradska Gora (Montenegro). *Plant Biosystems* 149:966–975. <https://doi.org/10.1080/11263504.2014.945978>
- Muth CC, Bazzaz FA (2002) Tree canopy displacement at forest gap edges. *Canadian Journal of Forest Research* 32:247–254. <https://doi.org/10.1139/x01-196>
- Nagel TA, Svoboda M (2008) Gap disturbance regime in an old-growth *Fagus* – *Abies* forest in the Dinaric Mountains, Bosnia-Herzegovina. *Canadian Journal of Forest Research* 38:2728–2737. <https://doi.org/10.1139/X08-110>
- Nyamgeroh BB, Groen TA, Weir MJC, et al (2018) Detection of forest canopy gaps from very high resolution aerial images. *Ecological Indicators* 95:629–636. <https://doi.org/10.1016/j.ecolind.2018.08.011>
- Petritan AM, Nuske RS, Petritan IC, Tudose NC (2013) Gap disturbance patterns in an old-growth sessile oak (*Quercus petraea* L.)–European beech (*Fagus sylvatica* L.) forest remnant in the Carpathian Mountains, Romania. *Forest Ecology and Management* 308:67–75. <https://doi.org/10.1016/j.foreco.2013.07.045>

- Rich Roy L, Frelich L, Reich PB, Bauer ME (2010) Detecting wind disturbance severity and canopy heterogeneity in boreal forest by coupling high-spatial resolution satellite imagery and field data. *Remote Sensing of Environment* 114:299–308. <https://doi.org/10.1016/j.rse.2009.09.005>
- Sabatini FM, Burrascano S, Keeton WS, et al (2018) Where are Europe’s last primary forests? Diversity and Distributions 24:1426–1439. <https://doi.org/10.1111/ddi.12778>
- Schliemann SA, Bockheim JG (2011) Methods for studying treefall gaps: A review. *Forest Ecology and Management* 261:1143–1151. <https://doi.org/10.1016/j.foreco.2011.01.011>
- Soille P (2004) *Morphological Image Analysis*. Springer Berlin Heidelberg, Berlin, Heidelberg
- Sun W, Chen B, Messinger DW (2014) Nearest-neighbor diffusion-based pan-sharpening algorithm for spectral images. *Optical Engineering* 53:013107-1-013107–2. <https://doi.org/10.1117/1.OE.53.1.013107>
- Torimaru T, Itaya A, Yamamoto S-I (2012) Quantification of repeated gap formation events and their spatial patterns in three types of old-growth forests: Analysis of long-term canopy dynamics using aerial photographs and digital surface models. *Forest Ecology and Management* 284:1–11. <https://doi.org/10.1016/j.foreco.2012.07.044>
- Tyrrell LE, Crow TR (1994) Structural Characteristics of Old-Growth Hemlock-Hardwood Forests in Relation to Age. *Ecology* 75:370–386. <https://doi.org/10.2307/1939541>
- Vepakomma U, St-Onge B, Kneeshaw D (2008) Spatially explicit characterization of boreal forest gap dynamics using multi-temporal lidar data. *Remote Sensing of Environment* 112:2326–2340. <https://doi.org/10.1016/j.rse.2007.10.001>
- Wirth C, Gleixner G, Heimann M (eds) (2009) *Old-growth forests: function, fate, and value*. Springer, Berlin
- Wright MN, Ziegler A (2017) ranger: A Fast Implementation of Random Forests for High Dimensional Data in C++ and R. *J Stat Soft* 77:1–17. <https://doi.org/10.18637/jss.v077.i01>
- Xu N, Tian J, Tian Q, et al (2019) Analysis of Vegetation Red Edge with Different Illuminated/Shaded Canopy Proportions and to Construct Normalized Difference Canopy Shadow Index. *Remote Sensing* 11:1192. <https://doi.org/10.3390/rs11101192>
- Yang J, Jones T, Caspersen J, He Y (2015) Object-Based Canopy Gap Segmentation and Classification: Quantifying the Pros and Cons of Integrating Optical and LiDAR Data. *Remote Sensing* 7:15917–15932. <https://doi.org/10.3390/rs71215811>
- Zielewska-Büttner K, Adler P, Ehmann M, Braunisch V (2016) Automated Detection of Forest Gaps in Spruce Dominated Stands Using Canopy Height Models Derived from Stereo Aerial Imagery. *Remote Sensing* 8:175. <https://doi.org/10.3390/rs8030175>

PAPER 2: Legacies of past human activities on one of the largest old-growth forests in south-east European mountains

Eleonora Cagliero^{1,2}, Donato Morresi³, Laure Paradis², Milić Čurović⁴, Velibor Spalevic⁵, Niccolò Marchi¹, Fabio Meloni³, Ilham Bentaleb², Renzo Motta³, Matteo Garbarino³, Emanuele Lingua¹, Walter Finsinger²

¹ Department of Land, Environment, Agriculture and Forestry (TESAF), University of Padova, 35020 Legnaro (PD), Italy

² University of Montpellier, ISEM, CNRS, IRD, EPHE, Montpellier, France

³ Department of Agricultural, Forest and Food Sciences (DISAFA), University of Torino, 10095 Grugliasco (TO), Italy

⁴ University of Montenegro, Biotechnical Faculty, Podgorica, Montenegro

⁵ University of Montenegro, Faculty of Philosophy – Geography Department, Nikšić, Montenegro

Based on the manuscript published in: *Vegetation History and Archaeobotany*, 2021

<https://doi.org/10.1007/s00334-021-00862-x>

Abstract

The Dinaric Mountains are a region considered as a hotspot for late-successional montane mixed *Abies alba*-*Fagus sylvatica*-*Picea abies* old-growth forests. This is likely due to historical deforestation levels being presumably lower than in other European regions. This paper provides new insights into the long-term vegetation dynamics and possible legacies of past human activities in old-growth forests in the montane zone of the Dinaric Mountains. Our extensive ground survey and the detailed land-cover types map show that the mixed *Abies alba*-*Fagus sylvatica* old-growth forest with sparse *Picea abies* is surrounded by almost pure *F. sylvatica* stands at Biogradska Gora. The well-dated stand-scale palaeoecological records (pollen, spores, stomata, macrofossils, macroscopic charcoal, and magnetic susceptibility) show that land use (cereal crop cultivation, cattle herding, and fire) during the Middle Ages caused a reduction of the *A. alba* and *P. abies*-dominated forest. After a major land abandonment around the Black Death pandemic (mid-14th century) and weaker land-use phases, *F. sylvatica*-dominated stands developed in the more accessible areas surrounding the old-growth forest. The legacy of past land uses is still visible as the almost pure *F. sylvatica* stands show less old growth characteristics than other European beech-dominated old-growth forests. Markedly in contrast to decreasing tree cover elsewhere in the region, tree cover increased several centuries before the formal protection of the forest (1878 CE). These results support the view that historical land-use pressures played an important role for the small extent and the continuity of disturbance-sensitive *A. alba* and *P. abies*-dominated old-growth forest stands.

Keywords

disturbance history, forest structure, land-use legacy, mountain ecosystem, old-growth forest, palaeoecology

Introduction

Forest ecosystems that have developed for a long period of time without important anthropogenic disturbance are small, fragmented and less abundant in Europe (< 3% of the total forest area) than in other regions (Sabatini et al. 2018; Barredo et al. 2021). The small extent of these remaining primary and old-growth forests is likely due to major human imprints on forest ecosystems since millennia (Nagel et al. 2017; Sabatini et al. 2020), including high conversion rates to agriculture (often with the use of fire) and intense forest exploitation (Kaplan et al. 2009; Birks and Tinner 2016). Despite their small extent, primary and old-growth forests provide valuable opportunities to study forest dynamics and biotic responses to non-anthropogenic disturbances (Foster et al. 1996). The study of these forests contributes to the development of close-to-nature forest management methods (Bauhus et al. 2009; Schütz et al. 2016), guiding restoration and adaptation to environmental changes (Mazziotta et al. 2016). Although generally protected, the smaller forests are vulnerable to both biotic and abiotic disturbances (Nagel et al. 2017; Sabatini et al. 2020), such as climate change (Elsen et al. 2020), land-use changes and fires that may hinder the development of features associated with the old-growth stage.

Old-growth forests are typically characterised by functional, structural and compositional features which distinguish them from forests of younger age classes: high amounts and size of deadwood, presence of old trees approaching their natural longevity and a mosaic of heterogeneous stands arising through gap dynamics (Wirth et al. 2009). These features indirectly reflect the length of time an area has been continuously wooded without human influence and major stand-replacing disturbances, as well as the history of land use and forest management (Buchwald 2005). However, features reflecting the current old-growthness cannot provide information on their longer-term history and dynamics. Paleoecology, instead, is sometimes the best and only tool for evaluating the history and ecosystem responses to past environmental changes such as climate, fire and land use (Whitlock et al. 2018). Moreover, palaeoecology can document the legacies of land-use history, climate change and disturbances such as fire on present-day forest composition (Lindbladh 1999; McLachlan et al. 2000; Birks 2019), which is a critical information for clarifying conservation objectives and evaluating outcomes (Whitlock et al. 2018; McMullin and Wiersma 2019).

The distribution of primary and old-growth forests is uneven in Europe (Sabatini et al., 2018). The Dinaric Mountains are considered a hotspot for late-successional montane old-growth forests (Sabatini et al. 2018) likely due to early protection of forests during the 19th century and lower historical human pressure compared to other mountain ranges in Europe (Sabatini et al. 2020). Indeed, the region is characterized by rugged mountain areas and land with low agricultural productivity (Diaci 1999; Kaplan et al. 2009; Nagel et al. 2017). However, records documenting long-term vegetation dynamics in conjunction with environmental changes are lacking for the montane zone in this region (Finsinger et al. 2017). Thus, the factors leading to the fragmentation of primary and old-growth forests and the extent to which the current landscape retains legacies of past land-uses and natural components (Vale 2002;

Whitlock et al. 2018) are largely unknown. For instance, in the montane zone of the Apennines, monospecific beech forests established in relatively recent times following the decline of *Abies alba* and other mesophilous deciduous trees due to enhanced fire activity and multi-millennial land use intensification superimposed on late-Holocene cooling and moistening (Morales-Molino et al. 2020). Here, we present novel multi-proxy palaeoecological data (pollen, spores, macrofossils, macroscopic charcoal, and magnetic susceptibility) and current forest structure data from Biogradska Gora (central Dinaric Mountains, Montenegro) to provide new insights into the long-term vegetation dynamics of old-growth forests in the montane zone of the Dinaric Mountains. The area has been continually under protection for the past 140 years. It includes one of the largest central-southern European old-growth stands dominated by mixed fir and beech with sparse spruce that is surrounded by almost pure beech stands (Motta et al. 2015a). Our specific aims are: (1) to assess differences in current forest structure between the old-growth forest stands and the surrounding pure beech forest (Fig. 1), (2) to track stand-scale long-term vegetation dynamics and occurrence of past disturbances by fire, and (3) to assess potential legacy effects on present-day forests.

Materials and Methods

Study area

The Biogradska Gora valley (Fig. 1) is located on the Bjelasica massif, which bears relatively small amounts of carbonate bedrocks compared to the rest of the Dinaric mountain system. Dystric cambisols (brown soils) on eruptive rock are the dominant type of soil (Čurović et al. 2011). The climate is influenced by continental and maritime airstreams, with annual average precipitation of c. 1960 mm, lowest rainfall in July-August and monthly temperatures ranging between -2 and 16 °C (Motta et al. 2015a; Fick and Hijmans 2017).

Tree cover in the valley is dominated by beech, fir and spruce, with minor amounts of *Acer pseudoplatanus* L., *A. platanoides* L. and *A. heldreichii* Orph. ex Boiss, *Fraxinus excelsior* L., *Ulmus montana* With., *Ulmus glabra* Huds., and *Sorbus aucuparia* L. (Stijovic 2017). *Betula* L. and *Pinus mugo* Turra occur at the upper treeline in adjacent valleys, and *Pinus peuce* Griseb, *P. leucodermis* Ant., and *P. sylvestris* L. are absent in the valley but sparsely occur on the Bjelasica (Černjavski 1937).

The area is protected since 1878 CE, when a royal hunting reserve was established (Motta et al. 2015a). The Biogradska Gora National Park was created in 1952 to protect the forest from exploitation by logging companies (Luburić 2016) and a part of the National Park was proclaimed Biosphere Reserve in 1977 (UNESCO 2010). This includes a 2830-ha strictly protected core area (IUCN category II) where land-use activities (logging, farming, grazing) are prohibited and which hosts the old-growth forest and

the surrounding pure beech forest. The core area is surrounded by a buffer zone characterised by meadows (Fig. 1) and groups of shepherds' huts whose presence possibly dates back to the Middle Ages when pasturing was widespread in Montenegro (Pluskowski and Seetah 2006). The number of occupied huts has declined considerably during the past decades due to depopulation of rural areas and many of them have been converted for tourism purposes.

Current forest composition and structure

We surveyed 51 plots (Fig. 1) choosing their location based on a preliminary segmentation of a SPOT5 satellite image that identified polygons of homogeneous forest canopy composition and structure (Motta et al. 2015a). In each circular plot (radius = 14 m), we recorded the species and measured the diameter at breast height (DBH) of all living stems with a $DBH \geq 7.5$ cm and the heights (H) of at least three individuals for each species and in different diameter classes when available. We measured the minimum and maximum diameter and length (D_{min} , D_{max} , L) of all coarse woody debris (CWD) with $L \geq 100$ cm and $D_{min} \geq 10$ cm, classifying the deadwood as snags (standing dead trees), logs (lying deadwood), or stumps ($H < 130$ cm). In a smaller area (radius = 6 m) centred on each plot centroid we identified and counted the regeneration ($DBH < 7.5$ cm).

We pooled our 51-plots dataset with the 30-plots dataset recorded by Motta et al. (2015a), which were concentrated in a small (50 ha) portion of the old-growth forest. For each plot we calculated variables to assess the current old-growthness and forest structure. Thus, we estimated the tree density (De ; #/ha), basal area (m^2/ha), and amount of regeneration (#/ha). To estimate the volume of living wood biomass (m^3/ha) we used a local volume table, deriving tree heights from species-specific hypsometric curves. We computed CWD volumes (m^3/ha) for CWD classes, and the dead to live wood ratio (Öder et al. 2021). To estimate tree species diversity, we computed the Brillouin index (Brillouin 1956). To measure the structural diversity, we calculated the DBH standard deviation, Tree Diameter Diversity index (TDD) to 5 cm DBH classes of living stems (Rouvinen and Kuuluvainen 2005), and the Gini coefficient (Gini 1912; Weiner and Solbrig 1984), which quantifies the structural heterogeneity in tree diameters (G_{DBH}) and basal areas (G_{BA}) (ESM Table S1).

Subsequently, we identified forest structural types (FST) using a Hierarchical Cluster Analysis (HCA) based on selected structural and compositional variables and tested the statistical differences among FSTs using a non-parametric Kruskal-Wallis test, followed, in the case of significance, by a Dunn's post hoc test (see ESM for further details).

To explore the influence of accessibility, we calculated Spearman's correlations between variables describing forest structure and a proxy for potential human pressure namely the cost of access, that is the minimum accumulative path distance (m) to each plot from the main roads (see ESM for further details), following Garbarino et al. (2013).

To assess the distribution of land-cover types and to upscale FSTs at a landscape scale we used an object-based image analysis of two high-resolution satellite Pléiades images. After pre-processing the images, we created image objects through the Large-Scale Mean-Shift segmentation algorithm (Michel et al. 2015) using a raster stack formed by the near infrared band (NIR), the Normalized Difference Vegetation Index (NDVI) and textural data that were derived from granulometric analysis based on the opening procedure (see ESM for further details). We performed a supervised classification of image objects using the Random Forest (RF) algorithm implemented in the ‘ranger’ R package (Wright and Ziegler 2017), employing their spectral and textural information as predictor variables (ESM Table S2-S3). We trained the RF model using 1457 objects that were classified through on-screen interpretation. Most of the training objects (n=1305) intersected the ground-survey plots and belonged to one of the following land-cover types: broadleaved trees, conifers and forest canopy gaps. Training objects of land-cover types that were not surveyed (grasslands, bare ground and water) were identified through on-screen interpretation. We assessed the performance of the RF model by computing the average overall accuracy and Cohen’s Kappa statistic obtained from a 5-fold cross-validation procedure. We performed the analyses separately for two satellite images and then merged the land-cover maps.

Long-term vegetation and fire disturbance histories

We collected a 245-cm long sediment sequence from a forest hollow (0.047 ha; 20-30 m in diameter; 42°54'5.898"N; 19°35'53.538"E; 1155 m asl.; Fig. 1) located in the beech-dominated forest to reconstruct stand-scale vegetation dynamics. We combined two parallel and overlapping cores (drives 1-m long and 8 cm in diameter) collected near to the centre of the basin with a Russian-type corer at 5 cm water depth.

To constrain the depth-age model, we used eight AMS ^{14}C dates from terrestrial plant macrofossils (ESM Table S4) calibrated using the IntCal13 dataset (Reimer et al. 2013). We built the model using the RBAcon v2.4.1 package (Blaauw and Christen 2011) and verified the accuracy in its most recent part by comparing the expected and actual ages of the first occurrence of *Ambrosia artemisiifolia* L. pollen. Documentary evidence (Makra et al. 2005; Csontos et al. 2010) indicates that ragweed (*Ambrosia*) became invasive in Central and Eastern Europe around 1910-1920 CE.

We measured the magnetic susceptibility at 1-cm intervals with a Bartington MS2E sensor following Nowaczyk (2001). Magnetic susceptibility is influenced by the amount of minerogenic input that results from erosion. Negative magnetic-susceptibility values are found in sediments with minerals that do not contain Fe (e.g. quartz and calcite) and in organic-rich sediments.

We used macroscopic charcoal analyses to reconstruct long-term fire activity (Whitlock and Larsen 2001; Conedera et al. 2009). We counted charcoal particles in contiguous 1-cm³ samples, and additionally measured areas of charcoal particles for 42 samples (6-cm resolution) using an image-

analysis software (see ESM). We transformed charcoal concentrations to charcoal accumulation rates (CHAR) based on the chronology.

To uncover local-scale vegetation dynamics, we analysed 41 plant macrofossil samples in conjunction with pollen and stomata (see ESM Fig. S1 and ESM for details of laboratory and identification methods used) (Birks and Birks 2000; Ammann et al. 2014; Finsinger and Tinner 2020). We calculated pollen percentages relative to the terrestrial pollen sum, which included pollen from trees, shrubs, herbs and *Pteridium* spores. A sum of at least 250 pollen and spores was counted for each sample. However, the lowermost sample has a substantially lower pollen sum (n=36) due to an extremely low pollen concentration.

To evaluate human impact, we considered the abundances of primary anthropogenic indicators, secondary adventives and apophytes (Behre 1981; Deza-Araujo et al. 2020), which include pollen of cultivated plants, ruderals, and plants of meadows. In addition, we used *Sporormiella*-type dung-fungi spores, which are linked to the presence and abundance of large herbivores (Davis 1987; Baker et al. 2013), and *Tilletia caries*-type spores (see ESM), a pathogen associated mostly with grasses, including cereals (Mazurkiewicz-Zapałowicz and Okuniewska-Nowaczyk 2015). Abundances of non-pollen palynomorphs are presented as influx (number cm⁻² year⁻¹).

We determined pollen assemblage zones based on terrestrial pollen taxa (excluding taxa with maximum abundance <5%) using optimal partitioning by sums-of-squares (Birks and Gordon 1985) in Pspoll v4.26 (Bennett 2008). The number of statistically significant zone boundaries was determined by comparison with the broken-stick model (Bennett 1996).

We analysed the charcoal data using CharAnalysis v1.1 (Higuera et al. 2009) to determine centennial-scale trends that were interpreted as relative changes in biomass burned over time (Marlon et al. 2008; Higuera et al. 2010a), and to identify peaks, which were interpreted as fire episodes. The analysis involved interpolating CHAR values to a constant sampling resolution, decomposing that record into a background and a peak component using robust locally weighted scatterplot smoothing (LOWESS), and evaluating peak samples using both the 99th percentile of the modelled noise distribution obtained with a Gaussian mixture model and a peak-screening test. The suitability of the record for peak detection was assessed with the signal-to-noise index (SNI; Kelly et al. 2011) before calculating fire return intervals (see ESM for details). We retained the results obtained using an interpolation to 8 years and with charcoal background modelled using a 500-years smoothing-window width. We used change-point analysis to determine significant changes in biomass burning and test the potential effect of sedimentation rates on change-point detection (Finsinger et al. 2018).

To test the simultaneity between fire and erosion events, thereby allowing identification of high-severity local catchment fires (Chileen et al. 2020), we used Event Coincidence Analysis (ECA; Siegmund et al. 2017). We determined erosion events as (i) peaks of magnetic susceptibility, which respond to increases in minerogenic input that often follow fire events as a result of erosion, and to in-washing of secondary ferromagnetic minerals that are formed when soils with a high concentration of convertible

Fe are heated (Thompson and Oldfield 1986; Millspaugh and Whitlock 1995), and (ii) peaks of *Cenococcum geophilum* Fr. sclerotia influx, whose abundances are linked to soil erosion (Van Geel 1978). The two datasets were analysed with a custom-made computer code (R Core Team 2020) in a similar way to the CHAR record to statistically identify peaks. We performed the ECA using two binary event time series (CHAR peaks and erosion peaks), a lag of 8 years, and a tolerance window 8-48 years that detects erosion events within 10-50 years of fire episodes. We tested the significance based on the assumption of independent and sparse Poisson processes ($\alpha=0.05$).

To identify leads and lags between fire activity (CHAR) and vegetation and land-use change (pollen percentages and dung-fungi spores' influx), we used cross-correlation analyses (Green 1981; Tinner et al. 1999; Valsecchi et al. 2008). We performed the analyses for two time intervals that show different intensity of human pressure: 970-1350 CE (higher pressure); 1600 CE to the present (lower pressure). Within the selected time intervals, the sampling resolution was relatively stable (32 ± 3 and 21 ± 3 years between samples, respectively). The cross-correlations' span was restricted to one-fourth of the sample number N (lag number $\leq N/4$).

Results and interpretation

Present vegetation composition and forest structure

The surveyed area includes plots characterized by large trees (up to 148 cm of DBH) and by a high CWD volume (up to $791.6 \text{ m}^3 \text{ ha}^{-1}$; Table 1 and ESM Table S5). Plots having a complex horizontal and vertical structure are present as shown by high volume of living trees (up to $1781.9 \text{ m}^3 \text{ ha}^{-1}$) and high values of structural diversity indices (G_{BA} up to 0.8; Fig. 2). CWD consists mostly of logs (65%) and snags (33%). Although beech is the species with the highest stem density, beech trees are generally smaller than fir and spruce trees (Table 1 and ESM Table S5).

The HCA (ESM Fig. S2) identified three forest structural types (FST) that differ significantly from each other (Fig. 2). Their overlap on the land-cover type map that we obtained through remote-sensing analysis (Fig. 1; ESM Table S6) shows that FST1 plots predominantly occur in the beech-dominated forest. These plots are dominated by small and mostly multi-stemmed beech trees (DBH generally <40 cm from single stools; Table 1). The amount of CWD, as well as the basal area and density of conifers and other deciduous species are negligible (Fig. 2). We found an inactive charcoal kiln in one of these plots at top of the valley, and cut stumps in two plots both at the top and on the bottom of the valley. FST2 and FST3 plots are in the c. 1000-ha conifer-dominated old-growth forest (34% of the core area). They are dominated by fir (FST3) and predominantly co-dominated by fir and spruce (FST2). FST2 plots also includes a plot dominated by sycamore maple. CWD and dead to live wood ratio values are

significantly higher, and basal area and density of beech are significantly lower than in FST1 plots (Fig. 2)

The indices of structural diversity (DBH_{SD} , G_{DBH} , G_{BA}) indicate that plots in the old-growth forest are structurally more heterogeneous than those in the beech-dominated forest. FST2 plots have the highest species and structural diversity as they consist of large fir and spruce trees (DBH: up to 148 cm), and small to intermediate beech trees (DBH: 10-65 cm). FST3 plots consist of intermediate and large fir trees and small to intermediate beech trees. Spruce trees are rare, the DBH_{mean} and volume are significantly lower than in FST2 plots and the amount of CWD and dead to live wood ratio values are significantly higher than in FST1 and FST2 plots. Regeneration of spruce is very scarce in all plots, while regeneration of fir and beech is significantly higher in FST1 and FST3 plots, respectively.

Median cost of access is lower for FST1 plots (Fig. 2). Cost of access is significantly correlated to basal area of fir (Spearman's $\rho=0.43$, $P<0.001$) and beech (Spearman's $\rho=-0.36$, $P<0.01$). Positive significant correlations are also found for CWD amount (Spearman's $\rho=0.44$, $P<0.001$), dead to live wood ratio (Spearman's $\rho=0.38$, $P<0.001$) and heterogeneity as described by the DBH standard deviation (Spearman's $\rho=0.29$, $P<0.05$) and Gini indices (Spearman's $\rho=0.35$ for G_{DBH} and 0.30 for G_{BA} , $P<0.01$).

The difference among forest structures is also supported by the analysis of the forest-canopy textures that we derived from the satellite images (ESM Fig. S3). The textures are finer and more homogeneous in the beech-dominated part, whereas more complex and heterogeneous textures, probably arising from gap dynamics, are common in the old-growth forest. About 99% of the detected gaps occur in the conifer-dominated area. Gap sizes are highly variable (mean: 210 m²; range: 3.33-5636 m²) and their distribution is right-skewed (76% of gaps <200 m²; 2% >1000 m²).

Long-term environmental changes

The sediment core spans the past c. 1000 years (Fig. 3). The reliability of the chronology in its most recent part is confirmed by the first occurrence of *Ambrosia* pollen around 1920 CE (Fig. 3). One of the ¹⁴C dates, which was measured on a piece of wood, was considered as an outlier by the depth-age modelling software. It is possible that it misrepresents the age of the sediment because of its longer terrestrial residence time and the potential in-built age of long-lived plants (Oswald et al. 2005). Sediment deposition time varies little (3-8 years cm⁻¹). Sediments deposited before 1300 CE are lighter in colour than the darker-brown detritus gyttja deposited thereafter (see ESM for further details).

The pollen record (Fig. 4; ESM Fig. S4) was divided into three statistically significant assemblage zones at 123.5 and 52 cm depth (c. 1600 and 1850 CE, respectively). To better illustrate the long-term vegetation changes we additionally selected a non-significant pollen zone boundary at 1350 CE.

The lowermost pollen assemblages (950-1150 CE) of zone 1a are characterized by decreasing abundance of tree pollen, particularly pollen of conifers (*Abies*, *Pinus sylvestris*-type and *Picea*) and of fern spores (e.g. *Athyrium filix-femina*), which grow in fresh and shaded understorey environments (Ellenberg 2009). The continuous finds of pollen and plant macrofossils (Fig. 4; ESM Fig. S5) of the semi-shade demanding *Sambucus* from 950 to 1150 CE indicate the presence of clearings. The high abundance of primary anthropogenic indicators, secondary adventives, and of *Sporormiella* and *Tilletia* spores indicate a land-use phase (1150-1350 CE) that is preceded by an increase of *Rhamnus* pollen and macrofossils (1050-1150 CE).

Anthropogenic indicators and herb pollen abundances distinctly decrease around 1350 CE (onset of zone 1b) indicating a sudden abandonment of pasture and cultivation. Trees and shrubs that typically colonise abandoned pastures (*Sambucus*, *Betula*, *Alnus*, *Ulmus* and *Acer*) expanded as shown by pollen and plant macrofossils. *Picea* was present in the surroundings as well, as shown by stomata and plant-macrofossil finds. A century later (around 1450 CE) pollen, stomata and plant-macrofossils of shade-tolerant *Abies* and *Fagus* trees increased. The development of a mixed woodland was interrupted by a short-term weak land-use phase (1500-1600 CE), as suggested by the slight rise of primary and secondary anthropogenic indicators, fire-adapted *Pteridium* and upland herbs.

Local conifer populations collapsed during this second land-use phase (onset of zone 2: 1590 CE) and a *Fagus*-dominated forest gradually established around the site. Pollen and plant macrofossils indicate that light-demanding woody species (*Corylus*, *Betula*) expanded faster than the shade-tolerant *Fagus*, which peaked around 100 years later (1700 CE). *Fagus* and *Fraxinus* pollen as well as their plant macrofossils markedly decreased between 1760 and 1850 CE in conjunction with a slight rise in *Sporormiella* and *Veratrum* spores, which indicates another weak land-use phase probably including mainly grazing activities.

During the past 170 years (zone 3; 1850 CE to present), a *Fagus*-dominated forest developed as shown by high values of stomata, macrofossils and pollen. This time interval also shows increasing abundance of *Ulmus*, *Alnus*, *Fraxinus* and *Acer*, low abundance of anthropogenic indicators, and decreasing abundance of pioneer trees and shrubs (*Corylus* and *Betula*). Tree cover is at its highest from 1950 CE. Macroscopic charcoal concentration values ranged between 0 and 271 (median = 34 pieces cm⁻³). Charcoal counts and charcoal areas are significantly correlated ($R^2=0.91$, $P<0.001$). Peak analyses based on different parameters are highly comparable among one another with mean SNI values generally higher than the critical threshold (ESM Table S7; Fig. S6-S7). The periods of shorter fire-return intervals (1000-1150 CE: FRI=25 years; 1460-1520 CE: FRI=60 years; and 1730-1810 CE: FRI=75 years) occur predominantly during phases of high biomass burning (1000-1030, 1340-1730, and 1730-1850 CE, ESM Fig. S8-S9). Most erosion events (75%, $P=0.05$) occurred 10-50 years after fire episodes (Fig. 5). This is the case for erosion events occurring at the onset of the Middle Ages (1050 CE), towards the end of the Middle Ages (1500-1550 CE), and during the 20th-century. The coincidence between fire episodes and erosion events suggests that these were triggered by higher-severity catchment fires,

whereas fire episodes occurring during the medieval land-use phase (1050-1150 CE) and around 1800 CE were of lower severity or occurred outside the catchment.

We used cross-correlation analyses (Fig. 6) to explore leads and lags between fire activity and vegetation and land-use change. For the time interval when human pressure was higher (970-1350 CE; zone 1b) *Abies*, *Picea*, *Fagus* and arboreal pollen are negatively correlated with charcoal-accumulation rates (CHAR), indicating that in the Middle Ages fires contributed to the decline of late seral species. We found the highest correlation coefficients when CHAR lagged primary indicators and dung spores by 30 years, consistent with mechanisms of charcoal taphonomy leading to delayed deposition at a coring location (Duffin et al., 2008; Higuera et al., 2010). Thus, the significant positive correlations between CHAR and primary anthropogenic indicators and dung spores at negative lags support the hypothesis of human-driven fires used to create open areas for agriculture and grazing.

For the time interval when human pressure was lower (1600 CE to the present) arboreal pollen is negatively correlated with fire, and primary anthropogenic indicators are positively correlated with fire at lag 0, thus corroborating the link between cultivation and fire. Dung fungi also show positive significant correlations with fire, though the highest coefficients are found at positive lags, suggesting a delayed increase of grazing ca. 60 years after fire activity rises. The correlation coefficients between CHAR and *Abies*, *Picea* and *Fagus* are not significant. However, *Corylus* and *Betula* show positive significant correlations ahead of the charcoal peaks (at lags -4 and -5), suggesting that these light-demanding pioneer species acted as fire precursors. *Fraxinus* shows a negative significant correlation at lag 0. It thus seems likely that land use and fires mainly occurred in gaps within the overall *Fagus*-dominated forest.

Discussion

Current forest structure within the old-growth stands and the surrounding forest

Our extensive ground surveys and the detailed remote-sensing analyses show that the forest is characterised by a large compositional and structural variability. We detected a fine-scale heterogeneity due to gap dynamics within the conifer-dominated old-growth forest. The formation of gaps allows the recruitment of more light-demanding species, like sycamore maple (Nagel et al. 2014). In addition to this fine-scale variability, we identified three forest structural types (FSTs) showing different degrees of old-growthness (Fig. 2) that are unevenly distributed within the forest (Fig. 1).

The structure of the old-growth forest (FST2 and FST3 plots) is comparable to that of other mixed old-growth forests in Bosnia-Herzegovina (Motta et al. 2011, 2015a, b; Keren et al. 2014, 2020; Zenner et

al. 2015; Chivulescu et al. 2020), both in terms of stand descriptors (basal area, volume, and coarse woody debris) previously assessed by Motta et al. (2015a) as well as in terms of dead to live wood ratio and structural diversity (Fig. 2; Table 1). Moreover, the heterogeneous texture of the forest canopy (ESM Fig. S3) also shows that the conifer-dominated stands likely had the time to develop typical old-growth attributes (Spies and Franklin 1988; Wirth et al. 2009).

The HCA confirms prior studies showing that the old-growth forest includes two structural types, their main differences being the rarity of spruce (Motta et al. 2015a) and significantly higher amount of dead biomass in the fir-dominated FST3 plots (Fig. 2). Because spruce is rare in these plots, the higher amount of dead biomass could be linked to higher spruce mortality. This would fit with the persisting decline of the spruce population, as indicated by its extremely low seedling regeneration and the absence of spruce saplings in all plots (Table 1). The decline of spruce may agree with evidence showing that the cold-adapted spruce populations at the southern boundary of the distributional range are more vulnerable to drought than fir and beech (Hanewinkel et al. 2013; Zang et al. 2014). In agreement with this, in the Dinaric Alps spruce-dominated stands are common in karst depressions and sinkholes where temperature inversions cause significantly colder microclimates (Nagel et al. 2017). Conversely, the low spruce regeneration could be explained by the scarcity of expanded gaps, as spruce is less shade tolerant than beech and fir (Stancioiu and O'Hara 2006a) and beech is the main gap filler in a small-scale disturbance regime (Petritan et al. 2014) typical of old-growth forests.

In the beech-dominated forest (FST1 plots), coarse woody debris consists mostly of logs with a lower number of snags (Fig. 2; ESM Table S5), as often observed in old-growth stands (Nilsson et al. 2003). However, the amount of coarse woody debris in these plots is substantially lower than in the old-growth forest plots (Fig. 2). While this is relatively unsurprising given that broadleaved trees produce a lower deadwood accumulation (Harmon et al. 2004) and their deadwood decays about 3-10 times faster than deadwood of conifer species (Vacek et al. 2015; Hararuk et al. 2020), the FST1 plots also have substantially lower amounts of coarse woody debris than other European beech-dominated old-growth forests (Burrascano et al. 2013; Meyer et al. 2021). Interestingly, coarse woody debris and dead to live wood ratio values of the FST1 plots are closer to those found in currently managed forests or in those recently withdrawn from regular management (Motta et al. 2015b). Moreover, the lower structural diversity of these plots (DBH_{SD} and G_{BA} , Fig. 2) and the finer texture of the forest canopy (ESM Fig. S3) rather reflect a homogeneous structure and even-aged cohorts. However, the age of trees remains unknown as, according to the protection status of the Park, the sampling of cores from living trees was forbidden.

Stand-scale long-term vegetation dynamics, land-use changes and disturbances by fire

The proportion of pollen loading coming to the 0.05-ha-forest hollow in the beech-dominated area is adequate to reflect local vegetation composition as the pollen source area is normally 200-300 m for such sites (Sugita 1994; Hofstetter et al. 2006). This is also supported by the coherence between the pollen and the plant-macrofossil and stomata records (Fig. 7) that are generally dispersed over substantially shorter distances than pollen (Birks and Bjune 2010; Ammann et al. 2014). Similarly, while the source area of macroscopic charcoal particles can be relatively large (up to 30-50 km; Oris et al. 2014; Adolf et al. 2018), both empirical and simulated data support the assumption that charcoal peaks most accurately reflect fire episodes within 1–3 km of coring sites (Higuera et al. 2010b). Moreover, the coincidence of fire and erosion events pinpoints the occurrence of higher-severity catchment fires (Fig. 5; Fig. 7). Thus, our palaeoecological record predominantly documents local-scale vegetation dynamics, land use and fire occurrence for the currently beech-dominated forest.

During the Middle Ages (1150-1350 CE), tree cover was substantially lower than today (trees and shrubs pollen: 40% vs 70%, respectively). Cereal crop cultivation and cattle herding were more widespread than today as confirmed by high values of primary anthropogenic indicators pollen and *Sporormiella*-type, and the occurrence of *Tilletia caries*-type spores (Fig. 7). In the Middle Ages bunt (*Tilletia sp.*) was one of the most severe diseases of winter wheat (Gaudet and Menzies 2012) causing devastating yield reductions by up to 50% (Kiesselbach and Lyness 1939). As winter rye (*Secale cereale*) is able to grow at high altitudes even in the continental areas of the inner Balkans (Behre 1992), it is likely that cultivation took place locally in openings in the forest cover interspersed with woodland pastures and forested areas. The end of this land-use phase broadly coincides with the Black Death pandemic (1350 CE) that spread rapidly and substantially reduced population density (Green 2014; Luterbacher et al. 2020).

Despite setbacks due to the occurrence of more moderate and transient local land-use phases with the use of fire (1500-1600 CE and 1760-1850 CE), tree cover increased after 1350 CE. This trajectory markedly contrasts with decreasing tree cover due to intensifying land use since the 15th-16th century (Fig. 7) documented for the nearby montane zones of Bosnia-Herzegovina (Prokoško Jezero; Dörfler 2013) and Serbia (Crveni Potok mire; Finsinger et al. 2017). A tree-cover reduction is also visible at lower elevation in Albania-Macedonia (Lake Ohrid; Wagner et al. 2009) and in the coastal region of Albania-Montenegro (Shkodra Jezero; Sadori et al. 2015), as well as elsewhere in Europe (Conedera et al. 2017), and as suggested by models (Kaplan et al. 2009). The absence of evidence for intensifying land use after the 15th century at Biogradska Gora could be due to the transition to cooler temperatures at the beginning of the Little Ice Age (LIA), which may have discouraged cultivation and pasturing in the valley. Indeed, years with unusually cold spring seasons during the LIA had serious consequences on grain harvests and on cattle in the meridional Balkans and in Serbia (Xoplaki et al. 2001; Mrgic

2018). In addition, harvest failures were important factors for social vulnerability, particularly for people living in rural areas in pre-industrial economies (Pfister and Brázdil 2006). An alternative, or additional, explanation could be the small pollen source area, which predominantly captured pollen from the surrounding expanding beech stand despite ongoing land use on the hilltops where meadows still exist today. Regardless, the tree-cover increase and decreasing land-use pressure that started around 1500-1600 CE suggests that the 19th century's formal protection of the Biogradska Gora forest eventually took advantage of the pre-existing situation. This supports the view that historical land-use pressure is a significant predictor for the occurrence of primary and old-growth forests (Sabatini et al. 2018).

The continuity of the conifer-dominated old-growth forest stands is currently not supported by firm evidence due to the lack of palaeoecological sites in that area. On the one hand, these stands may have developed after the 15th-16th century, when land use declined. This would fit with age estimates of deadwood showing that trees up to 400-500 years old occurred in the conifer-dominated stands (Motta et al. 2015a). On the other hand, the presence of stomata and plant macrofossils before the 15th-16th century in the currently beech-dominated forest (Fig. 4; Fig. 7) rather supports the hypothesis that the area of fir and spruce was reduced during the Middle Ages. Fires either did not propagate into the old-growth forest, or their severity was too low to affect the fire-sensitive fir population. In Central and in southern European mountains fir declined due to human-induced fires (Büntgen et al. 2014; Morales-Molino et al. 2020) several millennia earlier than at Biogradska Gora. It is plausible to hypothesise that land use was probably limited by cost of access, with more accessible mountain areas being more influenced by human activities, as observed at Biogradska Gora (Černjavski 1937) and as is often the case for protected ecosystems (Hansen and DeFries 2007). Overall, this supports the notions that human pressure played an important role for the small extent of old-growth forests (Nagel et al. 2017; Sabatini et al. 2018) and that buffer zones are key for protecting old-growth forests (Barredo et al. 2021).

Legacies of past human activities

Forest composition shifted from a mixed fir-spruce-broadleaf stand to one dominated by beech in conjunction with a decrease in land-use pressure around 1500-1600 CE and at the transition to cooler LIA temperatures (Fig. 7). Whereas cooling and increased precipitation have been identified as the main drivers of the Holocene broad-scale expansion of *Fagus* in Central Europe (Tinner and Lotter 2006), the Holocene range expansion of *Fagus* was possibly also influenced by competitive interactions among species, and by natural and anthropogenic disturbance events (Giesecke et al. 2007). Analogous expansions of beech at the expense of fir are well documented in mid-late Holocene pollen records from central-southern Europe. Evidence suggests that beech became more competitive after the decline of *Abies alba* due to the onset of cooler and moister summers and human-induced fires (Vescovi et al.

2010; Morales-Molino et al. 2020). While it is difficult to disentangle the effects of climate and land use in our record, it seems likely that land-use and fire occurrence, superimposed on the onset of favourable climatic conditions, probably played an important role in driving the vegetation shift. However, since the area is archaeologically poorly studied and historical information is not readily available, we do not know which ethnic groups may have been responsible for the different phases of land use at Biogradska Gora. The local conifer population was strongly reduced due to increased local fire activity in conjunction with land use during the Middle Ages (Fig. 6). Moreover, the conifer population finally collapsed in 1500 CE when two higher-severity catchment fires occurred at the onset of a weaker land-use phase (Fig. 7). This is in line with a wealth of evidence showing that conspicuous canopy gaps from fires and land use can cause a reshuffling of the dominant tree species in mixed fir, beech and spruce forests. Spruce, for instance, has traits promoting fires (high resin content, ladder canopy structure) and can persist with a low to moderate fire severity (Feurdean et al. 2017). However, it does not survive or re-sprout after high severity fires or when fires occur with a high frequency (Niklasson et al. 2010; Feurdean et al. 2019). Similarly, both large-infrequent and small-frequent fires lead to a rapid local extinction of the fire-intolerant *Abies* (Tinner et al. 2013). By contrast, human activities and disturbance by fire can favour the spread of beech at the stand level (Bradshaw and Lindbladh 2005; Tinner and Lotter 2006). Beech quickly re-sprouts and regenerates successfully after small or intermediate human and natural disturbances (windthrow, cutting, fire; Motta et al. 2011; Nagel et al. 2014; Maringer et al. 2016). Importantly, beech regenerates faster than fir and spruce in canopy gaps and overstorey releases (Stancioiu and O'Hara 2006b; Bolte et al. 2014). Additionally, beech encircles competitors and fills gaps after disturbances (Pretzsch and Schütze 2005; Bolte et al. 2014) as it rapidly takes advantage of more favourable light conditions due to higher morphological plasticity of foliage and crown structures (Dieler and Pretzsch 2013). An alternative explanation to the spread of beech at Biogradska Gora could involve a reduction of the local conifer population due to selective clear-cutting and extraction of timber in stands that are accessible for harvest (Büntgen et al. 2014), like the ones near the forest hollow. Traditionally, timber of *Abies* and *Picea* has been widely used as building material as the monochroic stems of conifers provides long structural elements. Moreover, as observed elsewhere in marginal areas of coniferous woodland in Central Europe (Winkler 1963), other forms of land-use, such as coppicing to obtain firewood or wood charcoal, also could have favoured *Fagus*. Beech trees, unlike conifer trees, re-sprout if coppiced and their wood has a high energetic potential (Packham et al. 2012). In temperate regions, wood charcoal production in wind-sheltered forest sites was the main source of energy since the Iron Age until the 19th century (Blondel 2006; Carrari et al. 2017). At Biogradska Gora, these practices are attested by multi-stemmed beech trees and a remnant of a charcoal kiln in the beech-dominated forest at the top of the valley. However, we do not have sufficient data to reconstruct when this activity started and when it was abandoned (e.g., ¹⁴C data on charred materials, age of the multi-stemmed beech trees, number and location of charcoal kilns remnants over the whole forest surface). Coppicing and clear-cutting practices could have been

developed greatly due to increasing wood demand since 1250-1300 CE following the opening of the Brskovo silver mines (at c. 30 km from Biogradska Gora, Longman et al. 2018) or as a result of demographic growth during the 16th-17th centuries and after 1850 CE (McEvedy and Jones 1978).

Old-growth forests in east-central Europe caught the attention of foresters long ago (Leibundgut 1959; Horvat et al. 1974) as their dominant tree species (*Abies alba*, *Fagus sylvatica*, and *Picea abies*) prevail in the montane belt of central Europe. The protected old-growth forest of Biogradska Gora should be sufficiently large (~1000 ha) to buffer the effects of small-scale natural disturbances (Sabatini et al. 2018). Moreover, in eastern Europe, human population density in mountain areas is predicted to decrease over the 21st century due to abandonment of pastoral and agricultural activities (Wu et al. 2015). This may be beneficial to the majority of primary and old-growth forests (Sabatini et al. 2018). However, old-growth forests may be at risk due to predicted environmental changes. Despite the rare natural fire occurrence (Nagel et al. 2017), forest fires are predicted to increase in the region, which could potentially become a new fire-prone area (Krawchuk et al. 2009; Wu et al. 2015). Warmer and drier conditions that may lead to increased fire activity will also affect the vegetation structure modifying fuel type, fuel load and therefore fire intensity and spread. For instance, as fir is known to be more drought tolerant than beech (Morales-Molino et al. 2020) its population may recover if fires do not prevent the expansion of this fire-sensitive tree species.

Conclusions

The multi-proxy palaeoecological records (pollen, spores, stomata, macrofossils, macroscopic charcoal, and magnetic susceptibility) from the Biogradska Gora forest provide new insights into the long-term vegetation dynamics of old-growth forests in the montane zone of the Dinaric Mountains. The area of fir and spruce-dominated forest was likely reduced during the Middle Ages by human activities (agriculture and pastures) as well as by fires, which are rare today in these forest types (Nagel et al. 2017). However, markedly in contrast to intensifying land use elsewhere in the region, human activities were strongly reduced several centuries before the formal protection of the forest (1878 CE). While this may have prevented the old-growth forest to be further reduced, the legacies of past land-use activities are still visible. The conifer-dominated mixed stands in the less accessible area have more old-growth characteristics than the almost pure beech stands surrounding the old-growth forest. These results support the view that historical land-use pressure played an important role for the small extent and the continuity of disturbance-sensitive *A. alba* and *P. abies*-dominated old-growth stands.

Our study shows that combining stand-scale long-term ecological records with assessments of contemporary forest structure can generate valuable insights (Foster et al. 1996). Structures and spatial patterns of ecosystems are often the result of legacy effects arising from complex interactions between

natural and human disturbances (McLachlan et al. 2000; Vale 2002; Willis and Birks 2006; Whitlock et al. 2018). Considering the longer-term history and its effects on forest ecosystems is essential for guiding their management and conservation measures (Conedera et al. 2017).

Acknowledgement

We are grateful to D. D'Aprile for help during fieldwork, to I. Figueras, L. Bouby and F. Wagner-Cremer for help with identification of plant-macrofossil, wood and charcoal pieces and *Fagus* stomata, and to R. Marzano, D. Ascoli, C. Urbinati, D. McKey, E. Ilardi, and D. Barbaro for discussions. We thank the Biogradska Gora National Park for granting permission to collect sediments and perform the field surveys.

Figures

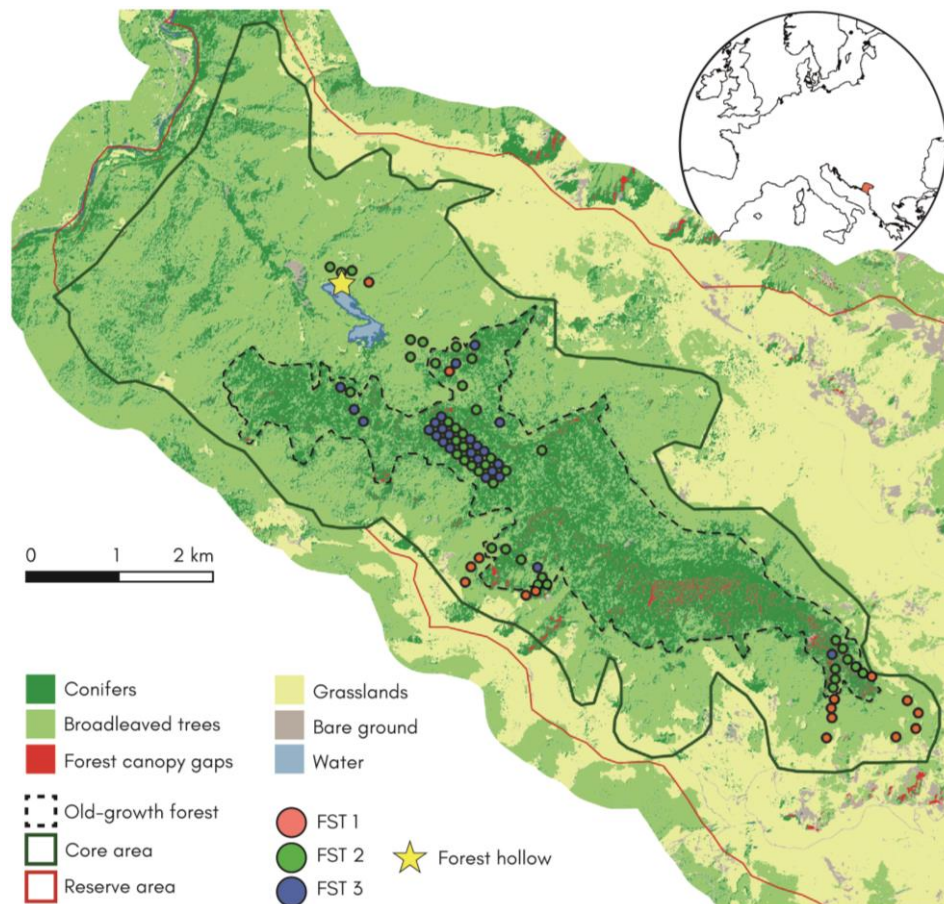


Fig. 1 Location and map showing the distribution of land-cover types in the Biogradska Gora National Park obtained through the remote-sensing analysis of Pléiades satellite images. Circles indicate the locations of field-survey plots (colour-coded by forest structural type, FST). The star shows the location of the forest hollow.

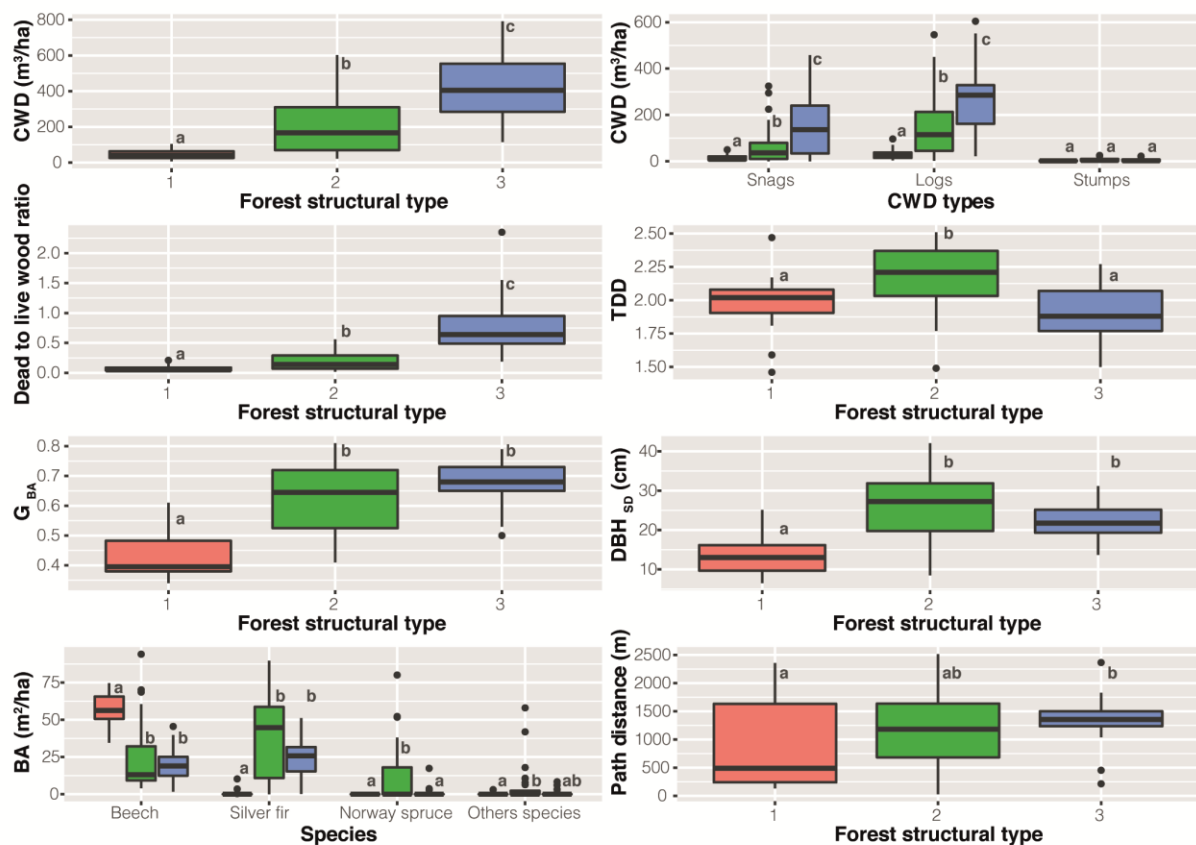


Fig. 2 Boxplots showing the distributions of selected variables used to assess the different forest structural types of the Biogradska Gora forest. Whiskers: first and third quartiles of the distributions; horizontal black lines: median values. Superscript letters indicate statistically significant differences between the mean values according to the Dunn's post hoc test ($\alpha=0.05$). CWD: coarse woody debris; TDD: Tree diameter diversity index, G_{BA} : Gini index referred to the basal area; DBH_{SP} : diameter standard deviation; BA: basal area.

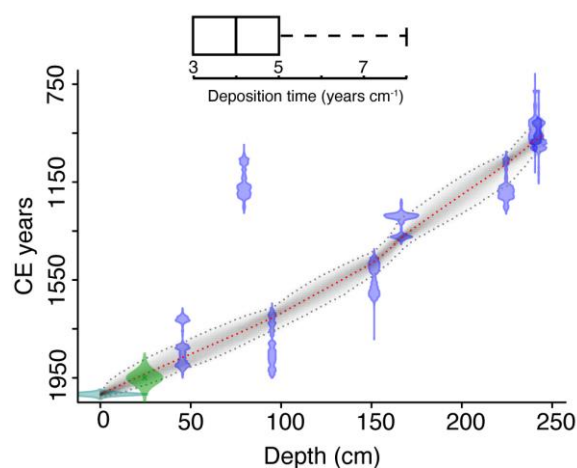


Fig. 3 Depth-age relationship of the sediments from the forest hollow as calculated using R Bacon software (Blaauw and Christen 2011). The inset shows the distribution of sediment deposition times within the sequence (median = c. 4 years cm^{-1}).

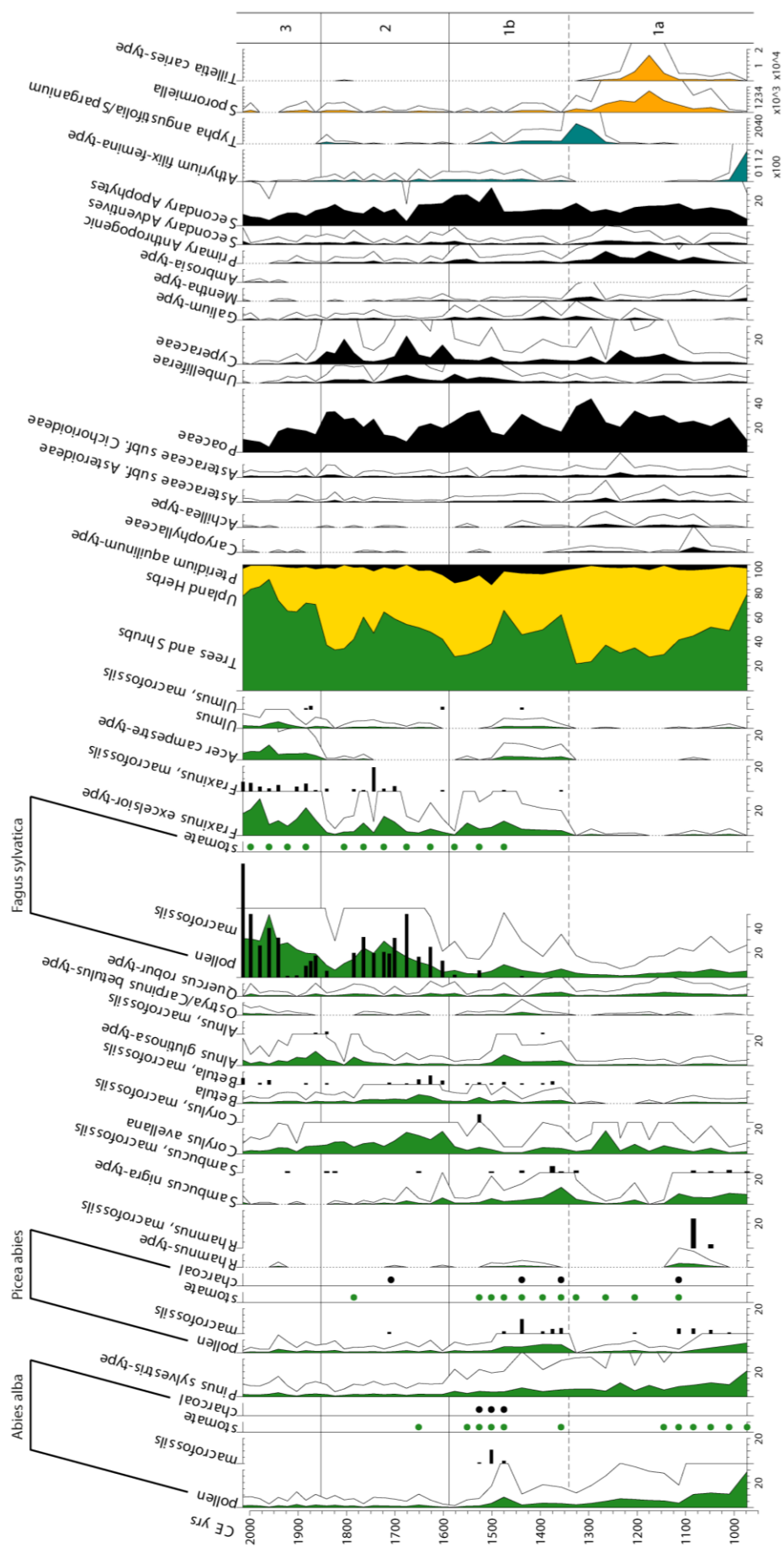


Fig. 4 Pollen and plant-macrofossil diagram (selected taxa) from the forest hollow at Biogradska Gora. Plant macrofossil concentrations are shown as black bar plots. Horizontal continuous and dotted lines represent significant and non-significant pollen zone boundaries, respectively. See ESM Fig. S4 and S5 for more detailed pollen and plant-macrofossil diagrams.

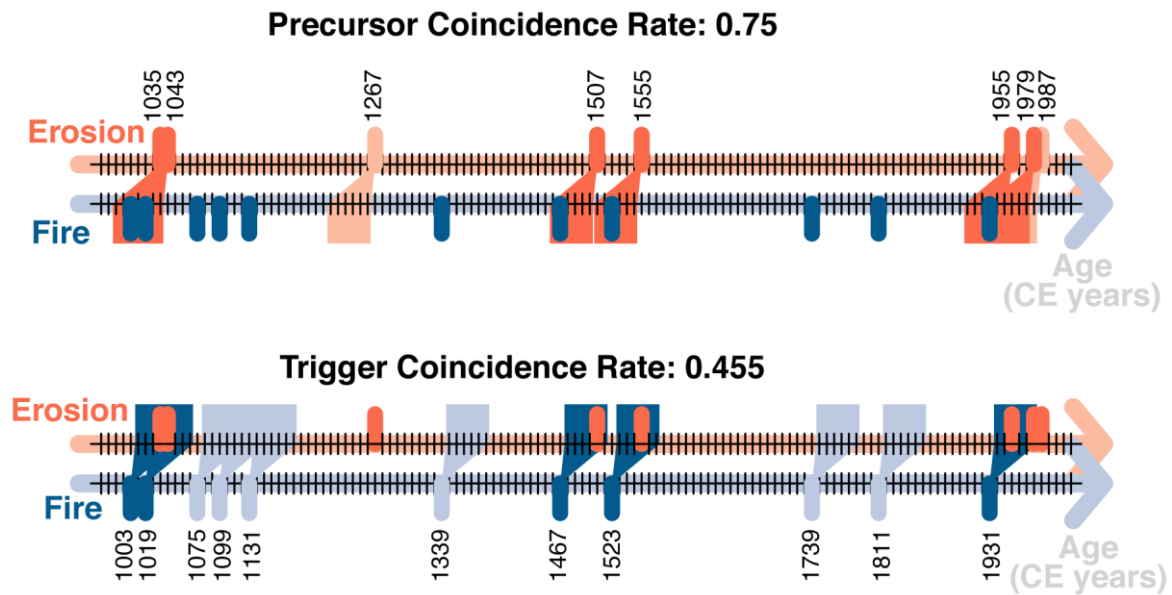


Fig. 5 Relationships between erosion and fire events as determined with Event Coincidence Analysis (ECA; Siegmund et al., 2017) showing higher-severity fire events (dark blue bars in the lower panel) that triggered erosion events in the catchment. About 75% of erosion events were preceded by fire events ($P=0.052$).

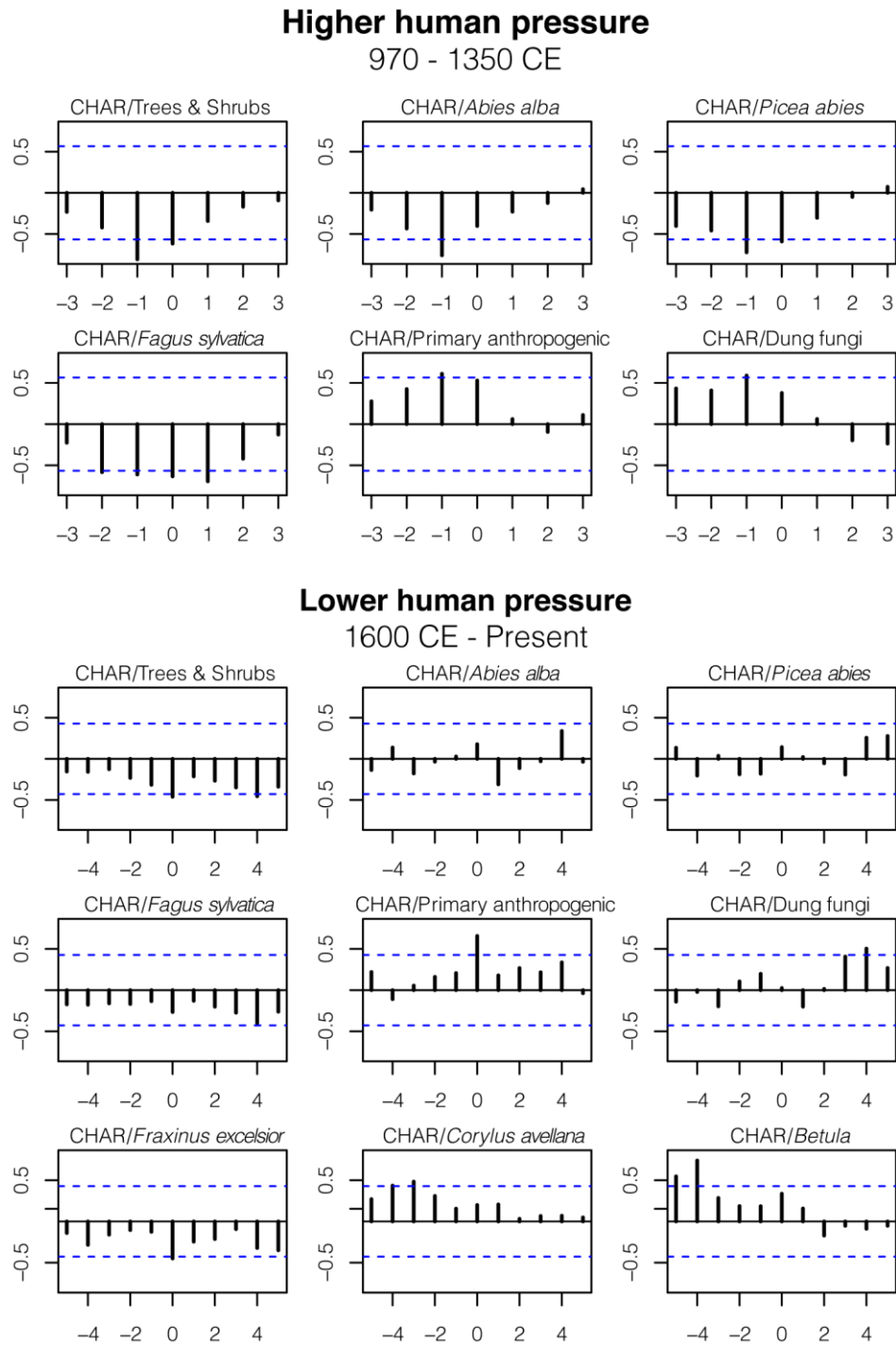


Fig. 6 Cross-correlograms of charcoal accumulation rates (CHAR), selected pollen percentages and dung-fungi spores' influxes for two phases of different intensity of human pressure. Horizontal axis shows the lag (one lag is equal to c. 20-30 years); vertical axis: correlation coefficients; dashed horizontal lines: 95% confidence limits.

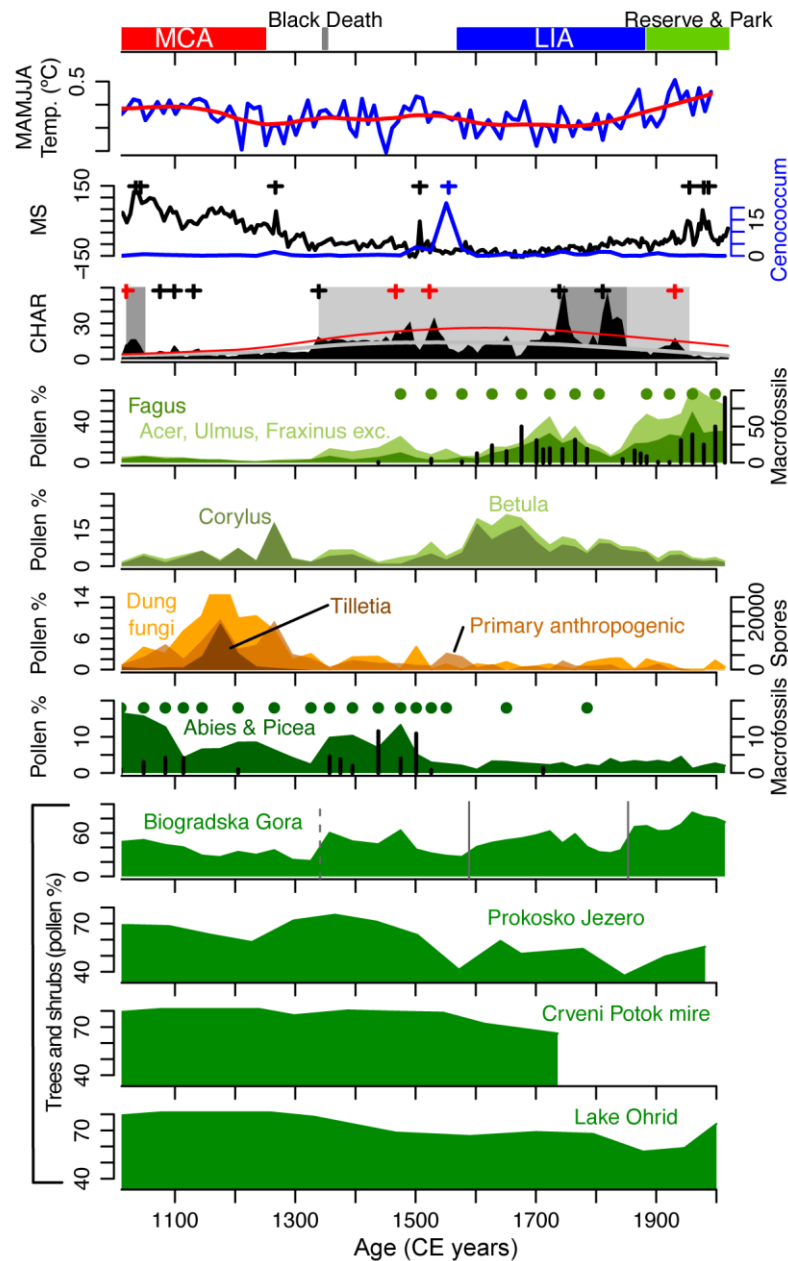


Fig. 7 Comparison between environmental changes at Biogradska Gora, regional warm-season (May–August, MAMJJA) air temperature anomalies (Ljungqvist et al. 2019; see ESM for further details), and tree cover at other sites in the Dinaric region. The data from Biogradska Gora include, from top to bottom: magnetic-susceptibility (MS) inferred erosion history (black and blue crosses: erosion events), macroscopic charcoal (CHAR) inferred fire history (black filled area: charcoal accumulation rate; grey line: charcoal background modelled using a 500-year smoothing window; red line: threshold used for fire peaks identification; black crosses: lower-intensity fire events; red crosses: higher-severity catchment fire events; shaded areas from white to grey: period of stable biomass burning, the darker the shade the higher the mean CHAR values), and vegetation dynamics (filled areas: pollen and non-pollen palynomorphs selection; black barplots: plant macrofossils selection; full circles: stomata). The bottom panels show the tree cover at Prokoško Jezero, Bosnia-Herzegovina (Dörfler, 2013), at the Crveni Potok mire, Serbia (Finsinger et al. 2017) and at Lake Ohrid, Albania-Macedonia (Wagner et al. 2009).

Table 1 Selected variables describing differences in forest composition, structure and regeneration among forest structural types (FST; see Fig. 1) as measured in the 81 plots in the Biogradska Gora forest (values for other variables are reported in Table S5). Superscript letters indicate statistically significant differences between the mean values according to the Dunn's post hoc test ($\alpha=0.05$). CWD=coarse woody debris; SD=standard deviation; DBH=diameter at breast height.

Variable	Mean FST1	Mean FST2	Mean FST3	Overall (mean $\pm$ SD)	Overall (range)
Density Beech (#/ha)	800 ^a	264 ^b	379 ^c	405 $\pm$ 350.42 (71.9%)	49-2160
Density Silver fir (#/ha)	18 ^a	188 ^b	77 ^c	120 $\pm$ 136.83 (21.3%)	0-780
Density Norway Spruce (#/ha)	0 ^a	26 ^b	2 ^a	14 $\pm$ 30.88 (2.4%)	0-146
Density Other species (#/ha)	3 ^a	45 ^b	7 ^{ab}	25 $\pm$ 112.52 (4.4%)	0-974
Density Total (#/ha)	821 ^a	523 ^{ab}	465 ^a	564 $\pm$ 349.50	211-2176
DBH mean (cm)	31.66 ^a	37.88 ^b	28.93 ^a	33.89 $\pm$ 9.34	15.74-62.14
DBH Beech (cm)	26.33	27.64	20.45	25.21 $\pm$ 16.64	8-140
DBH Silver fir (cm)	20.00	38.28	56.22	40.94 $\pm$ 30.47	8-147
DBH Norway spruce (cm)	/	68.51	65.00	68.37 $\pm$ 26.58	12-148
DBH Other species (cm)	28.00	30.51	33.37	30.65 $\pm$ 17.75	9-114
Basal area Total (m ² /ha)	57.86 ^a	77.74 ^b	44.82 ^c	63.65 $\pm$ 20.69	26.53-104.81
Volume Total (m ³ /ha)	678.26 ^a	1168.93 ^b	635.39 ^a	907.30 $\pm$ 380.00	336.6-1781.9
Brillouin species diversity index	0.07 ^a	0.77 ^b	0.51 ^c	0.55 $\pm$ 0.32	0-1.17
Gini index DBH	0.24 ^a	0.38 ^b	0.40 ^b	0.36 $\pm$ 0.09	0.18-0.54
Regeneration Beech (#/ha)	221.05 ^a	1176.81 ^{ab}	1815.47 ^b	1237.59 $\pm$ 2292.21 (39.2%)	0-12640.15
Regeneration Silver fir (#/ha)	1576.81 ^a	773.48 ^b	844.90 ^{ab}	927.90 $\pm$ 1548.32 (29.4%)	0-9107.2
Regeneration Norway Spruce (#/ha)	7.37 ^a	41.81 ^a	45.95 ^a	37.63 $\pm$ 124.87 (1.2%)	0-795.13
Regeneration Other species (#/ha)	633.67 ^a	827.90 ^a	1287.07 ^a	951.50 $\pm$ 1793.17 (30.2%)	0-9991.4
Regeneration Total (#/ha)	2438.90 ^a	2820.01 ^a	3993.39 ^a	3154.60 $\pm$ 3839.67	0-21928

References

- Adolf C, Wunderle S, Colombaroli D, et al (2018) The sedimentary and remote-sensing reflection of biomass burning in Europe. *Glob Ecol Biogeogr* 27:199–212. <https://doi.org/10.1111/geb.12682>
- Ammann B, Knaap WO van der, Lang G, et al (2014) The potential of stomata analysis in conifers to estimate presence of conifer trees: examples from the Alps. *Veg Hist Archaeobotany* 23:249–264. <https://doi.org/10.1007/s00334-014-0431-9>
- Baker AG, Bhagwat SA, Willis KJ (2013) Do dung fungal spores make a good proxy for past distribution of large herbivores? *Quat Sci Rev* 62:21–31. <https://doi.org/10.1016/j.quascirev.2012.11.018>
- Barredo JI, Brailescu C, Teller A, et al (2021) Mapping and assessment of primary and old-growth forests in Europe. Luxembourg
- Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. *For Ecol Manag* 258:525–537. <https://doi.org/10.1016/j.foreco.2009.01.053>
- Behre K-E (1981) The interpretation of anthropogenic indicators in pollen diagrams. *Pollen Spores* 23:225–245
- Behre K-E (1992) The history of rye cultivation in Europe. *Veget Hist Archaeobot* 1:141–156. <https://doi.org/10.1007/BF00191554>
- Bennett KD (2008) Psimpoll v. 4.26
- Bennett KD (1996) Determination of the number of zones in a biostratigraphical sequence. *New Phytol* 132:155–170
- Birks HH, Birks HJB (2000) Future uses of pollen analysis must include plant macrofossils. *J Biogeogr* 27:31–35
- Birks HH, Bjune AE (2010) Can we detect a west Norwegian tree line from modern samples of plant remains and pollen? Results from the DOORMAT project. *Veg Hist Archaeobotany* 19:325–340. <https://doi.org/10.1007/s00334-010-0256-0>
- Birks HJB (2019) Contributions of Quaternary botany to modern ecology and biogeography. *Plant Ecol Divers* 12:189–385. <https://doi.org/10.1080/17550874.2019.1646831>
- Birks HJB, Gordon AD (1985) *Numerical Methods in Quaternary Pollen Analysis*. Academic Press, London
- Birks HJB, Tinner W (2016) Past forests of Europe. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, et al. (eds) *European Atlas of Forest Tree Species*. Publications Office of the European Union, Luxembourg, pp 36–39
- Blaauw M, Christen JA (2011) Flexible Paleoclimate Age-Depth Models Using an Autoregressive Gamma Process. *Bayesian Anal* 6:457–474. <https://doi.org/10.1214/11-BA618>
- Blondel J (2006) The ‘Design’ of Mediterranean Landscapes: A Millennial Story of Humans and Ecological Systems during the Historic Period. *Hum Ecol* 34:713–729. <https://doi.org/10.1007/s10745-006-9030-4>
- Bolte A, Hilbrig L, Grundmann BM, Roloff A (2014) Understory dynamics after disturbance accelerate succession from spruce to beech-dominated forest—the Siggaboda case study. *Ann For Sci* 71:139–147. <https://doi.org/10.1007/s13595-013-0283-y>
- Bradshaw RHW, Lindbladh M (2005) Regional spread and stand-scale establishment of *Fagus sylvatica* and *Picea abies* in Scandinavia. *Ecology* 86:1679–1686
- Brillouin L (1956) *Science and Information Theory*. Academic Press, New York (USA)

- Buchwald E (2005) A hierarchical terminology for more or less natural forests in relation to sustainable management and biodiversity conservation. FAO, Rome, 17–19 January 2005, p 17
- Büntgen U, Tegel W, Kaplan JO, et al (2014) Placing unprecedented recent fir growth in a European-wide and Holocene-long context. *Front Ecol Environ* 12:100–106. <https://doi.org/10.1890/130089>
- Burrascano S, Keeton WS, Sabatini FM, Blasi C (2013) Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. *For Ecol Manag* 291:458–479. <https://doi.org/10.1016/j.foreco.2012.11.020>
- Carrari E, Ampoorter E, Verheyen K, et al (2017) Former charcoal platforms in Mediterranean forest areas: a hostile microhabitat for the recolonization by woody species. *iForest* 10:136–144. <https://doi.org/10.3832/ifer1701-009>
- Černjavski P (1937) Zur Kenntnis der Glaziation und des Buchenwaldes bei Biogradsko Jezero in Montenegro. *Bull Inst Jard Bot Univ Beogr* 4:24–41
- Chileen BV, McLauchlan KK, Higuera PE, et al (2020) Vegetation response to wildfire and climate forcing in a Rocky Mountain lodgepole pine forest over the past 2500 years. *The Holocene* 30:1493–1503. <https://doi.org/10.1177/0959683620941068>
- Chivulescu S, Ciceu A, Leca S, et al (2020) Development phases and structural characteristics of the Penteleu-Viforâta virgin forest in the Curvature Carpathians. *IForest - Biogeosciences For* 13:389. <https://doi.org/10.3832/ifer3094-013>
- Conedera M, Colombaroli D, Tinner W, et al (2017) Insights about past forest dynamics as a tool for present and future forest management in Switzerland. *For Ecol Manag* 388:100–112. <https://doi.org/10.1016/j.foreco.2016.10.027>
- Conedera M, Tinner W, Neff C, et al (2009) Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. *Quat Sci Rev* 28:555–576. <https://doi.org/10.1016/j.quascirev.2008.11.005>
- Csontos P, Vitalos M, Barina Z, Kiss L (2010) Early distribution and spread of *Ambrosia artemisiifolia* in Central and Eastern Europe. *Bot Helvetica* 120:75–78. <https://doi.org/10.1007/s00035-010-0072-2>
- Čurović M, Stešević D, Medarević M, et al (2011) Ecological and structural characteristics of monodominant montane beech forests in the National park Biogradska Gora, Montenegro. *Arch Biol Sci* 63:429–440
- Davis OK (1987) Spores of the dung fungus *Sporormiella*: increased abundance in historic sediments and before Pleistocene megafaunal extinction. *Quat Res* 28:290–294
- Deza-Araujo M, Morales-Molino C, Tinner W, et al (2020) A critical assessment of human-impact indices based on anthropogenic pollen indicators. *Quat Sci Rev* 236:106291. <https://doi.org/10.1016/j.quascirev.2020.106291>
- Diaci J (ed) (1999) Virgin forests and forest reserves in Central and East European countries: history, present status and future development: proceedings of the invited lecturers' reports presented at the COST E4 management committee and working groups meeting in Ljubljana, Slovenia, Ljubljana, 25-28 April, 1998. Dept. of Forestry and Renewable Forest Resources, Ljubljana
- Dieler J, Pretzsch H (2013) Morphological plasticity of European beech (*Fagus sylvatica* L.) in pure and mixed-species stands. *For Ecol Manag* 295:97–108. <https://doi.org/10.1016/j.foreco.2012.12.049>
- Dörfler W (2013) Prokoško Jezero: An environmental record from a subalpine lake in Bosnia-Herzegovina. In: Müller J, Rassmann K, Hofmann R (eds) *Okolište 1 – Untersuchungen einer spätneolithischen Siedlungskammer in Zentralbosnien*. Habelt Verlag, Bonn, pp 311–340

- Duffin KI, Gillson L, Willis KJ (2008) Testing the sensitivity of charcoal as an indicator of fire events in savanna environments: quantitative predictions of fire proximity, area and intensity. *The Holocene* 18:279–291. <https://doi.org/10.1177/0959683607086766>
- Ellenberg H (2009) *Vegetation ecology of Central Europe*, 4th Edition. Cambridge University Press
- Elsen PR, Monahan WB, Dougherty ER, Merenlender AM (2020) Keeping pace with climate change in global terrestrial protected areas. *Sci Adv* 6:eaay0814. <https://doi.org/10.1126/sciadv.aay0814>
- Feurdean A, Florescu G, Vannière B, et al (2017) Fire has been an important driver of forest dynamics in the Carpathian Mountains during the Holocene. *For Ecol Manag* 389:15–26. <https://doi.org/10.1016/j.foreco.2016.11.046>
- Feurdean A, Tonkov S, Pfeiffer M, et al (2019) Fire frequency and intensity associated with functional traits of dominant forest type in the Balkans during the Holocene. *Eur J For Res* 138:1049–1066. <https://doi.org/10.1007/s10342-019-01223-0>
- Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37:4302–4315. <https://doi.org/10.1002/joc.5086>
- Finsinger W, Fevre J, Orbán I, et al (2018) Holocene fire-regime changes near the treeline in the Retezat Mts. (Southern Carpathians, Romania). *Quat Int* 477:94–105. <https://doi.org/10.1016/j.quaint.2016.04.029>
- Finsinger W, Morales-Molino C, Gafka M, et al (2017) Holocene vegetation and fire dynamics at Crveni Potok, a small mire in the Dinaric Alps (Tara National Park, Serbia). *Quat Sci Rev* 167:63–77. <https://doi.org/10.1016/j.quascirev.2017.04.032>
- Finsinger W, Tinner W (2020) New insights on stomata analysis of European conifers 65 years after the pioneering study of Werner Trautmann (1953). *Veg Hist Archaeobotany* 29:393–406. <https://doi.org/10.1007/s00334-019-00754-1>
- Foster DR, Orwig DA, McLachlan JS (1996) Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Trends Ecol Evol* 11:419–424. [https://doi.org/10.1016/0169-5347\(96\)10047-1](https://doi.org/10.1016/0169-5347(96)10047-1)
- Garbarino M, Lingua E, Weisberg PJ, et al (2013) Land-use history and topographic gradients as driving factors of subalpine *Larix decidua* forests. *Landsc Ecol* 28:805–817. <https://doi.org/10.1007/s10980-012-9792-6>
- Gaudet D, Menzies J (2012) Common bunt of wheat: an old foe remains a current threat. In: Sharma I (ed) *Disease Resistance in Wheat*. CABI, pp 220–235
- Giesecke T, Hickler T, Kunkel T, et al (2007) Towards an understanding of the Holocene distribution of *Fagus sylvatica* L. *Journal of Biogeography* 34:118–131. <https://doi.org/10.1111/j.1365-2699.2006.01580.x>
- Gini C (1912) *Variabilità e Mutabilità (Variability and Mutability)*. C. Cuppini, Bologna, Italy
- Green DG (1981) Time Series and Postglacial Forest Ecology. *Quat Res* 15:265–277
- Green MH (2014) Taking “Pandemic” Seriously: Making the Black Death Global. *Mediev Globe* 1:27–62
- Hanewinkel M, Cullmann DA, Schelhaas M-J, et al (2013) Climate change may cause severe loss in the economic value of European forest land. *Nat Clim Change* 3:203–207. <https://doi.org/10.1038/nclimate1687>
- Hansen AJ, DeFries R (2007) Ecological mechanisms linking protected areas to surrounding lands. *Ecol Appl* 17:974–988. <https://doi.org/10.1890/05-1098>

- Hararuk O, Kurz WA, Didion M (2020) Dynamics of dead wood decay in Swiss forests. *For Ecosyst* 7:36. <https://doi.org/10.1186/s40663-020-00248-x>
- Harmon ME, Franklin JF, Swanson FJ, et al (2004) Ecology of coarse woody debris in temperate ecosystems. In: *Advances in Ecological Research*. Academic Press, pp 59–234
- Higuera PE, Brubaker LB, Anderson PM, et al (2009) Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecol Monogr* 79:201–219
- Higuera PE, Gavin DG, Bartlein PJ, Hallett DJ (2010a) Peak detection in sediment–charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *Int J Wildland Fire* 19:996. <https://doi.org/10.1071/WF09134>
- Higuera PE, Whitlock C, Gage JA (2010b) Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in subalpine forests of Yellowstone National Park, USA. *The Holocene* 21:327–341. <https://doi.org/10.1177/0959683610374882>
- Hofstetter S, Tinner W, Valsecchi V, et al (2006) Lateglacial and Holocene vegetation history in the Insubrian Southern Alps—New indications from a small-scale site. *Veg Hist Archaeobotany* 15:87–98. <https://doi.org/10.1007/s00334-005-0005-y>
- Horvat I, Glavač V, Ellenberg H (1974) *Vegetation of Southeast Europe*. Gustav Fischer Verlag, Stuttgart
- Kaplan JO, Krumhardt KM, Zimmermann N (2009) The prehistoric and preindustrial deforestation of Europe. *Quat Sci Rev* 28:3016–3034. <https://doi.org/10.1016/j.quascirev.2009.09.028>
- Kelly R, Higuera PE, Barrett CM, Hu FS (2011) A signal-to-noise index to quantify the potential for peak detection in sediment–charcoal records. *Quat Res* 75:11–17. <https://doi.org/10.1016/j.yqres.2010.07.011>
- Keren S, Motta R, Govedar Z, et al (2014) Comparative structural dynamics of the Janj mixed old-growth mountain forest in Bosnia and Herzegovina: Are conifers in a long-term decline? *Forests* 5:1243–1266. <https://doi.org/10.3390/f5061243>
- Keren S, Svoboda M, Janda P, Nagel TA (2020) Relationships between structural indices and conventional stand attributes in an old-growth forest in southeast Europe. *Forests* 11:4. <https://doi.org/10.3390/f11010004>
- Kiesselbach TA, Lyness WE (1939) The effects of stinking smut (Bunt) and seed treatment upon the yield of winter wheat. *Hist Res Bull Neb Agric Exp Stn* 1913-1993 110:1–25
- Krawchuk MA, Moritz MA, Parisien M-A, et al (2009) Global pyrogeography: the current and future distribution of wildfire. *PLOS ONE* 4:e5102. <https://doi.org/10.1371/journal.pone.0005102>
- Leibundgut H (1959) Über Zweck und Methodik der Struktur und Zuwachsanalyse von Urwäldern. *Schweiz Z Für Forstwes* 110:111–124
- Lindbladh M (1999) The influence of former land-use on vegetation and biodiversity in the boreo-nemoral zone of Sweden. *Ecography* 22:485–498. <https://doi.org/10.1111/j.1600-0587.1999.tb01277.x>
- Ljungqvist FC, Seim A, Krusic PJ, et al (2019) European warm-season temperature and hydroclimate since 850 CE. *Environ Res Lett* 14:084015. <https://doi.org/10.1088/1748-9326/ab2c7e>
- Luburić V (2016) The introduction of new management measures in protected areas with the aim of improving models of nature protection of Montenegro. PhD, University of Novi Sad
- Luterbacher J, Newfield TP, Xoplaki E, et al (2020) Past pandemics and climate variability across the Mediterranean. *Euro-Mediterr J Environ Integr* 5:46, s41207-020-00197–5. <https://doi.org/10.1007/s41207-020-00197-5>

- Makra L, Juhász M, Béczi R, Borsos E (2005) The history and impacts of airborne *Ambrosia* (Asteraceae) pollen in Hungary. *Grana* 44:57–64. <https://doi.org/10.1080/00173130510010558>
- Maringer J, Conedera M, Ascoli D, et al (2016) Resilience of European beech forests (*Fagus sylvatica* L.) after fire in a global change context. *Int J Wildland Fire* 25:699. <https://doi.org/10.1071/WF15127>
- Marlon JR, Bartlein PJ, Carcaillet C, et al (2008) Climate and human influences on global biomass burning over the past two millennia. *Nat Geosci* 1:697–702. <https://doi.org/10.1038/ngeo313>
- Mazurkiewicz-Zapałowicz K, Okuniewska-Nowaczyk I (2015) Mycological and palynological studies of early medieval cultural layers from strongholds in Pszczew and Santok (western Poland). 10
- Mazziotta A, Heilmann-Clausen J, Bruun HH, et al (2016) Restoring hydrology and old-growth structures in a former production forest: Modelling the long-term effects on biodiversity. *For Ecol Manag* 381:125–133. <https://doi.org/10.1016/j.foreco.2016.09.028>
- McEvedy C, Jones R (1978) *Atlas of World Population History*. Penguin Books, London
- McLachlan JS, Foster DR, Menalled F (2000) Anthropogenic ties to late-successional structure and composition in four New England Hemlock stands. *Ecology* 81:717–733. [https://doi.org/10.1890/0012-9658\(2000\)081\[0717:ATTLSS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0717:ATTLSS]2.0.CO;2)
- McMullin RT, Wiersma YF (2019) Out with OLD growth, in with ecological continNEWity: new perspectives on forest conservation. *Front Ecol Environ*. <https://doi.org/10.1002/fee.2016>
- Meyer P, Aljes M, Culmsee H, et al (2021) Quantifying old-growthness of lowland European beech forests by a multivariate indicator for forest structure. *Ecol Indic* 125:107575. <https://doi.org/10.1016/j.ecolind.2021.107575>
- Michel J, Youssefi D, Grizonnet M (2015) Stable mean-shift algorithm and Its application to the segmentation of arbitrarily large remote sensing images. *IEEE Trans Geosci Remote Sens* 53:952–964. <https://doi.org/10.1109/TGRS.2014.2330857>
- Millspaugh SH, Whitlock C (1995) A 750-year fire history based on lake sediment records in central Yellowstone National Park, USA. *The Holocene* 5:283–292. <https://doi.org/10.1177/095968369500500303>
- Morales-Molino C, Steffen M, Samartin S, et al (2020) Long-term responses of mediterranean mountain forests to climate change, fire and human activities in the northern Apennines (Italy). *Ecosystems*. <https://doi.org/10.1007/s10021-020-00587-4>
- Motta R, Berretti R, Castagneri D, et al (2011) Toward a definition of the range of variability of central European mixed *Fagus* – *Abies* – *Picea* forests: the nearly steady-state forest of Lom (Bosnia and Herzegovina). *Can J For Res* 41:1871–1884. <https://doi.org/10.1139/x11-098>
- Motta R, Garbarino M, Berretti R, et al (2015a) Structure, spatio-temporal dynamics and disturbance regime of the mixed beech–silver fir–Norway spruce old-growth forest of Biogradska Gora (Montenegro). *Plant Biosyst - Int J Deal Asp Plant Biol* 149:966–975. <https://doi.org/10.1080/11263504.2014.945978>
- Motta R, Garbarino M, Berretti R, et al (2015b) Development of old-growth characteristics in uneven-aged forests of the Italian Alps. *Eur J For Res* 134:19–31. <https://doi.org/10.1007/s10342-014-0830-6>
- Mrgic J (2018) Intemperate weather in violent times – narratives from the Western Balkans during the Little Ice Age (17–18th centuries). *Cuad Investig Geográfica* 44:137. <https://doi.org/10.18172/cig.3380>
- Nagel TA, Mikac S, Dolinar M, et al (2017) The natural disturbance regime in forests of the Dinaric Mountains: A synthesis of evidence. *For Ecol Manag* 388:29–42. <https://doi.org/10.1016/j.foreco.2016.07.047>

- Nagel TA, Svoboda M, Kobal M (2014) Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. *Ecol Appl* 24:663–679
- Niklasson M, Zin E, Zielonka T, et al (2010) A 350-year tree-ring fire record from Białowieża Primeval Forest, Poland: implications for Central European lowland fire history. *J Ecol* 98:1319–1329. <https://doi.org/10.1111/j.1365-2745.2010.01710.x>
- Nilsson SG, Niklasson M, Hedin J, et al (2003) Erratum to “Densities of large living and dead trees in old-growth temperate and boreal forests.” *For Ecol Manag* 178:355–370. [https://doi.org/10.1016/S0378-1127\(03\)00084-7](https://doi.org/10.1016/S0378-1127(03)00084-7)
- Nowaczyk NR (2001) Logging of magnetic susceptibility. In: *Tracking Environmental Change Using Lake Sediments. Volume 1: Basin Analysis, Coring, and Chronological Techniques*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 155–170
- Öder V, Petritan AM, Schellenberg J, et al (2021) Patterns and drivers of deadwood quantity and variation in mid-latitude deciduous forests. *For Ecol Manag* 487:118977. <https://doi.org/10.1016/j.foreco.2021.118977>
- Oris F, Ali AA, Asselin H, et al (2014) Charcoal dispersion and deposition in boreal lakes from 3 years of monitoring: Differences between local and regional fires. *Geophys Res Lett* 41:6743–6752. <https://doi.org/10.1002/2014GL060984>
- Oswald WW, Anderson PM, Brown TA, et al (2005) Effects of sample mass and macrofossil type on radiocarbon dating of arctic and boreal lake sediments. *The Holocene* 15:758–767. <https://doi.org/10.1191/0959683605hl849rr>
- Packham JR, Thomas PA, Atkinson MD, Degen T (2012) Biological Flora of the British Isles: *Fagus sylvatica*. *J Ecol* 100:1557–1608. <https://doi.org/10.1111/j.1365-2745.2012.02017.x>
- Petritan IC, Marzano R, Petritan AM, Lingua E (2014) Overstory succession in a mixed *Quercus petraea*–*Fagus sylvatica* old growth forest revealed through the spatial pattern of competition and mortality. *For Ecol Manag* 326:9–17. <https://doi.org/10.1016/j.foreco.2014.04.017>
- Pfister C, Brázdil R (2006) Social vulnerability to climate in the “Little Ice Age”: an example from Central Europe in the early 1770s. *Clim Past* 2:115–129. <https://doi.org/10.5194/cp-2-115-2006>
- Pluskowski A, Seetah K (2006) The animal bones from the 2004 excavation at Stari Bar, Montenegro. In: Gelichi S (ed) *The Archaeology of an abandoned town. The 2005 Project in Stari Bar*. All’Insegna del Giglio, Florence, pp 97–111
- Pretzsch H, Schütze G (2005) Crown allometry and growing space efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed stands. *Plant Biol Stuttg Ger* 7:628–639. <https://doi.org/10.1055/s-2005-865965>
- R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Reimer PJ, Bard E, Bayliss A, et al (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP
- Rouvinen S, Kuuluvainen T (2005) Tree diameter distributions in natural and managed old *Pinus sylvestris*-dominated forests. *For Ecol Manag* 208:45–61. <https://doi.org/10.1016/j.foreco.2004.11.021>
- Sabatini FM, Burrascano S, Keeton WS, et al (2018) Where are Europe’s last primary forests? *Divers Distrib* 24:1426–1439. <https://doi.org/10.1111/ddi.12778>
- Sabatini FM, Keeton WS, Lindner M, et al (2020) Protection gaps and restoration opportunities for primary forests in Europe. *Divers Distrib* 26:1646–1662. <https://doi.org/10.1111/ddi.13158>

- Sadori L, Giardini M, Gliozzi E, et al (2015) Vegetation, climate and environmental history of the last 4500 years at lake Shkodra (Albania/Montenegro). *The Holocene* 25:435–444. <https://doi.org/10.1177/0959683614561891>
- Schütz J-P, Saniga M, Diaci J, Vrška T (2016) Comparing close-to-nature silviculture with processes in pristine forests: lessons from Central Europe. *Ann For Sci* 73:911–921. <https://doi.org/10.1007/s13595-016-0579-9>
- Siegmund JF, Siegmund N, Donner RV (2017) CoinCalc —A new R package for quantifying simultaneities of event series. *Comput Geosci* 98:64–72. <https://doi.org/10.1016/j.cageo.2016.10.004>
- Spies TA, Franklin JF (1988) Old growth and forest dynamics in the Douglas-fir region of Western Oregon and Washington. *Nat Areas J* 8:190–201
- Stancioiu PT, O'Hara KL (2006a) Morphological plasticity of regeneration subject to different levels of canopy cover in mixed-species, multiaged forests of the Romanian Carpathians. *Trees* 20:196–209. <https://doi.org/10.1007/s00468-005-0026-2>
- Stancioiu PT, O'Hara KL (2006b) Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. *Eur J For Res* 125:151–162. <https://doi.org/10.1007/s10342-005-0069-3>
- Stijovic A (2017) Bazna studija o sumama u Nacionalnom parku Biogradska Gora (Podloga za upravljanje sumama). JP Nacionalni parkovi Crne Gore
- Sugita S (1994) Pollen representation of vegetation in Quaternary sediments - theory and method in patchy vegetation. *J Ecol* 82:881–897
- Thompson R, Oldfield F (1986) *Environmental magnetism*. Allen & Unwin Ltd, London
- Tinner W, Colombaroli D, Heiri O, et al (2013) The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. *Ecol Monogr* 83:419–439. <https://doi.org/10.1890/12-2231.1>
- Tinner W, Hubschmid P, Wehrli M, et al (1999) Long-term forest fire ecology and dynamics in southern Switzerland. *J Ecol* 87:273–289
- Tinner W, Lotter AF (2006) Holocene expansions of *Fagus sylvatica* and *Abies alba* in Central Europe: where are we after eight decades of debate? *Quat Sci Rev* 25:526–549
- UNESCO (2010) UNESCO Global Strategy: the Man and the Biosphere Programme. In: UNESCO World Herit. Cent. <https://whc.unesco.org/en/tentativelists/5569/>. Accessed 17 May 2021
- Vacek S, Vacek Z, Bílek L, et al (2015) The dynamics and structure of dead wood in natural spruce-beech forest stand – a 40 year case study in the Krkonoše National Park. *Dendrobiology* 73:21–32. <https://doi.org/10.12657/denbio.073.003>
- Vale TR (2002) The Pre-European landscape of the United States. In: Vale TR (ed) *Fire, native peoples, and the natural landscape*. Island Press, Washington, D.C.
- Valsecchi V, Finsinger W, Tinner W, Ammann B (2008) Testing the influence of climate, human impact, and fire on the Holocene population expansions of *Fagus sylvatica* in the southern Prealps (Italy). *The Holocene* 18:603–614. doi: 10.1177/0959683608089213
- Van Geel B (1978) A palaeoecological study of Holocene peat bog sections in Germany and The Netherlands, based on the analysis of pollen, spores and macro- and microscopic remains of fungi, algae, cormophytes and animals. *Rev Palaeobot Palynol* 25:1–120. [https://doi.org/10.1016/0034-6667\(78\)90040-4](https://doi.org/10.1016/0034-6667(78)90040-4)

- Vescovi E, Ammann B, Ravazzi C, Tinner W (2010) A new Late-glacial and Holocene record of vegetation and fire history from Lago del Greppo, northern Apennines, Italy. *Veg Hist Archaeobotany* 19:219–233. <https://doi.org/10.1007/s00334-010-0243-5>
- Wagner B, Lotter AF, Nowaczyk N, et al (2009) A 40,000-year record of environmental change from ancient Lake Ohrid (Albania and Macedonia). *J Paleolimnol* 41:407–430. <https://doi.org/10.1007/s10933-008-9234-2>
- Weiner J, Solbrig OT (1984) The meaning and measurement of size hierarchies in plant populations. *Oecologia* 61:334–336. <https://doi.org/10.1007/BF00379630>
- Whitlock C, Colombaroli D, Conedera M, Tinner W (2018) Land-use history as a guide for forest conservation and management. *Conserv Biol* 32:84–97. <https://doi.org/10.1111/cobi.12960>
- Whitlock C, Larsen C (2001) Charcoal as a fire proxy. In: Smol JP, Birks HJB, Last WM, Last WM (eds) *Terrestrial, Algal, and Siliceous Indicators*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 75–97
- Willis KJ, Birks HJB (2006) What is natural? The need for a long-term perspective in biodiversity conservation. *Science* 314:1261–1265
- Winkler E (1963) Beiträge zur Klimatologie hochalpiner Lagen der Zentralalpen. *Berichte Naturwissenschaftlich-Med Ver Innsbr* 53:209–223
- Wirth C, Messier C, Bergeron Y, et al (2009) Old-growth forest definitions: a pragmatic view. In: Wirth C, Gleixner G, Heimann M (eds) *Old-Growth Forests*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 11–33
- Wright MN, Ziegler A (2017) ranger: A fast implementation of random forests for high dimensional data in C++ and R. *J Stat Softw* 77:1–17. <https://doi.org/10.18637/jss.v077.i01>
- Wu M, Knorr W, Thonicke K, et al (2015) Sensitivity of burned area in Europe to climate change, atmospheric CO₂ levels, and demography: A comparison of two fire-vegetation models: Projected future burned area in Europe. *J Geophys Res Biogeosciences* 120:2256–2272. <https://doi.org/10.1002/2015JG003036>
- Xoplaki E, Maheras P, Luterbacher J (2001) Variability of climate in meridional Balkans during the periods 1675–1717 and 1780–1830 and its impact on human life. *Clim Change* 48:581–615. <https://doi.org/10.1023/A:1005616424463>
- Zang C, Hartl-Meier C, Dittmar C, et al (2014) Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. *Glob Change Biol* 20:3767–3779. <https://doi.org/10.1111/gcb.12637>
- Zenner EK, Sagheb-Talebi K, Akhavan R, Peck JE (2015) Integration of small-scale canopy dynamics smoothes live-tree structural complexity across development stages in old-growth Oriental beech (*Fagus orientalis* Lipsky) forests at the multi-gap scale. *For Ecol Manag* 335:26–36. <https://doi.org/10.1016/j.foreco.2014.09.023>

Electronic Supplementary Material

Materials and Methods

Tree species and forest structural diversity indices

Table S1 Compositional and structural diversity indices. n_i : number of individuals of the i^{th} species; n : total number of trees in a plot; p_i : proportion of stems in the i^{th} tree diameter class; j : rank of tree in ascending order from 1 to n ; x_j : diameter (cm) or basal area (m^2) of tree with rank j .

Diversity index	Source	Equation
<u>Tree species diversity</u> Brillouin index	Brillouin (1956)	$HB = \frac{\ln n! - \sum \ln ni!}{n}$
<u>Structural diversity</u> Tree Diameter Diversity	(Rouvinen and Kuuluvainen 2005)	$TDD = - \sum_{i=1}^s (p_i \ln p_i)$
Gini coefficient (with DBH and BA)	Keren et al. (2019)	$G = \frac{\sum_{j=1}^n (2j - 1 - n) x_j}{\sum_{j=1}^n x_j (n - 1)}$

Hierarchical Cluster Analysis

To group the plots into distinct forest structural types, we performed a Hierarchical Cluster Analysis (HCA) based on the total tree density, total basal area, basal areas of species in percentage, mean and standard deviation of DBH, dead to live wood ratio, Brillouin index, TDD, G_{BA} , total CWD, and proportion of CWD classes (snags, logs, and stumps). The HCA was performed using standardized data, Ward's agglomeration method, and Euclidean distance with the eclust R package (Bhatnagar et al. 2017). The number of retained clusters was determined using Monte Carlo ("bootstrap") resampling. We tested for the differences among forest-structural types using the non-parametric Kruskal-Wallis test, followed, in the case of significance, by a Dunn's post hoc test ($\alpha=0.05$) of multiple comparisons taking into account the unadjusted P-values (Dunn 1964).

Cost of Access

We estimated the cost of access to each plot using the Path Distance tool in ArcGIS Pro and the ALOS World 3D v2.2 30-m resolution digital surface model (Japan Aerospace Exploration Agency 2019). The function estimates the minimum accumulative distance (m) from roads and paths by taking into consideration topographic distance and the occurrence of horizontal and vertical barriers due to height and slope. We considered only the main roads, as we assumed they have been used since the Middle Ages. We did not estimate the cost of access from isolated shepherds' huts that are not located along the main roads because their period of construction and activity was unknown.

Remote sensing analysis

We pre-processed two high-resolution satellite images (Table S2) by pan-sharpening multispectral bands through the nearest neighbour diffusion (NNDiffuse) algorithm (Sun et al. 2014) and by co-registering them to the Bing satellite image with ENVI software (v5.3.1; Exelis Visual Information Solutions, Boulder, Colorado). We then created image objects through the Large-Scale Mean-Shift (LSMS) segmentation algorithm (Michel et al. 2015) implemented in Orfeo ToolBox v7.0 (Grizonnet et al. 2017), using a raster stack formed by the near infrared band, the Normalized Difference Vegetation Index (NDVI) and textural data derived from granulometric analysis based on the opening procedure. To obtain image objects representing small groups of crowns within the forested area, we selected the following parameters in the Large-Scale Mean-Shift (LSMS) segmentation algorithm: a spatial radius of 20 pixels, a range radius of 0.015 (all values in the raster stack ranged from 0 to 1) and a minimum region size of 200 pixels. To help the classifier disentangle among forest structure and composition we derived additional textural information from granulometric analysis of the Pléiades images based on the opening technique (Soille 2004). The opening procedure includes two mathematical morphology operations: an erosion followed by a dilation using a 2-dimensional structuring element (SE) and it is aimed at eliminating objects smaller than the SE. As SE we used a 7-pixel diameter disc (corresponding to 3.5 m) since this shape and size were well suited to the smallest tree crowns detectable in the satellite images. The opening procedure was done using the grey Values component after a Hue-Saturation-Value (HSV) transformation, which we applied to the red, green and blue bands of the Pléiades images. Since the Value component corresponds to the brightness of a surface, the opening procedure allowed us to maximize the contrast between sunlit crowns, which are generally located at the top of the forest stand, and darker portions in the background that correspond to smaller trees and canopy gaps.

Table S2 Details relative to Pléiades images employed to produce the land-cover map.

Satellite	Acquisition date	Spectral bands	Spatial resolution (m)	Geometric processing level	Radiometric processing level
Pléiades 1B	30/08/2015	Panchromatic (PAN); Multispectral (MS): Red, Green, Blue, Near infrared	0.5 (PAN) / 2 (MS)	Standard ortho (automatically processed with the best DEM available)	Reflectance imagery (radiometrically corrected from sensor calibration and systematic atmospheric effects of the atmosphere)
Pleiades 1A	01/08/2016				

Table S3 Summary statistics of spectral and textural layers employed as predictor variables in the Random Forest (RF) model.

Spectral and textural layers	Summary statistics
Pleiades reflectance bands (PAN and MS)	Min; max; range; sum; mean; variance; Gini coefficient; standard deviation; percentiles (5 th , 25 th , 50 th , 75 th , 95 th)
Spectral vegetation indices (NDVI; EVI; GNDVI; MSAVI; NDWI; SAVI; SR)	
Textures from the morphological opening procedure (kernels widths: 3; 5; 7; 9; 11; 13)	
Simple Haralick textures (Energy; Entropy; Correlation; Inverse Difference Moment; Inertia; Cluster Shade; Cluster Prominence; Haralick Correlation; square kernel of 9 pixels width and 1 pixel shift)	

To show differences among forest structures we selected a textural layer obtained from granulometric analysis based on the opening technique (Soille 2004) and a subsample of Haralick textural layers: Energy (Band=1) and Inverse Difference Moment (Band=4), as they measure the texture uniformity and texture homogeneity, respectively (Orfeo ToolBox, 2021).

Chronology of the sediment core

Table S4 Radiocarbon dates from the sediment core collected from the forest hollow (Biogradska Gora National Park).

Mid-depth (cm)	Lab code	Material dated	Dry weight (mg)	Sample thickness (cm)	¹⁴ C Age (year BP)
0	/	surface	/	1	-67 ± 5
24.5	/	<i>Ambrosia</i> pollen	/	1	0 ± 25
45.5	De-23155	Angiosperm leaf fragments; 1 petiole; angiosperm bud-scales	21.4	5	77 ± 26
79.5	Poz-116583	<i>Fagus</i> spp. wood*	100.5	1	885 ± 30
95	De-23156	Angiosperm leaf fragments; 1 petiole; bud-scales; 1 <i>Fagus</i> fruit	43.5	2	134 ± 27
151.5	Poz-116582	<i>Fraxinus</i> spp. wood*	588.8	3	365 ± 30
166.5	De-23157	Needles; 1 conifer bud-scale; 1 conifer seed; angiosperm leaf fragments; angiosperm bud-scales; 1 <i>Betula</i> seed; 1 <i>Betula</i> catkin scale; 1 <i>Sambucus</i> seed	23.6	3	696 ± 28
224.5	Poz-112247	<i>Rhamnus alpinus</i> wood	25	1	865 ± 30
240.5	Poz-112246	<i>Picea/Larix</i> type wood	31	1	1110 ± 30
242.5	Poz-109239	<i>Picea/Larix</i> type wood **	37	1	1070 ± 30

* = outer ring likely present but no bark

** = wood without bark

Charcoal, plant-macrofossils, and pollen and spores' analyses

Samples for macroscopic charcoal analysis were disaggregated in a 5% NaPO₃ solution overnight and then bleached for 24 hours with a 15% H₂O₂ solution (Schlachter and Horn 2010). Thereafter, samples were washed through a 150 µm mesh sieve (Higuera et al. 2005) and transferred to a petri dish for analysis at x7.5-60 magnification.

For plant-macrofossil analyses, we first measured sample volumes by water displacement (10 cm³ sample⁻¹ on average), then soaked samples in a 5% NaPO₃ solution overnight, and thereafter sieved them (200 µm mesh) under a gentle water jet.

Macrofossils were identified and counted at x7.5-60 magnification using atlases (Birks 2017; Cappers et al. 2006; Godet 1998; Katz et al. 1965; Schoch et al. 1988) and the reference collection at ISEM (Univ. Montpellier). Sufficiently large wood and charcoal pieces were identified using wood-anatomy keys and atlases (Schoch et al. 2004; Schweingruber 1990).

Pollen samples (1 cm³) were prepared following standard chemical (HCl, KOH, HF, acetolysis) and physical treatments (sieving at 500 µm and decanting), mounted on slides with glycerol and stained with Fuchsin. To calculate pollen concentrations, *Lycopodium* tablets were added prior to sample processing (Stockmarr 1971).

Pollen grains, spores, non-pollen palynomorphs and conifer stomata were identified and counted at x400 magnification using pollen keys and photographic atlases (Trautmann 1953; Reille 1992; Moore et al. 1998; Finsinger and Tinner 2019), and the reference collection at the University of Montpellier. *Fagus sylvatica*'s stomata were identified with comparison to type slides prepared from collected leaves (Fig. S1).

Details on *Fagus sylvatica* stomata and *Tilletia caries*-type spores

***Fagus sylvatica* stomata**

Stomata roundish, 20-30 µm in length (Kvaček and Walther 1991), T-shaped stem between the guard cells (Worobiec and Worobiec 2019).

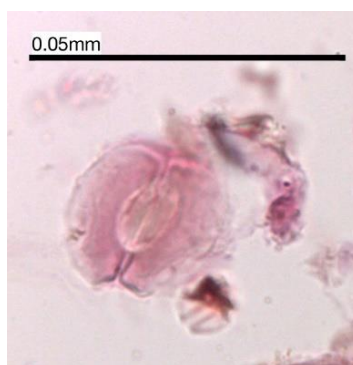


Fig. S1 *Fagus sylvatica*'s stomata found in the sediments of the forest hollow (Biogradska Gora National Park)

Tilletia-caries type spores

The spores identified as “*Tilletia cares*-type” in this study differ from spores called *Tilletia sphagni* Naw. (HdV-27; Van Geel 1978), because *Tilletia* spores have an external reticulation (Durán 1973), whilst in Type HdV-27 spores the network is formed by interconnected grooves.

Fire history reconstruction

We decomposed the charcoal-accumulation rate (CHAR) record into a background and a peak component. Charcoal background was modelled using a robust LOWESS with multiple smoothing-window widths (100, 200, 300, 400 and 500 years). Peak samples were calculated as residuals from the background and were evaluated using the 99th percentile of the modelled noise distribution obtained with a Gaussian mixture model for each 500-year portion of the record (Higuera et al. 2009). Identified peak samples were subjected to a peak-screening test (Higuera et al. 2010). To evaluate the suitability of the record for peak detection we used the signal-to-noise index (SNI) (Kelly et al. 2011). We calculated fire return intervals (FRI) using the screened peak records.

Climate data

We took the climate data from the ‘Last Millennium’ (850-1850 CE) and the ‘historical’ (1850-2005 CE) simulations of the Community Climate System Model, version 4 (CCSM4; Landrum et al. 2013) that were regridded to a 5° x 5° resolution and decadal filtered (Ljungqvist et al., 2019). We averaged the data over the grid cells located within a radius of 3° around Biogradska Gora, and determined the long-term trends using a loess smoothed curve that matches the centennially-filtered data (Ljungqvist et al. 2019). Consistently with other paleoclimate records (PAGES 2k Consortium 2013), the data show that temperatures were milder during the Medieval Climate Anomaly (MCA, in this work 950-1250 CE following Mann et al. 2009), thereafter transitioned to cooler temperatures and entered a protracted cold period (the Little Ice Age, LIA) between 1570 and 1880 CE.

Results

Hierarchical Cluster Analysis

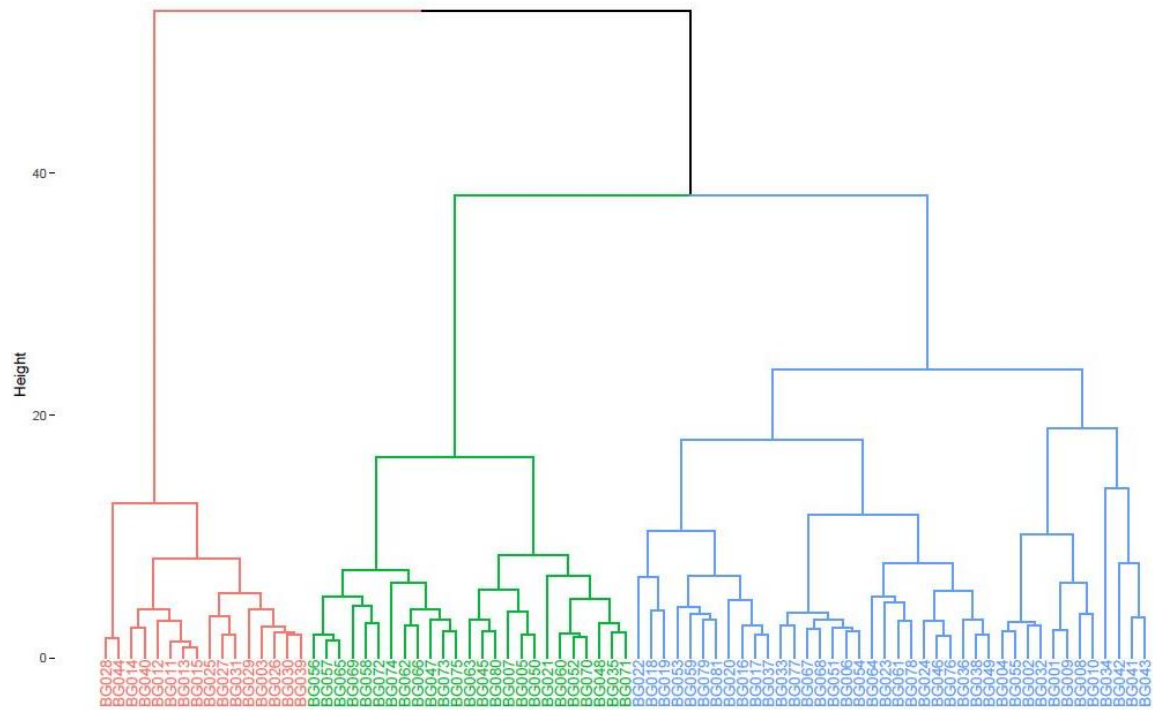


Fig. S2 Dendrogram showing the results of the hierarchical cluster analysis (HCA) of the field-survey plots. Colours denote the 3 types of vegetation structure and composition.

Differences in forest structure and composition among FSTs

Table S5 Variables describing differences in forest composition, structure and regeneration among forest structural types (FST; see Fig. 1) as measured in the 81 plots in the Biogradska Gora forest. Superscript letters indicate statistically significant differences between the mean values according to the Dunn's post hoc test ($\alpha=0.05$). CWD=coarse woody debris; SD=standard deviation; DBH=diameter at breast height.

Variable	Mean FST1	Mean FST2	Mean FST3	Overall (mean $\pm$ SD)	Overall (range)
Density Beech (#/ha)	800 ^a	264 ^b	379 ^c	405 $\pm$ 350.42 (71.9%)	49-2160
Density Silver fir (#/ha)	18 ^a	188 ^b	77 ^c	120 $\pm$ 136.83 (21.3%)	0-780
Density Norway spruce (#/ha)	0 ^a	26 ^b	2 ^a	14 $\pm$ 30.88 (2.4%)	0-146
Density Other species (#/ha)	3 ^a	45 ^b	7 ^{ab}	25 $\pm$ 112.52 (4.4%)	0-974
Density Total (#/ha)	821 ^a	523 ^{ab}	465 ^a	564 $\pm$ 349.50	211-2176
DBH mean (cm)	31.66 ^a	37.88 ^b	28.93 ^a	33.89 $\pm$ 9.34	15.74-62.14
DBH Beech (cm)	26.33	27.64	20.45	25.21 $\pm$ 16.64	8-140
DBH Silver fir (cm)	20.00	38.28	56.22	40.94 $\pm$ 30.47	8-147
DBH Norway spruce (cm)	/	68.51	65.00	68.37 $\pm$ 26.58	12-148
DBH Other species (cm)	28.00	30.51	33.37	30.65 $\pm$ 17.75	9-114
Basal area Beech (m ² /ha)	56.79 ^a	23.24 ^b	19.77 ^b	28.8 $\pm$ 21.99 (45.2%)	1.66-94.06
Basal area Silver fir (m ² /ha)	0.89 ^a	37.57 ^b	23.32 ^b	25.93 $\pm$ 24.98 (40.7%)	0-89.71
Basal area Norway spruce (m ² /ha)	0.00 ^a	12.68 ^b	0.96 ^a	6.558 $\pm$ 14.74 (10.3%)	0-80.07
Basal area Other species (m ² /ha)	0.19 ^a	4.25 ^b	0.77 ^{ab}	2.373 $\pm$ 8.30 (3.7%)	0-57.99
Basal area Total (m ² /ha)	57.86 ^a	77.74 ^b	44.82 ^c	63.65 $\pm$ 20.69	26.53-104.81
Volume Total (m ³ /ha)	678.26 ^a	1168.93 ^b	635.39 ^a	907.30 $\pm$ 380.00	336.6-1781.9
CWD Log (m ³ /ha)	31.22 ^a	150.47 ^b	268.24 ^c	163.27 $\pm$ 154.16 (65%)	2.16-604.27
CWD Snag (m ³ /ha)	14.35 ^a	62.26 ^b	160.40 ^c	83.08 $\pm$ 112.10 (33%)	0-457.86
CWD Stump (m ³ /ha)	2.46 ^a	6.21 ^a	5.40 ^a	5.22 $\pm$ 6.38 (2%)	0-25.24
CWD Total (m ³ /ha)	48.03 ^a	218.94 ^b	434.04 ^c	251.57 $\pm$ 208.91	7.36-791.64
Brillouin species diversity index	0.07 ^a	0.77 ^b	0.51 ^c	0.55 $\pm$ 0.32	0-1.17
Dead to live wood ratio	0.07 ^a	0.19 ^b	0.76 ^c	0.34 $\pm$ 0.39	0.01-2.35
DBH SD (cm)	13.65 ^a	26.61 ^b	22.37 ^b	22.74 $\pm$ 8.09	6.49-42.06
Tree diameter diversity index	1.99 ^a	2.18 ^b	1.90 ^a	2.06 $\pm$ 0.26	1.460-2.510
Gini index DBH	0.24 ^a	0.38 ^b	0.40 ^b	0.36 $\pm$ 0.09	0.18-0.54
Gini index Basal area	0.43 ^a	0.63 ^b	0.68 ^b	0.61 $\pm$ 0.13	0.34-0.81
Regeneration Beech (#/ha)	221.05 ^a	1176.81 ^{ab}	1815.47 ^b	1237.59 $\pm$ 2292.21 (39.2%)	0-12640.15
Regeneration Silver fir (#/ha)	1576.81 ^a	773.48 ^b	844.90 ^{ab}	927.90 $\pm$ 1548.32 (29.4%)	0-9107.2
Regeneration Norway spruce (#/ha)	7.37 ^a	41.81 ^a	45.95 ^a	37.63 $\pm$ 124.87 (1.2%)	0-795.13
Regeneration Other species (#/ha)	633.67 ^a	827.90 ^a	1287.07 ^a	951.50 $\pm$ 1793.17 (30.2%)	0-9991.4
Regeneration Total (#/ha)	2438.90 ^a	2820.01 ^a	3993.39 ^a	3154.60 $\pm$ 3839.67	0-21928
Path distance (m)	844.73 ^a	1182.19 ^{ab}	1358.72 ^b	/	/

Remote sensing analyses

The random-forest classifier performed very well as the average overall accuracy was higher than 95% for both Pléiades images and the Cohen's Kappa statistic ranged between 0.92 and 0.95 (Table S6). Producer's and user's accuracies of vegetated canopy gaps were the lowest among land-cover types and they varied between 75% and 100% and 54.5% and 66.7%, respectively (Table S6).

Table S6 Producer's accuracy, user's accuracy, overall accuracy and Cohen's Kappa of land-cover types (CO: conifers, BR: broadleaved trees, FG: forest canopy gaps, GR: grasslands, BG: bare ground, WA: water) obtained with each Pléiades image. Accuracies are reported in percentage.

	Pléiades 1B (30/08/2015)				Pléiades 1A (01/08/2016)			
Land-cover class	Producer's accuracy	User's accuracy	Overall accuracy	Cohen's Kappa	Producer's accuracy	User's accuracy	Overall accuracy	Cohen's Kappa
CO	95.8	96.1	95.6	0.92	92.9	97.8	96.5	0.95
BR	95.2	95.6			98.5	97.8		
FG	75.0	66.7			100.0	54.5		
GR	100.0	97.0			100.0	100.0		
BG	100.0	100.0			96.4	100.0		
WA	100.0	100.0			NA	NA		

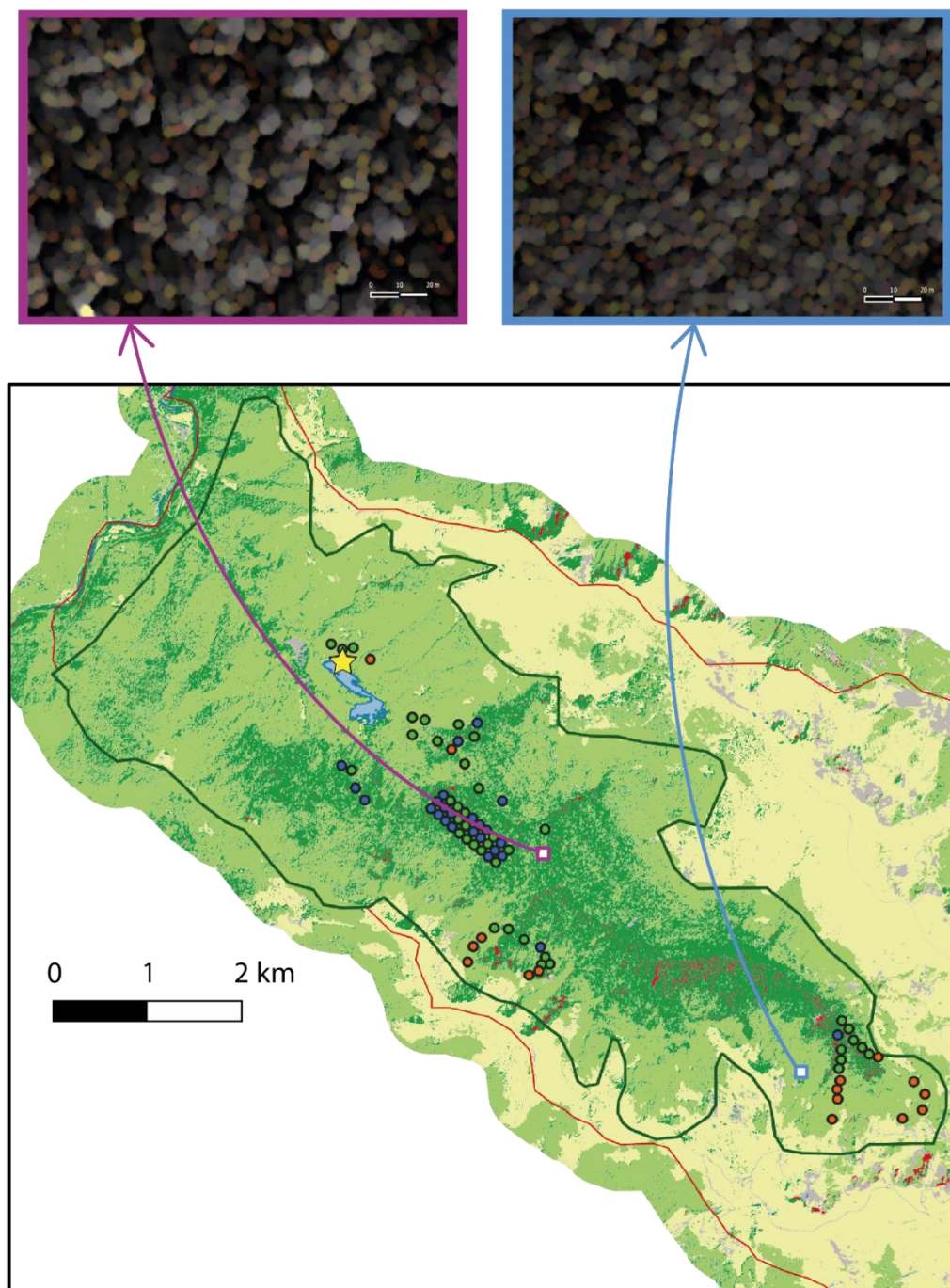


Fig. S3a Land-cover map of the Biogradska Gora National Park (core area: green continuous line). On the top, details of the textural layers obtained from the morphological opening procedure (Soille, 2004) for the conifer-dominated old-growth stands (left) and the beech-dominated stands (right) (structuring element = 5 pixels).

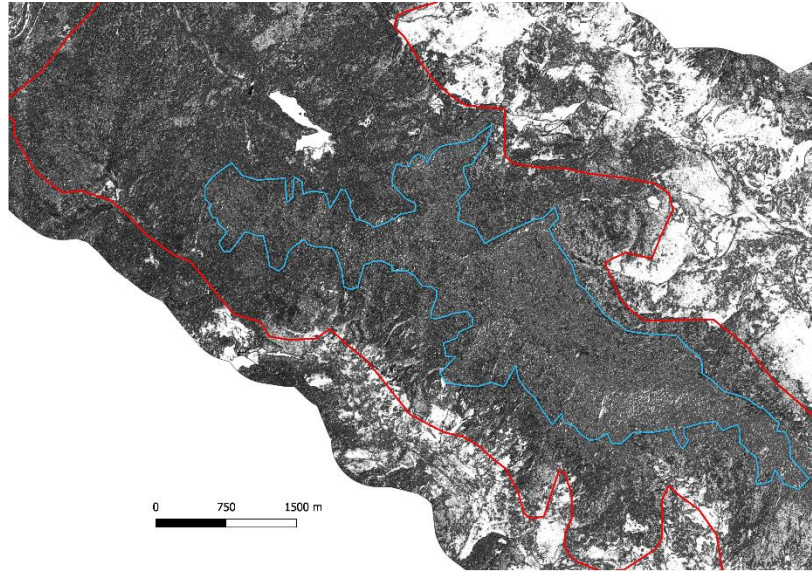


Fig. S3b Gray-scale map of Haralick's textural layer showing texture uniformity (Band 1, Energy). The red line delimits the core area while the blue line divides the conifer-dominated old-growth stands and the beech-dominated stands.

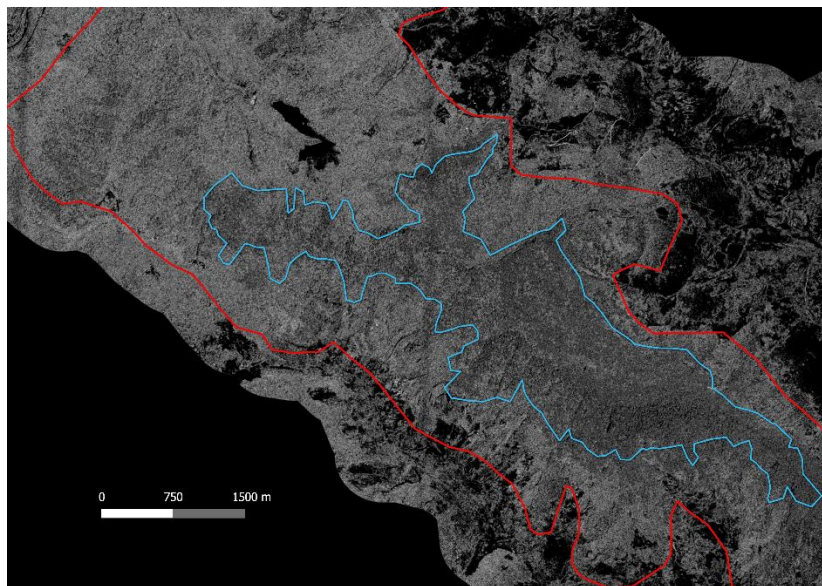


Fig. S3c Gray-scale map of Haralick's textural layer showing texture homogeneity (Band 4, Inverse Difference Moment). The red line delimits the core area while the blue line divides the conifer-dominated old-growth stands and the beech-dominated stands.

Description of the sediments

Sediments are mostly composed of dark-brown detritus gyttja. From 235 to 215 cm depth (1010 and 1120 CE) sediments gradually lighten and remain olive-green up to 175 cm depth. Above 175 cm sediments become darker and *Carex* stems are particularly abundant between 140 and 40 cm. In keeping with this, highest magnetic susceptibility values occur between 235 and 190 cm (1010-1250 CE), then gradually decrease until 170 cm (1350 CE) and level-off at lowest and negative values, and finally increase in the top 100 cm (from 1690 CE until the present day) (Fig. S8).

Plant macrofossils of wetland plants (*Juncus* and *Eleocharis*) are more abundant from the base of the core to c. 120 cm depth (Fig. S5). There is a peak of *Sparganium* at 180 cm (1350-1300 CE) that is followed first by high abundance of *Carex* fruits (170 to 150 cm; 1350-1470 CE), and then by high abundance of Cyperaceae pollen from 150 to 50 cm depth (1470-1850 CE) (Fig. 4).

Detailed pollen diagram

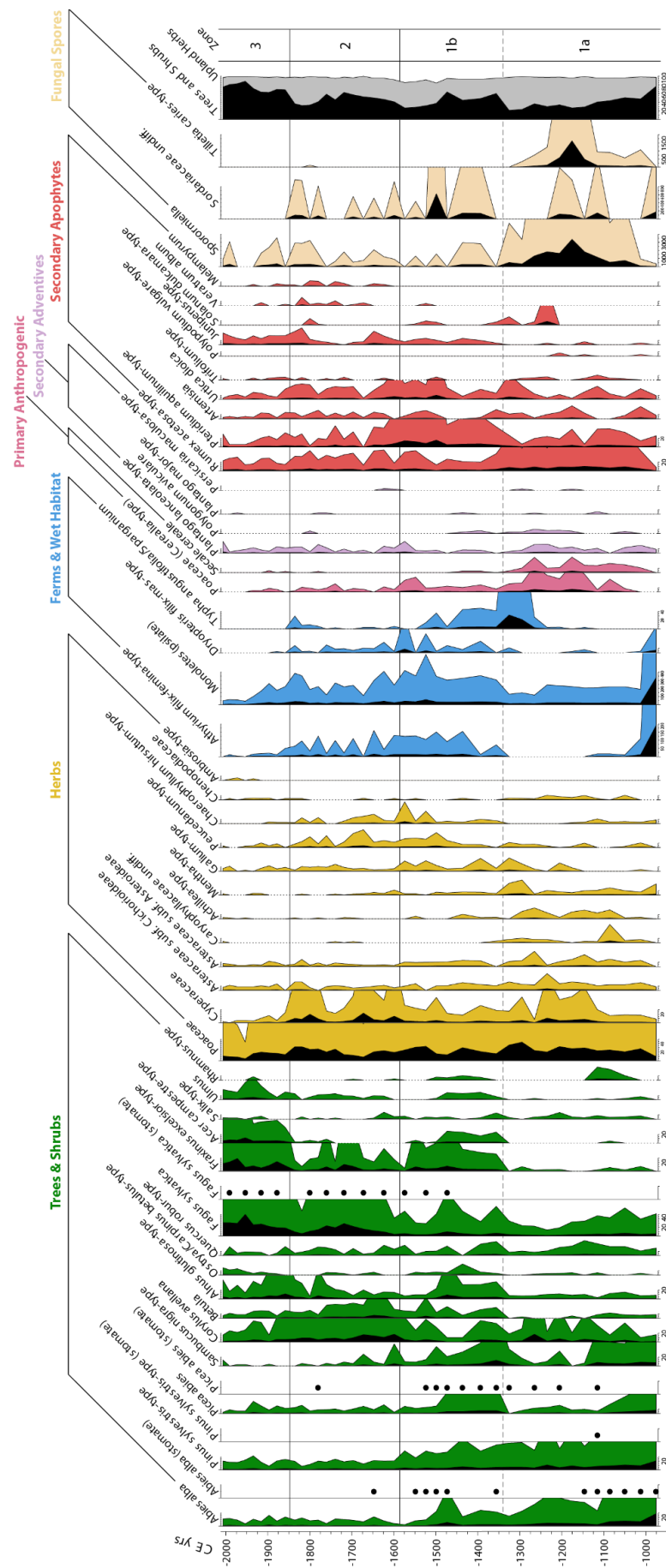


Fig. S4 Pollen diagram from the forest hollow situated in the Biogradska Gora National Park (selected taxa). Horizontal continuous and dashed lines represent significant and non-significant pollen zone boundaries, respectively. Black dots are stomata findings.

Detailed plant macrofossil diagram

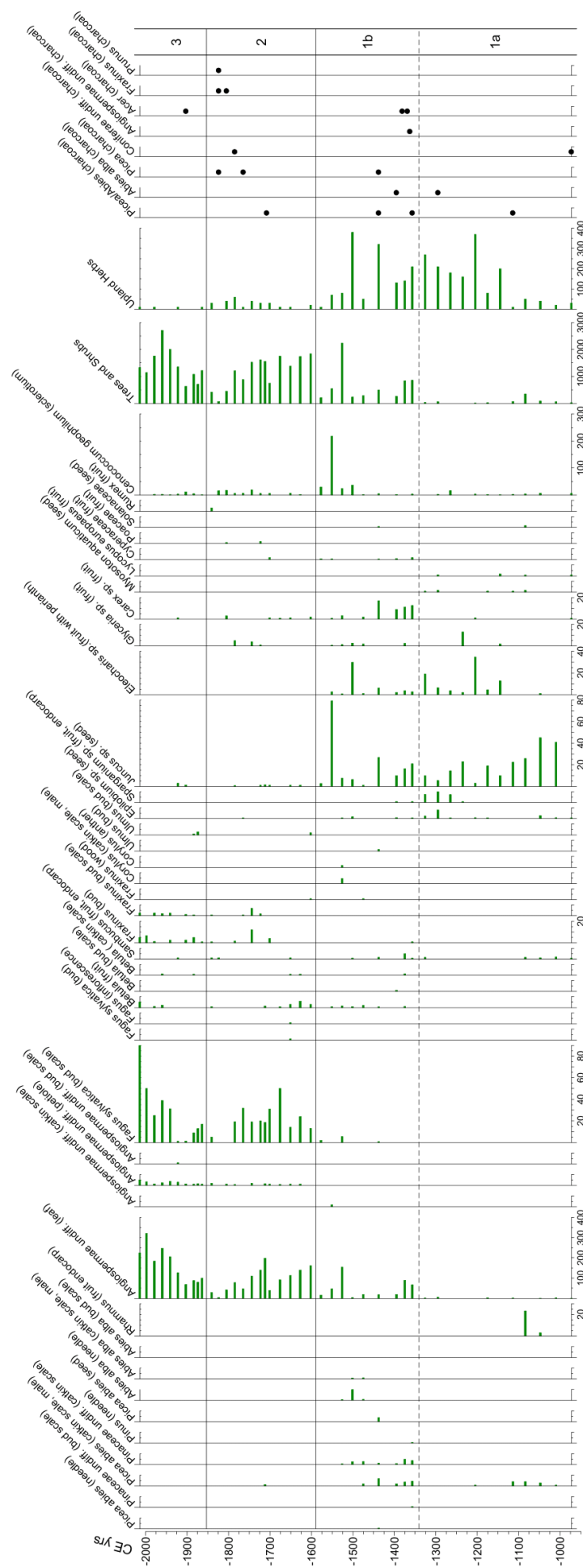


Fig. S5 Plant macrofossil diagram of selected taxa from the forest hollow (Biogradska Gora National Park). Horizontal continuous and dotted lines represent significant and non-significant pollen zone boundaries, respectively.

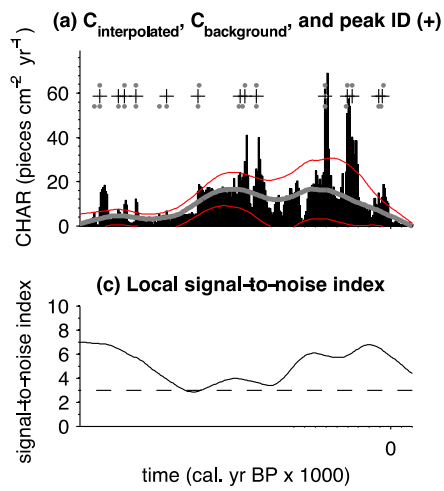
Fire history

Table S7 Number of fire episodes based on peak analyses using different user-determined parameters (interpolation years and smoothing moving-window widths). For each combination of variables, the mean value of the signal-to-noise index (Kelly et al. 2011) is reported, and an asterisk indicates the timeseries that are suitable for peak analyses (SNI>3).

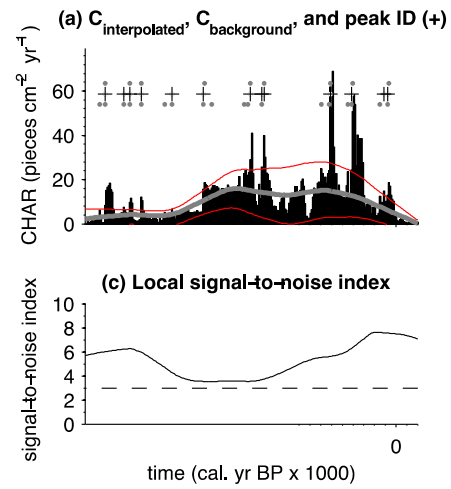
Interpolation (year)	Smoothing- window width (year)	Mean SNI	N° of detected fire episodes
8	100	2.95	12
	200	4.42*	9
	300	4.85*	9
	400	4.74*	9
	500	4.85*	11
4	100	3.50*	11
	200	5.29*	14
	300	5.49*	13
	400	5.27*	11
	500	5.29*	12

Resampling=4 years

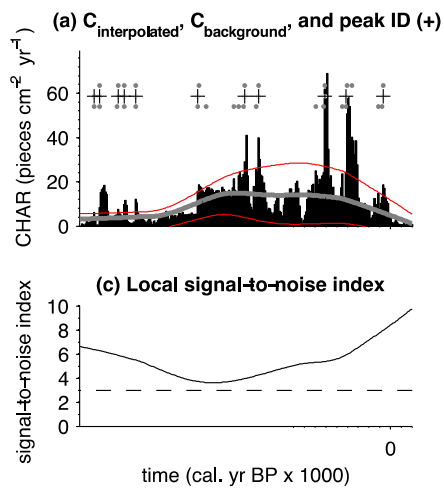
Smoothing-window width=200 years



Smoothing-window width=300 years



Smoothing-window width=400 years



Smoothing-window width=500 years

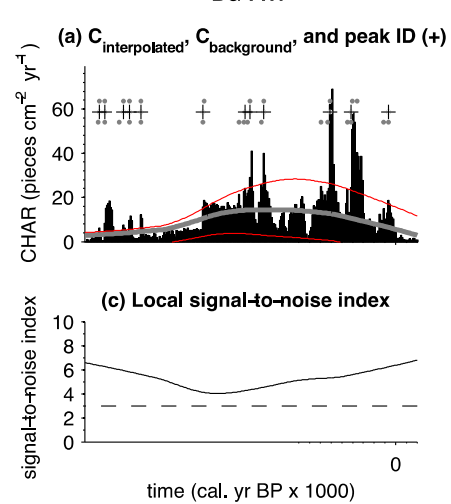
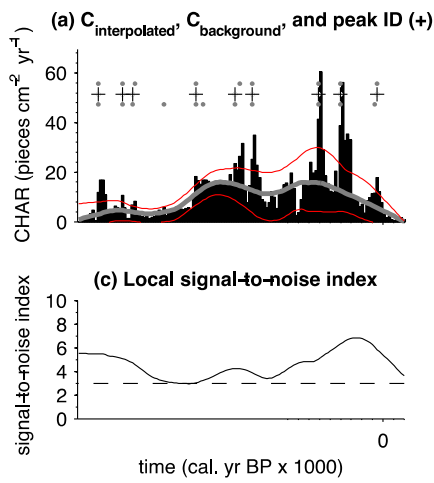


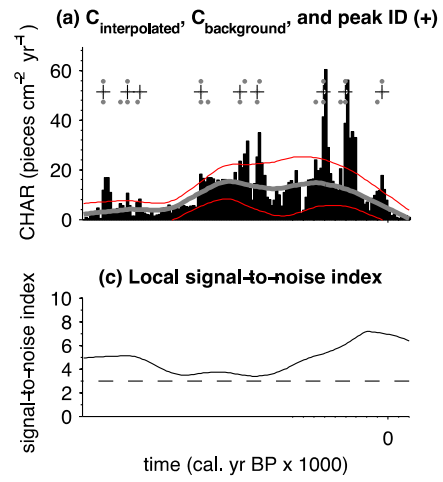
Fig. S6 Comparison between peak-analyses using a resampling at 4 years and different smoothing-window widths.

Resampling=8 years

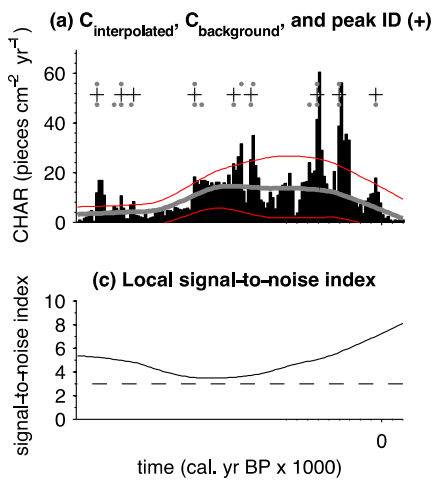
Smoothing-window width=200 years



Smoothing-window width=300 years



Smoothing-window width=400 years



Smoothing-window width=500 years

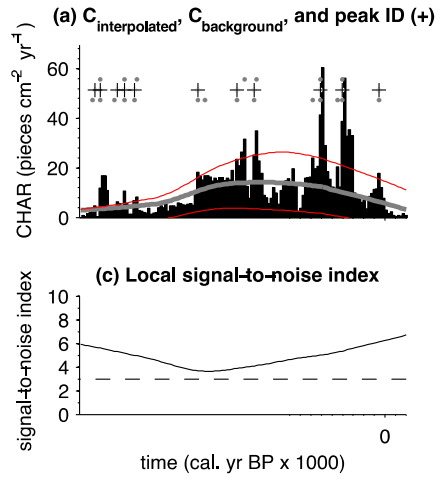


Fig. S7 Comparison between peak-analyses using a resampling at 8 years and different smoothing-window widths.

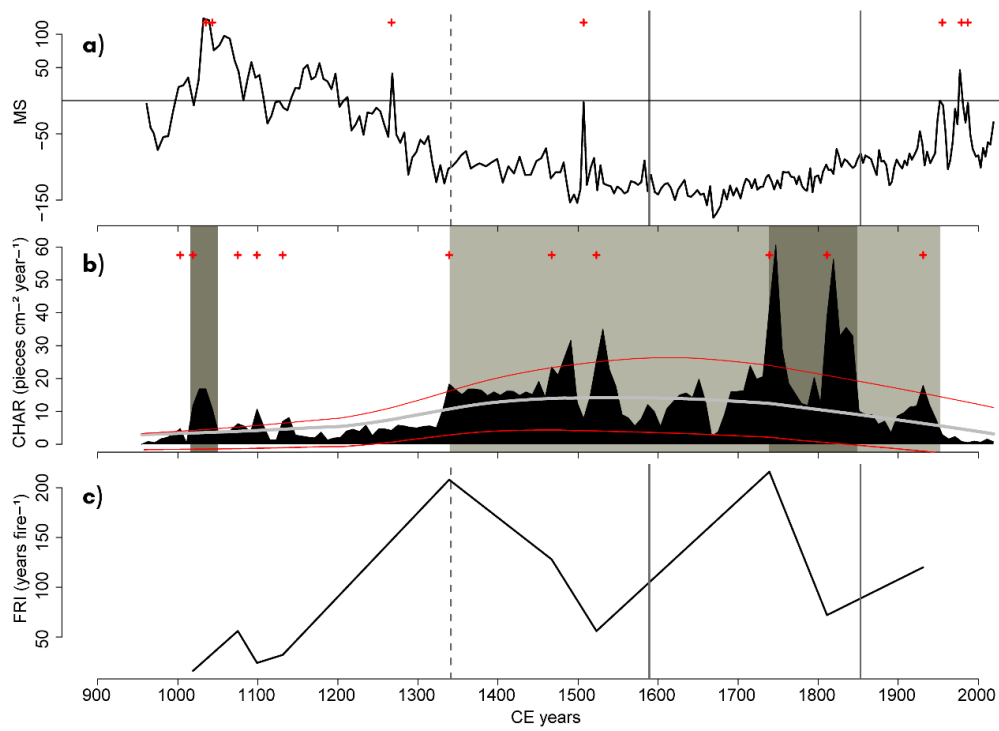


Fig. S8 Comparison between erosion and charcoal-derived fire history. a) Magnetic susceptibility (MS); b) Macroscopic charcoal accumulation rate (CHAR) interpolated to 8 years (black), charcoal background modelled using a 500-year smoothing window (grey line), final positive and negative threshold values for peaks identification (red lines). Identified CHAR peaks are marked with “+” symbols. Shaded areas from white to grey refer to periods of relatively stable biomass burning as determined by the change-point analysis, see Fig. S9 (the darker the shade, the higher the mean CHAR values are). c) Fire return interval (FRI) values. Vertical continuous and dotted lines represent significant and non-significant pollen zone boundaries, respectively.

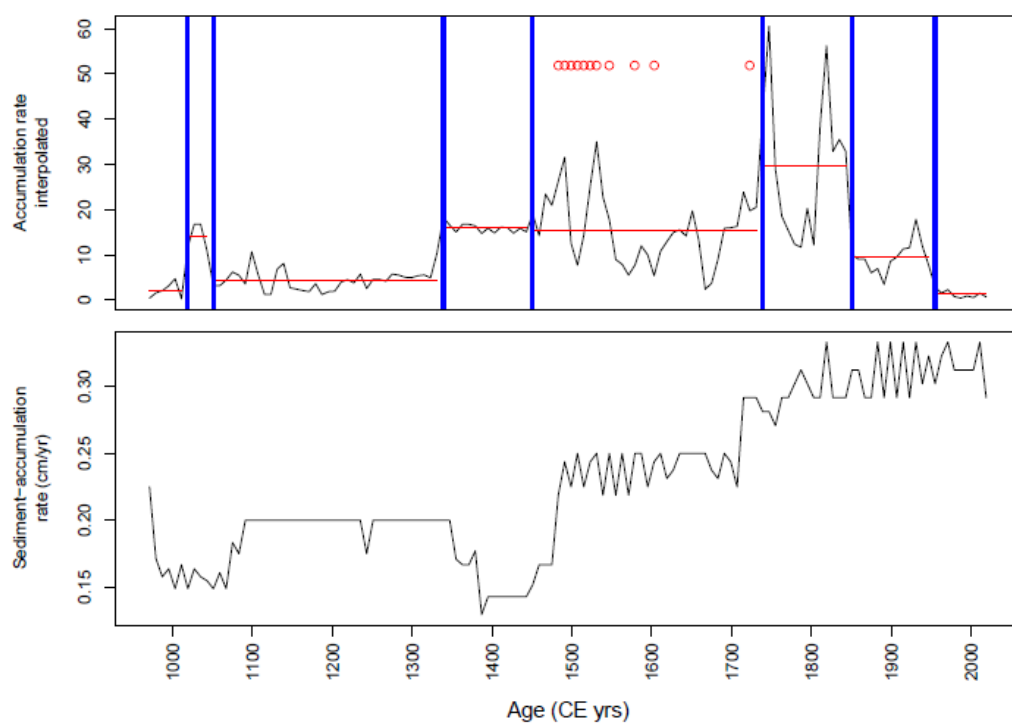


Fig. S9 Comparison between changes in biomass burning based on variations in both the mean (red horizontal lines) and variance of the total CHAR record and sediment-accumulation rates. Blue vertical lines: significant change points in biomass burning; red empty circles: change points determined by variations of the modelled sediment-accumulation rate.

References

- Bhatnagar SR, Yang Y, Khundrakpam B, et al (2017) An analytic approach for interpretable predictive models in high dimensional data, in the presence of interactions with exposures. *Genomics*
- Birks HH (2017) Plant Macrofossil Introduction. In: Reference Module in Earth Systems and Environmental Sciences. Elsevier
- Brillouin L (1956) Science and information theory. Academic Press, New York (USA)
- Cappers RTJ, Bekker RM, Jans JEA (2006) Digital Seed Atlas of the Netherlands. Barkhuis Publishing & Groningen University Library, Groningen (Netherlands)
- Dunn OJ (1964) Multiple comparisons using rank sums. 241–252
- Durán R (1973) Ustilaginales. In: Ainsworth GC, Sparrow FK, Sussman S (eds) *The Fungi*. Academic Press, New York (USA), pp 281–300
- Finsinger W, Tinner W (2019) New insights on stomata analysis of European conifers 65 years after the pioneering study of Werner Trautmann (1953). *Veget Hist Archaeobot*. <https://doi.org/10.1007/s00334-019-00754-1>
- Godet J-D (1998) *Einheimische Bäume und Sträucher*. Arboris Verlag, Hinterkappelen-Bern (Switzerland)
- Grizonnet M, Michel J, Poughon V, et al (2017) Orfeo ToolBox: open source processing of remote sensing images. *Open Geospatial Data, Software and Standards* 2:15. <https://doi.org/10.1186/s40965-017-0031-6>
- Higuera PE, Brubaker LB, Anderson PM, et al (2009) Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs* 79:201–219. <https://doi.org/10.1890/07-2019.1>
- Higuera PE, Gavin DG, Bartlein PJ, Hallett DJ (2010) Peak detection in sediment - charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *Int J Wildland Fire* 19:996–1014. <https://doi.org/10.1071/WF09134>
- Higuera PE, Sprugel DG, Brubaker LB (2005) Reconstructing fire regimes with charcoal from small-hollow sediments: a calibration with tree-ring records of fire. *The Holocene* 15:238–251. <https://doi.org/10.1191/0959683605hl789rp>
- Japan Aerospace Exploration Agency (2019) ALOS Global Digital Surface Model “ALOS World 3D - 30m” (AW3D30). <https://www.eorc.jaxa.jp/ALOS/en/aw3d30/index.htm>. Accessed 27 Oct 2020
- Katz NJ, Katz SV, Kipiani MG (1965) *Atlas and Keys of Fruits and Seeds Occurring in the Quaternary Deposits of the USSR*. NAUKA, Moscow (Russia)
- Kelly RF, Higuera PE, Barrett CM, Hu FS (2011) A signal-to-noise index to quantify the potential for peak detection in sediment–charcoal records. *Quat res* 75:11–17. <https://doi.org/10.1016/j.yqres.2010.07.011>
- Keren S, Svoboda M, Janda P, Nagel TA (2019) Relationships between structural indices and conventional stand attributes in an old-growth forest in Southeast Europe. *Forests* 11:4. <https://doi.org/10.3390/f11010004>
- Kvaček Z, Walther H (1991) Revision der mitteleuropäischen tertiären Fagaceen nach blattepidermalen Charakteristiken. IV. Teil *Fagus* Linné. *Feddes Repertorium* 102:471–534. <https://doi.org/doi:10.1002/fedr.19911020702>

- Landrum L, Otto-Bliesner BL, Wahl ER, et al (2013) Last Millennium climate and its variability in CCSM4. *Journal of Climate* 26:1085–1111. <https://doi.org/10.1175/JCLI-D-11-00326.1>
- Ljungqvist FC, Seim A, Krusic PJ, et al (2019) European warm-season temperature and hydroclimate since 850 CE. *Environ Res Lett* 14:084015. <https://doi.org/10.1088/1748-9326/ab2c7e>
- Mann ME, Zhang Z, Rutherford S, et al (2009) Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. *Science* 326:1256–1260
- Michel J, Youssefi D, Grizonnet M (2015) Stable mean-shift algorithm and Its application to the segmentation of arbitrarily large remote sensing images. *IEEE Trans Geosci Remote Sensing* 53:952–964. <https://doi.org/10.1109/TGRS.2014.2330857>
- Moore PD, Webb JA, Collinson ME (1998) *Pollen Analysis*. Blackwell Science Ltd., Oxford (UK)
- Orfeo ToolBox (2021). <https://www.orfeo-toolbox.org>
- PAGES 2k Consortium (2013) Continental-scale temperature variability during the past two millennia. *Nature Geosci* 6:339–346. <https://doi.org/10.1038/ngeo1797>
- Reille M (1992) *Pollen et spores d'Europe et d'Afrique du nord*. Laboratoire de Botanique Historique et Palynologie, Marseille (France)
- Rouvinen S, Kuuluvainen T (2005) Tree diameter distributions in natural and managed old *Pinus sylvestris*-dominated forests. *Forest Ecology and Management* 208:45–61. <https://doi.org/10.1016/j.foreco.2004.11.021>
- Schlachter KJ, Horn SP (2010) Sample preparation methods and replicability in macroscopic charcoal analysis. *J Paleolimnol* 44:701–708. <https://doi.org/10.1007/s10933-009-9305-z>
- Schoch W, Heller I, Schweingruber FH, Kienast F (2004) *Wood Anatomy of Central European Species*. www.woodanatomy.ch
- Schoch WH, Pawlik B, Schweingruber FH (1988) *Botanical Macro-remains: an Atlas for the Determination of Frequently Encountered and Ecologically Important Plant Seeds*. Paul Haupt, Bern (Switzerland)
- Schweingruber FH (1990) *European Wood Anatomy*. Paul Haupt, Bern (Switzerland)
- Soille P (2004) *Morphological Image Analysis*. Springer Berlin Heidelberg, Berlin, Heidelberg
- Stockmarr J (1971) Tablets with spores used in absolute pollen analysis. *Pollen Spores* 13:615–621
- Sun W, Chen B, Messinger D (2014) Nearest-neighbor diffusion-based pan-sharpening algorithm for spectral images. *OE* 53:013107. <https://doi.org/10.1117/1.OE.53.1.013107>
- Trautmann W (1953) Zur Unterscheidung fossiler Spaltöffnungen der mitteleuropäischen Coniferen. *Flora oder Allgemeine Botanische Zeitung* 140:523–533. [https://doi.org/10.1016/S0367-1615\(17\)31952-3](https://doi.org/10.1016/S0367-1615(17)31952-3)
- Van Geel B (1978) A palaeoecological study of holocene peat bog sections in Germany and The Netherlands, based on the analysis of pollen, spores and macro- and microscopic remains of fungi, algae, cormophytes and animals. *Review of Palaeobotany and Palynology* 25:1–120. [https://doi.org/10.1016/0034-6667\(78\)90040-4](https://doi.org/10.1016/0034-6667(78)90040-4)
- Worobiec G, Worobiec E (2019) Wetland vegetation from the Miocene deposits of the Bełchatów Lignite Mine (central Poland). *Palaeontologia Electronica* 22.3.63:1–38. <https://doi.org/doi:10.26879/871>

PAPER 3: The value of long-term history of small and fragmented old-growth forests for restoration ecology

Walter Finsinger¹, E. Cagliero¹⁻², D. Morresi³, L. Paradis¹, M. Čurović⁴, M. Garbarino³, N. Marchi², F. Meloni³, V. Spalević⁵, E. Lingua² and R. Motta³

¹ ISEM, Univ Montpellier, CNRS, EPHE, IRD, France

² Department of Land, Environment, Agriculture and Forestry, University of Padova, Legnaro, Italy

³ Department of Agricultural, Forest and Food Sciences, University of Torino, Grugliasco, Italy

⁴ Biotechnical Faculty, University of Montenegro, Podgorica, Montenegro

⁵ Geography Department, University of Montenegro, Nikšić, Montenegro

Published in: Past Global Changes Magazine, 30, vol 1, 8-9, 2022

doi.org/10.22498/pages.30.1.8

The long-term history of small and fragmented old-growth forests can provide insights into the legacies of past environmental changes and land-use history in the surrounding landscapes, which can support nature protection and restoration ecology measures.

The value of old-growth forests

Primary and old-growth forests are of great value for sustainable forest management and restoration. By virtue of their structural and compositional complexity, they are highly biodiverse when compared with managed forests in the same ecological region, as they offer a variety of microhabitats such as large pieces of coarse woody debris, providing shelter to a range of taxa. These naturally regenerated forests of native trees are thought to have developed dynamically for a long period of time without large stand-replacing disturbances, and show no indication of human activities (Barredo et al. 2021). They offer unique opportunities to characterize the effects of natural disturbances and the structural heterogeneity emerging from natural forest dynamics. This is important knowledge to develop close-to-nature forest management practices aimed at emulating natural processes and features in second-growth forests (Schütz et al. 2016).

In Europe, primary and old-growth forests are very rare, generally small, fragmented, and less abundant (< 3% of the total forest area) than on other continents (Sabatini et al. 2018). Currently, these forests are embedded in landscape mosaics bearing variously managed patches that are sometimes strikingly different in species composition and structure. Thus, the small and fragmented ecosystems are threatened along fragment edges by land-use activities (e.g. logging) and anthropogenic disturbances (e.g. fire ignitions) that may initiate long-term changes to the structure of the remaining fragments, thereby hindering the development or the continuity of the old-growth forest stage.

Old-growth forests are typically late-successional forests that contain structures and species that are markedly different from forests of earlier stages. Their distinguishing features include high amounts of deadwood, presence of old trees approaching their natural longevity (which is often much higher than the management rotation cycle for a given tree species), and a patchwork of heterogeneously aged stands arising through small-scale gap dynamics (Barredo et al. 2021).

The current old-growthness is generally assessed using field-based methods, such as dendroecology and forest surveys, and remote sensing (Barredo et al. 2021). However, these methods cannot provide information on the longer-term history of an area. Paleoecology, instead, is sometimes the best, and only, tool for documenting the continuity of forest ecosystems and the legacies of land-use history, climate change, and disturbances (such as fire) on present-day forest composition. This information is critical for clarifying conservation and restoration objectives because mosaic landscapes are often the result of legacy effects arising from complex interactions between natural and human disturbances (Whitlock et al. 2018). In this context, stand-scale paleoecology can be particularly valuable as it allows

us to address the history of small and fragmented ecosystems (Bradshaw and Zackrisson 1990; Foster et al. 1996).

Old-growth forests remnants in the Balkans

The causes of the current fragmented distribution of old-growth forests in Europe is a long-standing question in ecology. They are arguably remnants of formerly larger extents of “primeval forests”, “virgin forests”, “climax forests”, or “Urwald” that have been shattered due to major human imprints on forest ecosystems over past millennia (Birks and Tinner 2016). However, primary and old-growth forests are particularly abundant in some regions, such as the Dinaric Alps, possibly due to early protection of forests and lower historical human pressure compared to other mountain ranges in Europe (Sabatini et al. 2018). Indeed, this mountain region is characterized by rugged terrain and land with low agricultural productivity (Kaplan et al. 2009). Nonetheless, detailed records documenting long-term vegetation dynamics in conjunction with environmental changes are lacking for the montane zone in this region (Finsinger et al. 2017).

Legacies of past land uses at an old-growth forest’s fragment edge

Cagliero et al. (2021) recently presented stand-scale paleoecological records, an assessment of contemporary forest structure, and dendrochronological data from the edge of the Biogradska Gora old-growth forest (Dinaric Alps, Montenegro), one of the largest in Europe. It provides new insights into the long-term dynamics of these fragmented ecosystems. Like other old-growth forests in the montane zone of the Balkans, Biogradska Gora’s old-growth forest is dominated by fir (*Abies alba*) and beech (*Fagus sylvatica*) with sparse spruce (*Picea abies*) (Motta et al. 2015). However, unlike many other old-growth forests, this one is surrounded by grasslands and meadows, and by almost pure beech stands. These stands are characterized by small, mostly multi-stemmed trees, the amount of coarse woody debris is negligible (Fig. 1), and charcoal kilns are present. By contrast, the fir-beech-spruce dominated old-growth forest has a mixed and multilayered structure shaped by gaps of different sizes, a large amount of coarse woody debris, and very large and old trees (> 500 years old), indicating that this part of the forest developed dynamically for a long period of time without human and natural stand-replacing disturbances.

The well-dated pollen, spore, stomata, plant-macrofossil, and charcoal records from a small forest hollow at the current edge of the old-growth forest (Fig. 1) document the reduction of fir and spruce during the Middle Ages, when the land was used for cereal crop cultivation and cattle herding, and after

local, higher-severity catchment fires occurred (Fig. 2). This evidence supports the notion that historical land-use pressure reduced the extent of old-growth forests.

After intensive local land use ceased (in the mid-14th century, approximately at the time of the Black Death pandemic) and during the cooler Little Ice Age, beech-dominated stands developed in the area surrounding the old-growth (Fig. 2). The legacy of past land use is still visible as the almost pure beech stands show less old-growthness than other European beech-dominated old-growth forests. Conversely, the formal protection of the Biogradska Gora forest as a royal hunting reserve and as a national park since the late 19th century prevented intensive land use, and has strongly reduced biomass burned in recent times, which has allowed for the persistence of the beech stands in the buffer zone. This protected zone may offer a habitat for adaptation to future environmental changes, such as the expansion of the fir old-growth, as fir has more potential than spruce and beech under warmer and drier conditions (Vitasse et al. 2019).

Outlook

Old-growth forests have captured the attention of foresters and conservationists alike (Fröhlich 1930). However, there still are substantial conservation and restoration gaps, as primary and old-growth forests are only partially representative of the full range of European forest types (Sabatini et al. 2018). Paleoecology, in conjunction with structural and dendrochronological research, can unfold the history of Europe's primary and old-growth forests. Thereby, their responses to past environmental changes as well as legacy effects of past land use and of disturbances in surrounding landscapes can be assessed. This may be important as strategies for the preservation and restoration of old-growth forests should acknowledge past environmental changes, including land-use history, and anticipate future environmental changes.

Although primary and old-growth forests are generally included in protected areas (Sabatini et al. 2018), they may be vulnerable to climate change and associated changing disturbance regimes (wind, pathogens, or fire; Seidl et al. 2017). For instance, several of the smaller old-growth forests that bear fire-sensitive species such as *Abies alba* may be at risk if fire-frequency becomes excessive. In this context, identifying and protecting primary and old-growth areas and their buffer zones, as well as protecting and restoring secondary forests that may represent future primary and old-growth ecosystems (Barredo et al. 2021; EU's Biodiversity Strategy for 2030: ec.europa.eu/environment/strategy/biodiversity-strategy-2030_en) could be of paramount importance to promote native forests. Such actions may likely increase ecosystem resilience to future climate change and be helpful to anticipate environmental changes (Henne et al. 2015).

Figures

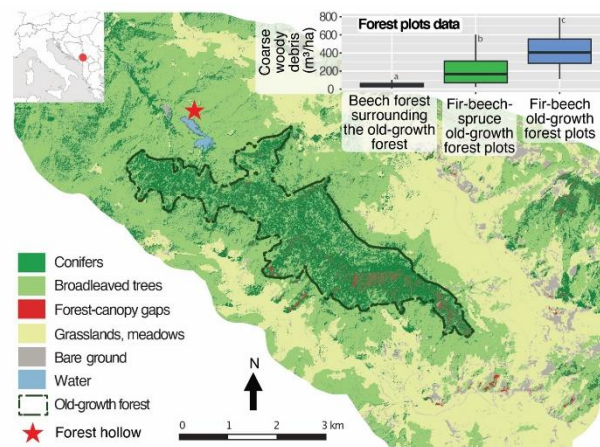


Fig. 1 Distribution of land-cover types in the Biogradska Gora valley (Dinaric Alps, Montenegro). The boxplots show the amount of coarse woody debris inside and outside of the old-growth forest (modified from Cagliero et al. 2021).

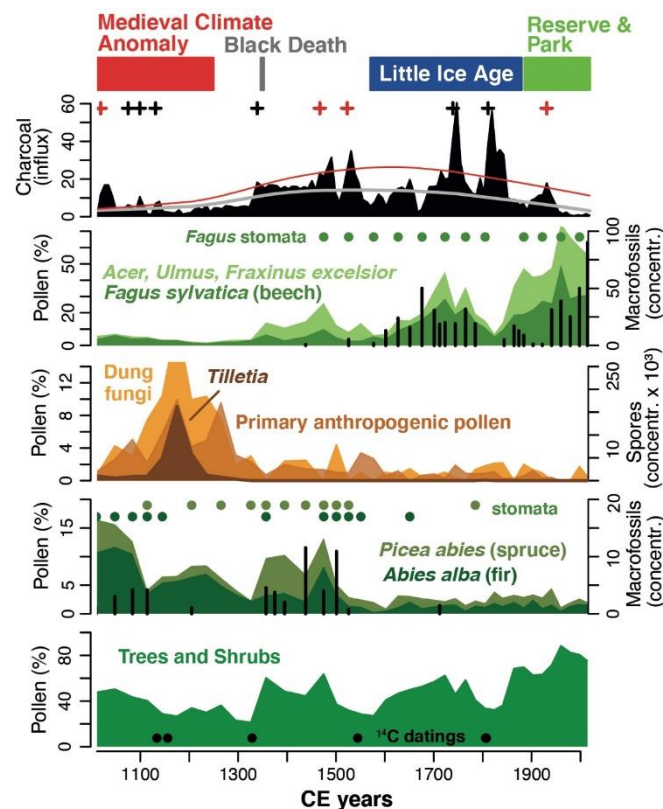


Fig. 2 Local vegetation and fire-disturbance dynamics at the current edge of Biogradska Gora's old-growth forest as reconstructed with the sediments from a small forest hollow. The charcoal-influx graph includes the long-term trend of charcoal accumulation (grey line) and identified fire episodes (crosses; red crosses: higher-severity catchment fires). Pollen and spores (filled areas), stomata (full circles), and plant macrofossils (black bars) illustrate the vegetation dynamics and land-use history (primary anthropogenic pollen and *Tilletia* spores: cereal crop cultivation; cattle herding: dung-fungi spores). Full black circles (bottom) show the location of radiocarbon dates (modified from Cagliero et al. 2021).

References

- Barredo JI, Brailescu C, Teller A, et al (2021) Mapping and assessment of primary and old-growth forests in Europe. Publications Office of the European Union, Luxembourg
- Birks HJB, Tinner W (2016) Past forests of Europe. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, et al. (eds) Past forests of Europe. European Atlas of Forest Tree Species. Publication Office of the European Union, Luxembourg, pp 36–39
- Bradshaw RHW, Zackrisson O (1990) A two thousand year history of a northern Swedish boreal forest stand. *Journal of Vegetation Science* 1:519–528. <https://doi.org/10.2307/3235786>
- Cagliero E, Morresi D, Paradis L, et al (2021) Legacies of past human activities on one of the largest old-growth forests in the south-east European mountains. *Veget Hist Archaeobot*. <https://doi.org/10.1007/s00334-021-00862-x>
- Finsinger W, Morales-Molino C, Gafka M, et al (2017) Holocene vegetation and fire dynamics at Crveni Potok, a small mire in the Dinaric Alps (Tara National Park, Serbia). *Quaternary Science Reviews* 167:63–77. <https://doi.org/10.1016/j.quascirev.2017.04.032>
- Foster DR, Orwig DA, McLachlan JS (1996) Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Trends in Ecology & Evolution* 11:419–424
- Fröhlich J (1930) Der südosteuropäische Urwald und seine Überführung in Wirtschaftswald. *Centralblatt für das Gesamte Forstwesen* 56:49–68
- Henne PD, Elkin C, Franke J, et al (2015) Reviving extinct Mediterranean forest communities may improve ecosystem potential in a warmer future. *Frontiers in Ecology and the Environment* 13:356–362. <https://doi.org/10.1890/150027>
- Kaplan JO, Krumhardt KM, Zimmermann N (2009) The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews* 28:3016–3034. <https://doi.org/10.1016/j.quascirev.2009.09.028>
- Motta R, Garbarino M, Berretti R, et al (2015) Structure, spatio-temporal dynamics and disturbance regime of the mixed beech–silver fir–Norway spruce old-growth forest of Biogradska Gora (Montenegro). *Plant Biosystems* 149:966–975. <https://doi.org/10.1080/11263504.2014.945978>
- Sabatini FM, Burrascano S, Keeton WS, et al (2018) Where are Europe’s last primary forests? *Diversity and Distributions* 24:1426–1439. <https://doi.org/10.1111/ddi.12778>
- Schütz J-P, Saniga M, Diaci J, Vrška T (2016) Comparing close-to-nature silviculture with processes in pristine forests: lessons from Central Europe. *Annals of Forest Science* 73:911–921. <https://doi.org/10.1007/s13595-016-0579-9>
- Seidl R, Thom D, Kautz M, et al (2017) Forest disturbances under climate change. *Nature Clim Change* 7:395–402. <https://doi.org/10.1038/nclimate3303>
- Vitasse Y, Bottero A, Rebetez M, et al (2019) What is the potential of silver fir to thrive under warmer and drier climate? *Eur J Forest Res* 138:547–560. <https://doi.org/10.1007/s10342-019-01192-4>
- Whitlock C, Colombaroli D, Conedera M, Tinner W (2018) Land-use history as a guide for forest conservation and management: Land-Use History. *Conservation Biology* 32:84–97. <https://doi.org/10.1111/cobi.12960>

PAPER 4: The role of fire disturbances, human activities and climate change on long-term mountain forest dynamics in the central Dinaric Alps

Eleonora Cagliero^{1,2}, Laure Paradis², Niccolò Marchi¹, Zsuzsanna Lisztes-Szabó³, Mihály Braun³, Ilham Bentaleb², Katalin Hubay³, Velibor Spalević⁵, Renzo Motta⁴, Emanuele Lingua¹, Walter Finsinger²

¹ Department of Land, Environment, Agriculture and Forestry (TESAF), University of Padova, 35020 Legnaro (PD), Italy

² University of Montpellier, ISEM, CNRS, IRD, EPHE, Montpellier, France

³ Isotope Climatology and Environmental Research Centre (ICER), Institute for Nuclear Research, Bemtér 18/C, H-4026 Debrecen, Hungary

⁴ Department of Agricultural, Forest and Food Sciences (DISAFA), University of Torino, 10095 Grugliasco (TO), Italy

⁵ Geography Department, University of Montenegro, Nikšić, Montenegro

Manuscript

Abstract

We present the first high-resolution Holocene fire, vegetation, and land-use pressure history records from the upper-montane zone in the central Dinaric Alps based on detailed palaeoecological analyses (including pollen, plant macrofossils, microscopic and macroscopic charcoal analyses) of a well-dated sediment core from Zminje jezero (Durmitor massif, Montenegro). We used Generalized Additive Models to investigate long-term responses of the dominant montane trees – spruce (*Picea abies*), fir (*Abies alba*), and beech (*Fagus sylvatica*) – to variations in climate, fire and human impact drawing on our new records and on chironomid-inferred summer temperatures from Lago Verdarolo (Northern Apennines, Italy), whose temperature variations are very likely representative for a wider area, including the Dinaric Alps.

During the Younger Dryas and until 10,000 cal yr BP, vegetation was dominated by *Pinus* and *Betula*. A mixed spruce-fir forest established in the upper-montane zone between 10,000 and 9000 cal yr BP and remained relatively stable until 5000 cal yr BP, when beech became co-dominant with the two conifers. Biomass burning gradually decreased during the past 8500 years, but higher-severity fires occurred more frequently since 5000 cal yr BP. Anthropogenic pollen indicators and independent archaeological evidence suggest that land-use pressure was overall remarkably low in the montane zone but rose since the Roman period. However, regional fire activity rose since c. 3000 cal yr BP (late Bronze Age) as a result of higher land-use pressure in the wider region.

Response curves show a significant positive relationship with biomass burning and summer temperature, indicating that fires in the upper-montane zone were mostly driven by variations of climatic conditions. Spruce was insensitive to variations in summer temperature, biomass burning and human impact, which supports the view that spruce forests may not be significantly impacted by fire. In contrast, fir shows a significant positive relationship with summer temperatures and a significant negative relationship with land-use pressure. This supports the notion that fir may be well-adapted to warmer-than present summer temperatures and that its populations declined in recent millennia due to land-use activities. Conversely, beech was sensitive to increasing summer temperatures but was promoted by low biomass burning, indicating that its expansion in the spruce-fir dominated forest was enhanced by the onset of cooler and possibly also moister climatic conditions as well as by fire disturbances.

Keywords: mountain forests, fire history, Holocene, vegetation-fire interactions, vegetation dynamics, Dinaric Alps

Introduction

Mountain forests provide important ecosystem services such as risk prevention (from avalanches, landslides or rockfall), recreation, and maintenance and promotion of biodiversity (Klopčič et al. 2017). Moreover, mountain forests are a main source of livelihood for rural communities providing goods (e.g. wood supply) and employment (Knorn et al. 2013; Quave and Pieroni 2015; Pieroni et al. 2015; European Environment Agency 2016). In Europe, they also host a large share of current primary and old-growth forests (Sabatini et al. 2018), which have high conservation value as they are important for developing close-to-nature forest management strategies (Bauhus et al. 2009) and serve as refuges or sources of propagules for rare or endangered species, especially for forest species sensitive to human disturbance (Wirth et al. 2009). Thus, it is critical to assess the responses of European mountain forests to changing environmental conditions in order to develop adaptation and management strategies to possible ecosystem shifts that may cause the loss of important ecosystem services. Such an assessment is particularly important given that there is strong support for the hypothesis that climate change could markedly modify disturbance regimes, with a likely increase of some disturbances (e.g. fire) in a warming world (Seidl et al. 2017).

However, understanding natural ecological processes is challenging as processes often play out over long time scales (centuries, millennia), particularly when long-lived species such as trees are involved. The long time horizon of palaeoecological records permits to study ecosystem responses under substantially different environmental conditions than the present ones, including temperatures analogous to those predicted by future climate changes (approximately 1-2°C higher than present; Samartin et al. 2017; Carter et al. 2018; Morales-Molino et al. 2020). Moreover, current ecosystems and ecological processes often still carry legacy effects of past environmental changes and anthropogenic impacts (Feurdean et al. 2009; Grindean et al. 2019; Morales-Molino et al. 2020; Cagliero et al. 2021), which have often altered species-environment relationships (Tinner et al., 2013). Thus, taking into account long-term records may be important to gain realistic environmental-change response assessments, especially in Europe, where anthropogenic manipulation of nature started several millennia ago (Tinner et al. 2013; Birks and Tinner 2016).

The long-term history of mountain ecosystems varies across regions and is arguably contingent on patterns of human settlement, land use, and socioeconomic development. In this context, the central Dinaric Alps are an interesting area as its land-use history may differ from land-use history in surrounding areas and in other European mountain regions. The Balkan Peninsula acted as a land bridge from the Near East, across Asia Minor and towards Central and Western Europe. Thus, the Neolithic culture arrived in the region quite early (6th millennium CE; 8000-7000 cal yr BP; Borić et al. 2019). However, the impact of Neolithic and of more recent cultures on the interior mountain region is weakly constrained. While it seems that the Neolithic spread mainly across the fertile plains along the Danube valley in the east (Starčevo culture) and along the Adriatic coastal strip in the west (Impresso culture),

there is evidence to suggest that the inland mountain area of the central Dinaric Alps either remained an agricultural frontier zone (Forenbaher and Miracle 2005; Mihailović 2007), or is simply archeologically under surveyed (Borić et al. 2019). Further, modelled anthropogenic deforestation suggests that during the past 3000 years relatively low forest clearance occurred in the region when compared to other regions of Europe and that a large fraction of usable land in the region was not heavily exploited until the Middle Ages (Kaplan et al. 2009). By contrast, charcoal production, mining activities, and grazing likely occurred in the interior area of the Dinaric Alps since the Bronze Age (3500 BCE) and intensified during the Iron Age and the Ottoman Empire (Kranjc 2009; Longman et al. 2018). However, it is not clear if these activities were widespread across the mountain region, as human activities may have concentrated in some areas. In the latter case, large forested regions in the interior range may have remained relatively intact until the present (Nagel et al. 2017) or managed with low intensity silvicultural systems during recent centuries (Boncina 2011).

Low historical forest clearance may have preserved old-growth forests in this mountain region (Sabatini et al. 2018; Cagliero et al. 2021) that is characterized by rugged terrain land with low agricultural productivity (Kaplan et al. 2009). Forests dominated by fir (*Abies alba* Mill.), beech (*Fagus sylvatica* L.), and spruce (*Picea abies* (L.) Karst.), are important in the Dinaric Alps montane zone over 500 m in elevation (Nagel et al. 2017). As these tree species are widespread components of European mountain forests, often forming mixed forests (Hilmers et al. 2019), knowledge of their long-term responses in forests having been possibly left relatively intact for several millennia may be useful to improve knowledge of the role of disturbances by fire and of climate.

Here, we focus on the Holocene vegetation dynamics and its responses to disturbances by fire, and to changes in climate and land use at Zminje jezero situated in the Durmitor National Park, montane belt of the central Dinaric Alps. The area is strongly understudied with very few long-term palaeoecological records documenting vegetation dynamics, disturbances by fire, and past land-use history (Finsinger et al. 2017; Cagliero et al. 2021). Whereas old-growth stands have not yet been reported in the Park, the presence of scattered old monumental trees and the informal protection of the area since 1907 suggest that patches with a high level of naturalness (*sensu* Buchwald 2005) could have been maintained or possibly restored. Our main aims are to (1) assess the long-term Holocene vegetation dynamics of mixed montane forests, (2) characterize the Holocene land-use history at different spatial scales (regional and local scales), (3) characterize the Holocene fire history at different spatial scales (regional, landscape, and local scales), and investigate the influence of the main drivers of fire dynamics (climate and human impact), and (4) track responses of the dominant montane trees (fir, beech, and spruce) to variations in climate, fire and human impact.

Material and methods

Study area and study site

In the Dinaric Alps, vegetation is influenced by the interaction of mountainous reliefs, pedological conditions, and proximity to the Adriatic coast (Horvat et al. 1974; Nagel et al. 2017). Mediterranean evergreen hard-leaf vegetation occurs near the coast and consist of *Pinus halepensis*, *Quercus ilex*, *Olea europaea* and other species of the Mediterranean maquis. Moving inwards (from the lowlands up to c. 700 m asl), the Mediterranean vegetation is replaced by mixed sub-Mediterranean deciduous woodlands, which consist of *Carpinus betulus*, *Fraxinus ornus*, *Quercus* sp. (such as *Q. petraea*, *Q. cerris*, and *Q. pubescens*), *Acer campestre*, *Ostrya carpinifolia*, *Carpinus orientalis*, and *Castanea sativa* (Polunin 1980). The valley floodplains are commonly occupied by *Alnus glutinosa*, *Quercus robur*, *Fraxinus* sp. and *Ulmus minor* with *Salix* sp. and *Populus* sp. in moist and naturally disturbed conditions (Horvat et al. 1974). In the montane belt (from 700 to 1700 m asl), forests are dominated by *Pinus nigra* or by *Fagus sylvatica*, and mixed *Fagus sylvatica*-*Abies alba*-*Picea abies* forests also occur. Other species occurring in the montane belt include *Pinus sylvestris*, *Ostrya carpinifolia*, *Acer* sp., *Tilia*, and *Fraxinus excelsior*. At altitudes higher than c. 1700 m asl, *Pinus mugo*, *Juniperus communis*, and *Alnus viridis* occur (Polunin 1980).

Zminje jezero (Snake lake; 43°09'21" N 19°04'14" E; 1535 m asl) is a small 1.2-ha large and 9.5-m deep glacial lake located on the north-west part of a high karst plateau of the Durmitor massif (Gachev and Mitkov 2019; Fig. 1). A stream drains the lake connecting it with the Crno Jezero (1460 m asl). A rich community of wetland plants occurs on the lake shores, which are covered mainly by *Molinia caerulea* and *Comarum palustre*, together with a minor share of *Carex* sp., *Sphagnum* sp., *Parnassia palustris*, *Filipendula ulmaria*, *Eriophorum vaginatum*. The lake is surrounded by dense mixed forests consisting mostly of conifers (*Picea abies*, *Abies alba*) with a lesser amount of *Fagus sylvatica*, *Acer* sp., *Sorbus aucuparia*, *Rhamnus fallax*, and *Vaccinium myrtillus*. *Pinus mugo*, *Salix nigricans* and *Populus tremula* are also present near the lake shores. The lake is c. 400 m below the current tree line (c. 1950 m asl), which is formed by *Pinus mugo*, *Juniperus communis*, and *Picea abies*.

The climate is continental with a mean annual air temperature of 4.7 °C and mean annual precipitation of c. 1450 mm at Žabljak (1,450 m asl), c. 4 km from Zminje jezero (Djurović 2012). In the northern and central part of the mountain range bedrock consists of Mesozoic sedimentary rocks and thick Middle and Upper Triassic and Upper Jurassic limestones, while in the southern part upper Cretaceous flysch are predominant (Mirković 1983).

Currently, the lake is in the Durmitor National Park (UNESCO 2005), which was already informally protected as royal reserve from 1907 to 1952 (Srdanović and Pavić 2013), when the National Park was established. In 1980 the National Park was listed as a UNESCO World Natural and Cultural Heritage

Site as it hosts rare Arcto-tertiary endemic plant species, six of them specific to the Durmitor (Birks and Walters 1973; World Heritage Committee 2017). Zminje jezero is located in a zone of special protection, where a limited and controlled use of natural resources is allowed, such as the cutting of naturally collapsed trees (so-called “sanitary cuttings”), clearing of forest roads, and tourism (Srdanović and Pavić 2013; UNESCO and IUCN 2018).

Field work and sediment-core correlation

We scanned the lake with an echo sounder connected to a Garmin GPS device from an inflatable rubber boat to study the floor of the lake (Fig. 1d). Thereafter, we collected two overlapping sediment cores (sections 1-m long and 6 cm in diameter) in September 2019 from the center of the lake at a water depth of 9.3 m using a modified Livingstone piston corer from a floating platform (Hubay et al. 2018). We collected the sediment-water interface using an UWITEC gravity corer in 2017 and in 2019. All core sections were split longitudinally into halves and photographed with a digital camera at ISEM (University of Montpellier). To correlate the core sections and determine the 615-cm-long master core, we used visual variations in lithology and changes in element concentration values obtained from the XRF records. Thereafter, one core half was cut into 1-cm thick slices and the samples were stored in zip-lock bags at 4°C for further analyses.

Sediment composition and chronology

We assessed the composition of the sediments visually with the aid of Corelyzer v2.1.1 (CSDCO/LacCore-University of Minnesota). In addition, we quantified the abundance of specific elements using an X-ray fluorescence (XRF) AVAATECH scanner (at the EDYTEM Laboratory, University of Savoie Mont-Blanc, France) at 5 mm resolution with a live time of 15-20 s on the archive core half (ESM Fig. S1). Element concentrations are expressed in counts per second (cps).

The depth-age relationship was modeled using RBacon v2.4.1 (Blaauw and Christen 2011). To constrain the depth-age model (Fig. 2), we used 15 control points: 12 AMS ^{14}C dates from terrestrial plant macrofossils calibrated using the IntCal20 dataset (Reimer et al. 2020), and two pollen-inferred ages, and the estimated age of the sediment surface (Table 1). To constrain the model in the lowermost part, we used a statistically significant pollen-zone boundary indicating the onset of the Holocene, following Giesecke et al. (2014). To better constrain the most recent part of the age-depth model, we used the first appearance of *Ambrosia artemisiifolia* L. pollen. According to high temporal resolution palynological studies, the first occurrence of *Ambrosia* pollen in the Alps is dated to c. 1950 AD (van der Knaap et al. 2000). Moreover, documentary evidence (Makra et al. 2005; Csontos et al. 2010) specifies that ragweed (*Ambrosia*) became invasive in Central and Eastern Europe c. 1910-1920 AD.

We identified visible turbidite layers and checked the match with increases in the baseline concentrations of K, Ti, Rb, Zr and Al (Fig. 2), which indicate phases of greater run-off and soil erosion in the catchment (Davies et al. 2015; Carter et al. 2020). We excised these sediments from the depth-age model (Heiri et al. 2003) because they were likely deposited over a short period of time (days, weeks) (Finsinger et al. 2021). Finally, we verified the accuracy of the depth-age model in its most recent part by comparing the expected and actual ages of two Pb peaks during the Roman period (McConnell et al. 2018; Sabatier et al. 2020) and one peak during the Middle Ages (Fig. 2; Renberg et al., 2001).

Pollen, non-pollen palynomorphs, and plant macrofossils analyses

We processed 78 1-cm³ samples for pollen analysis following standard physical and chemical treatments: HCl, KOH, sieving with a 500-µm mesh and decanting, HF, Acetolysis, staining with Fuchsin and mounting on slides with glycerol. To calculate concentrations (# cm⁻³) and influxes (# cm⁻² yr⁻¹), we added two *Lycopodium* tablets (Batch #1031; Stockmarr 1971). We identified pollen, stomata, the dung-fungi *Sporormiella* spore using determination keys, photographic atlases (Davis 1987; Reille 1992; Moore et al. 1998; Beug 2004; Finsinger and Tinner 2019; Cagliero et al. 2021) and the pollen and stomata reference collections at ISEM (University of Montpellier). At least 300 terrestrial pollen grains was counted at x400 magnification. Pollen abundances are presented as percentages of the terrestrial pollen sum, which includes pollen from trees, shrubs, herbs, and fern spores and exclude pollen of aquatic plants. *Sporormiella* spores' abundance is presented as percentage of the terrestrial pollen sum and stomata are presented as presence/absence.

The pollen diagram was divided into pollen assemblage zones using the optimal partitioning by sums-of-squares method with square-root-transformed proportions of pollen types included in the terrestrial pollen sum and exclusion of rare taxa (abundance <5%; Birks and Gordon 1985). The number of statistically significant zones was determined by comparison with the broken-stick model (Bennett 1996), as implemented Psimpoll v4.26 (Bennett 2008).

For plant macrofossils analyses, we processed 203 samples. We measured sample volumes (c. 6 cm³) by water displacement and then sieved them with using a 100-µm mesh sieve. We identified and counted macrofossils with a stereomicroscope at x7.5-60 magnification using atlases (Birks, 2017; Cappiers et al., 2006; Godet, 1998; Katz et al., 1965; Schoch et al., 1988) and the reference collection at ISEM (University of Montpellier). Identified plant macrofossils were picked and stored at -18°C in Milli-Q water. Plant-macrofossil abundances are expressed as concentrations (# cm⁻³).

We assessed human impact using the abundances of *Secale cereale* pollen (a primary anthropogenic indicator; PI), secondary indicators (SI, as the sum of adventives and apophytes; Behre 1981), and cultural indicators (CI, as the sum of Cerealia-type and *Plantago lanceolata* type pollen; Tinner et al., 2003). These indexes include pollen of cultivated plants, ruderals, and plants of meadows (Deza-Araujo

et al. 2020). *Veratrum album* was added to the apophytes category, as it is avoided by cattle due to its toxicity (Spiegelberger et al. 2006). We also assessed human impact in the wider region using the OJC index (Mercuri et al. 2013), which is based on the abundance of woody crops (*Olea europaea*, *Juglans regia*, and *Castanea sativa*) that grow at lower elevations and along the coast of the Adriatic Sea where the eu-mediterranean climate predominates. Despite their presence in uncultivated areas along the coast of the Mediterranean Sea, an increase in their abundances is often due to broad-scale cultivation (Deza-Araujo et al. 2020). For details on indexes of human impact see ESM Table S1.

Charcoal analyses

We counted microscopic charcoal particles in 42 pollen slides spread along the sediment core (Tinner and Hu 2003; Finsinger and Tinner 2005). For macroscopic charcoal analyses, contiguous 1-cm³ samples were taken between 0 and 432 cm depth. Other 19 samples were taken discontinuously down to the bottom of the sequence, at the same depths of the pollen samples. Samples were disaggregated overnight in a 5% NaPO₃ solution, bleached for 24 hours in a 15% H₂O₂ solution (Schlachter and Horn 2010), sieved through a 150-μm mesh (Higuera et al. 2005) and counted with a stereomicroscope at x7.5-60 magnification. The area of charcoal particles was not estimated since they are generally highly correlated to charcoal counts (Tinner et al. 1998; Finsinger et al. 2014; Cagliero et al. 2021). To account for variations in sedimentation rate (Whitlock and Larsen 2001), both microscopic and macroscopic charcoal counts were converted to charcoal accumulation rates (# cm⁻² yr⁻¹), hereafter mCHAR and MCHAR, respectively.

Fire-events detection, change point analysis, and ECA

The MCHAR record was used to reconstruct the local fire history using CharAnalysis v1.1 (Higuera et al. 2009). The contiguously sampled section of the macroscopic charcoal record was first interpolated to a constant temporal resolution of 31 years (third quartile of the distribution of the sediment accumulation rate values). The record was decomposed into a low-frequency background component (MCHAR_{back}) and a peak component (MCHAR_{peak}) using a locally weighted polynomial regression (LOWESS) robust to outliers with a smoothing-window width of 500 years. The suitability of the record for peak detection was evaluated through the signal-to-noise index according to Kelly et al. (2011) (SNI>3). Peaks were detected as residuals from the background and evaluated using the 99th percentile of the modelled noise distribution obtained with locally defined Gaussian mixture models for each 500-year portion of the record (Higuera et al. 2009). The evaluated peaks were further screened using the minimum count test (Higuera et al. 2010a). Fire return intervals (FRI: number of years between adjacent fire episodes) were calculated using the screened peak records and were smoothed using a 1000-year window.

We smoothed the mCHAR record to infer the long-term trend of regional fire activity in a 20-120 km radius from the study site (Whitlock and Larsen 2001). The low-frequency variation of total MCHAR reflects overall landscape-scale biomass burning at c. 50 km (Higuera et al. 2007, 2010b; Carter et al. 2018). Interpreting fire history from macroscopic-charcoal stratigraphy assumes that secondary charcoal deposition via slope wash or within-lake redeposition does not obscure patterns of primary charcoal deposition (Higuera et al. 2007).

To determine significant changes in landscape-scale biomass burning, we performed a change-point analysis. The analysis used the ‘changept’ v2.2.2 package (Killick and Eckley 2014; R Core Team 2020) and considered the variations of both the mean and the variance in the MCHAR record, as well as the potential effect of the modelled sediment-accumulation-rates on change-point detection (ESM Fig. S2; Finsinger et al. 2018).

The MCHAR peaks represent fire episodes that occurred nearer to the site (c. <3 km) (Higuera et al., 2007, 2010b). To characterize the fire severity, we distinguished between higher-severity catchment fires and lower-severity catchment fires or fires outside the catchment (Chileen et al. 2020), by testing the simultaneity between fire and erosion events using the Coincidence Analysis (ECA; Siegmund et al., 2017). Following Cagliero et al. (2021), we determined erosion events as peaks in selected XRF records (K, Ti, Rb, Zr, and Al) using a similar method to that applied to MCHAR values to identify fire peaks (ESM Fig. S3). We performed the ECA using two binary event time series (MCHAR peaks and erosion peaks), a lag of 0 years, and a tolerance window of 31-93 years that detects erosion events within c. 0-90 years of fire episodes. We chose a maximum value of 90 years being an ecologically realistic time for the complete regeneration of the forest, even after a severe fire or erosion event. Fire return intervals were calculated for the identified high-severity catchment fires (FRI_C).

Climate data

To investigate the response of fire activity and vegetation changes to variations in climate, we used summer (July) surface air temperature reconstructions based on fossil chironomid assemblages. Given the lack of paleoclimate records in the study area, we selected records from a site in biogeographically comparable ecosystems. Lago Verdarolo (1390 m asl) is located in the Tuscan-Emilian Apennines and vegetation in its surroundings is dominated by *Abies alba* and *Fagus sylvatica* (Samartin et al. 2017). The July air-temperature reconstruction from this site is expressed as anomalies (in °C) with respect to the late-Holocene pre-industrial mean (2000-100 cal yr BP). Comparisons between instrumental data and climate models runs show that at interannual to multidecadal timescales summer temperature variations in the Tuscan-Emilian Apennines are representative for a wider area, which include the central Dinaric Alps (Samartin et al. 2017). Specifically, the Pearson correlation between the summer temperature variations at Lago Verdarolo, and grid cells in Montenegro, is about 0.8-1 for multi-decadal variability and 0.6-0.7 for interannual variability.

Generalized additive models

Generalized additive models (GAMs) employ a link function to explore the relationship between the mean of the response variable (dependent variable) and a smoothed function of the predictor variable (independent variable) (Hastie and Tibshirani 1986; Carter et al. 2020). In this study, we used GAMs to investigate the response of dominant forest canopy taxa (pollen percentages of *Picea abies*, *Abies alba*, and *Fagus sylvatica*) to variations of climate (T_{July} anomalies of Lago Verdarolo, in °C), landscape-scale biomass burning ($\text{MCHAR}_{\text{back}}$), and human impact (sum of primary and secondary anthropogenic indicators and of the OJC index). Moreover, we investigated the response of regional fire activity and landscape-scale biomass burning (mCHAR and $\text{MCHAR}_{\text{back}}$) to variations of climate and human impact. Species responses to environmental changes (climate, biomass burning, human impact) are useful for identifying species' environmental optima and disturbance tolerance (Colombaroli et al. 2010). Conversely, the response of biomass burning to changes in temperature, human impact is essential to understand how the fire regime was influenced by natural and anthropogenic drivers of environmental change.

GAMs were performed using the *mgcv* v1.8-38 R package (Wood 2017). We assumed a quasi-Poisson distribution and we log-transformed both the response and the predictor variables to stabilize the variance among datasets. GAMs were fitted using restricted maximum likelihood (REML) smoothness selection (Wood 2011; Carter et al. 2020). We chose a base period from 8000 cal yr BP to the present (Carter et al. 2020), because many taxa classified as secondary anthropogenic indicators were very abundant during the early Holocene when human impact was negligible (Feurdean et al. 2017b).

Results and interpretation

Lithology and chronology

At the base, from 614.5 cm to 575 cm, the sediments consist of light-brown silty clay. From 575 cm to 529 cm and from 500 cm to 479 cm, 1-2-cm thick light grey silty-clay layers alternate with darker and organic-rich layers (gradual boundaries). Between these sections with alternating light-grey and dark-brown organic layers, there is a c. 28-cm thick sequence of five turbidites (529-500 cm), each one characterized by a distinct fining upward trend. Above 479 cm, sediments are composed mainly of dark-brown organic gyttja. The gyttja deposition was interrupted by distinct minerogenic layers of fine grey detrital clay with sharp stratigraphic boundaries at 604-602 cm, 445-441 cm, 413-410 cm, 283-281 cm depths (Fig. 2).

The sediment core covers part of the Younger Dryas and the entire Holocene, from c. 12,450 cal yr BP to present. One ^{14}C date (DeA-23963) was rejected because it has an unrealistic young age compared

to other age determinations from samples at lower depths. The dated material was found near to the top of a sediment-core section and likely contained contaminated sediments that are not included in the master core. The reliability of the chronology in its most recent part is confirmed by the matches between the predicted and actual ages of the two Pb peaks during the Roman period and the Pb peak during the Middle Ages (Fig. 2). The chronology below the lowermost date (at 566.5 cm depth, $11,500 \pm 250$ cal yr BP) is inferred from the depth-age model and it is therefore unsecure for ages older than c. 11,800. Sediment deposition times (Fig. 2) vary between 6-65 years cm^{-1} (median = 21.6 years cm^{-1}).

Long-term vegetation dynamics

The pollen diagram (Fig. 3) was divided into four statistically significant assemblage zones at 566.5, 455.5, and 359.5 cm (corresponding to 11,497, 9413, and 6348 cal yr BP). To better illustrate the vegetation changes, we selected two additional non-significant pollen zone boundaries at 200.5 cm and 58.5 cm (2098 and 481 cal yr BP).

Pollen assemblages in zone 1 (615-566.5 cm; 12,430-11,500 cal yr BP) are dominated by *Artemisia*, Poaceae, Chenopodiaceae, and *Pinus* pollen, with minor amounts of *Juniperus*, Asteraceae subf. Asteroideae, *Galium*, *Thalictrum*, and Poaceae Cerealina-type. Such assemblages are typical of Central European Late Glacial pollen assemblages (Younger Dryas; 12,850-11,650 cal yr BP; Rasmussen et al., 2014) and are indicative of an open steppe environment and a semi-arid continental climate. *Pinus* is generally over-represented in pollen diagrams, being a high pollen producer with a high pollen dispersal capacity (Birks 2003). However, its local presence is attested by stomata and needle finds (Fig. 4), presumably as low-density stands of dwarf pine (*Pinus mugo*) or pine trees (*Pinus sylvestris*, *Pinus heldreichii*, or *Pinus nigra*). The presence of Cerealina-type pollen is likely associated with wild Poaceae, as high values of Cerealina-type pollen were found in the region since 18,000 cal yr BP, long before the development of agriculture (Dörfler 2013). During the final phase of the Younger Dryas, arboreal pollen increased (from c. 45 to 65%) and *Artemisia* pollen decreased (from c. 20% to 10%). This may indicate an initial closure of the woodland, possibly due to a climate warming. A *Picea abies* stoma was found around 11,600 cal yr BP, indicating a rapid altitudinal shift of this tree species at the Younger Dryas-Holocene transition.

The onset of zone 2 (566.5-455.5 cm; 11,500-9410 cal yr BP) marks the start of the Holocene. The steppe vegetation started to be replaced by woodland as attested by a further increase of arboreal pollen (from c. 65% to 80%) in conjunction with a decrease in *Artemisia* and others herbs (Chenopodiaceae, Poaceae, and *Thalictrum*) and of *Pinus* pollen. *Quercus robur*-type and later *Ulmus* and *Fraxinus* sp. pollen abundances rose, indicating that thermophilus tree populations expanded, probably at lower elevation, in response to the on-going Holocene warming. *Betula* pollen peaked around 10,750 cal yr BP and thereafter declined until c. 10,000 cal yr BP. The presence of *Ephedra* pollen at the beginning

of the zone and relatively high values of light-demanding Apiaceae pollen suggest the presence of an open woodland until c. 10,000 cal yr BP, when *Picea* and *Abies* populations began to expand as evidenced by a rise in pollen, and by the presence of *Picea* macrofossils. However, finds of *Betula* and *Pinus sylvestris*-type plant macrofossils and stomata from 10,500 to 9500 cal yr BP indicate that *Pinus* trees or shrubs and *Betula* were still present in the surroundings. Finds of *Sporormiella* dung-fungi indicate the presence of wild large herbivores in the nearby of the lake.

Arboreal pollen percentage values further increase during zone 3 (455.5-359.5 cm; 9410-6350 cal yr BP), reaching values of c. 85-90%. The transition to a more closed woodland occurred in conjunction with a further decline of *Pinus* and *Betula* and the expansion of *Picea* and *Abies* populations. Increasing abundances of *Picea* and *Abies* plant macrofossils and finds of stomata attest to the development of a mixed *Picea-Abies* forest with minor shares of *Pinus* and *Betula*. *Picea* was perhaps locally dominant over *Abies*, as indicated by higher concentrations of macrofossils and by a greater abundance of stomata. However, this remains a working hypothesis given that the production and dispersal of plant macrofossils for *Picea* and *Abies* are not constrained (Blarquez et al. 2012). Monolete and *Dryopteris filix-mas* spores as well as Bryophyta macrofossils increased during this zone. As these plants grow in fresh and shaded understory (Ellenberg 2009) and require moist conditions for their development, the closed forest probably favored them. The continuous pollen curve of *Fagus* from 8000 cal yr BP onwards indicates the establishment of beech in the surroundings. *Corylus* pollen abundance was higher throughout this zone, indicating the presence of forest edges that were colonized by this pioneer light-demanding shrub (Enescu et al. 2016). Towards the end of the zone (c. 7250 cal yr BP), *Ostrya*-type pollen increased. *Ostrya*-type pollen includes pollen produced by both *Ostrya carpinifolia* and *Carpinus orientalis* (Beug 2004). *Carpinus orientalis* is a thermophilus tree with a wide distribution range being found both with Mediterranean oaks communities and with *Ostrya carpinifolia* and *Fraxinus ornus* on the hillsides and mountains of the western part of Balkans up to 900 m (Pasta et al. 2016; Sikkema and Caudullo 2016). Therefore, the *Ostrya*-type pollen reflects vegetation changes at lower altitudes. None of the anthropogenic indicators increase during this zone.

At the onset of zone 4a (359.5-200.5 cm; 6350-2100 cal yr BP) *Abies* pollen distinctly declined, and *Fagus* as well as *Carpinus betulus* pollen rose. The *Abies* population recovered about 1000-1500 years later (5000 cal yr BP), and starting from 4500 cal yr BP *Fagus* was admixed in the *Picea-Abies*-dominated forest, as attested by *Fagus* stomata and plant macrofossils. *Picea* pollen gradually increases during the zone reaching values >25%. Other distinct features of the pollen record include the rise of *Alnus glutinosa* pollen around 5500 cal yr BP. The shade-tolerant *Carpinus betulus* and *Fagus* together with the light-demanding pioneer *Alnus glutinosa* are favored by moist habitats on upland soils (Houston Durrant et al. 2016; Sikkema et al. 2016). Therefore, their increase could suggest an increase in humidity during the growing season (Finsinger et al. 2017). *Pinus* macrofossils are absent in this zone, but a single stoma indicates that *Pinus* was still locally present. Reductions of arboreal pollen percentages together with increases of pollen of light-demanding herbs (such as *Artemisia*, Poaceae,

and Chenopodiaceae) and of *Juniperus* indicate mild phases of forest-cover openings. However, anthropogenic indicators do not increase, suggesting that human activities did not contribute substantially to these mild forest-cover openings.

During zone 4b (200.5-58.5 cm; 2100-480 cal yr BP), a mixed *Abies-Picea-Fagus* was still present locally as confirmed by stomata and plant macrofossils. However, *Abies* pollen abundance sharply decreased and *Fagus* locally expanded between 1200 and 480 cal yr BP, as shown by stomata and plant macrofossils as well as by an increase in Angiospermae leaf fragments. During this local *Fagus* expansion, *Picea* pollen decreased (from 25% to 15%). Around 2000 cal yr BP, a rise in SI, CI, as well as frequent finds of *Olea europea*, *Juglans*, and *Castanea sativa* pollen and thus higher OJC index values indicate an increased land-use pressure in the area and the development of orchards at lower altitudes (<700 m asl) since Roman times. Pollen of *Juniperus* and PI increase from 750 cal yr BP (Middle Ages) together with a further increase in SI and CI, a rise in *Artemisia*, *Poaceae* pollen and a sharp decrease in arboreal pollen (from c. 85% to 65%). The pollen assemblages suggest the onset of a land-use phase involving both cultivation (*Secale cereale* pollen) and pastoralism (*Juniperus*, *Rumex acetosa*-type, and *Veratrum* pollen).

Pollen percentages of *Fagus* decreased during zone 4c (58.5-0 cm; 480-0 cal yr BP). Plant macrofossils of *Fagus* are absent and those of *Abies* occur rarely. The rise of *Picea* pollen and the continuous finds of its macrofossils and stomata attest the local establishment of a *Picea*-dominated forest with minor occurrence of *Abies* and *Fagus*. Anthropogenic indicators (PI, SI, and CI), as well as *Juniperus*, *Artemisia*, and *Poaceae* increased documenting a rise in human impact. The regular finds and increase of *Olea*, *Juglans*, and *Castanea* pollen (OJC index) indicate the development of orchards at lower altitudes. Forest cover increased during the last century, perhaps due to the protection of the area since 1907 CE.

Charcoal-inferred fire history

Regional fire activity, inferred based on the smoothed microscopic charcoal record (mCHAR), was high between c. 12,000 and 10,000 cal yr BP as well as over the past 2500 years (Fig. 7). Macroscopic charcoal concentration values ranged between 0 and 89 (median = 3 pieces cm⁻³; mean = 6 pieces cm⁻³). From 12,400 to 8500 cal yr BP the trend of the charcoal-accumulation rate records is weakly constrained due to the low resolution of the data (Fig. 7). However, from 8500 cal yr BP onwards, the change-point analysis captures three periods of decreasing landscape-scale biomass burning: 8500-5750 cal yr BP, 5750-1500 cal yr BP, and the past 1500 years (Fig. 8).

The median signal-to-noise index (SNI = 4.99) shows that the macroscopic charcoal-accumulation rate (MCHAR) record is suitable for peak-detection analysis (Kelly et al. 2011). A total of 25 fire episodes were identified over the past 8500 years, with a mean fire-return interval (mFRI) of c. 300 years (FRI range: 154-388 years). Although the distributions of FRIs overlap among pollen zones, periods of

reduced FRI are centered between 8500 and 7750 cal yr BP, 5000-4000 cal yr BP, and 2750-2000 cal yr BP (Fig. 7).

Only 24% of the fire events occurred 0 to 90 years before distinct erosion events (Fig. 5; Fig. 8). We assume that the coincidence between these fire and erosion events indicates the effect of higher-severity catchment fires, which occurred mostly after 5000 cal yr BP with a mean fire-return interval (mFRI_C) of c. 950 years (FRI_C range: 341-1643 years). Other erosion events in the catchment (ca. 80% of the identified erosion events) might have been triggered by other disturbances, such as avalanches and landslides.

Response of fire to variations in climate and human impact

Landscape-scale biomass burning (as inferred from macroscopic charcoal accumulation rates; MCHAR) and regional fire activity (as inferred from microscopic charcoal accumulation rates; mCHAR) show opposite responses to climate and human impact. While landscape-scale biomass burning significantly increases in response to increasing summer temperatures (Fig. 7a; Table 2), regional fire activity significantly decreases (Fig. 7b). Similarly, while landscape-scale biomass burning significantly decreases in response to human impact, regional fire activity increases (Fig. 7c).

Response of dominant forest canopy species to variations in climate, fire and human impact

The dominant trees respond in a similar way to summer temperature and biomass burning. Whereas *Picea*'s responses are not statistically significant (Fig. 7d-e; Table 2), *Fagus* shows a significant negative response, and *Abies* shows a significant positive response to both summer temperature and landscape-scale biomass burning (Fig. 7d-e). Among the three dominant trees, *Abies* is the only one showing a significant (negative) response to human impact (Fig. 7f).

Discussion

The well-dated and high-resolution pollen, plant macrofossil, stomata, and charcoal records from Zminje jezero provide valuable insights into the long-term vegetation dynamics and fire ecology of mountain forests in the central Dinaric Alps. However, the investigation of long-term vegetation dynamics in relation to changes in land-use pressure requires a detailed understanding of land-use history. This is particularly important for southern Europe, where continued forest clearances and agriculture (often with the use of fire), interspersed by periods of abandonment and secondary regeneration, occurred for millennia since the late Neolithic as the result of the development and expansion of more permanent land-use practices (e.g. animal husbandry, ploughing, crop cultivation,

woodland management; Birks and Tinner, 2016). We therefore first assess our results in comparison to other records from the region and evaluate past land-use pressure and fire activity in the framework of archaeological evidences and historic societal changes in the region.

Long-term vegetation dynamics in a regional setting

The vegetation changes documented by the pollen, plant-macrofossil, and stomata records from Zminje jezero (Fig. 7) are overall consistent with those that are documented based on pollen from sites in the surrounding region. During the Younger Dryas, vegetation in the region consisted mainly of an arid steppe-tundra or alpine vegetation characterized by herbs (*Artemisia*, Poaceae, Chenopodiaceae) and cold-tolerant pine woodlands, probably due to dry and continental climatic conditions. At the onset of the Holocene, vegetation drastically changed in response to a rapid climatic change including a warming of c. 2-4°C (Heiri et al. 2014; Tóth et al. 2015). While mixed deciduous thermophilus woodlands with *Quercus*, *Ulmus*, *Fraxinus* sp. formed at lower elevation (Fig. 3), in the surroundings of Zminje jezero the light-demanding pioneer *Betula* expanded first (Fig. 3; Fig. 4), followed shortly thereafter by the expansion of both *Picea* and *Abies*, indicating a relatively rapid altitudinal shift of the montane vegetation belt. The early-Holocene rapid expansion of thermophilus trees is a characteristic feature of pollen records at sites further to the north, east, and south on the Balkan Peninsula (Willis 1994). Similarly, the expansion of *Picea* and *Abies*, two dominant trees in mountain forests, occurred between 9000 and 8000 cal yr BP both at Zminje jezero and at other mountain sites such as Rezina marsh (1800 m asl, Greece; Willis, 1992, 1994) and Prokoško Jezero (1670 m asl, Bosnia Herzegovina; Dörfler, 2013). Further, although *Fagus* expanded only around 6350 cal yr BP in the Durmitor, i.e. about 2000-1000 years later than at other sites, the pollen record from Zminje jezero shows that expansion of *Fagus* broadly coincided with the expansion of *Ostrya* and *Carpinus betulus* (Fig. 3), as often seen in other pollen records from the region (Prokoško Jezero, Lake Ohrid, Lake Prespa, Crveni Potok mire; Dörfler, 2013; Finsinger et al., 2017; Panagiotopoulos et al., 2013; Wagner et al., 2009). However, the plant-macrofossil record indicates that *Fagus* contributed to form a mixed *Picea-Abies-Fagus* forest only around 4500 cal yr BP (Fig. 7). As *Fagus* is sensitive to low winter temperatures and spring frosts (Cheddadi et al. 2016; Allevato et al. 2019), it is likely that the spread of beech in the Durmitor prior to 6500 cal yr BP was limited by colder-than-present winter temperatures (Perşoiu et al. 2017), this aspect may have been accentuated by altitude. In addition to climatic variations, other possible explanations for the later onset of the expansion of *Fagus* at Zminje jezero include the influence of site-specific factors (e.g. competition and disturbances) and slow population growth, which is typical of *Fagus* (Giesecke et al. 2007). Continuous finds of *Olea europea*, *Juglans*, and *Castanea sativa* pollen since 480 cal yr BP point to the development of arboriculture probably in the western foothills of the Dinaric Alps (Fig. 8). The cultivation of these species became widespread from Roman times and intensified during the Middle Ages in Roman territories (Mercuri et al. 2013). Montenegro was conquered by the

Romans during the 2nd century BCE. Thus, finds of *Castanea* pollen after 2000 cal yr BP are in line with the hypothesis of human-mediated spread of chestnut populations since Roman times (Conedera et al. 2004). Further, as in other records in the region (Dörfler 2013; Finsinger et al. 2017), pollen of *Juglans* first appear at c. 1500 cal yr BP and occur more regularly after 500 cal yr BP.

Regional vs local land-use

Identifying the start and inferring the intensity of land-use pressure using palaeoecological records is challenging, particularly in regions where independent documentation by archaeological evidence is poor (Deza-Araujo et al., 2020), as is the case for the Durmitor.

On the one hand, the continuous presence of plant macrofossils and stomata of trees (*Picea*, *Abies*, and *Fagus*) in the sediments of Zminje jezero (Fig. 7) indicates that tree cover persisted in the surroundings of the lake at least throughout the past 9000 years. In keeping with this, the high values of arboreal pollen (generally >80%; Fig. 7), as well as the AP/NAP ratio values (generally >4; Fig. 8), qualitatively support the interpretation of the persistence of close forest (Deza-Araujo et al., 2020). A similarly high long-term forest cover was also found in the internal Dinaric Alps, at Crveni potok (1090 m asl; Finsinger et al., 2017), but contrasts with results from Prokoško Jezero (Bosnia-Herzegovina, 1670 m asl; Dörfler, 2013) where arboreal pollen values decreased to 50% during the past 2000 years. This would support the hypothesis that some of the forested regions in the interior range of the Dinaric Alps have been left relatively intact until the present (Nagel et al. 2017).

On the other hand, the detailed interpretation of arboreal pollen values is unclear, particularly when intermediate AP/NAP ratio values occur (Deza-Araujo et al., 2020). Moreover, stomata and plant macrofossils indicate the local presence of the taxa, within some decameters around a site (Ammann et al. 2014; Birks 2017). By contrast, even if the relevant pollen source area of small lakes such as Zminje jezero is relatively small (some kilometers at most; Sugita, 1994), pollen from the wider region as well as from lower elevations may reach the site (Markgraf 1980; Finsinger et al. 2007). Thus, reconstructions based on local-scale proxies (plant macrofossils and stomata) and those based on a landscape-to-regional-scale proxy (pollen, including anthropogenic indicators) may not necessarily covary if land-use pressure was not homogeneous across the region.

Indeed, despite agriculture and forest clearances did not reach the surroundings of the lake during the past 9000 years, anthropogenic pollen indicators document land use in the region (Fig. 7). The presence of primary anthropogenic indicator pollen (*Secale cereale*) unambiguously documents that cultivation started in the region at least around 6000 cal yr BP, during the Copper Age. While this is about 1000 years later than the age of Neolithic settlements on the shores of the lowland Lake Ohrid (Hafner et al. 2021) and 2000 years later than the earliest Starčevo-culture Neolithic settlements in the inland of Bosnia-Herzegovina (Vander Linden et al. 2014), the *Secale* pollen finds support the view that Neolithic novelties, albeit with a certain time lag, spread in the hinterland of Montenegro (Borić et al. 2021).

However, the sparse occurrence of *Secale* pollen may agree with both alternative hypotheses: (i) that the mountain hinterland remained an agricultural frontier zone (Forenbaher and Miracle 2005; Mihailović 2007) for much of the Neolithic and the Copper Age, and (ii) that while there is some evidence for Neolithic occupation sites in the inland, such as the Odmut and the Trilca caves 20-35 km from the Durmitor (Vislobokova et al. 2020; Borić et al. 2021), the mountain inland may be archeologically undersurveyed (Vander Linden et al. 2014; Borić et al. 2021). Similarly, anthropogenic indicators do not show distinct signs of stronger land-use pressure for the Bronze and Iron Ages, despite overland connections probably existed between coastal and inland settlements during the Bronze Age (Bulatović et al. 2020) and Montenegro was inhabited by Illyrian and Celtic groups between the 5th and the 2nd century BCE (World Heritage Committee 2017; Cozzolino et al. 2020). By contrast, anthropogenic indicators indicate that land-use pressure increased both within as well as at lower elevation around the Durmitor since the Roman period. Cultural indicators, secondary indicators, as well as OJC index values rise around 2000 cal yr BP, when the region currently belonging to Montenegro was conquered by the Romans (2nd century BCE). At that time, land-use pressure probably reached the Durmitor, as attested by the construction of roads, including the one connecting Nikšić and Komini that probably passed through Zabljak. The further rise of anthropogenic indicators around the 15th century CE is coherent with the first local settlements in the Durmitor. The so-called stećci sites (medieval tombstones and graveyards from the 13th to the 17th century; Erdeljan, 2018) near Zabljak attest to the local presence of settlements on the Durmitor during the Middle Ages and the Ottoman Empire. Churches and monasteries from the 15th to the 19th century CE attest settlements during the Ottoman Empire.

A shift from a *Picea-Abies-Fagus* mixed forest to one dominated by *Picea* occurred in the surroundings of Zminje jezero around 1400-1600 CE (from the end of the 15th to the 17th century CE). Beech and fir populations, which are more sensitive to browsing than *Picea* (Feurdean et al. 2009; Klopčič et al. 2017) could have been reduced by an increase in grazing pressure due to the establishment of the local pastoral katun society from c. 1477 CE (Turkish Land Registry). An alternative explanation could involve silvicultural practices which may have locally favored spruce. Around 1400 CE, the Balkan Peninsula was under the influence of the Republic of Venice and from 1496 CE Montenegro fell under the domain of the Ottoman Empire (Rastoder 2003). In the mid-16th century, local land-owners started seizing monastery estates and hunting grounds in the lower parts of Montenegro, which resulted in the retreat of considerable parts of the population in mountain areas (Rastoder 2003), including the Durmitor (Karadzic and Sibalic 1997), whose forests probably started to be more intensively exploited. As spruce is able to withstand lower winter temperatures compared to *Fagus* and *Abies* (Cheddadi et al. 2016), the development of a *Picea*-dominated forest at Durmitor could also be linked to the onset of cooler conditions during the Little Ice Age (1450-1850 CE).

Regional vs local fires

We found contrasting trends and responses of fire to climate and human impact over the past 8500 years (Fig. 6), pointing to different drivers of fire dynamics at regional and landscape scales. Biomass burning responded negatively to human impact (Fig. 6c). It is unlikely that this relationship is the result of negative feedbacks arising from human-induced deforestation (e.g. lower fuel availability, fragmentation; Bowman et al., 2011) because biomass burning decreased predominantly during the Neolithic, when land-use was probably mild. By contrast, landscape-scale biomass burning responded positively and significantly to summer temperature, as expected based on the strong influence (summer) temperature has on fire activity (Westerling et al. 2006; Jain et al. 2022) and as often observed with sedimentary charcoal records (Power et al. 2008; Daniau et al. 2012). Thus, climate very likely was the main driver of fire dynamics in the mountain area. As fuel was not a limiting factor in the moist and productive mixed and broadleaf mountain forests, higher mean July temperatures perhaps coupled with prolonged dry seasons (Holocene Thermal Maximum; Samartin et al., 2017) improved fuel flammability (Pausas and Paula 2012). Conversely, the positive albeit non-significant response of mCHAR to human impact suggests that human-activities contributed to increased regional fire activity (Fig. 6c). Given the large potential source area of microscopic charcoal (Tinner et al. 1998; Whitlock and Larsen 2001), the mCHAR record likely records fire activity within a wide region, possibly even including the lowlands along the coast, where land-use change rose since 2000 cal yr BP as shown by the OJC pollen index (Fig. 8). The slightly earlier rise of regional fire activity, which started around the Bronze Age-Iron Age transition, may be connected to land use in the region that remained undetected by the anthropogenic indicators from Zminje jezero.

A disconnect between charcoal-based fire-history reconstructions can arise both when comparing records from sites located near to each other (Gavin et al. 2006; Finsinger et al. 2018), as well as proxies of fire from the same sediment core (Finsinger et al. 2017) if fire occurrence was not spatially homogeneous. Additional macroscopic-charcoal records from lakes may be necessary to better constrain the spatial heterogeneity of past fire occurrence in the Durmitor. However, regardless of these uncertainties, it is likely that land use activities were not limited to coastal area during the past 2000 years. Resources from the inland mountains (e.g. timber) were probably useful to the economies of surrounding settlements and the lack of rising biomass burning at Zminje jezero possibly indicates that humans did not extensively use fire in the Durmitor to clear the forests and make space for other types of land use. Moreover, the lower biomass burning rates in recent millennia fit with the notion that fires are rare in the mountain forests in the Dinaric Alps (Nagel et al. 2017). Yet, the identification of higher-severity catchment fires (24% of fire episodes; FRIs >350 years) as well as of charred *Picea* and *Abies* needles may be useful to nuance the importance of fires in these mountain forest.

Response of dominant forest canopy species to variations in climate, fire and human impact

Picea, *Abies*, and *Fagus* show similar responses to both summer temperature and biomass burning (Fig. 6d-e). Given the strong and positive relationship among the two predictors (Fig. 6a), it is difficult to disentangle their roles separately. However, as (summer) temperature currently has a strong influence on fire activity (Westerling et al. 2006; Jain et al. 2022), the species responses to variations in climate, biomass burning, and human impact may yield valuable insights into the long-term fire ecology of these three species that are widespread and often dominant in European mountain forests.

Our response curves show that *Fagus* is sensitive to summer temperatures and that its response to biomass burning is more complex (Fig. 6d-e). The right-skewed response to biomass burning suggests that *Fagus* was favored under low biomass burning conditions and became sensitive to fires under higher biomass burning rates. Overall, both response curves from Zminje jezero strikingly match those obtained with long-term ecological observations from the Northern Apennines (Morales-Molino et al. 2020), and suggest that also in the central Dinaric Alps *Fagus* became more competitive in mixed fir-spruce forests with the onset of cooler and moister summers and fire disturbance (Fig. 7). Indeed, *Fagus* requires moist summers for its germination (Giesecke et al. 2014) and is more sensitive than *Abies* to drought due to its shallow root system (Tinner et al. 2013; Cheddadi et al. 2016). *Fagus* is a shade tolerant species and its regeneration can establish and grow with very low light levels under the existing forest canopy for years before rapidly expanding and achieving the dominance when light conditions improved after disturbances (Gardner and Willis 1999). Thus, the occurrence of both high and low severity fires after 5000 cal yr BP may have promoted the recruitment of *Fagus* and its admixture into the mixed *Picea-Abies* forest. This matches with evidence suggesting that during the initial phase of stand establishment *Fagus* is favored by mixed-severity fire and intermediate human disturbances (Bradshaw and Lindbladh 2005; Giesecke et al. 2007; Tinner and Lotter 2006) thanks to its capacity to occupy newly exposed soils and canopy openings (Carter et al. 2018) more rapidly than its two main competitors (*Abies* and *Picea*). However, lacking ecological adaptations to fire, *Fagus* is a fire-sensitive species that was negatively affected by higher biomass burning and higher temperatures (Tinner et al. 2000; Carter et al. 2018; Morales-Molino et al. 2020) prior to 5500 cal yr BP. In keeping with this, the change-point analysis shows a decrease in landscape-scale biomass burning after the establishment of *Fagus* (Fig. 7), corroborating the view that beech establishment occurs in conjunction with a shift to a lower fire activity (Feurdean et al. 2017a; Bobek et al. 2019).

Picea can persist with a low to moderate fire severity (Feurdean et al. 2017) but it does not survive or re-sprout after high severity fires (Feurdean et al. 2019). Moreover, due to its shallow root system *Picea* is more vulnerable to drought than *Abies* (Henne et al. 2011). In agreement with these notions, spruce dominated stands in the Dinaric Alps are mostly common in habitats with significantly colder and moister microclimates (Nagel et al. 2017). However, we found that neither temperature nor biomass burning significantly influenced *Picea* (Fig. 6a-b), and its population remained relatively stable (Fig. 7)

even under higher-than-present summer temperatures, as also observed in the Carpathians (Carter et al. 2018). Its insensitivity to summer temperatures may simply imply that past climatic conditions did not exceed the species' tolerance range. Moreover, the lack of a significant response to biomass burning agrees with evidence showing that *Picea* can persist thanks to vigorous post-fire regeneration (Bobek et al. 2018) even with FRI as low as 200-300 years (Brown and Giesecke 2014; Feurdean et al. 2017a; Finsinger et al. 2018). Although fires may have been fueled by *Picea*'s traits that promote fire spread (high resin content, flammable litter, and a ladder canopy structure), its well-established populations persisted at Zminje jezero, despite higher-severity catchment fires occurred with fire-return intervals >350 years (Fig. 7).

We found that *Abies* was promoted by warmer-than-present summer temperatures (up to c. 2.5°C), similarly to observations from the Northern Apennines (Morales-Molino et al. 2020). However, our findings also suggest that *Abies* responded positively to increasing landscape-scale biomass burning (Fig. 6e). This contrasts with a number of records showing that *Abies* is a fire-sensitive species and that both high-severity infrequent fires and low-severity frequent fires led to its rapid decline and to local extinctions in recent millennia (Tinner et al. 2000, 2013; Morales-Molino et al. 2020). On the one hand, the striking positive response of *Abies* to biomass burning could simply arise from the positive relationship between biomass burning and summer temperatures (Fig. 6a). On the other hand, most records showing a negative influence of fires on *Abies* also document excessive human-induced fire activity in recent millennia (Feurdean and Willis 2008; Tinner et al. 2013). While the biomass burning record from Zminje jezero does not support a rise of fire activity, the mCHAR record does. Thus, given the significant negative response of *Abies* to increasing human impact (Fig. 6f), it seems likely that land use rather than fires substantially contributed to the decline of *Abies* in the Durmitor. Indeed, the rise in human impact (pasturing and small-scale cultivation) since 2000 cal yr BP coincides with the gradual decline of *Abies*. Conversely, its local persistence in the surroundings of Zminje jezero could support the view that *Abies* is resistant to low fire frequencies or even rare high-severity fires (Tinner et al. 2005; Henne et al. 2013; Feurdean et al. 2019).

Conclusions

Vegetation of forest ecosystems often is the result of complex interactions between vegetation dynamics and variations in climate, disturbances (e.g. fire), and human activities. However, understanding ecological processes is challenging as processes often play out over long time scales (centuries, millennia), particularly for forests where long-lived species such as trees are involved. The long time horizon of palaeoecological records permits to study ecosystem responses under substantially different environmental conditions than the present ones, including higher-than-present temperatures as well as

different degrees of land-use pressure and associated fire disturbances (Tinner et al. 2013; Carter et al. 2018; Morales-Molino et al. 2020).

In this study, we sought to investigate the Holocene vegetation and fire history in the upper-montane zone of the central Dinaric Alps, where fires are rare and forests mainly include beech dominated forests and mixed forests dominated by varying amounts of beech, fir, and occasionally spruce (Nagel et al., 2017). We performed the first detailed palaeoecological study from this region (including pollen, plant macrofossils, microscopic and macroscopic charcoal analysis) on well-dated sediments from Zminje jezero (Durmitor massif, Montenegro) and assessed the response of the dominant canopy taxa (*Picea*, *Abies*, *Fagus*) to variations in climate, fire and land-use pressure.

The results indicate that vegetation was dominated by *Pinus* and *Betula* during the Younger Dryas and the early Holocene. A mixed *Picea-Abies* forest established in the upper-montane zone between 10,000 and 9000 cal yr BP and remained relatively stable until 5000 cal yr BP, when *Fagus* became co-dominant with the two conifers. Biomass burning gradually decreased during the past 8500 years in the upper-montane zone, though higher-severity fires became more frequent since 5000 cal yr BP. Anthropogenic pollen indicators only rose after 2000 cal yr BP indicating that land-use pressure was overall remarkably low in the montane zone until the Roman period, in agreement with the (albeit sparse) independent archaeological evidence. Regional fire activity rose since c. 3000 cal yr BP (late Bronze Age) as a result of higher land-use pressure in the wider region, probably including the coastal area. While additional records may be necessary to better support these results, they may support the view that the inland central Dinaric remained an agricultural frontier zone during the Neolithic (Forenbaher and Miracle 2005; Mihailović 2007) and suggest that land-use pressure in the upper-montane zone was also low during most of the Bronze Age.

Response curves show a positive relationship with regional fire activity and human impact, and a significant positive relationship with biomass burning and summer temperature. The curves thus indicate that fires in the upper-montane zone were mostly driven by variations of climatic conditions, as expected based on the strong influence (summer) temperature has on fire activity today (Westerling et al. 2006; Jain et al. 2022) and as often observed with sedimentary charcoal records (Power et al. 2008; Danialu et al. 2012). *Picea* was insensitive to variations in summer temperature, biomass burning and human impact, which supports the view that spruce forests may not be significantly impacted by fire (Carter et al. 2018). In contrast, *Abies* shows a significant positive relationship with summer temperatures and a significant negative relationship with land-use pressure. This supports the notion that *Abies* may be well-adapted to warmer-than present summer temperatures and that its populations declined in recent millennia due to land-use activities (Tinner et al. 2000, 2013; Morales-Molino et al. 2020). Conversely, *Fagus* emerges as a species sensitive to summer temperatures that is promoted by low biomass burning. This indicates that its expansion in the *Picea-Abies* dominated forest was enhanced by the onset of cooler, and possibly also moister, climatic conditions as well as by fire disturbances.

Acknowledgements

We are grateful to S. Rouland, S. Canal, and A. Haliuc for their help during the lab work, to I. Figueral for help with identification of plant-macrofossil and wood, as well as to M. Curovic, and K. Escobar-Torrez for discussions. We are further thankful to Oliver Heiri (University of Basel, Switzerland) for funding some of the radiocarbon dates that are used in this study.

Figures

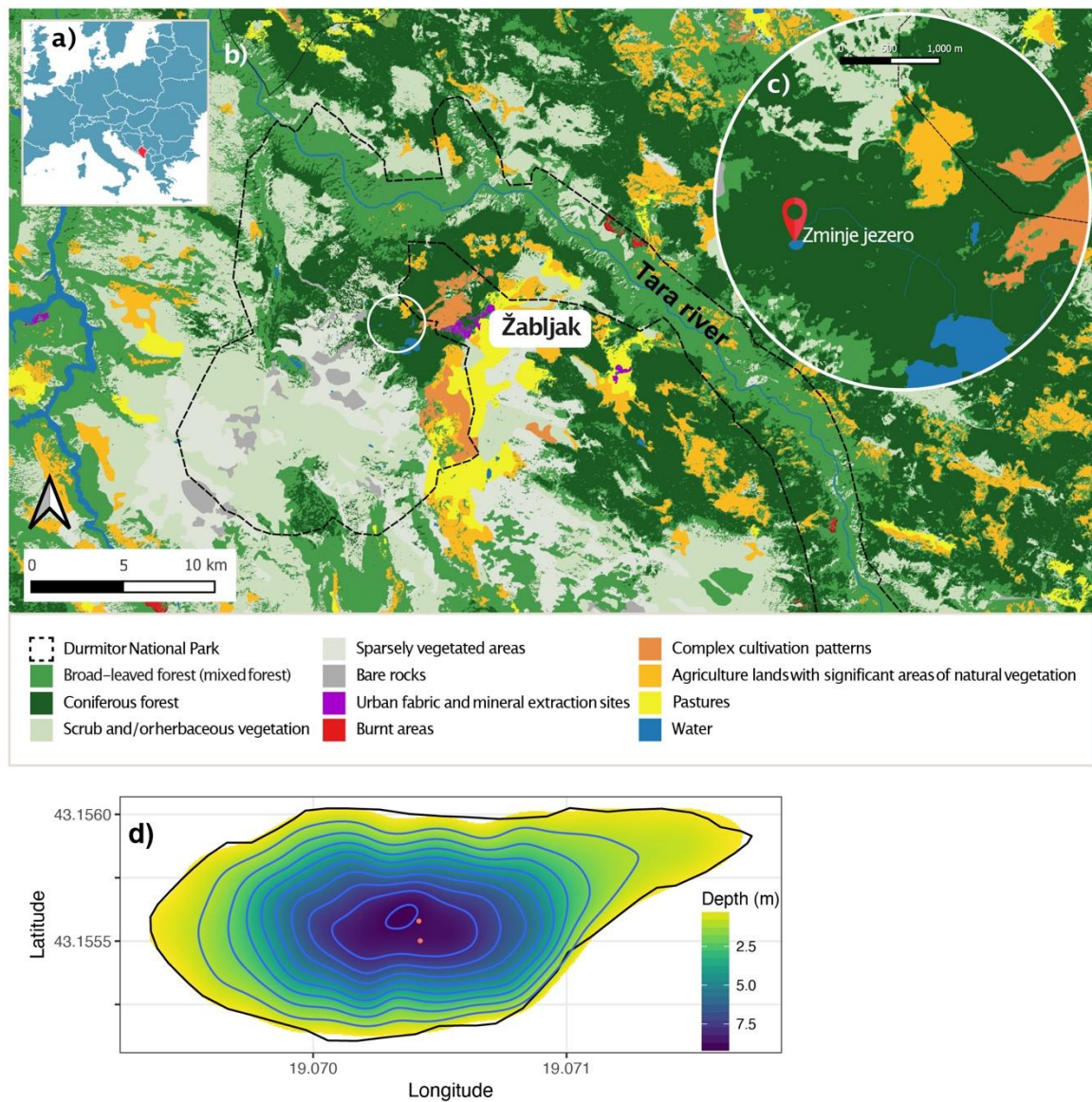


Fig. 1 a-c) Location of the study site at decreasing spatial scales. b-c) Map showing the distribution of land cover types (CORINE Land Cover 2018; <https://land.copernicus.eu/pan-european>) in the Durmitor National Park and surroundings, and d) bathymetric map of Zminje jezero with contour lines at 1-m intervals and coring locations (red circles).

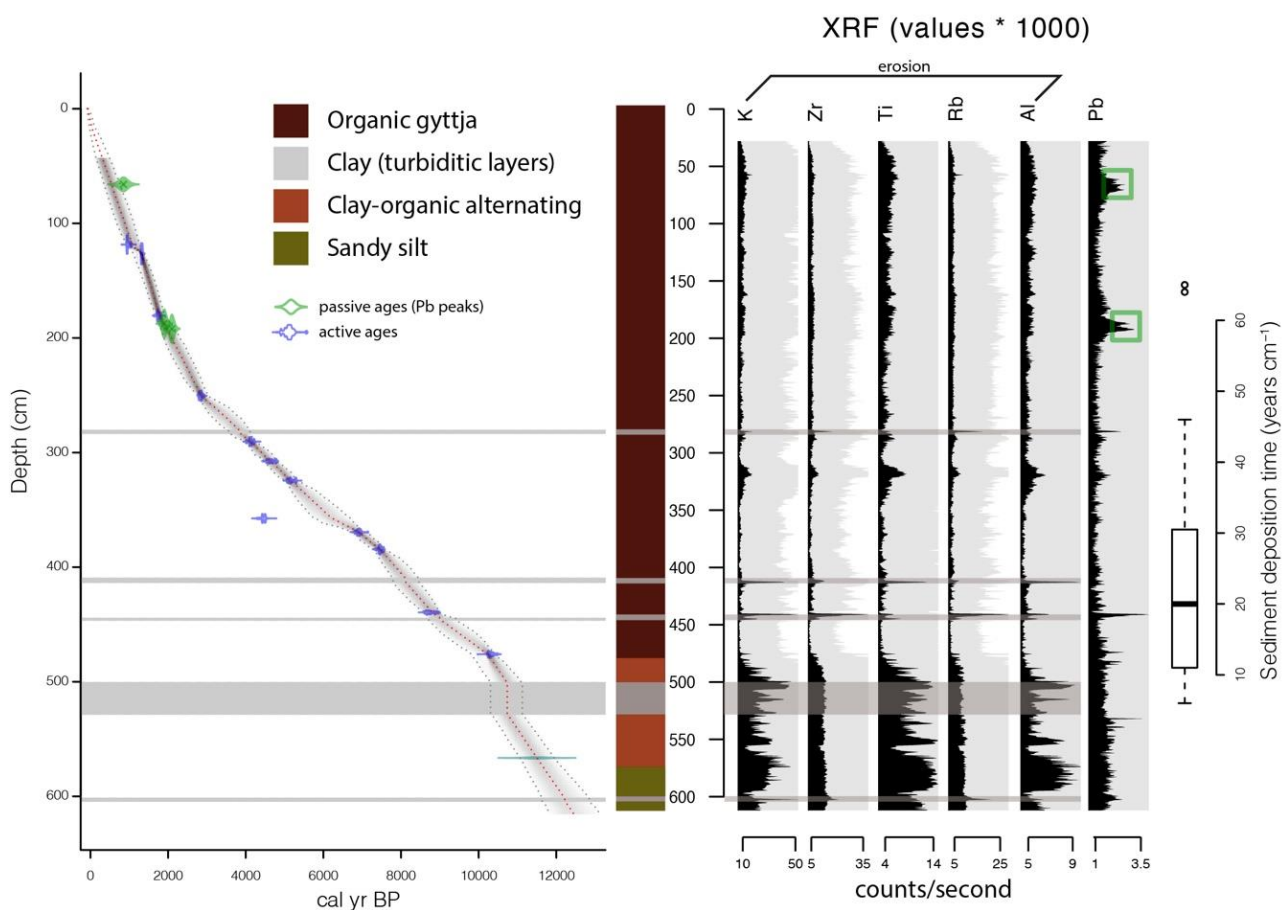


Fig. 2 Depth-age model for the Zminje jezero sediment core. The active control points used to constrain the model include 12 ^{14}C dates from terrestrial plant-macrofossils (blue) and two pollen-inferred ages (light-blue) (Table 1). Passive control points based on Pb peaks (Renberg et al. 2001; McConnell et al. 2018) are shown in green. Grey horizontal bands indicate turbidite layers that were excluded from the model. Lithological and XRF geochemical profiles of the sediment core are shown on the right. The inset shows the distribution of sediment deposition time within the sequence (median = 21.6 years cm^{-1}).

Fig. 3 Abundance of selected pollen and spores from the Zminje jezero sediment profile, expressed as percentages of the terrestrial pollen sum. The continuous horizontal and dashed lines indicate statistically significant and non-significant pollen-assemblage zones, respectively. Empty curves show 7x exaggerations.

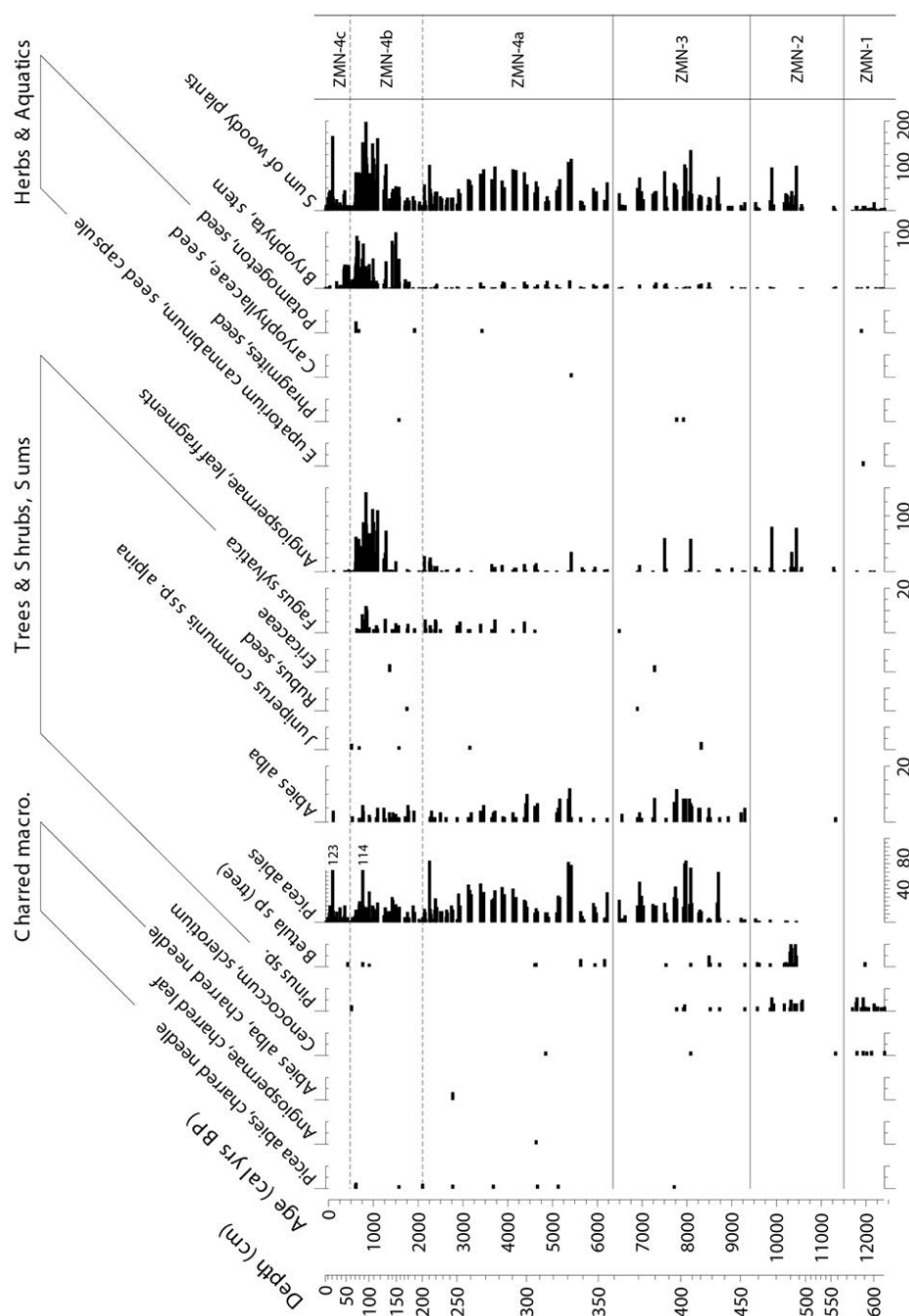


Fig. 4 Plant-macrofossil concentration record for 10 ml from the Zminje jezero sediment profile. The continuous horizontal and dashed lines indicate statistically significant and non-significant pollen-assemblage zones, respectively.

Trigger Coincidence Rate : 0.24

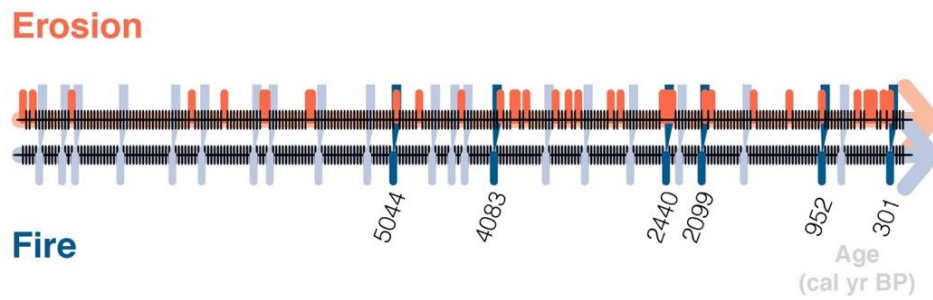


Fig. 5 Synchronicity between erosion and fire events as derived from the Event Coincidence Analysis (Siegmond et al. 2017). About 24% of fire events can be regarded as higher-severity catchment fire events since they triggered erosion events.

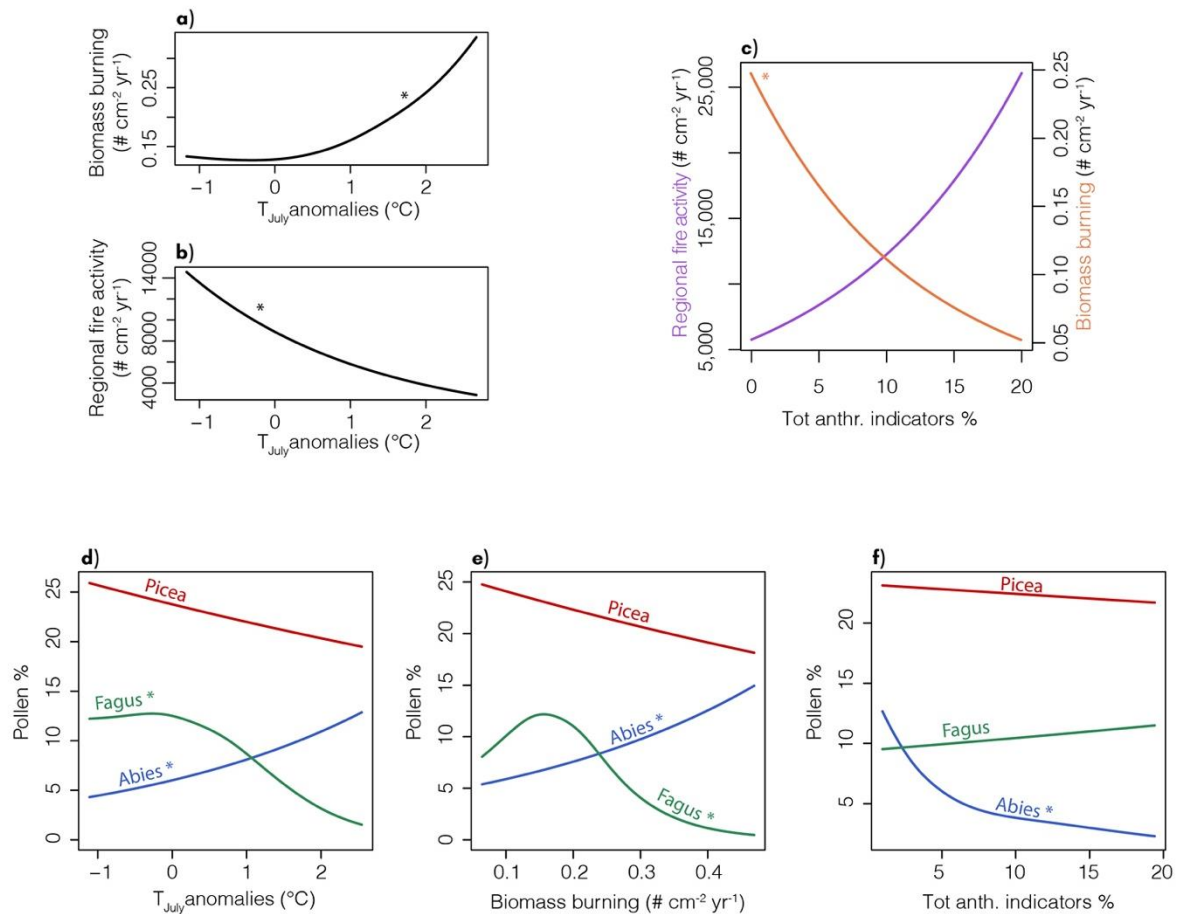


Fig. 6 Generalized Additive Models showing (a-c) landscape-scale biomass burning and regional fire activity (MCHAR_{back} and mCHAR) responses to climate and human impact, and (d-f) responses of dominant forest canopy taxa to climate (T_{July} anomalies of Lago Verdarolo; Samartin et al., 2017) landscape-scale biomass burning (MCHAR_{back}), and human impact (pollen % of anthropogenic indicators).

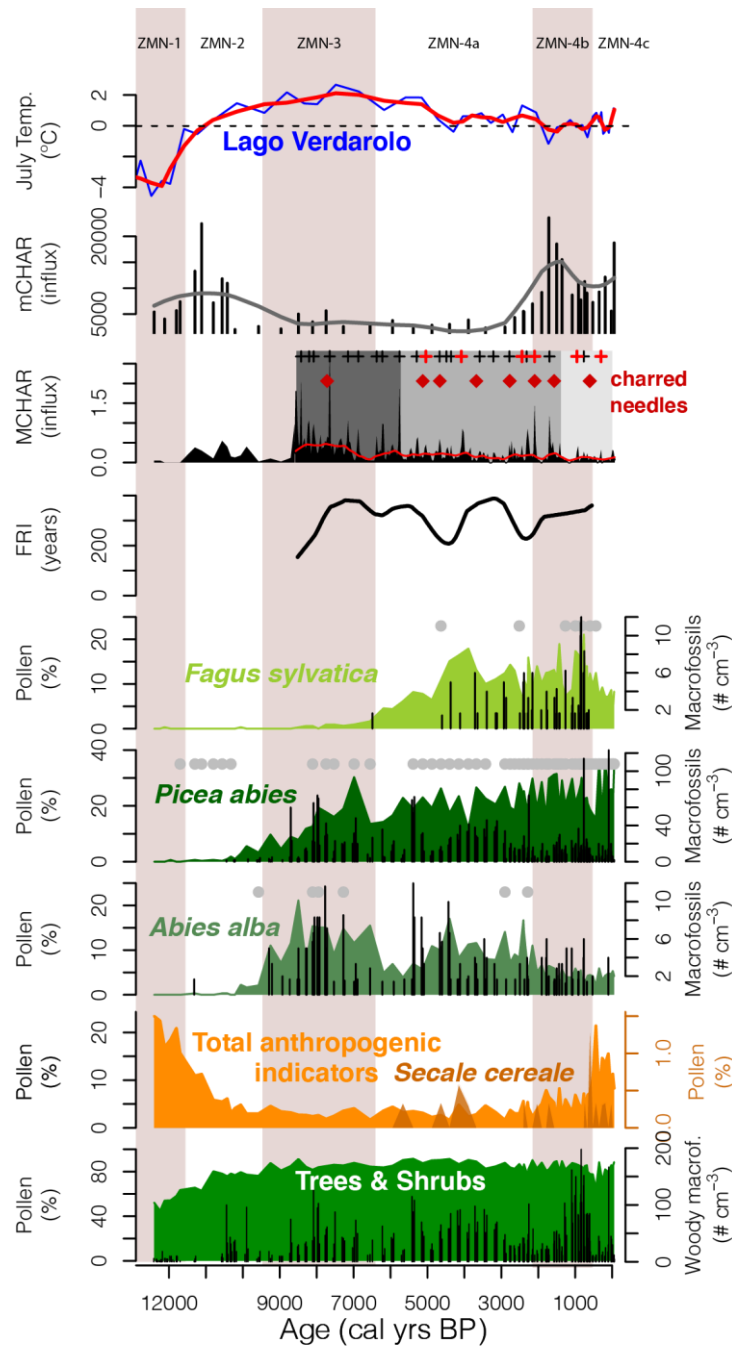


Fig. 7 Comparison of the main proxies for vegetation dynamics, fire and land-use history from Zminje jezero, and chironomid-inferred July-air temperature (T_{July}) anomalies from Lago Verdarolo (Samartin et al. 2017). Microscopic charcoal (mCHAR) inferred regional fire activity; macroscopic charcoal (MCHAR) inferred landscape-scale biomass burning and local fire events (black filled area: charcoal accumulation rate; red line: charcoal background modelled using a 500-years smoothing window; shaded area from grey to white: decreasing periods of relatively stable biomass burning as determined by the change-point analysis; black crosses: low-severity catchment fire events or high-severity fire events outside the catchment; red crosses: high-severity catchment fire events as inferred from the ECA analysis; diamonds: charred needles of *Picea* and *Abies*); fire return intervals (FRI); temporal changes of dominant forest canopy taxa and of human impact (filled polygons: pollen percentages; back vertical bars: plant macrofossils concentrations; grey circles: stomata). Pink vertical bands represent significant and non-significant pollen zone boundaries, respectively.

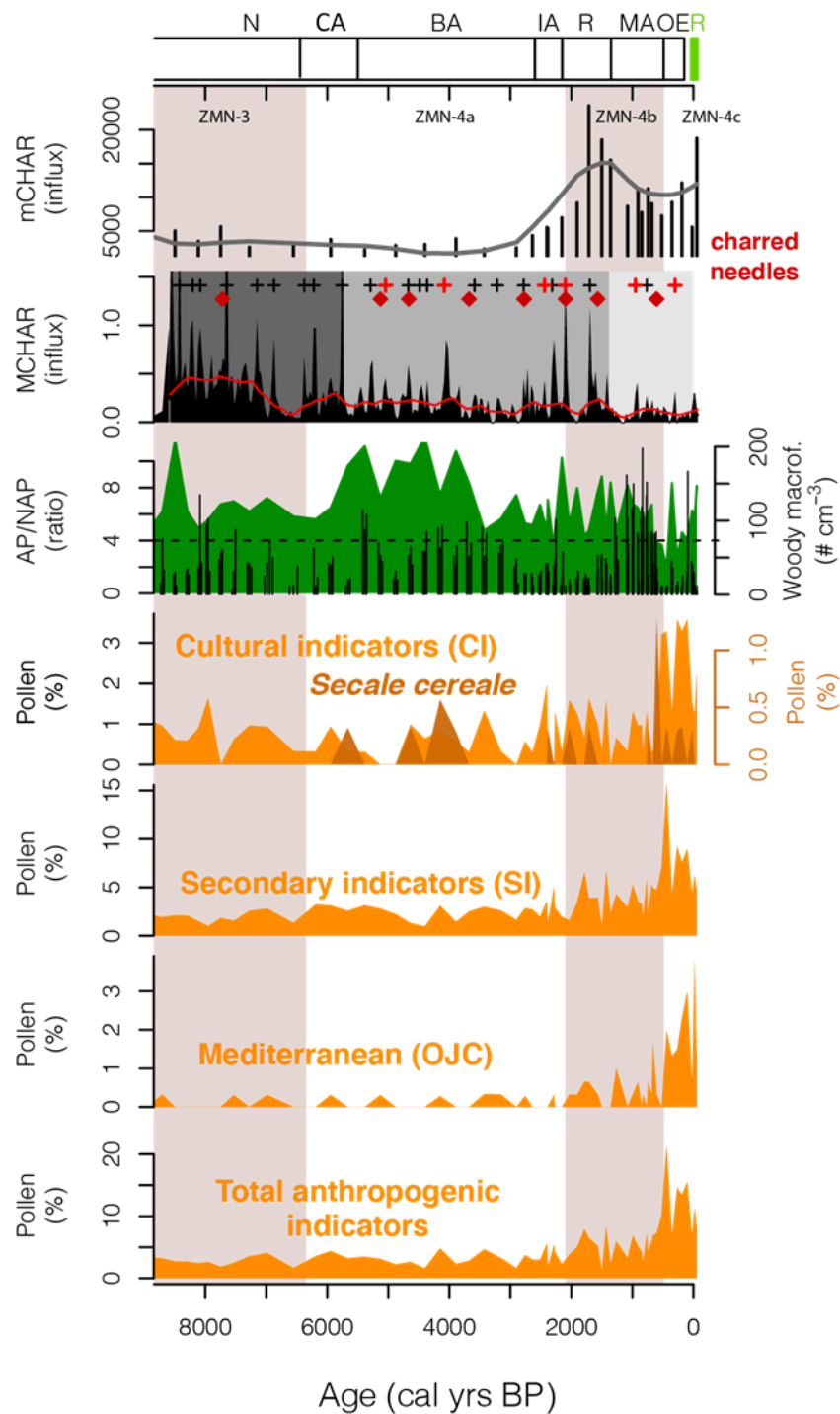


Fig. 8 Comparison between the fire and the land-use histories from the Zmnje jezero record in relation to archaeological cultural periods (N: Neolithic, CA: Copper Age, BA: Bronze Age, IA: Iron Age, R: Roman period, MA: Middle Ages, OE: Ottoman Empire, R: Reserve and Park). From top to bottom: microscopic charcoal (mCHAR) inferred regional fire activity; macroscopic charcoal (MCHAR) inferred landscape-scale biomass burning and local-scale fire events (see Fig. 7); filled green area: arboreal-non arboreal pollen ratio (dashed line separates forests with small openings from closed forest); black vertical bars: total woody plant macrofossils concentrations; orange filled areas: anthropogenic indicators including *Secale cereale* (as primary indicator, PI), cultural indicators (CI), secondary indicators (SI), Olea-Juglans-Castanea index (OJC), and the total sum of anthropogenic indicators. Pink vertical bands represent significant and non-significant pollen zone boundaries, respectively.

Table 1 Control points used to establish the depth-age model for the ZMN-19 sediment core collected from Zminje jezero (Durmitor Massif, Montenegro). * = Rejected dates

Depth (cm)	Lab-code	Material dated	Dry weight (mg)	Sample Thickness (cm)	Age (^{14}C yr BP)	Age (cal yr BP)
0	/	surface	/	1	/	-70 $\pm$ 5
14.5	/	Pollen-inferred age (<i>Ambrosia</i>)	/	1	/	0 $\pm$ 30
118.5	DeA-23961	1 complete leaf and 1 leaf rachis of <i>Fagus sylvatica</i> ; 2 <i>Picea abies</i> needles	20	1	1054 $\pm$ 24	/
126.5	DeA-32618	11 <i>P. abies</i> needles; 2 <i>P. abies</i> seeds; 1 <i>P. abies</i> seed wing; 1 <i>Abies alba</i> needle; 1 Conifer periderm	16.8	1	1427 $\pm$ 20	/
180.5	DeA-31441	1 <i>A. alba</i> seed wing; 1 <i>A. alba</i> needle; 1 <i>P. abies</i> floral bract	9.8	1	1844 $\pm$ 23	/
250.5	DeA-31442	2 <i>P. abies</i> complete needles; 1 <i>A. alba</i> complete needle; 1 <i>F. sylvatica</i> bud scale; 1 <i>F. sylvatica</i> leaf with margin	8	1	2755 $\pm$ 22	/
290.5	DeA-31091	2 Conifer bud scales; 9 Conifer periderms; 1 <i>P. abies</i> seed coat; 1 <i>P. abies</i> seed wing; 3 <i>P. abies</i> needle bases; 4 <i>P. abies</i> needle points; 2 <i>P. abies</i> complete needles; 10 <i>P. abies</i> floral bracts	8.5	1	3762 $\pm$ 22	/
307.5	DeA-23962	<i>A. alba</i> wood w/out bark	194	1	4108 $\pm$ 30	/
324.5	DeA-31093	2 <i>A. alba</i> needles; 3 <i>P. abies</i> needles; 2 conifer bark pieces; 1 <i>P. abies</i> seed wing; 3 branchlets with bark; 1 <i>P. abies</i> seed, 1 Conifer bud scale	17.8	1	4532 $\pm$ 25	/

357.5	DeA-23963	<i>A. alba</i> branch w/out bark	266.5	1	3980 ± 30*	/
369.5	DeA-31440	1 <i>P. abies</i> seed wing; 6 <i>P. abies</i> complete needles; 3 <i>P. abies</i> needle bases; 2 <i>A. alba</i> needle bases; 1 Conifer bud scale; 6 <i>P. abies</i> floral bracts; 4 <i>P. abies</i> needle fragments; 5 Angiosperm leaf fragments	17.6	1	6060 ± 28	/
384.5	DeA-23964	<i>Salix/Populus</i> wood w/out bark	170.2	1	6552 ± 37	/
439.5	DeA-23967	<i>Pinus</i> sp. cone, 1 <i>P.</i> <i>abies</i> needle	148.5	1	7908 ± 39	/
476	DeA-23965	Conifer bark	532.3	0.5	9139 ± 44	/
566.5	HOL-begin	Pollen-inferred age	/	1	11500 ± 250	/

Table 2 Responses of dependent variables to variations of the independent variables at Zminje jezero (Durmitor Massif, Montenegro), as determined by Generalized Additive Models. Dominant forest canopy species and anthropogenic indicators (pollen %); landscape-scale biomass burning and regional fire activity (MCHAR_{back} and mCHAR); climate (T_{July} anomalies of Lago Verdarolo) (Samartin et al., 2017). Edf = effective degree of freedom which indicate the complexity of the smooth (edf = 1 indicate a straight line). Ref.df = reference degrees of freedom used in computing test statistic and the P-values.

Independent variable	Dependent variable	edf	ref.df	F value	Deviance explained
Climate	<i>Picea abies</i>	1	1	3.676	6.52%
Climate	<i>Abies alba</i> ***	1	1	16.67	24.4%
Climate	<i>Fagus sylvatica</i> ***	2.997	3.782	10.46	52.1%
Climate	Biomass burning**	2.121	2.667	5.788	34.6%
Climate	Regional fire activity**	1	1	11.42	29.3%
Biomass burning	<i>Picea abies</i>	1	1	3.674	6.63%
Biomass burning	<i>Abies alba</i> ***	1	1	15.94	23%
Biomass burning	<i>Fagus sylvatica</i> ***	3.176	3.933	5.693	49%
Anthr. indicators	<i>Picea abies</i>	1.002	1.005	0.11	0.215%
Anthr. indicators	<i>Abies alba</i> ***	2.322	2.92	12.53	44.3%
Anthr. indicators	<i>Fagus sylvatica</i>	1.002	1.004	0.288	0.441%
Anthr. indicators	Biomass burning**	1.054	1.106	11.04	23.3%
Anthr. indicators	Regional fire activity	1	1	2.512	9.37%

* = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$

References

- Allevato E, Saulino L, Cesarano G, et al (2019) Canopy damage by spring frost in European beech along the Apennines: effect of latitude, altitude and aspect. *Remote Sensing of Environment* 225:431–440. <https://doi.org/10.1016/j.rse.2019.03.023>
- Ammann B, van der Knaap WO, Lang G, et al (2014) The potential of stomata analysis in conifers to estimate presence of conifer trees: examples from the Alps. *Veget Hist Archaeobot* 23:249–264. <https://doi.org/10.1007/s00334-014-0431-9>
- Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. *Forest Ecology and Management* 258:525–537. <https://doi.org/10.1016/j.foreco.2009.01.053>
- Behre K-E (1981) The interpretation of anthropogenic indicators in pollen diagrams. *Pollen et Spores* 23:225–245
- Bennett KD (1996) Determination of the number of zones in a biostratigraphical sequence. *New Phytologist* 132:155–170
- Bennett KD (2008) *Psimpoll v. 4.26*
- Beug H-J (2004) *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete*, Verlag Dr Friedrich Pfeil, Munich
- Birks H, Walters S (1973) *The flora and vegetation of Barro jezero, Durmitor, Montenegro*. Titograd
- Birks HH (2017) *Plant Macrofossil Introduction*. In: *Reference Module in Earth Systems and Environmental Sciences*. Elsevier
- Birks HH (2003) The importance of plant macrofossils in the reconstruction of Lateglacial vegetation and climate: examples from Scotland, western Norway, and Minnesota, USA. *Quaternary Science Reviews* 22:453–473. [https://doi.org/10.1016/S0277-3791\(02\)00248-2](https://doi.org/10.1016/S0277-3791(02)00248-2)
- Birks HJB, Gordon AD (1985) *Numerical Methods in Quaternary Pollen Analysis*. Academic Press, London
- Birks HJB, Tinner W (2016) Past forests of Europe. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, et al. (eds) *Past forests of Europe. European Atlas of Forest Tree Species*. Publication Office of the European Union, Luxembourg, pp 36–39
- Blaauw M, Christen JA (2011) Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Anal* 6:457–474. <https://doi.org/10.1214/11-BA618>
- Blarquez O, Carcaillet C, Elzein TM, Roiron P (2012) Needle accumulation rate model-based reconstruction of palaeo-tree biomass in the western subalpine Alps. *The Holocene* 22:579–587. <https://doi.org/10.1177/0959683611427333>
- Bobek P, Šamonil P, Jamrichová E (2018) Biotic controls on Holocene fire frequency in a temperate mountain forest, Czech Republic. *J Quaternary Sci* 33:892–904. <https://doi.org/10.1002/jqs.3067>
- Bobek P, Svobodová-Svitavská H, Pokorný P, et al (2019) Divergent fire history trajectories in Central European temperate forests revealed a pronounced influence of broadleaved trees on fire dynamics. *Quaternary Science Reviews* 222:105865. <https://doi.org/10.1016/j.quascirev.2019.105865>
- Boncina A (2011) History, current status and future prospects of uneven-aged forest management in the Dinaric region: an overview. *Forestry* 84:467–478. <https://doi.org/10.1093/forestry/cpr023>
- Borić D, Borovinić N, Đuričić L, et al (2019) Spearheading into the Neolithic: Last Foragers and First Farmers in the Dinaric Alps of Montenegro. *Eur j archaeol* 22:470–498. <https://doi.org/10.1017/ear.2019.14>

- Borić D, Cristiani E, Đuricic L, et al (2021) Holocene foraging in the Dinaric Alps: Current research on the Mesolithic of Montenegro. In: Borić D, Antonovic D, Mihailovic B (eds) FORAGING Assemblages Vol. 1. Serbian Archaeological Society -The Italian Academy for Advanced Studies in America, Belgrade, Republic of Serbia - Columbia University, New York
- Bowman DMJS, Balch J, Artaxo P, et al (2011) The human dimension of fire regimes on Earth: The human dimension of fire regimes on Earth. *Journal of Biogeography* 38:2223–2236. <https://doi.org/10.1111/j.1365-2699.2011.02595.x>
- Bradshaw RHW, Lindbladh M (2005) Regional spread and stand-scale establishment of *Fagus sylvatica* and *Picea abies* in Scandinavia. *Ecology* 86:1679–1686. <https://doi.org/10.1890/03-0785>
- Brown KJ, Giesecke T (2014) Holocene fire disturbance in the boreal forest of central Sweden: Holocene fire disturbance in the boreal forest, central Sweden. *Boreas* 43:639–651. <https://doi.org/10.1111/bor.12056>
- Buchwald E (2005) A hierarchical terminology for more or less natural forests in relation to sustainable management and biodiversity conservation. In: Third expert meeting on harmonizing forest-related definitions for use by various stakeholders Food and Agriculture Organization of the United Nations. Rome, pp 111–127
- Bulatović A, Gori M, Vander Linden M (2020) Radiocarbon dating the 3rd millennium BC in the Central Balkans: a re-examination of the early Bronze Age sequence. *Radiocarbon* 62:1163–1191. <https://doi.org/10.1017/RDC.2020.61>
- Cagliero E, Morresi D, Paradis L, et al (2021) Legacies of past human activities on one of the largest old-growth forests in the south-east European mountains. *Veget Hist Archaeobot*. <https://doi.org/10.1007/s00334-021-00862-x>
- Cappers RTJ, Bekker RM, Jans JEA (2006) Digital Seed Atlas of the Netherlands. Barkhuis Publishing & Groningen University Library, Groningen (Netherlands)
- Carter VA, Bobek P, Moravcová A, et al (2020) The role of climate-fuel feedbacks on Holocene biomass burning in upper-montane Carpathian forests. *Global and Planetary Change* 193:103264. <https://doi.org/10.1016/j.gloplacha.2020.103264>
- Carter VA, Moravcová A, Chiverrell RC, et al (2018) Holocene-scale fire dynamics of central European temperate spruce-beech forests. *Quaternary Science Reviews* 191:15–30. <https://doi.org/10.1016/j.quascirev.2018.05.001>
- Cheddadi R, Araújo MB, Maiorano L, et al (2016) Temperature range shifts for three European tree species over the last 10,000 years. *Front Plant Sci* 7:1581. <https://doi.org/10.3389/fpls.2016.01581>
- Chileen BV, McLauchlan KK, Higuera PE, et al (2020) Vegetation response to wildfire and climate forcing in a Rocky Mountain lodgepole pine forest over the past 2500 years. *The Holocene* 30:1493–1503
- Colombaroli D, Henne PD, Kaltenrieder P, et al (2010) Species responses to fire, climate and human impact at tree line in the Alps as evidenced by palaeo-environmental records and a dynamic simulation model. *Journal of Ecology* 98:1346–1357. <https://doi.org/10.1111/j.1365-2745.2010.01723.x>
- Conedera M, Krebs P, Tinner W, et al (2004) The cultivation of *Castanea sativa* Mill.) in Europe, from its origin to its diffusion on a continental scale. *Veget Hist Archaeobot* 13:161–179. <https://doi.org/10.1007/s00334-004-0038-7>
- Cozzolino M, Baković M, Borovinić N, et al (2020) The Contribution of Geophysics to the Knowledge of the Hidden Archaeological Heritage of Montenegro. *Geosciences* 10:187. <https://doi.org/10.3390/geosciences10050187>
- Csontos P, Vitalos M, Barina Z, Kiss L (2010) Early distribution and spread of *Ambrosia artemisiifolia* in Central and Eastern Europe. *Bot Helv* 120:75–78. <https://doi.org/10.1007/s00035-010-0072-2>

- Daniau A -L., Bartlein PJ, Harrison SP, et al (2012) Predictability of biomass burning in response to climate changes. *Global Biogeochem Cycles* 26:GB4007. <https://doi.org/10.1029/2011GB004249>
- Davies S, Lamb H, Roberts SJ (2015) Micro-XRF Core Scanning in Palaeolimnology: Recent Developments. In: Croudace IW, Rothwell RG (eds) *Micro-XRF Studies of Sediment Cores: Applications of a non-destructive tool for the environmental sciences*, Springer Nature
- Davis OK (1987) Spores of the dung fungus *Sporormiella*: Increased abundance in historic sediments and before Pleistocene megafaunal extinction. *Quaternary Research* 28:290–294. [https://doi.org/10.1016/0033-5894\(87\)90067-6](https://doi.org/10.1016/0033-5894(87)90067-6)
- Deza-Araujo M, Morales-Molino C, Tinner W, et al (2020) A critical assessment of human-impact indices based on anthropogenic pollen indicators. *Quaternary Science Reviews* 236:106291. <https://doi.org/10.1016/j.quascirev.2020.106291>
- Djurović P (2012) The Debeli Namet glacier (Durmitor, Montenegro) – from the second half of the 20th century to the present. *AGS* 52:277–301. <https://doi.org/10.3986/AGS52201>
- Dörfler W (2013) Prokoško Jezero: An environmental record from a subalpine lake in Bosnia-Herzegovina. In: Müller J, Rassmann K, Hofmann R (eds) *Okolište 1 – Untersuchungen Einer Späneolithischen Siedlungskammer in Zentralbosnien*, Universitätsforschungen Zur Prähistorischen Archäologie. Habelt Verlag, Bonn, pp 311–340
- Ellenberg H (2009) *Vegetation Ecology of Central Europe*, Fourth Edition. Cambridge University Press
- Enescu CM, Durrant TH, de Rigo D, Caudullo G (2016) *Corylus avellana* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, et al. (eds) *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, p e015486+
- Erdeljan J (2018) Cultural-historical heritage - a key to sustainable development of mountain areas. In: Jaćimović M (ed) *Sustainable Development of Mountain Areas - Experiences, Challenges and Perspectives*, Scientific Meetings. Montenegrin Academy of Sciences and Arts, Podgorica, pp 185–189
- European Environment Agency (2016) *European forest ecosystems: state and trends*. Publications Office, LU
- Feurdean A, Florescu G, Vannière B, et al (2017a) Fire has been an important driver of forest dynamics in the Carpathian Mountains during the Holocene. *Forest Ecology and Management* 389:15–26. <https://doi.org/10.1016/j.foreco.2016.11.046>
- Feurdean A, Tonkov S, Pfeiffer M, et al (2019) Fire frequency and intensity associated with functional traits of dominant forest type in the Balkans during the Holocene. *Eur J Forest Res* 138:1049–1066. <https://doi.org/10.1007/s10342-019-01223-0>
- Feurdean A, Veski S, Florescu G, et al (2017b) Broadleaf deciduous forest counterbalanced the direct effect of climate on Holocene fire regime in hemiboreal/boreal region (NE Europe). *Quaternary Science Reviews* 169:378–390. <https://doi.org/10.1016/j.quascirev.2017.05.024>
- Feurdean A, Willis KJ (2008) Long-term variability of *Abies alba* in NW Romania: implications for its conservation management. *Diversity and Distributions* 14:1004–1017. <https://doi.org/10.1111/j.1472-4642.2008.00514.x>
- Feurdean AN, Willis KJ, Astaloş C (2009) Legacy of the past land-use changes and management on the ‘natural’ upland forest composition in the Apuseni Natural Park, Romania. *The Holocene* 19:967–981. <https://doi.org/10.1177/0959683609337358>
- Finsinger W, Fevre J, Orbán I, et al (2018) Holocene fire-regime changes near the treeline in the Retezat Mts. (Southern Carpathians, Romania). *Quaternary International* 477:94–105. <https://doi.org/10.1016/j.quaint.2016.04.029>

- Finsinger W, Heiri O, Valsecchi V, et al (2007) Modern pollen assemblages as climate indicators in southern Europe. *Global Ecology and Biogeography* 16:567–582. <https://doi.org/10.1111/j.1466-8238.2007.00313.x>
- Finsinger W, Kelly R, Fevre J, Magyari EK (2014) A guide to screening charcoal peaks in macrocharcoal-area records for fire-episode reconstructions. *The Holocene* 24:1002–1008. <https://doi.org/10.1177/0959683614534737>
- Finsinger W, Morales-Molino C, Galka M, et al (2017) Holocene vegetation and fire dynamics at Crveni Potok, a small mire in the Dinaric Alps (Tara National Park, Serbia). *Quaternary Science Reviews* 167:63–77. <https://doi.org/10.1016/j.quascirev.2017.04.032>
- Finsinger W, Tinner W (2019) New insights on stomata analysis of European conifers 65 years after the pioneering study of Werner Trautmann (1953). *Veget Hist Archaeobot* 29:393–406. <https://doi.org/10.1007/s00334-019-00754-1>
- Finsinger W, Tinner W (2005) Minimum count sums for charcoal concentration estimates in pollen slides: accuracy and potential errors. *The Holocene* 15:293–297. <https://doi.org/10.1191/0959683605hl808rr>
- Finsinger W, Vanel Q, Ribolini A, Tinner W (2021) Early to late Holocene vegetation and fire dynamics at the treeline in the Maritime Alps. *Veget Hist Archaeobot* 30:507–524. <https://doi.org/10.1007/s00334-020-00795-x>
- Forenbahe S, Miracle PT (2005) The spread of farming in the Eastern Adriatic. *Antiquity* 79:514–528
- Gachev E, Mitkov I (2019) Small glaciers in Pirin (Bulgaria) and Durmitor (Montenegro) as glacio-karstic features. Similarities and differences in their recent behaviour. *Quaternary International* 504:153–170. <https://doi.org/10.1016/j.quaint.2018.03.032>
- Gardner AR, Willis KJ (1999) Prehistoric farming and the postglacial expansion of beech and hombeam: a comment on Küster. *The Holocene* 9:119–121. <https://doi.org/10.1191/09596839968254353>
- Gavin DG, Hu SH, Lertzman K, Corbett P (2006) Weak climatic control of stand-scale fire history during the late Holocene. *Ecology* 87:1722–1732
- Giesecke T, Davis B, Brewer S, et al (2014) Towards mapping the late Quaternary vegetation change of Europe. *Veget Hist Archaeobot* 23:75–86. <https://doi.org/10.1007/s00334-012-0390-y>
- Giesecke T, Hickler T, Kunkel T, et al (2007) Towards an understanding of the Holocene distribution of *Fagus sylvatica* L. *Journal of Biogeography* 34:118–131. <https://doi.org/10.1111/j.1365-2699.2006.01580.x>
- Godet J-D (1998) *Einheimische Bäume und Sträucher*. Arboris Verlag, Hinterkappelen-Bern (Switzerland)
- Grindean R, Tanțău I, Feurdean A (2019) Linking vegetation dynamics and stability in the old-growth forests of Central Eastern Europe: Implications for forest conservation and management. *Biological Conservation* 229:160–169. <https://doi.org/10.1016/j.biocon.2018.11.019>
- Hafner A, Reich J, Ballmer A, et al (2021) First absolute chronologies of Neolithic and bronze age settlements at Lake Ohrid based on dendrochronology and radiocarbon dating. *Journal of Archaeological Science: Reports* 38:103107. <https://doi.org/10.1016/j.jasrep.2021.103107>
- Hastie T, Tibshirani R (1986) Generalized Additive Models. *Statistical Science* 1:297–318
- Heiri O, Brooks SJ, Renssen H, et al (2014) Validation of climate model-inferred regional temperature change for late-glacial Europe. *Nat Commun* 5:4914. <https://doi.org/10.1038/ncomms5914>
- Heiri O, Wick L, van Leeuwen JFN, et al (2003) Holocene tree immigration and the chironomid fauna of a small Swiss subalpine lake (Hinterburgsee, 1515 m asl). *Palaeogeography, Palaeoclimatology, Palaeoecology* 189:35–53. [https://doi.org/10.1016/S0031-0182\(02\)00592-8](https://doi.org/10.1016/S0031-0182(02)00592-8)

- Henne PD, Elkin C, Colombaroli D, et al (2013) Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modeling. *Landscape Ecol* 28:819–833. <https://doi.org/10.1007/s10980-012-9782-8>
- Henne PD, Elkin CM, Reineking B, et al (2011) Did soil development limit spruce (*Picea abies*) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model: Soil depth limits spruce expansion in the Alps. *Journal of Biogeography* 38:933–949. <https://doi.org/10.1111/j.1365-2699.2010.02460.x>
- Higuera P, Peters M, Brubaker L, Gavin D (2007) Understanding the origin and analysis of sediment-charcoal records with a simulation model. *Quaternary Science Reviews* 26:1790–1809. <https://doi.org/10.1016/j.quascirev.2007.03.010>
- Higuera PE, Brubaker LB, Anderson PM, et al (2009) Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs* 79:201–219. <https://doi.org/10.1890/07-2019.1>
- Higuera PE, Gavin DG, Bartlein PJ, Hallett DJ (2010a) Peak detection in sediment - charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *Int J Wildland Fire* 19:996–1014. <https://doi.org/10.1071/WF09134>
- Higuera PE, Gavin DG, Bartlein PJ, Hallett DJ (2010b) Peak detection in sediment - charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *Int J Wildland Fire* 19:996–1014. <https://doi.org/10.1071/WF09134>
- Higuera PE, Sprugel DG, Brubaker LB (2005) Reconstructing fire regimes with charcoal from small-hollow sediments: a calibration with tree-ring records of fire. *The Holocene* 15:238–251. <https://doi.org/10.1191/0959683605hl789rp>
- Hilmers T, Avdagić A, Bartkiewicz L, et al (2019) The productivity of mixed mountain forests comprised of *Fagus sylvatica*, *Picea abies*, and *Abies alba* across Europe. *Forestry: An International Journal of Forest Research* 92:512–522. <https://doi.org/10.1093/forestry/cpz035>
- Horvat I, Glavač V, Ellenberg H (1974) *Vegetation of Southeast Europe*. Gustav Fischer Verlag, Stuttgart
- Houston Durrant T, de Rigo D, Caudullo G (2016) *Alnus glutinosa* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, et al. (eds) *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, p e01f3c0+
- Hubay K, Braun M, Harangi S, et al (2018) High-resolution peat core chronology covering the last 12 KYR applying an improved peat bog sampling. *Radiocarbon* 60:1367–1378. <https://doi.org/10.1017/RDC.2018.113>
- Jain P, Castellanos-Acuna D, Coogan SCP, et al (2022) Observed increases in extreme fire weather driven by atmospheric humidity and temperature. *Nature Climate Change* 12:63–70. <https://doi.org/10.1038/s41558-021-01224-1>
- Kaplan JO, Krumhardt KM, Zimmermann N (2009) The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews* 28:3016–3034. <https://doi.org/10.1016/j.quascirev.2009.09.028>
- Karadzic S, Sibalic V (1997) Drobnjak, porodice u Drobnjaku i njihovo porijeklo: Drobnjak, Jezera, Uskoci i Šaranci, IŠ “Stručna knjiga.” Beograd
- Katz NJ, Katz SV, Kipiani MG (1965) *Atlas and Keys of Fruits and Seeds Occurring in the Quaternary Deposits of the USSR*. NAUKA, Moscow (Russia)
- Kelly RF, Higuera PE, Barrett CM, Hu FS (2011) A signal-to-noise index to quantify the potential for peak detection in sediment–charcoal records. *Quat res* 75:11–17. <https://doi.org/10.1016/j.yqres.2010.07.011>

- Killick R, Eckley IA (2014) **change**point : An R Package for Changepoint Analysis. J Stat Soft 58:1–19. <https://doi.org/10.18637/jss.v058.i03>
- Klopcic M, Mina M, Bugmann H, Boncina A (2017) The prospects of silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst) in mixed mountain forests under various management strategies, climate change and high browsing pressure. European Journal of Forest Research 136:1071–1090. <https://doi.org/DOI.10.1007/s10342-017-1052-5>
- Knorn J, Kuemmerle T, Radeloff VC, et al (2013) Continued loss of temperate old-growth forests in the Romanian Carpathians despite an increasing protected area network. Envir Conserv 40:182–193. <https://doi.org/10.1017/S0376892912000355>
- Kranjc A (2009) History of deforestation and reforestation in the Dinaric karst. Geographical Research 47:15–23. <https://doi.org/10.1111/j.1745-5871.2008.00552.x>
- Longman J, Veres D, Finsinger W, Ersek V (2018) Exceptionally high levels of lead pollution in the Balkans from the Early Bronze Age to the Industrial Revolution. Proc Natl Acad Sci USA 115:E5661–E5668. <https://doi.org/10.1073/pnas.1721546115>
- Makra L, Juhász M, Béczi R, Borsos E (2005) The history and impacts of airborne *Ambrosia* (Asteraceae) pollen in Hungary. Grana 44:57–64. <https://doi.org/10.1080/00173130510010558>
- Markgraf V (1980) Pollen Dispersal in a Mountain Area. Grana 19:127–146. <https://doi.org/10.1080/00173138009424995>
- McConnell JR, Wilson AI, Stohl A, et al (2018) Lead pollution recorded in Greenland ice indicates European emissions tracked plagues, wars, and imperial expansion during antiquity. Proc Natl Acad Sci USA 115:5726–5731. <https://doi.org/10.1073/pnas.1721818115>
- Mercuri AM, Bandini Mazzanti M, Florenzano A, et al (2013) *Olea*, *Juglans* and *Castanea*: The OJC group as pollen evidence of the development of human-induced environments in the Italian peninsula. Quaternary International 303:24–42. <https://doi.org/10.1016/j.quaint.2013.01.005>
- Mihailović D (2007) Social aspects of the transition to farming in the Balkans. Doc praeh 34:72–88. <https://doi.org/10.4312/dp.34.6>
- Mirković M (1983) Geological Composition and Tectonic Setting of Durmitor, Pivske Planine Geološki and Volujak - Geološki sastav i tektonski sklop Durmitora, Pivske planine i Volujka, Geološki Glasnik. Zavod za geološka istraživanja, Titograd
- Moore PD, Webb JA, Collinson ME (1998) Pollen Analysis. Blackwell Science Ltd., Oxford (UK)
- Morales-Molino C, Steffen M, Samartin S, et al (2020) Long-Term responses of Mediterranean mountain forests to climate change, fire and human activities in the Northern Apennines (Italy). Ecosystems. <https://doi.org/10.1007/s10021-020-00587-4>
- Nagel TA, Mikac S, Dolinar M, et al (2017) The natural disturbance regime in forests of the Dinaric Mountains: A synthesis of evidence. Forest Ecology and Management 388:29–42. <https://doi.org/10.1016/j.foreco.2016.07.047>
- Panagiotopoulos K, Aufgebauer A, Schäbitz F, Wagner B (2013) Vegetation and climate history of the Lake Prespa region since the Lateglacial. Quaternary International 293:157–169. <https://doi.org/10.1016/j.quaint.2012.05.048>
- Pasta S, de Rigo D, Caudullo G (2016) *Ostrya carpinifolia* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, et al. (eds) European Atlas of Forest Tree Species. Publ. Off. EU, Luxembourg, p e01fd3d+

- Pausas JG, Paula S (2012) Fuel shapes the fire-climate relationship: evidence from Mediterranean ecosystems: Fuel shapes the fire-climate relationship. *Global Ecology and Biogeography* 21:1074–1082. <https://doi.org/10.1111/j.1466-8238.2012.00769.x>
- Perşoiu A, Onac BP, Wynn JG, et al (2017) Holocene winter climate variability in Central and Eastern Europe. *Sci Rep* 7:1196. <https://doi.org/10.1038/s41598-017-01397-w>
- Pieroni A, Ibraliu A, Abbasi AM, Papajani-Toska V (2015) An ethnobotanical study among Albanians and Aromanians living in the Rraicë and Mokra areas of Eastern Albania. *Genet Resour Crop Evol* 62:477–500. <https://doi.org/10.1007/s10722-014-0174-6>
- Polunin O (1980) *Flowers of Greece and the Balkans: A field guide*. Oxford University Press, Oxford
- Power MJ, Marlon J, Ortiz N, et al (2008) Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data. *Clim Dyn* 30:887–907. <https://doi.org/10.1007/s00382-007-0334-x>
- Quave CL, Pieroni A (2015) A reservoir of ethnobotanical knowledge informs resilient food security and health strategies in the Balkans. *Nature Plants* 1:14021. <https://doi.org/10.1038/nplants.2014.21>
- R Core Team (2020) *R: a Language and Environment for Statistical Computing*
- Rasmussen SO, Bigler M, Blockley SP, et al (2014) A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. *Quaternary Science Reviews* 106:14–28. <https://doi.org/10.1016/j.quascirev.2014.09.007>
- Rastoder Š (2003) A short review of the history of Montenegro. In: Bieber F (ed) *Montenegro in transition: problems of identity and statehood*. Nomos Verlagsgesellschaft, Baden-Baden, pp 107–140
- Reille M (1992) *Pollen et Spores d'Europe et d'Afrique du Nord*. Laboratoire de Botanique Historique et Palynologie, Marseille (France)
- Reimer PJ, Austin WEN, Bard E, et al (2020) The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). *Radiocarbon* 62:725–757. <https://doi.org/10.1017/RDC.2020.41>
- Renberg I, Bindler R, Brännvall M-L (2001) Using the historical atmospheric lead-deposition record as a chronological marker in sediment deposits in Europe. *The Holocene* 11:511–516. <https://doi.org/10.1191/095968301680223468>
- Sabatier P, Nicolle M, Piot C, et al (2020) Past African dust inputs in the western Mediterranean area controlled by the complex interaction between the Intertropical Convergence Zone, the North Atlantic Oscillation, and total solar irradiance. *Clim Past* 16:283–298. <https://doi.org/10.5194/cp-16-283-2020>
- Sabatini FM, Burrascano S, Keeton WS, et al (2018) Where are Europe's last primary forests? Diversity and Distributions 24:1426–1439. <https://doi.org/10.1111/ddi.12778>
- Samartin S, Heiri O, Joos F, et al (2017) Warm Mediterranean mid-Holocene summers inferred from fossil midge assemblages. *Nature Geosci* 10:207–212. <https://doi.org/10.1038/ngeo2891>
- Schlachter KJ, Horn SP (2010) Sample preparation methods and replicability in macroscopic charcoal analysis. *J Paleolimnol* 44:701–708. <https://doi.org/10.1007/s10933-009-9305-z>
- Schoch WH, Pawlik B, Schweingruber FH (1988) *Botanical Macro-remains: an Atlas for the Determination of Frequently Encountered and Ecologically Important Plant Seeds*. Paul Haupt, Bern (Switzerland)
- Seidl R, Thom D, Kautz M, et al (2017) Forest disturbances under climate change. *Nature Clim Change* 7:395–402. <https://doi.org/10.1038/nclimate3303>

- Siegmund JF, Siegmund N, Donner RV (2017) CoinCalc -- A new R package for quantifying simultaneities of event series. *Computers & Geosciences* 98:64–72. <https://doi.org/10.1016/j.cageo.2016.10.004>
- Sikkema R, Caudullo G (2016) *Carpinus orientalis* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, et al. (eds) *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, p e01bf18+
- Sikkema R, Caudullo G, de Rigo D (2016) *Carpinus betulus* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, et al. (eds) *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, p e01d8cf+
- Spiegelberger T, Matthies D, Müller-Schärer H, Schaffner U (2006) Scale-dependent effects of land use on plant species richness of mountain grassland in the European Alps. *Ecography* 29:541–548. <https://doi.org/10.1111/j.0906-7590.2006.04631.x>
- Srdanović M, Pavić D (2013) Environmental protection and major ecological problems in the National Park Durmitor. *Researches Reviews of the Department of Geography, Tourism and Hotel Management* 42:82–90
- Stockmarr J (1971) Tablets with spores used in absolute pollen analysis. *Pollen Spores* 13:615–621
- Sugita S (1994) Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *The Journal of Ecology* 82:881–897. <https://doi.org/10.2307/2261452>
- Tinner W, Colombaroli D, Heiri O, et al (2013) The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. *Ecological Monographs* 83:419–439. <https://doi.org/10.1890/12-2231.1>
- Tinner W, Conedera M, Ammann B, et al (1998) Pollen and charcoal in lake sediments compared with historically documented forest fires in southern Switzerland since AD 1920. *The Holocene* 8:31–42. <https://doi.org/10.1191/095968398667205430>
- Tinner W, Conedera M, Ammann B, Lotter AF (2005) Fire ecology north and south of the Alps since the last ice age. *The Holocene* 15:1214–1226. <https://doi.org/10.1191/0959683605hl892rp>
- Tinner W, Conedera M, Gobet E, et al (2000) A palaeoecological attempt to classify fire sensitivity of trees in the southern Alps. *The Holocene* 10:565–574. <https://doi.org/10.1191/095968300674242447>
- Tinner W, Hu FS (2003) Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. *The Holocene* 13:499–505. <https://doi.org/10.1191/0959683603hl615rp>
- Tinner W, Lotter A (2006) Holocene expansions of *Fagus sylvatica* and *Abies alba* in Central Europe: where are we after eight decades of debate? *Quaternary Science Reviews* 25:526–549. <https://doi.org/10.1016/j.quascirev.2005.03.017>
- Tinner W, Lotter AF, Ammann B, et al (2003) Climatic change and contemporaneous land-use phases north and south of the Alps 2300 BC to 800 AD. *Quaternary Science Reviews* 22:1447–1460. [https://doi.org/10.1016/S0277-3791\(03\)00083-0](https://doi.org/10.1016/S0277-3791(03)00083-0)
- Tóth M, Magyari EK, Buczkó K, et al (2015) Chironomid-inferred Holocene temperature changes in the South Carpathians (Romania). *The Holocene* 25:569–582. <https://doi.org/10.1177/0959683614565953>
- UNESCO (2005) UNESCO Global Strategy. <https://whc.unesco.org/en/list/100/>. Accessed 8 Nov 2021
- UNESCO and IUCN (2018) Joint World Heritage Centre/IUCN Advisory mission to the World Heritage property “Durmitor National Park” (Montenegro). UNESCO World Heritage Centre and IUCN, Paris, France and Gland, Switzerland

- van der Knaap WO, van Leeuwen JFN, Fankhauser A, Ammann B (2000) Palynostratigraphy of the last centuries in Switzerland based on 23 lake and mire deposits: chronostratigraphic pollen markers, regional patterns, and local histories. *Review of Palaeobotany and Palynology* 108:85–142. [https://doi.org/10.1016/S0034-6667\(99\)00035-4](https://doi.org/10.1016/S0034-6667(99)00035-4)
- Vander Linden M, Pandžić I, Orton D (2014) New radiocarbon dates for the Neolithic period in Bosnia & Herzegovina. *Godišnjak* 43:7–34. <https://doi.org/10.5644/Godisnjak.CBI.ANUBiH-43.35>
- Vislobokova IA, Agadzhanyan AK, Lopatin AV (2020) The case of Trlica TRL11–10 (Montenegro): Implications for possible early hominin dispersals into the Balkans in the middle of the Early Pleistocene. *Quaternary International* 554:15–35. <https://doi.org/10.1016/j.quaint.2020.06.025>
- Wagner B, Lotter AF, Nowaczyk N, et al (2009) A 40,000-year record of environmental change from ancient Lake Ohrid (Albania and Macedonia). *J Paleolimnol* 41:407–430. <https://doi.org/10.1007/s10933-008-9234-2>
- Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and Earlier Spring Increase Western U.S. Forest Wildfire Activity. *Science* 313:940–943. <https://doi.org/10.1126/science.1128834>
- Whitlock C, Larsen C (2001) Charcoal as a fire proxy. In: Smol JP, Birks HJB, Last WM, et al. (eds) *Tracking Environmental Change Using Lake Sediments*. Springer Netherlands, Dordrecht, pp 75–97
- Willis KJ (1994) The vegetational history of the Balkans. *Quaternary Science Reviews* 13:769–788. [https://doi.org/10.1016/0277-3791\(94\)90104-X](https://doi.org/10.1016/0277-3791(94)90104-X)
- Willis KJ (1992) The late Quaternary vegetational history of northwest Greece. II. Rezina marsh. *New Phytol* 121:119–138. <https://doi.org/10.1111/j.1469-8137.1992.tb01098.x>
- Wirth C, Gleixner G, Heimann M (eds) (2009) *Old-growth forests: function, fate, and value*. Springer, Berlin
- Wood SN (2017) *Generalized additive models: an introduction with R*, Second edition. CRC Press/Taylor & Francis Group, Boca Raton
- Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models: Estimation of Semiparametric Generalized Linear Models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 73:3–36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>
- World Heritage Committee (2017) *Durmitor National Park*. <http://world-heritage-datasheets.unep-wcmc.org/datasheet/output/site/durmitor-national-park/>

Electronic Supplementary Material

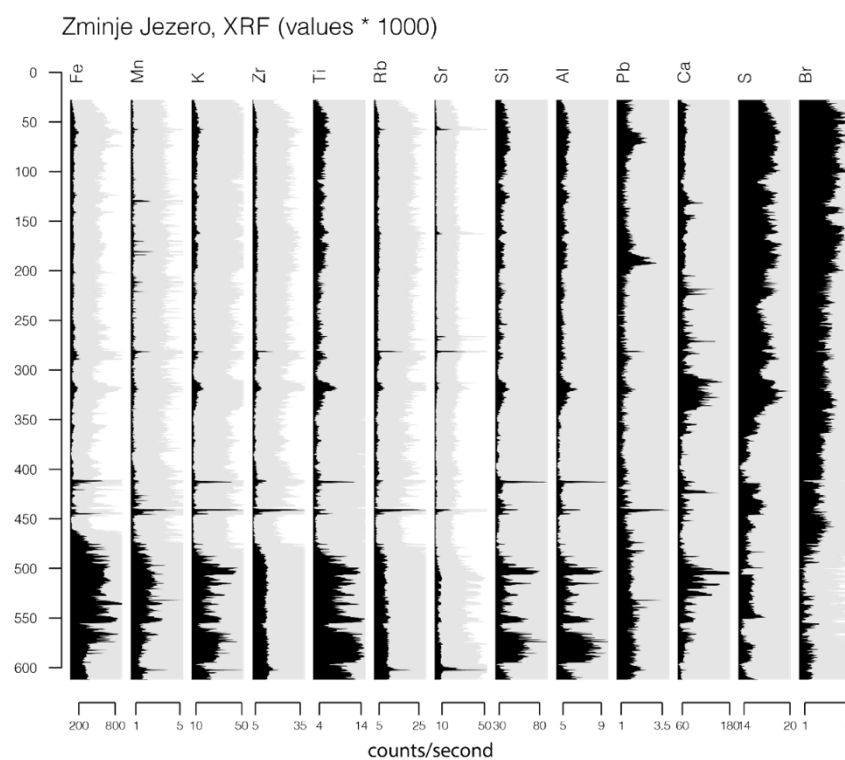


Fig. S1 XRF geochemical profiles of the sediment core extracted from Zminje jezero (Durmitor Massif, Montenegro).

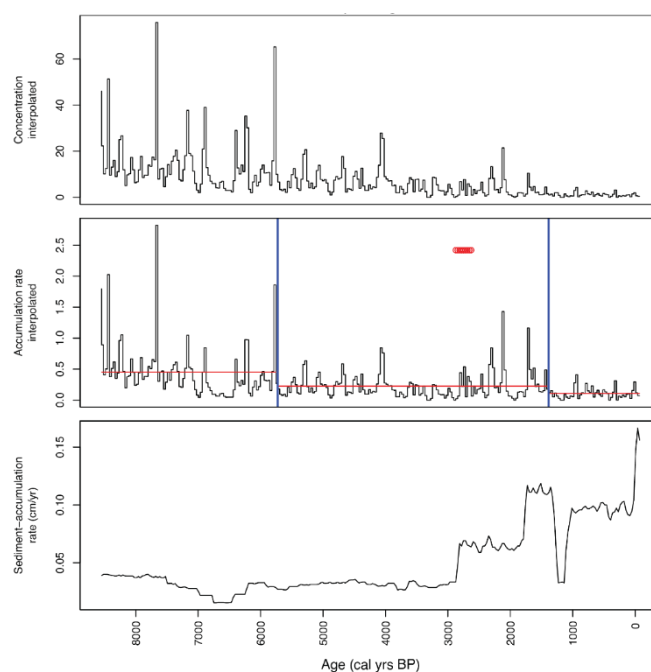


Fig. S2 Interpolated charcoal concentration (top panel), charcoal accumulation rate (MCHAR, middle panel) and sample accumulation rate (bottom panel) for Zminje Jezero. Vertical blue lines indicate change points in the MCHAR records, red empty circles represent change points in the randomly generated CHAR records.

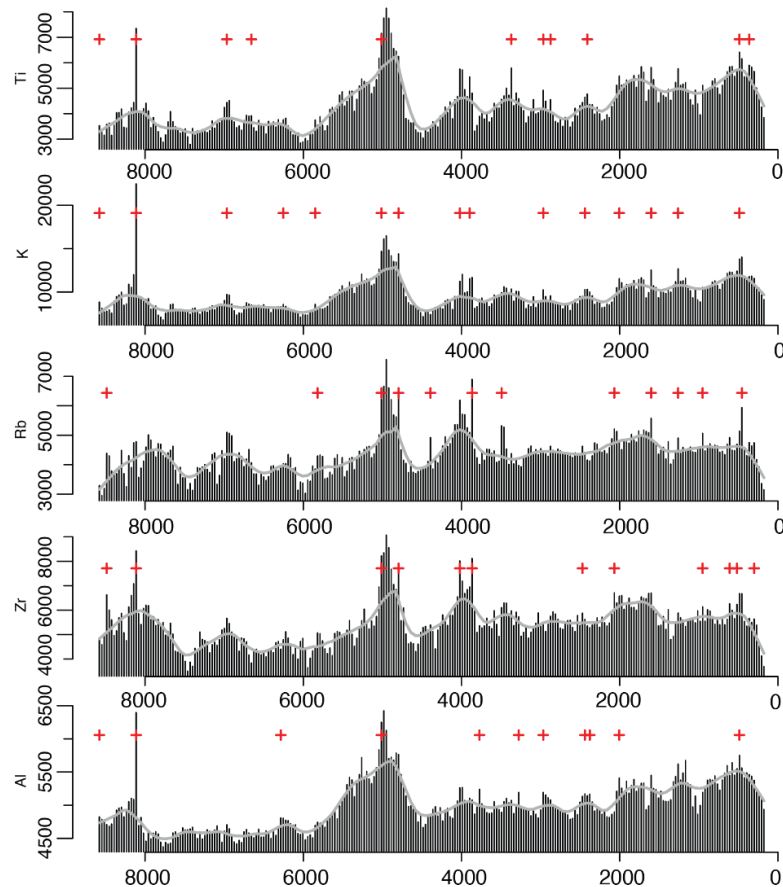


Fig. S3 Peak analysis results of the XRF elements indicating erosion (titanium, potassium, rubidium, zirconium, aluminium). Elements accumulation rates were interpolated to 31 years (black bars) and elements backgrounds were modelled using a 500-year smoothing window (grey line). Identified elements peaks are marked with red “+” symbols.

Table S1 List of taxa of anthropogenic indicator pollen used to calculate indexes of human impact at Zminje jezero following Deza-Araujo et al. (2020).

Approach	Pollen types included
PI Primary anthropogenic indicators (Behre 1981; Lang 1994)	<i>Secale cereale</i>
SI Secondary anthropogenic indicators (Behre 1981; Lang 1994)	Adventives: <i>Plantago lanceolata</i> -type, <i>Plantago major/media</i> -type Apophytes: <i>Rumex acetosa</i> -type, <i>Jasione/Campanula</i> -type, <i>Urtica</i> -type, <i>Artemisia</i> , <i>Melampyrum</i> , <i>Pteridium aquilinum</i> -type, <i>Polypodium vulgare</i> -type, <i>Juniperus</i> -type, <i>Veratrum album</i>
CI Cultural indicators (Tinner et al. 2003)	<i>Plantago lanceolata</i> -type, Poaceae Cerealia-type
OJC (Mercuri et al. 2013)	<i>Olea europea</i> , <i>Juglans regia</i> , <i>Castanea sativa</i>

References

- Behre K-E (1981) The interpretation of anthropogenic indicators in pollen diagrams. *Pollen et Spores* 23:225–245
- Deza-Araujo M, Morales-Molino C, Tinner W, et al (2020) A critical assessment of human-impact indices based on anthropogenic pollen indicators. *Quaternary Science Reviews* 236:106291. <https://doi.org/10.1016/j.quascirev.2020.106291>
- Lang G (1994) *Quartäre Vegetationsgeschichte Europas: Methoden und Ergebnisse*. Gustav Fischer, Jena/Stuttgart/New York
- Mercuri AM, Bandini Mazzanti M, Florenzano A, et al (2013) *Olea*, *Juglans* and *Castanea*: The OJC group as pollen evidence of the development of human-induced environments in the Italian peninsula. *Quaternary International* 303:24–42. <https://doi.org/10.1016/j.quaint.2013.01.005>
- Tinner W, Lotter AF, Ammann B, et al (2003) Climatic change and contemporaneous land-use phases north and south of the Alps 2300 BC to 800 AD. *Quaternary Science Reviews* 22:1447–1460. [https://doi.org/10.1016/S0277-3791\(03\)00083-0](https://doi.org/10.1016/S0277-3791(03)00083-0)

Discussion and Conclusion

By combining assessments of contemporary forests structure and composition, remote sensing analyses and multi-proxy palaeoecological records (pollen, spores, stomata, plant macrofossils, microscopic and macroscopic charcoal, magnetic susceptibility and geochemical analyses of sediment composition) from two study sites, this dissertation advanced our knowledge on the long-term vegetation dynamics of mixed spruce-fir-beech mountain forest ecosystems of the central Dinaric Alps over the past c. 12,500 years. The dissertation contributed to gain insights on the role of human impact and fire in shaping mountain forests and on the responses of fir, beech, and spruce to variations in climate, fire, and human impact (Papers 2 and 4). To our knowledge, this dissertation presented the first records of fire, vegetation, and land-use pressure history from the montane zone of the Dinaric Alps that span most of the Holocene (Paper 4), i.e. the last 11,700 years b2k (before CE 2000) (Walker et al. 2009). Moreover, it showed how fires and land-use influenced the long-term dynamics of currently small and fragmented primary and old-growth forests in the inner Dinaric Alps (Papers 2 and 3). From a methodological perspective, the dissertation demonstrated ways to integrate neoecology and palaeoecology (Rull 2010) in order to better understand ecological processes in mountain forest ecosystems (Papers 2 and 3), and applied a novel methodological approach to distinguish between high-severity catchment fires and lower severity/extra-local fires using sedimentary charcoal records (Papers 2 and 4). Additionally, it pointed out the limitations of coupling an object-based image analysis (OBIA) and a Random Forest classifier on very-high-resolution satellite imagery for mapping forest canopy gaps (Paper 1). Finally, it used two different methods to explore species responses to environmental changes: cross-correlations (CCs, Paper 2) and generalized additive models (GAMs, Paper 4). CCs display the relationship between two independent variables within a chosen time lag providing evidence for direction and rates of succession of forest vegetation (Green 1981; Tinner et al. 1999; Valsecchi et al. 2008). GAMs, instead, employ a link function to illustrate the relationship between the mean of the response variable and a smoothed function of the predictor variable over the whole time series, unfolding species' optima and tolerance towards climate conditions (e.g., summer temperatures) and disturbances (e.g., human impact, fire) (Hastie and Tibshirani 1986; Colombaroli et al. 2010; Carter et al. 2020).

General findings

Results of this dissertation seem to confirm, as suggested by the modelled retrospective study of Kaplan et al. (2009), that forests of southeastern Europe (in this case of Montenegro) were not heavily exploited or cleared until the Middle Ages. Moreover, the findings seem to support the presumed high naturalness of some mountain forest ecosystems located in the central Dinaric Alps (Boncina 2011; Nagel et al.

2017). Both palaeoecological records (Papers 2 and 4) showed an unusual late-Holocene persistence of high tree cover that contrasts with the majority of European tree cover records, which show massive anthropogenic land-cover changes in the past two-three millennia (Fyfe et al. 2015). However, land-use pressure (agriculture and pastures) as well as fires (possibly human-induced) likely played an important role in reducing the area of fir-spruce-beech old-growth forests during the Middle Ages (Papers 2 and 3). The legacies of these past land-use activities could be visible in the composition and structure of current forests (Papers 2 and 3). A greater human impact in the mountain areas of the Dinaric Alps during the past 500-1000 years could have been responsible for the reduction in species richness of mixed forests, leading to the dominance of a single species (*P. abies* in the Durmitor and *F. sylvatica* at Biogradska Gora). Contrary to the view that fire is considered a negligible disturbance agent in spruce-fir-beech mountain forests of the Dinaric region (Nagel et al. 2017), the new records presented in this dissertation (Paper 4) support emerging literature demonstrating that fires have been an important disturbance agent throughout the Holocene in such ecosystems (Niklasson et al. 2010; Carter et al. 2018; Bobek et al. 2018a).

Species responses

Global surface temperature has increased by 0.99°C during the period 2001-2020 CE and will further increase in the coming decades (IPCC 2021). In Europe, regional climate scenarios predict warmer temperatures (> 2.5°C) and an increased frequency of severe drought events (Christensen et al. 2007; Kovats et al. 2014). Prolonged periods of drought will, on the one hand, promote forest fires, which are expected to increase even in areas where they have historically been of minor importance (Schmuck et al. 2015; Wu et al. 2015). On the other hand, they will cause drought stress on vegetation by further increasing the vulnerability of mountain forests to fire and other disturbances. In this context, knowledge of the responses of silver fir, European beech, and Norway spruce to variations in climate, fire, and human activity offers critical information to identify species' environmental optima and disturbance tolerance (Colombaroli et al. 2010) and to infer the future vulnerability of a large part of European mountain forest ecosystems. However, to be effective, the prediction of future species distributions and their sensitivity to future environmental changes should not only be based on the current ecology of the species as inferred from modern ecosystems, but should also take into account past variation in environmental changes that drive species' ranges (Tinner et al. 2013; Cheddadi et al. 2016; Finsinger et al. 2021). In this dissertation, the use of palaeoecological records allowed detecting responses of beech, spruce, and fir to environmental changes under substantially different environmental conditions than the present ones, including temperatures analogous to those predicted by future climate changes (approximately 1-2°C higher than present) (Samartin et al. 2017; Carter et al. 2018; Morales-Molino et al. 2020). As the three species considered in this thesis show a different

tolerance to a large number of climatic parameters (e.g. winter cold, available humidity in summer), we are aware of the limitation of using the average July temperatures as the only climatic proxy. Therefore, investigating the long-term responses of *A. alba*, *F. sylvatica* and *P. abies* to winter temperatures and precipitation reconstructed by models (e.g. CCSM3, Fordham et al. 2017; MCM, Kuneš et al. 2015) or by other types of proxies (e.g. isotopes) would be an avenue worth exploring in future researches.

Silver fir

From the new records it emerges that *A. alba* was promoted by warmer-than-present summer temperatures (up to c. 2.5 °C) (Paper 4). A similar response curve was obtained by Morales-Molino et al. (2020) from long-term ecological observations in the Northern Apennines. This is not surprising considering that *A. alba* co-occurred with thermophilus taxa in meso- and sub-Mediterranean forests during the mid-Holocene (c. 6000 cal yr BP) (Tinner et al. 2013; Di Pasquale et al. 2014; Henne et al. 2015). In keeping with this, warming temperatures led to an increase in *A. alba* growth rates in European mountain forests during the last four decades (Büntgen et al. 2014; Gazol et al. 2015; Bosela et al. 2018; Hilmers et al. 2019).

However, strikingly the new record also shows that *A. alba* responded positively to increasing landscape-scale biomass burning (Paper 4). This contrasts with a number of records showing that *A. alba* is a fire-sensitive species and that both high-severity infrequent and low-severity frequent fires led to its rapid decline or to local extinctions in recent millennia (Tinner et al. 2000, 2013; Morales-Molino et al. 2020). On the one hand, the positive response of *A. alba* to biomass burning could simply arise from the positive relationship between biomass burning and summer temperatures. On the other hand, most records showing a negative influence of fires on *A. alba* also document excessive human-induced fire activity, supporting the view that the combined effects of land use and human-driven fires were the main causes of *A. alba* population reduction in recent millennia (Feurdean and Willis 2008; Tinner et al. 2013). In contrast, the new record shows that fire activity did not increase in conjunction with the decline of *A. alba*. Moreover, the persistence of *A. alba* in the surroundings of Zminje jezero supports the view that *A. alba* could be relatively resistant to low frequency and low severity fires or even rare high-severity fires (Tinner et al. 2005; Wick and Möhl 2006; Henne et al. 2013; Feurdean et al. 2019). However, human impact increased, suggesting that humans did not extensively use fire to clear the forests in the Durmitor and that land use rather than fires substantially contributed to the decline of *A. alba* populations, as also supported by the significant negative response of *A. alba* to increasing human impact (Paper 4). The generality of this notion is, however, possibly limited, as human-driven fires likely led to the *A. alba* decline in the Biogradska Gora valley (Paper 2). At this site, the sensitivity of *A. alba* to human impact is also evidenced by a positive correlation between the cost of access (as proxy of potential human pressure) and the basal area of *A. alba*, indicating that in the more accessible areas

of the valley, and thus more prone to anthropogenic disturbances, the abundance of *A. alba* is significantly lower. Thus, the insights from this dissertation support the view that although *A. alba* is a good competitor when disturbances are small or infrequent, its regeneration success is limited when the frequency and severity of disturbances increase, due to the lack of re-sprouting capacity (e.g., after a fire or a cutting), a late reproductive maturity (Feurdean and Willis 2008; Feurdean et al. 2019), and palatable regeneration extremely sensitive to browsing by wild and domestic ungulates (Motta 1996; Diaci et al. 2011; Klopčič et al. 2017).

European beech

F. sylvatica emerged as a species sensitive to increasing summer temperatures (Paper 4). In line with this, even if the response is strongly dependent from altitude, site, and water supply, beech growth generally declined over the last three decades in European mountain areas due to the increase of drought stress and of late frost events (Dittmar et al. 2003; Allevato et al. 2019), particularly in southern Europe (Piovesan et al. 2008; Linares and Camarero 2012; Castagneri et al. 2014; Bosela et al. 2018). However, some studies have also detected an increase of productivity in beech mountain forests (Tognetti et al. 2014; Bosela et al. 2016). The right-skewed response to biomass burning indicates that *F. sylvatica* was favored under low biomass burning conditions while it became sensitive to fires under higher biomass burning rates (Paper 4). *F. sylvatica*'s responses to summer temperatures and biomass burning match those obtained by Morales-Molino et al. (2020) from the northern Apennines and suggest that, in the central Dinaric Alps, *F. sylvatica* became more competitive with the onset of cooler and possibly moister summers, and fire disturbance.

While it is difficult to disentangle the effect of climate (e.g., the transition to cooler LIA temperatures) and land use, it seems likely that both land use and fire occurrence, superimposed on climatic changes, favored the establishment of *F. sylvatica* at the expense of *A. alba* at the current edge of the Biogradska Gora old-growth forest (Papers 2 and 3). Analogous reduction of *A. alba* coupled with the expansion of *F. sylvatica* between 6500 and 5000 cal yr BP are well documented in the palaeoecological studies from central-southern Europe and have ascribed the expansion of beech to the combined effects of favorable cooler climatic conditions, increased fire activity and human impact (Vescovi et al. 2010b, a; Branch 2013; Guido et al. 2013; Branch and Marini 2014; Morales-Molino et al. 2020). This matches evidence suggesting that mixed-severity fire and intermediate human disturbance can favor the establishment of *F. sylvatica* at the stand level (Bradshaw and Lindbladh 2005; Giesecke et al. 2007; Tinner and Lotter 2006). Indeed, *F. sylvatica* has the capacity of occupying newly exposed soils and canopy openings more rapidly than its two competitors (*A. alba* and *P. abies*) (Pretzsch and Schütze 2005; Bolte et al. 2014; Maringer et al. 2016) because it can regenerate and grow under the existing forest canopy for years and rapidly achieve the dominance when the light conditions improve following human and

natural disturbances (wind, logging, fire) (Nagel et al. 2010; Motta et al. 2011, 2015; Maringer et al. 2016).

These auto-ecological characters may explain the reason why *F. sylvatica* expanded around 5000 cal yr BP, when high severity fires permitted its admixture with the two conifers. Our findings show that *F. sylvatica* is sensitive to fires under high biomass burning rates, as also shown by Carter et al. (2018) and Tinner et al. (2000). Thus, its expansion in the Durmitor occurred in conjunction with a shift to a period of lower fire activity, as identified by the change point analysis (Tinner et al. 2000; Feurdean et al. 2017a; Bobek et al. 2019). In keeping with this, at Biogradska Gora *F. sylvatica*'s main expansions matched with periods of reduced biomass burning, as inferred by the change point analysis. However, it is important to take into account that a reduction in fire activity could also arise from the vegetation change itself (bottom-up effect), as the establishment of *F. sylvatica* could affect the moisture conditions and fuels characteristics (Bobek et al. 2018b, 2019; Carter et al. 2018). Although human impact probably played a main role for the establishment of *F. sylvatica* at Biogradska Gora, the response of *F. sylvatica* toward increasing human impact was not significant at the Durmitor. On the one hand, a non-significant relationship could derive by the fact that human only indirectly favored *F. sylvatica* by eliminating one of its competitors (*A. alba*). On the other hand, a non-significant relationship could derive by an overall low human impact in the mountain areas throughout the whole Holocene, as supported by the persistence of a closed forest in the surrounding of Zminje jezero in the past 9000 years. Possibly for the same reason, biomass burning responded negatively to human impact, suggesting that climate was the dominant driver of fires in the Durmitor mountain areas.

Norway spruce

P. abies emerged as a species relatively insensitive to long-term variations in summer temperatures and its population remained relatively stable in the mountain area of the Durmitor even under higher-than-present summer temperatures (Paper 4), as also observed in the Carpathians (Carter et al. 2018). *P. abies*' insensitivity to summer temperatures may simply imply that temperature did not exceed the species' climatic tolerance range. In addition, as *P. abies* is particularly sensitive to late-summer drought stress due to its shallow root system (Henne et al. 2011), particularly in southern latitudes and at low elevations (Spiecker 1995; Büntgen et al. 2006; Castagneri et al. 2014; Bosela et al. 2021), it is plausible to argue that moisture availability was not a limiting factor for spruce populations in the Durmitor. In keeping with this, the growth of spruce is positively correlated with summer temperatures if spring moisture is assured (Schurman et al. 2019).

The behavior of *P. abies* to fire is not well understood. On the one hand, the species has traits promoting fire, such as accumulation of flammable debris and litter on forest floor, high resin content, ladder canopy structure (Feurdean et al. 2019). On the other hand, *P. abies* is considered a fire-intolerant species due to its thin-bark, no-resprouting capacity, relatively long life cycle, and shallow roots that

are easily killed by fire (Feurdean et al. 2019). Moreover, *P. abies* has a vigorous post-fire regeneration (Bobek et al. 2018b) but it does not survive after high severity fires and shows a negative response to increased fire frequency (Niklasson et al. 2010; Feurdean et al. 2019; Spînu et al. 2020). At Biogradska Gora, *P. abies* strongly declined during the Middle Ages due to high-severity and high-frequency fires in conjunction with land use (grazing and cultivation) (Papers 2 and 3). However, neither human impact nor biomass burning significantly influenced *P. abies* in the Durmitor. A similar insensitivity of *P. abies* to biomass burning was found by Carter et al. (2018) in long-term ecological reconstructions from the Carpathians. The long-term stability of *P. abies* during the whole Holocene agrees with evidence showing that *P. abies* can persist even with FRI as low as 200-300 years (Brown and Giesecke 2014; Feurdean et al. 2017a, b; Finsinger et al. 2018). Finally, its well-established population in the surrounding of Zminje jezero supports the view that high-severity fires do not affect *P. abies* populations if they remained rare (FRI > 350 years).

Although further research from European mixed spruce-beech-fir forests is necessary to validate the species' responses to fire, climate, and human impact that are presented in Paper 4, the information obtained in this study could help to set silvicultural priorities and guide management strategies (e.g., conservation measures, adaptive forestry) to ensure the provision of ecosystem services of these European mixed mountain forests in the future (Bolte et al. 2009; Temperli et al. 2012; Conedera et al. 2017). Considering future climatic projections, forest management strategies should seek to reduce the risk of fire occurrence and to increase both the resistance and resilience of stands to drought and fires. In the light of our observations, maintain or re-establish a mixed composition in mountain forests could be a good choice from different perspectives. The simultaneous presence of spruce, fir and beech offers the opportunity to take advantage of the different characteristics of each species. *A. alba* could be more adapted to future higher temperatures and more drought-tolerant compared to *P. abies* and *F. sylvatica* (Ellenberg 2009; Henne et al. 2011). *F. sylvatica* could act as a fire-suppressing landscape element (Feurdean et al. 2017b; Carter et al. 2018; Bobek et al. 2018a). *P. abies* could be used thanks to its vigorous post fire regeneration (Bobek et al. 2018a) and its persistence under a fire-return interval as low as 200-300 years. Adaptive forest management strategies (Bolte et al. 2009) have already included the transformation of secondary monospecific stands of spruce into more stable mixed uneven-aged mountain forests (Hilmers et al. 2020). A higher number of tree species of mixed forests improves forests' resilience to extreme climatic events by mitigating their effects on tree-growth performance, resistance and recovery (Metz et al. 2016; Gazol and Camarero 2016). Moreover, a higher number of species can reduce the fire risk by increasing forest heterogeneity and creating points of discontinuity in the biomass, making fire dispersal more difficult (Feurdean et al. 2019). Finally, species diversity, besides maintaining a high level of biodiversity, has also a positive effect on forest productivity (increase in volume of trees) and thus on forests carbon adsorption, which is particularly important for climate change mitigation (Zhang et al. 2012; Toïgo et al. 2015; Liang et al. 2016).

References

- Allevato E, Saulino L, Cesarano G, et al (2019) Canopy damage by spring frost in European beech along the Apennines: effect of latitude, altitude and aspect. *Remote Sensing of Environment* 225:431–440. <https://doi.org/10.1016/j.rse.2019.03.023>
- Bobek P, Šamonil P, Jamrichová E (2018a) Biotic controls on Holocene fire frequency in a temperate mountain forest, Czech Republic. *J Quaternary Sci* 33:892–904. <https://doi.org/10.1002/jqs.3067>
- Bobek P, Svobodová HS, Werchan B, et al (2018b) Human-induced changes in fire regime and subsequent alteration of the sandstone landscape of Northern Bohemia (Czech Republic). *The Holocene* 28:427–443. <https://doi.org/10.1177/0959683617729443>
- Bobek P, Svobodová-Svitavská H, Pokorný P, et al (2019) Divergent fire history trajectories in Central European temperate forests revealed a pronounced influence of broadleaved trees on fire dynamics. *Quaternary Science Reviews* 222:105865. <https://doi.org/10.1016/j.quascirev.2019.105865>
- Bolte A, Ammer C, Löf M, et al (2009) Adaptive forest management in central Europe: Climate change impacts, strategies and integrative concept. *Scandinavian Journal of Forest Research* 24:473–482. <https://doi.org/10.1080/02827580903418224>
- Bolte A, Hilbrig L, Grundmann BM, Roloff A (2014) Understory dynamics after disturbance accelerate succession from spruce to beech-dominated forest—the Siggaboda case study. *Annals of Forest Science* 71:139–147. <https://doi.org/10.1007/s13595-013-0283-y>
- Boncina A (2011) History, current status and future prospects of uneven-aged forest management in the Dinaric region: an overview. *Forestry* 84:467–478. <https://doi.org/10.1093/forestry/cpr023>
- Bosela M, Lukac M, Castagneri D, et al (2018) Contrasting effects of environmental change on the radial growth of co-occurring beech and fir trees across Europe. *Science of the Total Environment* 615:1460–1469
- Bosela M, Štefančík I, Petráš R, Vacek S (2016) The effects of climate warming on the growth of European beech forests depend critically on thinning strategy and site productivity. *Agricultural and Forest Meteorology* 222:21–31. <https://doi.org/10.1016/j.agrformet.2016.03.005>
- Bosela M, Tumajer J, Cienciala E, et al (2021) Climate warming induced synchronous growth decline in Norway spruce populations across biogeographical gradients since 2000. *Science of The Total Environment* 752:141794. <https://doi.org/10.1016/j.scitotenv.2020.141794>
- Bradshaw RHW, Lindbladh M (2005) Regional spread and stand-scale establishment of *Fagus sylvatica* and *Picea abies* in Scandinavia. *Ecology* 86:1679–1686. <https://doi.org/10.1890/03-0785>
- Branch NP (2013) Early–Middle Holocene vegetation history, climate change and human activities at Lago Riane (Ligurian Apennines, NW Italy). *Veget Hist Archaeobot* 22:315–334. <https://doi.org/10.1007/s00334-012-0384-9>
- Branch NP, Marini NAF (2014) Mid-Late Holocene environmental change and human activities in the northern Apennines, Italy. *Quaternary International* 353:34–51. <https://doi.org/10.1016/j.quaint.2013.07.053>
- Brown KJ, Giesecke T (2014) Holocene fire disturbance in the boreal forest of central Sweden: Holocene fire disturbance in the boreal forest, central Sweden. *Boreas* 43:639–651. <https://doi.org/10.1111/bor.12056>
- Büntgen U, Frank DC, Schmidhalter M, et al (2006) Growth/climate response shift in a long subalpine spruce chronology. *Trees* 20:99–110. <https://doi.org/10.1007/s00468-005-0017-3>
- Büntgen U, Tegel W, Kaplan JO, et al (2014) Placing unprecedented recent fir growth in a European-wide and Holocene-long context. *Frontiers in Ecology and the Environment* 12:100–106. <https://doi.org/10.1890/130089>

- Carter VA, Bobek P, Moravcová A, et al (2020) The role of climate-fuel feedbacks on Holocene biomass burning in upper-montane Carpathian forests. *Global and Planetary Change* 193:103264. <https://doi.org/10.1016/j.gloplacha.2020.103264>
- Carter VA, Moravcová A, Chiverrell RC, et al (2018) Holocene-scale fire dynamics of central European temperate spruce-beech forests. *Quaternary Science Reviews* 191:15–30. <https://doi.org/10.1016/j.quascirev.2018.05.001>
- Castagneri D, Nola P, Motta R, Carrer M (2014) Summer climate variability over the last 250 years differently affected tree species radial growth in a mesic *Fagus–Abies–Picea* old-growth forest. *Forest Ecology and Management* 320:21–29. <https://doi.org/10.1016/j.foreco.2014.02.023>
- Cheddadi R, Araújo MB, Maiorano L, et al (2016) Temperature range shifts for three European tree species over the last 10,000 years. *Front Plant Sci* 7:1581. <https://doi.org/10.3389/fpls.2016.01581>
- Christensen JH, Hewitson B, Busuioc A, et al (2007) Regional Climate Projections. In: Solomon S, Qin D, Manning M, et al. (eds) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press. Cambridge UK and New York USA
- Colombaroli D, Henne PD, Kaltenrieder P, et al (2010) Species responses to fire, climate and human impact at tree line in the Alps as evidenced by palaeo-environmental records and a dynamic simulation model. *Journal of Ecology* 98:1346–1357. <https://doi.org/10.1111/j.1365-2745.2010.01723.x>
- Conedera M, Colombaroli D, Tinner W, et al (2017) Insights about past forest dynamics as a tool for present and future forest management in Switzerland. *Forest Ecology and Management* 388:100–112
- Diaci J, Rozenbergar D, Anic I, et al (2011) Structural dynamics and synchronous silver fir decline in mixed old-growth mountain forests in Eastern and Southeastern Europe. *Forestry* 84:479–491. <https://doi.org/10.1093/forestry/cpr030>
- Di Pasquale G, Allevato E, Cocchiararo A, et al (2014) Late Holocene persistence of *Abies alba* in low-mid altitude deciduous forests of central and southern Italy: new perspectives from charcoal data. *J Veg Sci* 25:1299–1310. <https://doi.org/10.1111/jvs.12196>
- Dittmar C, Zech W, Elling W (2003) Growth variations of Common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe - a dendroecological study. *Forest Ecology and Management* 173:63–78
- Ellenberg H (2009) *Vegetation Ecology of Central Europe*, Fourth Edition. Cambridge University Press
- Feurdean A, Florescu G, Vannière B, et al (2017a) Fire has been an important driver of forest dynamics in the Carpathian Mountains during the Holocene. *Forest Ecology and Management* 389:15–26. <https://doi.org/10.1016/j.foreco.2016.11.046>
- Feurdean A, Tonkov S, Pfeiffer M, et al (2019) Fire frequency and intensity associated with functional traits of dominant forest type in the Balkans during the Holocene. *Eur J Forest Res* 138:1049–1066. <https://doi.org/10.1007/s10342-019-01223-0>
- Feurdean A, Veski S, Florescu G, et al (2017b) Broadleaf deciduous forest counterbalanced the direct effect of climate on Holocene fire regime in hemiboreal/boreal region (NE Europe). *Quaternary Science Reviews* 169:378–390. <https://doi.org/10.1016/j.quascirev.2017.05.024>
- Feurdean A, Willis KJ (2008) Long-term variability of *Abies alba* in NW Romania: implications for its conservation management. *Diversity and Distributions* 14:1004–1017. <https://doi.org/10.1111/j.1472-4642.2008.00514.x>
- Finsinger W, Fevre J, Orbán I, et al (2018) Holocene fire-regime changes near the treeline in the Retezat Mts. (Southern Carpathians, Romania). *Quaternary International* 477:94–105. <https://doi.org/10.1016/j.quaint.2016.04.029>

- Finsinger W, Vanel Q, Ribolini A, Tinner W (2021) Early to late Holocene vegetation and fire dynamics at the treeline in the Maritime Alps. *Veget Hist Archaeobot* 30:507–524. <https://doi.org/10.1007/s00334-020-00795-x>
- Fordham DA, Saltré F, Haythorne S, et al (2017) PaleoView: a tool for generating continuous climate projections spanning the last 21 000 years at regional and global scales. *Ecography* 40:1348–1358. <https://doi.org/10.1111/ecog.03031>
- Fyfe RM, Woodbridge J, Roberts N (2015) From forest to farmland: pollen-inferred land cover change across Europe using the pseudobiomization approach. *Glob Change Biol* 21:1197–1212. <https://doi.org/10.1111/gcb.12776>
- Gazol A, Camarero JJ (2016) Functional diversity enhances silver fir growth resilience to an extreme drought. *J Ecol* 104:1063–1075. <https://doi.org/10.1111/1365-2745.12575>
- Gazol A, Camarero JJ, Gutiérrez E, et al (2015) Distinct effects of climate warming on populations of silver fir (*Abies alba*) across Europe. *J Biogeogr* 42:1150–1162. <https://doi.org/10.1111/jbi.12512>
- Giesecke T, Hickler T, Kunkel T, et al (2007) Towards an understanding of the Holocene distribution of *Fagus sylvatica* L. *Journal of Biogeography* 34:118–131. <https://doi.org/10.1111/j.1365-2699.2006.01580.x>
- Green DG (1981) Time series and postglacial forest ecology. *Quat res* 15:265–277. [https://doi.org/10.1016/0033-5894\(81\)90030-2](https://doi.org/10.1016/0033-5894(81)90030-2)
- Guido MA, Menozzi BI, Bellini C, et al (2013) A palynological contribution to the environmental archaeology of a Mediterranean mountain wetland (North West Apennines, Italy). *The Holocene* 23:1517–1527. <https://doi.org/10.1177/0959683613496294>
- Hastie T, Tibshirani R (1986) Generalized Additive Models. *Statistical Science* 1:297–318
- Henne PD, Elkin C, Colombaroli D, et al (2013) Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modeling. *Landscape Ecol* 28:819–833. <https://doi.org/10.1007/s10980-012-9782-8>
- Henne PD, Elkin C, Franke J, et al (2015) Reviving extinct Mediterranean forest communities may improve ecosystem potential in a warmer future. *Frontiers in Ecology and the Environment* 13:356–362. <https://doi.org/10.1890/150027>
- Henne PD, Elkin CM, Reineking B, et al (2011) Did soil development limit spruce (*Picea abies*) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model: Soil depth limits spruce expansion in the Alps. *Journal of Biogeography* 38:933–949. <https://doi.org/10.1111/j.1365-2699.2010.02460.x>
- Hilmers T, Avdagić A, Bartkowicz L, et al (2019) The productivity of mixed mountain forests comprised of *Fagus sylvatica*, *Picea abies*, and *Abies alba* across Europe. *Forestry: An International Journal of Forest Research* 92:512–522. <https://doi.org/10.1093/forestry/cpz035>
- Hilmers T, Biber P, Knoke T, Pretzsch H (2020) Assessing transformation scenarios from pure Norway spruce to mixed uneven-aged forests in mountain areas. *Eur J Forest Res* 139:567–584. <https://doi.org/10.1007/s10342-020-01270-y>
- IPCC (2021) Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press
- Kaplan JO, Krumhardt KM, Zimmermann N (2009) The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews* 28:3016–3034. <https://doi.org/10.1016/j.quascirev.2009.09.028>
- Klopčič M, Mina M, Bugmann H, Boncina A (2017) The prospects of silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst) in mixed mountain forests under various management strategies,

- climate change and high browsing pressure. *European Journal of Forest Research* 136:1071–1090. <https://doi.org/DOI.10.1007/s10342-017-1052-5>
- Kovats RS, Valentini R, Bouwer LM, et al (2014) Europe. In: Barros VR, Field CB, Dokken DJ, et al. (eds) *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, USA, pp 1267–1326.
- Kuneš P, Svobodová-Svitavská H, Kolář J, et al (2015) The origin of grasslands in the temperate forest zone of east-central Europe: long-term legacy of climate and human impact. *Quaternary Science Reviews* 116:15–27. <https://doi.org/10.1016/j.quascirev.2015.03.014>
- Liang J, Crowther TW, Picard N, et al (2016) Positive biodiversity-productivity relationship predominant in global forests. *Science* 354:aaf8957. <https://doi.org/10.1126/science.aaf8957>
- Linares JC, Camarero JJ (2012) From pattern to process: linking intrinsic water-use efficiency to drought-induced forest decline. *Glob Change Biol* 18:1000–1015. <https://doi.org/10.1111/j.1365-2486.2011.02566.x>
- Maringer J, Conedera M, Ascoli D, et al (2016) Resilience of European beech forests (*Fagus sylvatica* L.) after fire in a global change context. *Int J Wildland Fire* 25:699–710. <https://doi.org/10.1071/WF15127>
- Metz J, Annighöfer P, Schall P, et al (2016) Site-adapted admixed tree species reduce drought susceptibility of mature European beech. *Glob Change Biol* 22:903–920. <https://doi.org/10.1111/gcb.13113>
- Morales-Molino C, Steffen M, Samartin S, et al (2020) Long-Term responses of Mediterranean mountain forests to climate change, fire and human activities in the Northern Apennines (Italy). *Ecosystems*. <https://doi.org/10.1007/s10021-020-00587-4>
- Motta R (1996) Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the Western Italian Alps. *Forest Ecology and Management* 88:93–98. [https://doi.org/10.1016/S0378-1127\(96\)03814-5](https://doi.org/10.1016/S0378-1127(96)03814-5)
- Motta R, Berretti R, Castagneri D, et al (2011) Toward a definition of the range of variability of central European mixed *Fagus – Abies – Picea* forests: the nearly steady-state forest of Lom (Bosnia and Herzegovina). *Can J For Res* 41:1871–1884. <https://doi.org/10.1139/x11-098>
- Motta R, Garbarino M, Berretti R, et al (2015) Structure, spatio-temporal dynamics and disturbance regime of the mixed beech–silver fir–Norway spruce old-growth forest of Biogradska Gora (Montenegro). *Plant Biosystems* 149:966–975. <https://doi.org/10.1080/11263504.2014.945978>
- Nagel TA, Mikac S, Dolinar M, et al (2017) The natural disturbance regime in forests of the Dinaric Mountains: A synthesis of evidence. *Forest Ecology and Management* 388:29–42. <https://doi.org/10.1016/j.foreco.2016.07.047>
- Nagel TA, Svoboda M, Rugani T, Diaci J (2010) Gap regeneration and replacement patterns in an old-growth *Fagus – Abies* forest of Bosnia–Herzegovina. *Plant Ecol* 208:307–318. <https://doi.org/10.1007/s11258-009-9707-z>
- Niklasson M, Zin E, Zielonka T, et al (2010) A 350-year tree-ring fire record from Białowieża Primeval Forest, Poland: implications for Central European lowland fire history. *Journal of Ecology* 98:1319–1329. <https://doi.org/10.1111/j.1365-2745.2010.01710.x>
- Piovesan G, Biondi F, Filippo AD, et al (2008) Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Global Change Biology* 14:1–17. <https://doi.org/10.1111/j.1365-2486.2008.01570.x>

- Pretzsch H, Schütze G (2005) Crown allometry and growing space efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed stands. *Plant Biology* 7:628–639. <https://doi.org/10.1055/s-2005-865965>
- Rull V (2010) Ecology and Palaeoecology: Two Approaches, One Objective. *TOECOLJ* 3:1–5. <https://doi.org/10.2174/1874213001003020001>
- Samartin S, Heiri O, Joos F, et al (2017) Warm Mediterranean mid-Holocene summers inferred from fossil midge assemblages. *Nature Geosci* 10:207–212. <https://doi.org/10.1038/ngeo2891>
- Schmuck G, San-Miguel-Ayaz J, Durrant T, et al (2015) Forest Fires in Europe, Middle East and North Africa 2014. Publications Office of the European Union, Luxembourg
- Schurman JS, Babst F, Björklund J, et al (2019) The climatic drivers of primary *Picea* forest growth along the Carpathian arc are changing under rising temperatures. *Glob Change Biol* 25:3136–3150. <https://doi.org/10.1111/gcb.14721>
- Spiecker H (1995) Growth dynamics in a changing environment - long-term observations. *Plant and Soil* 168:555–561
- Spînu AP, Niklasson M, Zin E (2020) Mesophication in temperate Europe: A dendrochronological reconstruction of tree succession and fires in a mixed deciduous stand in Białowieża Forest. *Ecol Evol* 10:1029–1041. <https://doi.org/10.1002/ece3.5966>
- Temperli C, Bugmann H, Elkin C (2012) Adaptive management for competing forest goods and services under climate change. *Ecological Applications* 22:2065–2077. <https://doi.org/10.1890/12-0210.1>
- Tinner W, Colombaroli D, Heiri O, et al (2013) The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. *Ecological Monographs* 83:419–439. <https://doi.org/10.1890/12-2231.1>
- Tinner W, Conedera M, Ammann B, Lotter AF (2005) Fire ecology north and south of the Alps since the last ice age. *The Holocene* 15:1214–1226. <https://doi.org/10.1191/0959683605hl892rp>
- Tinner W, Conedera M, Gobet E, et al (2000) A palaeoecological attempt to classify fire sensitivity of trees in the southern Alps. *The Holocene* 10:565–574. <https://doi.org/10.1191/095968300674242447>
- Tinner W, Hubschmid P, Wehrli M, et al (1999) Long-term forest fire ecology and dynamics in southern Switzerland. *Journal of Ecology* 87:273–289. <https://doi.org/10.1046/j.1365-2745.1999.00346.x>
- Tinner W, Lotter A (2006) Holocene expansions of *Fagus sylvatica* and *Abies alba* in Central Europe: where are we after eight decades of debate? *Quaternary Science Reviews* 25:526–549. <https://doi.org/10.1016/j.quascirev.2005.03.017>
- Tognetti R, Lombardi F, Lasserre B, et al (2014) Tree-Ring Stable Isotopes Reveal Twentieth-Century Increases in Water-Use Efficiency of *Fagus sylvatica* and *Nothofagus* spp. in Italian and Chilean Mountains. *PLoS ONE* 9:e113136. <https://doi.org/10.1371/journal.pone.0113136>
- Toïgo M, Vallet P, Perot T, et al (2015) Overyielding in mixed forests decreases with site productivity. *J Ecol* 103:502–512. <https://doi.org/10.1111/1365-2745.12353>
- Valsecchi V, Finsinger W, Tinner W, Ammann B (2008) Testing the influence of climate, human impact and fire on the Holocene population expansion of *Fagus sylvatica* in the southern Prealps (Italy). *The Holocene* 18:603–614. <https://doi.org/10.1177/0959683608089213>
- Vescovi E, Ammann B, Ravazzi C, Tinner W (2010a) A new Late-glacial and Holocene record of vegetation and fire history from Lago del Greppo, northern Apennines, Italy. *Veget Hist Archaeobot* 19:219–233. <https://doi.org/10.1007/s00334-010-0243-5>

- Vescovi E, Kaltenrieder P, Tinner W (2010b) Late-Glacial and Holocene vegetation history of Pavullo nel Frignano (Northern Apennines, Italy). *Review of Palaeobotany and Palynology* 160:32–45. <https://doi.org/10.1016/j.revpalbo.2010.01.002>
- Walker M, Johnsen S, Rasmussen SO, et al (2009) Formal definition and dating of the GSSP (Global Stratotype Section and Point) for the base of the Holocene using the Greenland NGRIP ice core, and selected auxiliary records. *J Quaternary Sci* 24:3–17. <https://doi.org/10.1002/jqs.1227>
- Wick L, Möhl A (2006) The mid-Holocene extinction of silver fir (*Abies alba*) in the Southern Alps: a consequence of forest fires? Palaeobotanical records and forest simulations. *Veget Hist Archaeobot* 15:435–444. <https://doi.org/10.1007/s00334-006-0051-0>
- Wu M, Knorr W, Thonicke K, et al (2015) Sensitivity of burned area in Europe to climate change, atmospheric CO₂ levels, and demography: A comparison of two fire-vegetation models. *J Geophys Res Biogeosci* 120:2256–2272. <https://doi.org/10.1002/2015JG003036>
- Zhang Y, Chen HYH, Reich PB (2012) Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *Journal of Ecology* 100:742–749. <https://doi.org/10.1111/j.1365-2745.2011.01944.x>

APPENDIX 1: Introduction, Discussion, and Conclusion in French

Introduction

Motivation

Écosystèmes forestiers de montagne : valeur et menaces

Les forêts de montagne occupent 23 % du couvert forestier de la Terre, abritent un huitième de la population mondiale et fournissent des biens et services essentiels à la subsistance des communautés, des hautes et basses terres (FAO 2011). Elles fournissent une diversité de produits (par exemple, de l'eau douce, du bois, du combustible, des plantes médicinales et aromatiques, du fourrage et des aliments), et sont appréciées pour leurs fonctions de protection contre les risques naturels (tels que les glissements de terrain, les avalanches et les inondations), ainsi que pour leurs valeurs culturelles (c'est-à-dire les valeurs spirituelles et récréatives). De plus, puits de carbone majeur, elles contribuent à ralentir le changement climatique (Mina et al. 2017). La grande hétérogénéité des niches et des gradients climatiques altitudinaux fait que les forêts de montagne abritent un grand nombre d'espèces végétales et animales endémiques et menacées (FAO 2011). Globalement, un tiers des zones protégées de la planète sont situées en montagne et certaines d'entre elles abritent actuellement des forêts primaires et subnaturelles (FAO 2011). Les forêts primaires et subnaturelles sont des systèmes de référence précieux pour l'étude des perturbations naturelles, de la dynamique de succession dans les différents biomes forestiers (Burrascano et al. 2013; Sabatini et al. 2018) et sont des points chauds de la biodiversité, pour les espèces sensibles aux perturbations humaines (Paillet et al. 2015).

Cependant, dans les décennies à venir, la capacité des forêts de montagne à fournir des services écosystémiques pourrait être gravement remise en cause. On s'attend à ce que les écosystèmes de montagne soient particulièrement menacés par les changements climatiques induits par l'homme (IPCC 2014, 2021). Les forêts de montagne connaîtront des changements plus rapides que les écosystèmes situés à des altitudes plus basses, car le taux de réchauffement s'amplifie avec l'altitude (Mountain Research Initiative EDW Working Group 2015). D'autre part, il existe des preuves solides que le changement climatique modifiera sensiblement les régimes de perturbation des forêts, avec une augmentation de la fréquence et de la sévérité des perturbations (par exemple, les incendies, les invasions d'insectes et les sécheresses) (Seidl et al. 2017). Les effets directs du climat sur la végétation comprennent la modification des taux de mortalité, de croissance et de régénération des arbres, qui interagissent et affectent finalement la répartition des espèces (Hansen et al. 2001). Dans un monde qui se réchauffe, la réponse des écosystèmes de montagne à des conditions qui changent rapidement

dépendra de la capacité des espèces de montagne à s'adapter à ces nouvelles conditions (European Environment Agency 2016) et de l'adoption de stratégies de gestion appropriées. Dans cette optique, l'Agenda 2030 pour le développement durable (UN General Assembly 2015) indique que la mise en œuvre de mesures concrètes et durables est hautement nécessaire pour renforcer la résilience des zones de montagne aux changements futurs (Gratzer and Keeton 2017; Wymann Von Dach et al. 2018). Une résilience accrue des forêts de montagne permettra probablement de minimiser la perte des services écosystémiques et de préserver la biodiversité (Millar and Stephenson 2015).

Des recherches récentes ont montré que les forêts présentant un degré de naturalité moyen à élevé, (*sensu* Buchwald 2005) sont censées être plus résistantes et résilientes aux changements environnementaux, en raison de leur grande diversité de traits structurels et fonctionnels (Messier et al. 2013; Sabatini et al. 2020). Dans ce contexte, l'étude des modèles et des processus des forêts primaires et subnaturelles, pourrait contribuer à guider le développement de méthodes sylvicoles efficaces, capables d'augmenter ou de restaurer la stabilité et la continuité à long terme des forêts de montagne gérées à l'avenir (sylviculture proche de la nature ; Bauhus et al. 2009; Schütz et al. 2016). En outre, l'évaluation des réactions des espèces de montagne au réchauffement des températures et à la modification des régimes de perturbation pourrait être utile, pour prévoir les changements potentiels dans les écosystèmes et pour adopter des mesures préventives (par exemple, promotion d'espèces plus tolérantes à la sécheresse, migration assistée, éclaircissement) susceptibles de préserver les services écosystémiques. Cependant, l'étude des réponses des plantes est un défi car les processus (tels que les changements de température ou les régimes de perturbation) opèrent généralement sur des échelles spatiales multiples et leurs effets sont perceptibles sur des échelles de temps longues, en particulier lorsque des espèces à longue durée de vie, comme les arbres sont impliquées.

La nécessité d'approches méthodologiques intégratives

Les structures forestières, la composition des espèces et les schémas spatiaux résultent des interactions complexes et à long terme entre les perturbations naturelles, l'impact humain et le climat (Frelich 2016, Fig. 1). Plusieurs approches méthodologiques peuvent être employées pour étudier la dynamique des forêts, chacune ayant sa propre échelle temporelle et spatiale.

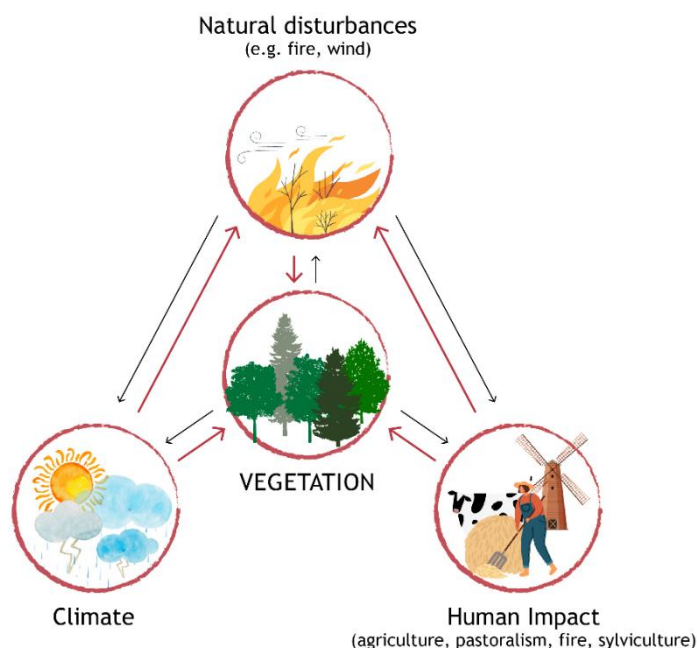


Fig. 1 Schéma simplifié des interactions entre le climat, les perturbations naturelles, l'impact humain et la végétation. Flèches rouges : interactions étudiées dans cette étude.

L'échelle fine des relevés de terrain permet de décrire la composition et la structure des espèces (par exemple, la surface terrière, les indices de diversité structurale, la quantité de débris ligneux grossiers) à l'échelle du peuplement, et de détecter le stade de croissance actuel du peuplement (Bauhus et al. 2009). Ces caractéristiques, ainsi que l'âge maximal atteint par les arbres, permettent de retracer indirectement la durée pendant laquelle un site a été continuellement boisé sans impact humain majeur (par exemple, récolte forestière, changements d'utilisation du sol) et sans perturbations de remplacement du peuplement, telles que les chablis et les incendies. Les observations sur le terrain peuvent fournir des preuves du type de perturbations, qui ont pu affecter un peuplement forestier (par exemple, l'impact humain : souches coupées, fours à charbon de bois ; les incendies : cicatrices de feu ; le vent : arbres déracinés ou cassés). Cependant, pour capturer la variabilité structurale et compositionnelle d'une forêt, un certain nombre d'observations effectuées de façon aléatoire sont nécessaires, ce qui demande du temps, de l'énergie et de l'argent (Carrer et al. 2018 ; Mikoláš et al. 2019). Souvent, les analyses de

télédétection sont combinées avec des enquêtes sur le terrain, afin de mettre à l'échelle les observations faites au niveau du peuplement sur une grande zone (niveau du paysage ou de la région). Les analyses d'images satellites multispectrales à haute ou très haute résolution spatiale (c. $< 5\text{m}$) permettent de cartographier les types de couverture terrestre avec une grande précision. En outre, l'imagerie satellitaire peut montrer des modèles de distribution des espèces, ainsi que la détection et la quantification des changements de la couverture forestière dus à des perturbations naturelles ou anthropiques (Brandt et al. 2012; Knorn et al. 2013). Cependant, l'identification des espèces au-delà des grandes catégories (par exemple, les conifères, les feuillus) et leur attribution aux agents de perturbation est souvent une tâche difficile (Wagner et al. 2018; Huo et al. 2019). De plus, les informations sur les structures forestières font défaut et l'horizon temporel des analyses multi-temporelles est limité par la disponibilité des images (jusqu'à 20-40 ans, selon la résolution spatiale).

Malgré la pertinence des relevés de terrain et de la télédétection, pour décrire les conditions actuelles et la dynamique des écosystèmes forestiers, leur court intervalle d'observation (de quelques décennies à quelques siècles) ne permet pas de saisir les réponses de la végétation, qui se jouent sur des échelles de temps plus longues (siècles, millénaires). Il s'agit, par exemple, de réponses à des perturbations peu fréquentes, de changements dans la fréquence ou la sévérité des incendies, ou encore de réponses des écosystèmes forestiers aux changements environnementaux dus au climat ou à l'impact humain (Swetnam et al. 1999). À cet égard, la vision temporelle étendue (plusieurs millénaires) fournie par les données paléoécologiques des archives naturelles (par exemple, sédiments lacustres, tourbières, cavités forestières) est particulièrement utile (Birks 2019). Alors que l'intervalle de temps couvert par les archives paléoécologiques dépend de l'âge maximal atteint par les sédiments, leur résolution temporelle varie en fonction de la période de dépôt et du nombre d'échantillons analysés (Foster et al. 1990). Bien que les archives paléoécologiques proviennent généralement d'un seul site d'étude, l'échelle spatiale de leurs reconstructions varie, selon que les sédiments sont collectés dans des cavités forestières ou des lacs (Foster et al. 1990) et selon le type d'indicateur considéré (par exemple, les macrofossiles végétaux vs le pollen, Birks 2002 ; charbon de bois macroscopique vs charbon de bois microscopique, Whitlock and Larsen 2001). Les sédiments extraits des cavités forestières, qui sont de petits sites humides dans les forêts, d'environ 5 m de diamètre, reflètent la végétation locale dans un rayon de quelques centaines de mètres (Calcote 1995, 1998). Les lacs, selon leur taille, sont capables de refléter la végétation à l'échelle du paysage ou de la région jusqu'à quelques kilomètres au maximum (Sugita 1994; Hofstetter et al. 2006; Seppä 2013). Les macrofossiles végétaux et les stomates permettent une reconstruction réaliste de la végétation locale dans un rayon de quelques décamètres autour d'un site (Ammann et al. 2014; Birks 2017). Les charbons microscopiques (10 - 100 μm) reflètent principalement l'histoire des incendies régionaux dans un rayon de 20-120 km (Whitlock and Larsen 2001) tandis que les charbons macroscopiques ($> 150 \mu\text{m}$) sont appropriés pour déduire le brûlage de la biomasse à l'échelle du paysage à environ 50 km du site d'étude, ainsi que les épisodes d'incendie locaux (environ $< 3 \text{ km}$) (Higuera et al. 2007, 2010; Carter et al. 2018). L'utilisation de plusieurs proxies paléoécologiques

indépendants (tels que le pollen, les palynomorphes non polliniques, les charbons microscopiques et macroscopiques, les macrofossiles végétaux, les chironomes et les stomates) présente l'avantage de reconstruire l'histoire à long terme de la végétation, des perturbations par le feu, du climat et de l'impact humain à différentes échelles spatiales et d'étudier les interactions possibles entre eux (par exemple, les réponses des plantes au changement climatique, à l'utilisation du sol ou au feu). Le niveau de l'impact humain est généralement reconstitué à partir des abondances relatives de pollen d'indicateurs anthropiques primaires (PI), d'indicateurs secondaires (SI), d'indicateurs culturels (CI), d'*Olea*, *Juglans* et *Castanea* (indice OJC), et du rapport AP/NAP (pollen arboricole/pollen non arboricole ; Deza-Araujo et al. 2020). Les spores des champignons des bouses (*Sporormiella-type*) peuvent être utilisées comme indicateur du pâturage (Davis 1987; Baker et al. 2013). L'histoire à long terme de la végétation, combinée à celle de l'impact humain, permet d'évaluer le degré d'altération des écosystèmes forestiers et la mesure dans laquelle ils conservent des composantes naturelles (Whitlock et al. 2018).

Les forêts primaires et subnaturelles d'Europe : définition, dynamique et menaces

Le caractère naturel est l'un des critères les plus importants de la conservation de la nature et de nombreuses tentatives ont été faites pour attribuer un degré de naturalité aux écosystèmes (Reif and Walentowski 2008).

Le degré de naturalité est souvent évalué par la similitude d'une biocénose avec l'état naturel présumé, avant que l'homme ne fasse obstacle aux successions naturelles (Reif and Walentowski 2008). Selon Peterken (1996), le concept de naturalité dépend principalement du fait que les humains sont considérés ou non comme faisant partie de la nature. Cependant, il n'est pas simple de discerner quel niveau d'impact permet de classer les humains comme faisant partie de la nature. Buchwald (2005) suggère de considérer les antonymes *nature* vs *culture* et *naturel* vs *artificiel*. Ces mots sont dérivés du latin *natura*, nature (< *natus*, né) ; *cultura*, culture des plantes (< *colere*, labourer) et *arte factum*, œuvre d'art. Le sens de ces mots nous permet d'établir que l'homme s'est distingué de la nature lorsqu'il a commencé à cultiver les plantes (labourer, semer et planter) et à produire de l'art et de l'artisanat. En effet, la conséquence directe et indirecte du développement culturel, a été un impact accru sur la faune et le paysage (Buchwald 2005). D'après les preuves archéologiques, l'éloignement de la nature peut être établi dans la période qui suit les premières œuvres d'art et qui précède le début de l'agriculture néolithique (Buchwald 2005) à partir de 10 000 ans avant notre ère en Europe (Roberts 2014). Cependant, l'homme est présent depuis des centaines de milliers d'années et a probablement eu un impact sur les écosystèmes forestiers au moins depuis qu'il a commencé à utiliser le feu, il y a plus de 200 000 ans (Sabatini 2014) indiquant que l'homme ait eu un impact sur la nature avant de cesser d'en faire partie (Buchwald 2005). De ce point de vue, l'idée selon laquelle les forêts étaient totalement épargnées par l'homme jusqu'à il y a quelques siècles est une idée fausse (Sabatini 2014).

Buchwald (2005) définit 14 classes ordinales de naturalité : degré de naturalité presque nul (plantations forestières p1-p4 et forêts naturelles semblable à une plantation ou exploitées n1-n2), degré de naturalité moyen-moderé (forêts spécialement gérées avec une exploitation de faible intensité et forêts intactes depuis moins de 60 à 80 ans n3-n4) et haut degré de naturalité (n5-n10). Selon Buchwald (2005), la catégorie *forêts primaires* regroupe les forêts appartenant aux cinq degrés de naturalité les plus élevés (n5-n10), y compris les forêts dites *subnaturelles* (voir le glossaire). Cependant, comme l'indique la FAO (2015) les forêts subnaturelles peuvent être soit primaires, soit secondaires, selon leur origine. Les forêts primaires subnaturelles sont des forêts d'espèces indigènes qui se régénèrent naturellement, où il n'y a pas de signes clairement visibles d'activités humaines passées et où les processus écologiques n'ont pas été perturbés de manière significative (FAO 2015). En revanche, les forêts subnaturelles secondaires sont issues de la repousse de la végétation ligneuse après d'importantes perturbations humaines et/ou naturelles de la végétation forestière d'origine (FAO 2015). Les forêts subnaturelles sont donc des forêts primaires ou secondaires qui ont atteint un âge auquel les structures et les espèces normalement associées aux forêts primaires anciennes de ce type spécifique se sont suffisamment développées (UNEP/CBD/SBSTTA 2001). Le vieillissement sans impact humain significatif est la condition nécessaire pour permettre à un peuplement forestier d'atteindre un statut de forêt subnaturelles en termes de structure, de biomasse vivante, de caractéristiques du bois mort et de diversité biologique (Spies 2004; Badalamenti et al. 2019). Le stade auquel les peuplements forestiers expriment les caractéristiques structurelles et fonctionnelles associées à des conditions anciennes est appelé le niveau de sub-naturalité (Bauhus et al. 2009). Dans cette optique, nous avons opté dans cette thèse pour le terme " forêt primaire et subnaturelle " afin d'englober toutes les catégories incluses dans les forêts primaires (*sensu* Buchwald, 2005) et dans les forêts subnaturelles (*sensu* FAO, 2015).

De plus, pour Buchwald (2005), l'évaluation de la continuité forestière est intéressante et se définit comme la durée pendant laquelle une zone a été continuellement boisée. Faisant suite à la définition des Peterken (1996) selon laquelle, les forêts avec une continuité longue, dites *forêts anciennes*, sont des sites forestiers qui ont été continuellement boisés pendant plusieurs centaines d'années ou millénaires. La continuité n'est pas rompue par l'abattage, le taillis, la plantation ou toute autre opération forestière si les espèces forestières se régénèrent immédiatement, mais elle est rompue s'il y a une autre utilisation du sol, comme le pâturage non boisé ou la culture. Les forêts anciennes, malgré leur degré de naturalité moyen ou assez faible (*sensu* Buchwald, 2005), ont une grande valeur de conservation : plus un terrain est boisé depuis longtemps, plus les espèces ont eu le temps de le coloniser et de nombreux habitats de se former (McMullin and Wiersma 2019).

En Europe, où des millénaires d'utilisation intensive du sol ont profondément transformé les paysages forestiers de plaine et de montagne et altéré les relations naturelles espèces-environnement (Kaplan et al. 2009; Birks and Tinner 2016; Bebi et al. 2017) depuis le Néolithique (European Environment

Agency 2007), les forêts primaires et subnaturelles sont rares (< 3 % de la superficie forestière totale ; Barredo et al. 2021) et petites (taille médiane de 24 ha et seulement 4,3 % des forêts de plus de 1 000 ha ; Sabatini et al. 2018). Les vestiges de forêts primaires et subnaturelles sont principalement situés dans les chaînes de montagnes éloignées d'Europe centrale et orientale (Alpes orientales, Carpates et montagnes Dinariques ; Parviainen 2005; Sabatini et al. 2018) et sont en grande partie composés de différentes proportions de sapins (*Abies alba* Miller), d'épicéas (*Picea abies* (L.) Karst.) et de hêtres (*Fagus sylvatica* L.) selon l'altitude et les conditions du site (Burrascano et al. 2013).

Dans les forêts primaires et subnaturelles d'Europe, les perturbations qui remplacent les peuplements sont rares. La dynamique forestière naturelle est principalement dirigée par des perturbations naturelles de petite et moyenne envergure (par exemple, le vent, la glace, la neige et les champignons) et par la mortalité d'arbres uniques ou de groupes d'arbres dominants de la canopée forestière (dynamique des *gaps*, Spies et al. 1990; Frankovič et al. 2021). Cette dynamique se traduit par une structure forestière horizontale complexe et à plusieurs niveaux, constituée d'une mosaïque de peuplements à différents stades de croissance (des groupes de régénération aux vieux arbres approchant leur longévité maximale) et d'une grande quantité de débris ligneux grossiers à différents stades de décomposition (Wirth et al. 2009). La plupart des *gaps* sont généralement de petite taille (c. < 100-250 m² ; Nagel and Svoboda 2008; Garbarino et al. 2012; Motta et al. 2015), cependant, des perturbations épisodiques de sévérité intermédiaire associées à des tempêtes de vent peuvent causer des ouvertures de plusieurs milliers de mètres carrés (Drößler and von Lüpke 2005; Nagel et al. 2007; Frankovič et al. 2021). Les différences de taille et de fréquence des *gaps* jouent un rôle clé dans le maintien de la diversité des espèces. Les espèces exigeantes en lumière, comme l'érable (*Acer* sp.) et, dans une moindre mesure, l'épicéa, se régénèrent dans les *gaps* de taille moyenne à grande (Stancioiu and O'Hara 2006; Nagel et al. 2010). Les perturbations peu fréquentes et de faible intensité favorisent la régénération avancée du sapin, tandis que les périodes où les perturbations de faible à moyenne intensité sont plus fréquentes favorisent la régénération avancée du hêtre en raison de sa capacité à surpasser le sapin, lorsque les conditions de lumière s'améliorent (Nagel et al. 2010; Motta et al. 2015).

Le feu est traditionnellement considéré comme un agent de perturbation faible dans la dynamique des forêts primaires et subnaturelles de sapin-épicéa-hêtre d'Europe centrale et orientale (Adámek et al. 2015). Dans ces écosystèmes, les incendies naturels (par exemple, les incendies provoqués par la foudre) sont extrêmement sporadiques (Niklasson et al. 2010; Nagel et al. 2017). Malgré tout, la littérature scientifique émergente a démontré que les incendies se produisent depuis des millénaires dans les écosystèmes de forêts mixtes d'Europe centrale et orientale, sous l'effet de facteurs descendants (par exemple, le climat) et ascendants (par exemple, l'impact humain et les changements de végétation) (Bobek et al., 2018b, 2018a ; Carter et al., 2018, 2020 ; Feurdean et al., 2017, 2019). De plus, les futurs changements environnementaux modifieront probablement le rôle du feu dans ces écosystèmes. Le

réchauffement des températures, l'augmentation de la fréquence des événements extrêmes, tels que les vagues de chaleur et les sécheresses (Seneviratne et al. 2012; Rajczak et al. 2013) couplés à l'absence de changements significatifs dans les précipitations (Auer et al. 2007; Bircher et al. 2016) augmentera probablement le risque d'incendie. Ainsi, une augmentation de la durée de la saison des feux et des zones brûlées a déjà été observée au cours des dernières décennies (San-Miguel-Ayaz et al., 2021 ; Schmuck et al., 2015). Et l'on s'attend à ce que les montagnes d'Europe de l'Est deviennent une nouvelle zone sujette aux incendies, en raison de l'effet additionnel de l'accumulation de combustible et de paysages moins fragmentés, suite à l'abandon du sol dû à l'exode rural (Krawchuk et al., 2009 ; Wu et al., 2015). Au cours des dernières décennies, l'essor du tourisme dans les parcs nationaux d'Europe de l'Est a pu accroître les possibilités de déclenchement d'incendies (Buckley 1991; Hall 2004). L'augmentation du risque d'incendie peut particulièrement mettre en danger les petites forêts primaires et subnaturelles, mais ce n'est pas la seule menace qui pèse sur ces forêts.

Bien qu'elles soient généralement protégées, les petites forêts primaires et subnaturelles sont également vulnérables à un impact humain direct (par exemple, les coupes, l'exploitation forestière de récupération, le braconnage, le pâturage) et indirect (par exemple, la modification du régime du feu et les changements d'utilisation du sol dans les zones non protégées environnantes) qui peuvent entraver le développement des attributs, associés au stade subnaturel. Même dans les régions où les forêts sont en expansion, les forêts primaires et subnaturelles continuent à disparaître (Watson et al. 2016, 2018; Potapov et al. 2017; Song et al. 2018) en raison de l'absence d'une protection adéquate, notamment en Europe de l'Est (Knorn et al. 2013; Grindean et al. 2019). Leur disparition et la réduction de leur surface sont préoccupantes, car les forêts primaires et subnaturelles sont particulièrement importantes pour la conservation et la promotion de la biodiversité, car elles constituent une source de propagules pour les espèces forestières rares ou menacées, sensibles aux perturbations humaines (Paillet et al. 2015).

Les forêts primaires et subnaturelles de montagne sont également menacées par le changement climatique en cours. Certaines espèces de montagne (par exemple, le hêtre et l'épicéa) ont déjà connu des baisses de croissance liées au réchauffement des températures et aux épisodes de sécheresse (Castagneri et al. 2014) et les premières modifications de l'aire de répartition des espèces sont déjà visibles (Hanewinkel et al. 2013). À cet égard, les forêts primaires et subnaturelles de montagne constituent un cadre unique pour l'étude de la réponse naturelle des plantes aux changements climatiques, car les arbres poussant à haute altitude sont souvent proches de leurs limites thermiques et les changements dans la durée de la saison de croissance, associés aux extrêmes de froid hivernal ou de chaleur estivale, peuvent modifier rapidement et fortement la répartition et la productivité des espèces (Henne et al. 2011).

Dans ce contexte, la prédiction des réponses des espèces d'arbres dominantes des forêts primaires et subnaturelles (sapin, hêtre et épicéa) aux variations du climat, aux incendies et à l'impact humain est importante, également parce que ces espèces sont des composantes répandues des écosystèmes montagneux européens (> 10 millions d'ha, c. 600-1400 m d'altitude ; Hilmers et al. 2020) et ont une grande valeur socio-économique (Vacek et al. 2021). En outre, la mise en évidence de l'héritage, de l'impact humain passé et présent dans les forêts primaires et subnaturelles et dans leurs environs peut être utile pour détecter d'éventuelles pertes ou réductions de surface et pour orienter les mesures de protection (par exemple, les zones tampons) et de restauration des forêts (Foster et al. 1996; Swetnam et al. 1999; Mazziotta et al. 2016; Barredo et al. 2021). De plus, la détection des héritages historiques est particulièrement importante parce qu'ils déterminent la vulnérabilité des forêts aux changements climatiques prévus et aux régimes de perturbation associés (Conedera et al. 2017). Par exemple, une réduction de la diversité des espèces d'arbres dominantes (d'une forêt mixte hêtre-sapin-épicéa à une forêt dominée par l'épicéa ou le hêtre) ou un changement dans les structures forestières (d'une forêt inéquienne à une forêt équienne) dû à l'impact humain passé pourrait réduire la résilience des écosystèmes forestiers aux perturbations.

Les Alpes Dinariques : une région de montagne présumée très naturelle avec une histoire de la végétation mal connue

Les Alpes Dinariques sont situées dans la partie occidentale de la péninsule des Balkans (sud-est de l'Europe). Elles constituent l'une des plus grandes régions montagneuses d'Europe, s'étendant de la bordure sud des Alpes orientales en Slovénie au massif du Šar-Korab en Albanie. Elles sont délimitées par la mer Adriatique le long de leur frontière occidentale et par le bassin pannonien à l'est (Fig. 2) (Nagel et al. 2017). Les Alpes Dinariques englobent des parties de la Slovénie, de la Croatie, de la Bosnie-Herzégovine, de la Serbie, du Kosovo, du Monténégro et de l'Albanie (Boncina 2011). La chaîne est formée par des roches mésozoïques, principalement constituées de calcaire et en partie de dolomite, ce qui entraîne la présence abondante de phénomènes karstiques (Kranjc 2009). Les sols prédominants sont les cambisols et les leptosols de différentes profondeurs (Sirotkovic 1987). La majeure partie de la chaîne se situe à plus de 500 m d'altitude, avec des sommets atteignant généralement 1500 m d'altitude et des sommets plus élevés (environ 2500 m d'altitude) en Bosnie-Herzégovine, au Monténégro et en Albanie (Nagel et al. 2017). La chaîne est située dans la zone climatique tempérée avec une température annuelle moyenne de 6-8 °C, chutant à environ 3 °C en haute altitude, et une quantité élevée de précipitations (environ 1500-2500 mm par an).



Fig. 2 Carte de la chaîne de montagnes dinariques. Lignes pointillées rouges : limites approximatives nord et sud de la chaîne ; lignes pointillées noires : délimitation des Alpes Dinariques centrales ; carrés rouges : localisation des sites étudiés dans cette recherche.

Les précipitations sont particulièrement élevées le long de la côte ouest de la chaîne en raison des grandes quantités d'humidité transportées par les vents d'ouest, soufflant sur la mer Adriatique (Mihevc et al. 2010).

De la côte adriatique au plateau dinarique, le gradient de végétation prononcé (Fig. 3) peut être résumé comme suit : Arbustes sempervirents de type méditerranéen - Forêts thermophiles mixtes subméditerranéennes - Forêts dominées par le hêtre - Forêts de montagne de hêtre, sapin et épicéa en différentes proportions (Jovanovic et al. 1986; Nagel et al. 2017). Les sites très escarpés et rocheux abritent souvent des peuplements de *Pinus nigra* Arnold, tandis que les peuplements dominés par l'épicéa se trouvent principalement dans les dépressions karstiques et les dolines où les inversions de température provoquent des microclimats froids (Nagel et al. 2017). En altitude, des hêtraies pures forment parfois la limite supérieure des arbres et au-dessus d'elles, on trouve des pins nains (*Pinus mugo* Turra) (Boncina 2011). Cette région forestière fournit des habitats pour de nombreuses espèces végétales endémiques (par exemple, l'épicéa de Serbie, *Picea omorika* (Pancic) Purk.) et menacées, y compris des reliques de l'Arcto-tertiaire (Boncina 2011).

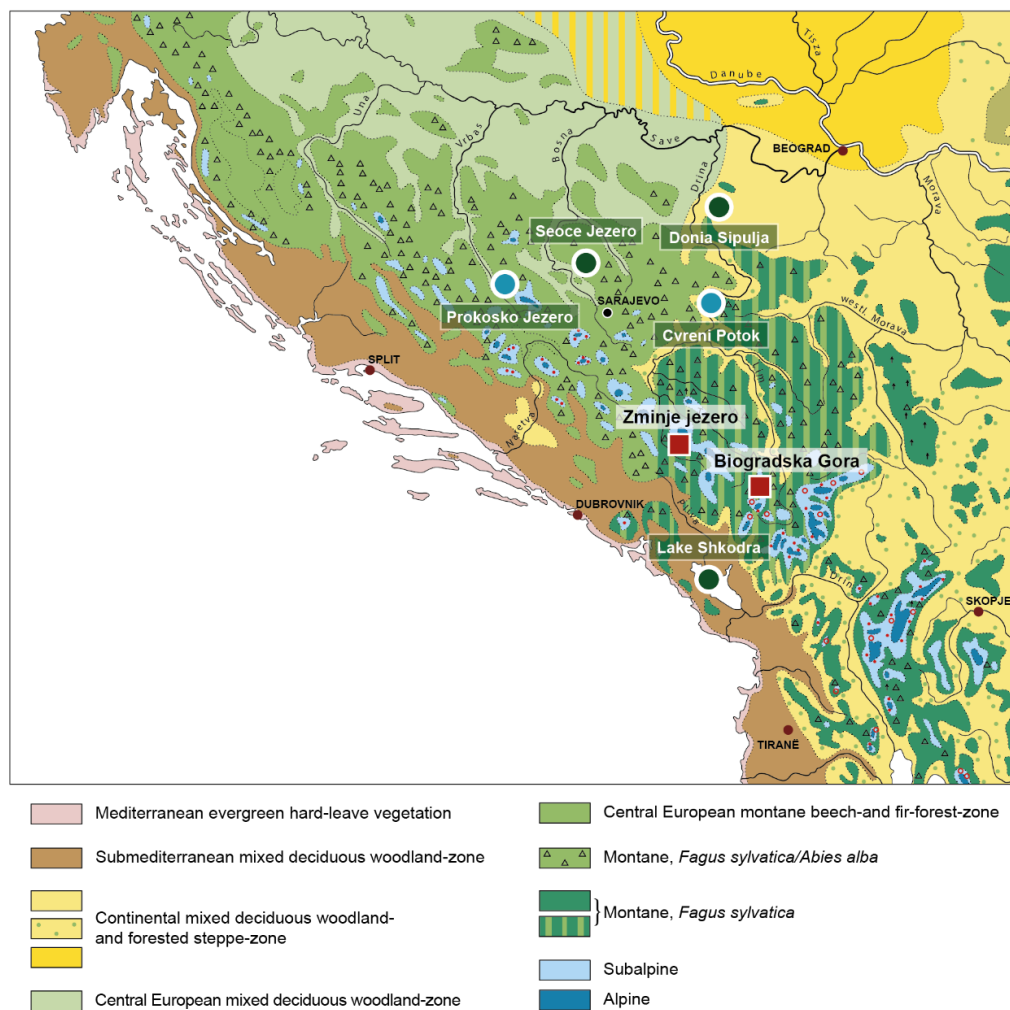


Fig. 3 Carte de végétation potentielle de Horvat et al. (1974) avec la localisation des sites d'étude des archives paléoécologiques dans les Alpes Dinariques mentionnés dans le texte : Prokoško Jezero (Dörfler 2013), Seoce Jezero (Wolters et al. 2010), Donja Sipulja (Kulkarni et al. 2016) et le lac Shkodra (Sadori et al. 2015). Cercles bleus : sites d'étude dans les zones de montagne ; carrés rouges : emplacement des sites dans cette étude.

Une étude rétrospective modélisée couvrant les trois derniers millénaires suggère que les forêts du Sud-Est de l'Europe (y compris la Slovénie, la Croatie, la Bosnie-Herzégovine, le Monténégro, la Serbie et la Macédoine) n'ont pas été fortement exploitée ou déboisées jusqu'au Moyen Âge en raison de terrains accidentés, d'une faible productivité agricole et d'une faible densité de population (Kaplan et al. 2009). Le résultat du modèle correspond à l'idée que certaines forêts situées dans l'intérieur, éloignées des chaînes de montagnes, comme dans les Alpes Dinariques centrales, ont pu être laissées relativement intactes ou ont été gérées avec des systèmes sylvicoles de faible intensité jusqu'à aujourd'hui (Boncina 2011; Nagel et al. 2017). Ainsi, la région de la chaîne de montagnes Dinaric a montré une probabilité forte d'abriter des forêts primaires et subnaturelles (Sabatini et al. 2018) et abrite actuellement des forêts

primaires et subnaturelles mixtes de sapin-épicéa-hêtre plus grand (> 1000 ha) que d'autres chaînes de montagnes, telles que les Alpes et les Carpates (Diaci 1999; Nagel et al. 2017; Sabatini et al. 2018). L'histoire de la végétation à long terme des écosystèmes forestiers de montagne dans les Alpes Dinariques est particulièrement intéressante car les espèces d'arbres dominantes de ces forêts de montagne (épicéa, sapin et hêtre) sont parmi les plus répandues et les plus précieuses du point de vue socio-économique dans les écosystèmes forestiers européens (Euforgen 2009; Vacek et al. 2021). De plus, la grande naturalité présumée de ces forêts permet d'étudier les interactions naturelles entre les espèces et l'environnement et de mieux démêler les effets possibles des impacts humains passés sur les écosystèmes de montagne. Cependant, l'histoire de la végétation des Alpes Dinariques est mal connue en raison de la faible couverture des données (Finsinger et al. 2017). Les archives paléoécologiques disponibles sont généralement situés loin des zones de montagne pour permettre la reconstruction de la dynamique des forêts de montagne (Seoce Jezero, Wolters et al. 2010; Donja Sipulja, Kulkarni et al. 2016; Lac Shkodra, Sadori et al. 2015; Fig. 3), à quelques exceptions près (Prokoško Jezero, Alpes Dinariques centrales, Dörfler 2013; Crveni potok, Alpes Dinariques internes, Finsinger et al. 2017; Fig. 3).

Pour les raisons évoquées ci-dessus, nous avons sélectionné deux sites d'étude situés dans la zone montagnarde des Alpes Dinariques centrales, sur les massifs de Bjelasica (documents 1, 2 et 3) et de Durmitor (document 4), respectivement dans le nord-est et le nord-ouest du Monténégro (Fig. 2). Leur protection précoce, en tant que réserves royales respectivement depuis 1907 et 1878, et en tant que parcs nationaux depuis 1952 (le parc national de Durmitor et le parc national de Biogradska Gora) a probablement permis le maintien ou la récupération d'un haut degré de naturalité, jusqu'à aujourd'hui. Le parc national de Biogradska Gora comprend actuellement l'un des plus grands peuplements subnaturels d'Europe centrale et méridionale, dont la grande surface est propice au développement d'une dynamique forestière naturelle (dynamique des *gaps*) avec la mosaïque qui en résulte d'une grande variété de phases de développement des peuplements forestiers (Motta et al. 2015; Barredo et al. 2021). Aucun peuplement subnaturel n'a encore été signalé dans le parc national de Durmitor, mais de vieux arbres monumentaux épars sont présents. Une description détaillée des sites d'étude se trouve dans les articles 1, 2 et 4.

Objectifs

Le projet de recherche vise à étudier les effets du climat, de l'histoire des incendies, de l'impact de l'homme et de leurs interactions possibles sur la dynamique de la végétation à long terme des écosystèmes forestiers de montagne mixtes épicéa-sapin-hêtre des Alpes Dinariques. Les quatre articles inclus dans cette thèse, chacun avec ses propres objectifs spécifiques, contribuent de manière différente mais complémentaire à répondre aux objectifs principaux.

Les objectifs individuels des études sont les suivants :

- Évaluer la pertinence de l'utilisation de l'imagerie satellitaire à très haute résolution pour cartographier les classes de couverture terrestre, y compris les *gaps* dans la canopée des forêts subnaturelles. **L'article 1** répond à cet objectif en couplant une analyse d'image basée sur les objets (OBIA) et un classificateur Random Forest sur des images Pléiades à très haute résolution de la forêt de Biogradska Gora.
- Identifier l'étendue actuelle de la forêt primaire et subnaturelle de Biogradska Gora, démontrer l'influence possible des incendies et de l'impact humain, qui ont pu réduire ou fragmenter les zones de forêt primaire et subnaturelle, et clarifier l'héritage des perturbations passées sur les écosystèmes forestiers actuels. **L'article 2** aborde ces objectifs en combinant des enquêtes de terrain sur la structure forestière contemporaine avec des analyses de télédétection et des archives paléoécologiques de la forêt primaire et subnaturelle de Biogradska Gora et de ses environs (massif de Bjelasica, Monténégro). **L'article 3** se concentre sur l'importance de l'histoire à long terme des forêts primaires et subnaturelles et de leurs paysages environnants, pour la protection de la nature et pour le développement de mesures de restauration.
- Évaluer la végétation holocène, la dynamique des incendies et l'histoire de l'utilisation du sol des écosystèmes forestiers mixtes de montagne et suivre les réponses des arbres dominants de la montagne (sapin, hêtre et épicéa) aux variations du climat, aux incendies et à l'impact humain. **L'article 4** aborde ces objectifs en présentant une nouvelle étude paléoécologique multi-proxy détaillée (comprenant du pollen, des macrofossiles végétaux, des analyses microscopiques et macroscopiques de charbon de bois) sur des sédiments bien datés, de la zone de montagne supérieure (Zminje jezero, massif de Durmitor, Monténégro) et en utilisant des modèles additifs généralisés (GAMs) pour évaluer la réponse des taxons dominants de la canopée, aux variations du climat, du feu et de l'impact humain.

Principaux résultats

Cartographie de la couverture terrestre à l'aide d'images satellite à très haute résolution

Le couplage d'une analyse d'image basée sur l'objet (OBIA) et d'un classificateur Random Forest, utilisant des échantillons partiellement dérivés de données de terrain, sur des images satellite à très haute résolution (imagerie satellite Pléiades avec une bande panchromatique de 0,5 m, PAN ; bandes multispectrales de résolution 2 m, RGB et NIR), a révélé une bonne performance globale dans la cartographie des classes de couverture terrestre (précision globale > 95,6 %, et a Cohen's Kappa précision > 92,5 %). Selon la classification des images, la partie centrale du parc national de Biogradska Gora est principalement constituée de forêts (92,5 %). Plus précisément, la partie intérieure est dominée par des conifères alors que les zones environnantes sont dominées par des hêtraies pures. Bien qu'une grande précision ait été obtenue pour les principales classes de couverture terrestre (conifères, feuillus, prairies, sols nus et eau), la classe des *gaps* dans le couvert forestier a été classée avec une faible précision. La classification des classes de conifères et d'arbres à feuilles larges a montré une précision minimale du producteur et de l'utilisateur, respectivement de 92,9 % et 95,6 %, tandis que les *gaps* du couvert forestier ont été classés avec une précision minimale du producteur et de l'utilisateur, respectivement de 75 % et 54,5 %. L'utilisation de métriques texturales pendant les phases de segmentation et de classification des images a probablement amélioré la circonscription des *gaps* et la distinction entre les couches dominantes et inférieures de la canopée. Cependant, le manque de données de télédétection fournissant des informations sur la structure verticale de la forêt a probablement été la principale raison des faibles précisions dans cette catégorie. Dans le même ordre d'idées, une fraction de *gaps* (< 2 %), qui est constamment inférieure aux valeurs dérivées des méthodes terrestres (toujours > 15 % d'après la littérature), suggère que la méthode de classification a sous-estimé le nombre de *gaps*, n'étant probablement pas en mesure de détecter les *gaps* anciennes (c'est-à-dire les *gaps* presque fermés par la régénération) et les *gaps* de petite taille (c'est-à-dire formées par la mort d'un seul arbre). La difficulté à détecter les *gaps* a été accentuée par la présence de feuillus (hêtres), qui ont tendance à fermer ou à réduire la taille des *gaps* avec la croissance latérale de la couronne. Par conséquent, seulement 1% de tous les *gaps* observés ont été détectés dans les peuplements dominés par le hêtre. Cependant, la découverte de 99% des *gaps* dans les peuplements dominés par les conifères pourrait également suggérer que ces peuplements ont une majeure sub-naturalité. Dans ce contexte, le couplage d'un OBIA et d'un classificateur Random Forest sur des images satellites Pléiades à très haute résolution a permis de détecter uniquement des *gaps* récents et de grande taille, dans lesquelles la régénération n'a pas encore atteint de grandes hauteurs ou n'a pas complètement colonisé la surface du *gap*.

Héritages des activités humaines passées sur les forêts subnaturelles et l'importance de l'histoire sur le long terme pour la restauration et la protection des forêts subnaturelles

Les enquêtes de terrain et la carte détaillée du type de couverture terrestre montrent que la forêt primaire et subnaturelle dominée par les conifères (*Abies-Picea-Fagus*), est entourée de peuplements de *Fagus* presque purs à Biogradska Gora. Les archives paléoécologiques à haute résolution et à l'échelle du peuplement (temps médian de dépôt des sédiments = 4 ans cm⁻¹) provenant d'un *forest hollow* situé dans la forêt de hêtres, à la limite actuelle de la forêt subnaturelle, montrent que les cultures, le pâturage, ainsi que les incendies provoqués par l'homme pour créer des zones ouvertes pour l'agriculture et le pâturage, ont provoqué une réduction d'*Abies* et de *Picea* au cours du Moyen Âge. Ces pratiques sont attestées par une faible couverture arborée (abondances de pollen arboricole autour de 40 %), des valeurs élevées d'indicateurs polliniques primaires anthropogéniques et de spores de *Sporormiella*-type entre 1150-1350 CE. Après un abandon des terres autour de la pandémie de peste noire (milieu du 14^{ème} siècle) et une phase d'utilisation plus faible du sol (1500-1600 CE), qui a provoqué l'effondrement des populations locales de conifères, la pression humaine a diminué. Contrairement à la diminution de la couverture forestière ailleurs dans la région, due à l'intensification de l'utilisation du sol depuis les 15th-16th siècles, la couverture forestière a progressivement augmenté et une forêt dominée par le *Fagus* s'est établie à partir de 1850, à la transition vers le petit âge glaciaire. L'héritage des utilisations passées du sol est encore visible dans les hêtres de petite taille et, pour la plupart, à tiges multiples (diamètres généralement < 40 cm à partir d'un seul pied). Les faibles valeurs des débris ligneux grossiers, du rapport bois mort/bois vivant et de la diversité structurale reflètent une structure homogène et des groupes d'âges égaux. En revanche, la forêt subnaturelle de sapin-épicéa-hêtre présente une structure mixte et multicouche façonnée par des *gaps*, une grande quantité de débris ligneux grossiers et un rapport bois mort/bois vivant indiquant que cette partie de la forêt s'est développée de manière dynamique, pendant une longue période sans perturbations humaines. Les peuplements dominés par les conifères ont probablement été préservés des perturbations humaines en raison de leur emplacement plus éloigné et de leur accès difficile, comme le confirment les résultats de la *path analysis*, depuis au moins 1500 CE. Cette hypothèse correspond à l'âge des arbres les plus anciens (> 500 ans).

La présence de stomates et de macro-fossiles végétaux de *Picea* et d'*Abies* dans la forêt actuellement dominée par *Fagus* depuis 950 CE soutient l'hypothèse que la superficie de ces deux conifères a été réduite au cours du Moyen Âge. Ces résultats attestent qu'au moins à partir du Moyen-Âge, une pression historique constante d'utilisation du sol s'est produite même dans les zones reculées de l'arrière-pays des Alpes Dinariques centrales et a joué un rôle important dans la réduction de la superficie des forêts primaires et subnaturelles existantes, conduisant à des surfaces forestières de petite taille et fortement fragmentées.

La paléoécologie, ainsi que la recherche structurale et dendrochronologique, peuvent retracer l'histoire des forêts primaires et subnaturelles d'Europe et évaluer leurs réponses aux changements

environnementaux passés, ainsi que les effets de l'utilisation passée du sol. Les informations sur l'histoire à long terme des écosystèmes forestiers peuvent être utiles pour définir des mesures de conservation ou de restauration et pour orienter les stratégies de gestion, afin de maintenir des forêts résistantes et résilientes, compte tenu du changement climatique et des modifications associées des régimes de perturbation.

L'impact des perturbations dues aux incendies, des activités humaines et du changement climatique sur la dynamique à long terme des forêts de montagne

L'archive de Zminje jezero (massif de Durmitor) couvre une partie du Dryas jeune et la totalité de l'Holocène, depuis environ 12 450 années cal. BP jusqu'à aujourd'hui (temps médian de dépôt des sédiments = 21,6 ans cm⁻¹). Pendant le Dryas jeune et jusqu'à 10 000 années cal. BP, la végétation était dominée par *Pinus* sp. et *Betula* sp. Entre 10 000 et 9 000 années cal. BP, une forêt mixte *Picea-Abies* s'est établie dans la zone de montagne supérieure et à partir de 5 000 années cal. BP, *Fagus* est devenu co-dominant avec les deux conifères.

Le climat a probablement été le principal moteur de la dynamique des incendies dans la zone de montagne. Le brûlage de la biomasse a progressivement diminué au cours des 8500 dernières années et la majorité des épisodes d'incendie locaux étaient de faible sévérité. Cependant, les incendies de forte sévérité sont devenus plus fréquents depuis 5000 ans. L'activité régionale des incendies a augmenté depuis la fin de l'âge du bronze (3000 cal. BP) en raison d'une pression plus forte de l'utilisation du sol dans la région. Néanmoins, dans la zone montagnarde, les indicateurs polliniques anthropiques n'ont augmenté que depuis 2000 ans, ce qui suggère une pression d'utilisation du sol remarquablement faible jusqu'à la période romaine. Après 2000 cal. BP, le pollen d'*Abies* a fortement diminué et, à partir de 1200 cal. BP, *Fagus* s'est développé localement. À partir de 480 cal. BP, une pression humaine plus forte dans les zones montagneuses a probablement été responsable du passage d'une forêt mixte *Picea-Abies-Fagus* à une forêt dominée par *Picea* dans les environs de Zminje jezero. La forte pression humaine a été soutenue par une nouvelle augmentation des indicateurs polliniques anthropogéniques et par la présence d'établissements archéologiques dans le Durmitor. Cependant, la présence continue de macrofossiles végétaux et de stomates d'arbres (*Picea*, *Abies* et *Fagus*), ainsi que l'abondance de pollen arboricole généralement > 80 % et un rapport AP/NAP généralement > 4 au cours des 9000 dernières années, pourraient suggérer qu'une couverture forestière élevée a persisté dans les environs de Zminje Jezero pendant tout l'Holocène. De plus, l'agriculture et les défrichements forestiers n'ont probablement pas atteint les environs du lac. Les courbes de réponse des arbres montagnards dominants aux variations environnementales montrent que *Picea* était relativement insensible aux variations à long terme des températures estivales, aux incendies et à l'impact humain. Ainsi, les forêts d'épicéas pourraient ne pas être significativement affectées par le feu et par des températures plus chaudes que celles d'aujourd'hui.

dans le futur. *Abies* a été favorisé par des températures estivales plus élevées que celles d'aujourd'hui, tout en présentant une relation négative significative avec l'augmentation de l'impact humain. Enfin, *Fagus* est apparu comme une espèce sensible à l'augmentation des températures estivales et à une forte intensité de feu, mais favorisée par une faible intensité de feu.

Discussion et conclusion

En combinant des études de la structure et de la composition des forêts contemporaines, des analyses de télédétection et des enregistrements paléoécologiques multi-proxy (pollen, spores, stomates, macrofossiles végétaux, charbon microscopique et macroscopique, susceptibilité magnétique et analyses géochimiques de la composition des sédiments) provenant de deux sites d'étude, cette thèse a fait progresser nos connaissances sur la dynamique de la végétation à long terme, des écosystèmes forestiers de montagne mixtes épicéa-sapin-hêtre, des Alpes Dinariques centrales au cours des 12 500 dernières années. La thèse a permis de mieux comprendre le rôle de l'impact humain et du feu dans le façonnement des forêts de montagne et les réponses du sapin, du hêtre et de l'épicéa aux variations du climat, du feu et de l'impact humain (articles 2 et 4). A notre connaissance, cette thèse a présenté les premiers enregistrements de l'histoire des incendies, de la végétation et de la pression de utilisation du sol dans la zone montagnarde des Alpes Dinariques, qui couvrent la majeure partie de l'Holocène (article 4), c'est-à-dire les 11 700 dernières années b2k (avant 2000 CE) (Walker et al. 2009). En outre, elle a montré comment les incendies et l'utilisation du sol ont influencé la dynamique à long terme des forêts primaires et subnaturelles, actuellement petites et fragmentées, dans les Alpes Dinariques intérieures (articles 2 et 3). D'un point de vue méthodologique, la thèse a démontré la possibilité d'intégrer la néoécologie et la paléoécologie (Rull 2010) afin de mieux comprendre les processus écologiques dans les écosystèmes forestiers de montagne (articles 2 et 3), et a appliqué une nouvelle approche méthodologique pour distinguer les feux de captage de haute sévérité, des feux de moindre sévérité/extra-locaux, en utilisant les sédiments de charbons de bois fossiles (articles 2 et 4). Elle a également mis en évidence les limites du couplage d'une analyse d'image basée sur l'objet (OBIA) et d'un classificateur Random Forest sur des images satellite à très haute résolution, pour la cartographie des *gaps* de la canopée forestière (article 1). Enfin, elle a utilisé deux méthodes différentes pour explorer les réponses des espèces aux changements environnementaux : les corrélations croisées (CCs, article 2) et les modèles additifs généralisés (GAMs, article 4). Les CCs montrent la relation entre deux variables indépendantes dans un laps de temps donné, ce qui permet de déterminer la direction et les taux de succession de la végétation forestière (Green 1981; Tinner et al. 1999; Valsecchi et al. 2008). Tandis que les GAMs utilisent une fonction de liaison, pour illustrer la relation entre la moyenne de la variable de réponse et une fonction lissée de la variable prédictive, sur l'ensemble de la série temporelle, révélant

les optima des espèces et leur tolérance aux conditions climatiques (par exemple, les températures estivales) et aux perturbations (par exemple, l'impact humain, le feu) (Hastie and Tibshirani 1986; Colombaroli et al. 2010; Carter et al. 2020).

Observations générales

Les résultats de cette thèse semblent confirmer, comme le suggère l'étude rétrospective modélisée de Kaplan et al. (2009), que les forêts du sud-est de l'Europe (dans ce cas du Monténégro) n'ont pas été fortement exploitées ou défrichées jusqu'au Moyen Âge. De plus, les résultats semblent confirmer le caractère présumé hautement naturel de certains écosystèmes forestiers de montagne, situés dans les Alpes Dinariques centrales (Boncina 2011; Nagel et al. 2017). Les deux archives paléoécologiques (articles 2 et 4) ont montré une persistance inhabituelle d'une couverture arborée élevée à la fin de l'Holocène qui contraste avec la majorité des documents européens montrant des changements anthropiques massifs de la couverture arborée au cours des deux ou trois derniers millénaires (Fyfe et al. 2015). Cependant, la pression exercée par l'utilisation du sol (agriculture et pâturages) ainsi que les incendies (probablement d'origine humaine) ont probablement joué un rôle important dans la réduction de la superficie des forêts subnaturelles de sapins, d'épicéas et de hêtres au cours du Moyen Âge (articles 2 et 3). L'héritage de ces activités passées d'utilisation du sol pourraient être visibles dans la composition et la structure des forêts actuelles (articles 2 et 3). Un impact humain plus important dans les zones montagneuses des Alpes dinariques, au cours des 500 à 1000 dernières années pourrait être responsable de la diminution de la richesse en espèces des forêts mixtes, conduisant à la domination d'une seule espèce (*P. abies* dans le Durmitor et *F. sylvatica* à Biogradska Gora). Contrairement à l'opinion selon laquelle le feu est considéré comme un agent perturbateur négligeable dans les forêts de montagne d'épicéas, de sapins et de hêtres de la région dinarique, (Nagel et al. 2017) les nouvelles données présentées dans cette thèse (article 4) soutiennent la littérature émergente, qui démontre que les incendies ont été un agent de perturbation important tout au long de l'Holocène dans ces écosystèmes (Niklasson et al. 2010; Carter et al. 2018; Bobek et al. 2018a).

Réponses des espèces

La température à la surface du globe a augmenté de 0,99°C au cours de la période 2001-2020 CE et continuera d'augmenter au cours des prochaines décennies (IPCC 2021). En Europe, les scénarios climatiques régionaux prévoient des températures plus élevées (> 2,5°C) et une augmentation de la fréquence des épisodes de sécheresse sévère (Christensen et al. 2007; Kovats et al. 2014). Les périodes

de sécheresse prolongées favoriseront, d'une part, les incendies de forêt, qui devraient augmenter même dans les régions où ils ont toujours été de faible importance (Schmuck et al. 2015; Wu et al. 2015). D'autre part, elles provoqueront un stress sur la végétation en augmentant encore la vulnérabilité des forêts de montagne aux incendies et autres perturbations. Dans ce contexte, la connaissance des réponses du sapin blanc, du hêtre commun et de l'épicéa commun aux variations du climat, des incendies et de l'activité humaine offre des informations précieuses pour identifier les optimum environnementaux des espèces et leur tolérance aux perturbations (Colombaroli et al. 2010) et déduire la vulnérabilité future d'une grande partie des écosystèmes forestiers de montagne européens. Cependant, pour être efficace, la prédiction de la répartition future des espèces et de leur sensibilité aux changements environnementaux futurs ne doit pas seulement être basée sur l'écologie actuelle de l'espèce, telle qu'elle est déduite des écosystèmes modernes, mais doit également prendre en compte les variations passées des changements environnementaux, qui déterminent les aires de répartition des espèces (Tinner et al. 2013; Cheddadi et al. 2016; Finsinger et al. 2021). Dans cette thèse, l'utilisation d'archives paléoécologiques a permis de détecter les réponses du hêtre, de l'épicéa et du sapin aux changements environnementaux, dans des conditions environnementales substantiellement différentes de celles d'aujourd'hui, y compris des températures analogues à celles prévues par les changements climatiques futurs (environ 1-2°C de plus qu'actuellement) (Samartin et al. 2017; Carter et al. 2018; Morales-Molino et al. 2020). Comme les trois espèces considérées dans cette thèse montrent une tolérance différente à un grand nombre de paramètres climatiques (par exemple le froid hivernal, l'humidité disponible en été), nous sommes conscients de la limitation de l'utilisation des températures moyennes de juillet comme seul proxy climatique. Par conséquent, l'étude des réponses à long terme de *A. alba*, *F. sylvatica* et *P. abies* aux températures et précipitations hivernales reconstruites par des modèles (par exemple CCSM3, Fordham et al. 2017 ; MCM, Kuneš et al. 2015) ou par d'autres types d'indicateurs (par exemple les isotopes) serait une voie à explorer dans les recherches futures.

Le sapin blanc

Il ressort de ces nouvelles données qu'*A. alba* a été favorisé par des températures estivales plus élevées que celles d'aujourd'hui (jusqu'à environ 2,5 °C) (article 4). Une courbe de réponse similaire a été obtenue par Morales-Molino et al. (2020) à partir d'observations écologiques à long terme dans les Apennins du Nord. Ceci n'est pas surprenant si l'on considère que *A. alba* coexistait avec des taxons thermophiles dans les forêts méso et sub-méditerranéennes au cours de l'Holocène moyen (environ 6000 années cal. BP) (Tinner et al. 2013; Di Pasquale et al. 2014; Henne et al. 2015). En accord avec ces éléments, on observe qu'au cours des quatre dernières décennies, le réchauffement des températures a conduit à une augmentation des taux de croissance d'*A. alba* dans les forêts de montagne européennes (Büntgen et al. 2014; Gazol et al. 2015; Bosela et al. 2018; Hilmers et al. 2019).

Cependant, de façon frappante, le nouveau rapport montre également que *A. alba* a répondu positivement à l'augmentation des incendies à l'échelle du paysage (document 4). Cela contraste avec un certain nombre de données montrant que *A. alba* est une espèce sensible au feu et que les feux fréquents de haute sévérité et de faible sévérité ont conduit à son déclin rapide ou à des extinctions locales au cours des derniers millénaires (Tinner et al. 2000, 2013 ; Morales-Molino et al. 2020). D'un côté, la réponse positive d'*A. alba* aux incendies pourrait simplement découler de la relation positive, entre les incendies et les températures estivales. Tandis que d'un autre côté, la plupart des données montrant une influence négative des incendies sur *A. alba*, documentent également une activité haut des incendies d'origine humaine, soutenant l'idée que les effets combinés de l'utilisation du sol et des incendies d'origine humaine ont été les principales causes de la réduction de la population d'*A. alba* au cours des derniers millénaires (Feurdean and Willis 2008; Tinner et al. 2013). En revanche, les nouvelles données montrent que l'activité des feux n'a pas augmenté en même temps que le déclin d'*A. alba*. De plus, la persistance d'*A. alba* dans les environs de Zminje jezero soutient l'idée qu'*A. alba* pourrait être relativement résistant aux incendies de faible fréquence et de faible sévérité, voire aux rares incendies de forte sévérité (Tinner et al. 2005; Wick and Möhl 2006; Henne et al. 2013; Feurdean et al. 2019). Cependant, l'impact humain a augmenté, ce qui suggère que les humains n'ont pas utilisé le feu de manière extensive pour défricher les forêts du Durmitor et que l'utilisation du sol, plutôt que les incendies ont contribué de manière substantielle au déclin des populations d'*A. alba*, comme le soutient également la réponse négative significative d'*A. alba* à l'augmentation de l'impact humain (article 4). La généralité de cette notion est, cependant, peut-être limitée, car les incendies provoqués par l'homme ont probablement conduit au déclin d'*A. alba* dans la vallée de Biogradska Gora (article 2). Sur ce site, la sensibilité d'*A. alba* à l'impact humain est également mise en évidence par une corrélation positive entre le coût d'accès (comme indicateur de la pression humaine potentielle) et la *basal area* d'*A. alba*, ce qui indique que dans les zones les plus accessibles de la vallée, et donc les plus exposées aux perturbations anthropiques, l'abondance d'*A. alba* est significativement plus faible. Ainsi, les résultats de cette thèse soutiennent l'idée que, bien que *A. alba* soit un bon compétiteur lorsque les perturbations sont faibles ou peu fréquentes, son succès de régénération est limité lorsque la fréquence et la sévérité des perturbations augmentent, en raison du manque de capacité de repousse (par exemple, après un incendie ou une coupe), d'une maturité reproductive tardive (Feurdean and Willis 2008; Feurdean et al. 2019) et d'une régénération extrêmement sensible au pâturage par les ongulés sauvages et domestiques (Motta 1996; Diaci et al. 2011; Klopčič et al. 2017).

L' hêtre commun

F. sylvatica est apparu comme une espèce sensible à l'augmentation des températures estivales (article 4). Dans ce sens, même si la réponse dépend fortement de l'altitude, du site et de l'approvisionnement

en eau, la croissance du hêtre a généralement diminué au cours des trois dernières décennies dans les zones montagneuses européennes en raison de l'augmentation du stress, dû à la sécheresse et des épisodes de gel tardif (Dittmar et al. 2003; Allevato et al. 2019) en particulier dans le sud de l'Europe (Piovesan et al. 2008; Linares and Camarero 2012; Castagneri et al. 2014; Bosela et al. 2018). Cependant, certaines études ont également détecté une augmentation de la productivité dans les forêts de hêtres de montagne (Tognetti et al. 2014; Bosela et al. 2016). Le résultat asymétrique à droite au brûlage de la biomasse indique que *F. sylvatica* a été favorisé dans des conditions de faible brûlage de la biomasse alors qu'il est devenu sensible aux incendies, dans des conditions de brûlage de la biomasse plus élevées (article 4). Les réponses de *F. sylvatica* aux températures estivales et aux incendies correspondent à celles obtenues par Morales-Molino et al. (2020) des Apennins septentrionaux et suggèrent que, dans les Alpes dinariques centrales, *F. sylvatica* est devenu plus compétitif avec l'arrivée d'étés plus frais et peut-être plus humides, et de perturbations par le feu.

Bien qu'il soit difficile de dissocier l'effet du climat (par exemple, la transition vers des températures plus fraîches lors de petit âge glaciaire) de l'utilisation du sol, il semble probable que l'utilisation du sol et les incendies aient favorisé le développement de *F. sylvatica* au détriment de *A. alba* à la lisière actuelle de la forêt subnaturelle de Biogradska Gora (articles 2 et 3). Une réduction analogue d'*A. alba*, associée à l'expansion de *F. sylvatica* entre 6500 et 5000 cal. BP est bien documentée dans les études paléoécologiques de l'Europe centrale et méridionale, qui attribuent l'expansion du hêtre aux effets combinés de conditions climatiques favorables et plus fraîches, d'une activité accrue des feux et de l'impact humain (Vescovi et al. 2010b, a; Branch 2013; Guido et al. 2013; Branch and Marini 2014; Morales-Molino et al. 2020). Cela coïncide avec des preuves suggérant que des feux de sévérité mixte et des perturbations humaines intermédiaires peuvent favoriser l'établissement de *F. sylvatica* au niveau du peuplement (Bradshaw and Lindbladh 2005; Giesecke et al. 2007; Tinner and Lotter 2006). En effet, *F. sylvatica* a la capacité de coloniser des sols nouvellement exposés et les ouvertures de canopée plus rapidement que ses deux concurrents (*A. alba* et *P. abies*) (Pretzsch and Schütze 2005; Bolte et al. 2014; Maringer et al. 2016) parce qu'il peut se régénérer et croître sous la canopée forestière existante pendant des années, puis dominer rapidement lorsque les conditions de lumière s'améliorent, à la suite de perturbations humaines et naturelles (vent, exploitation forestière, feu) (Nagel et al. 2010; Motta et al. 2011, 2015; Maringer et al. 2016).

Ces caractères auto-écologiques peuvent expliquer la raison de l'expansion de *F. sylvatica* autour de 5000 cal. BP, lorsque des feux de forte intensité ont permis son mélange avec les deux conifères. Nos résultats montrent que *F. sylvatica* est sensible aux incendies à des taux élevés de combustion de la biomasse, comme l'ont également montré Carter et al. (2018) et Tinner et al. (2000). Ainsi, son développement dans le Durmitor s'est produit en même temps qu'un passage d'une activité de feu plus faible, comme l'a identifié le *change point analysis* (Tinner et al. 2000; Feurdean et al. 2017a; Bobek et al. 2019). De façon similaire, à Biogradska Gora, les principales expansions de *F. sylvatica* correspondent à des périodes de réduction du brûlage de la biomasse, comme l'a déduit le *change point*

analysis. Cependant, il est important de prendre en compte le fait qu'une réduction de l'activité du feu pourrait également provenir du changement de végétation lui-même (effet ascendant), puisque l'établissement de *F. sylvatica* pourrait affecter les conditions d'humidité et les caractéristiques des combustibles (Bobek et al. 2018b, 2019; Carter et al. 2018). Bien que l'impact humain ait probablement joué un rôle principal dans l'établissement de *F. sylvatica* à Biogradska Gora, la réponse de *F. sylvatica* à un impact humain croissant n'était pas significative à Durmitor. D'une part, une relation non significative pourrait provenir du fait que l'homme n'a favorisé qu'indirectement *F. sylvatica* en éliminant un de ses concurrents (*A. alba*). D'autre part, une relation non significative pourrait découler d'un impact humain généralement faible dans les zones de montagne tout au long de l'Holocène, comme le montre la persistance d'une forêt fermée dans les environs de Zminje jezero au cours des 9000 dernières années. Peut-être que pour la même raison, le brûlage de la biomasse a répondu négativement à l'impact humain, ce qui suggère que le climat a été le moteur dominant des incendies dans les zones montagneuses de Durmitor.

L'épicéa commun

P. abies est apparu comme une espèce relativement insensible aux variations à long terme des températures estivales et sa population est restée relativement stable dans la zone montagneuse du Durmitor, même lorsque les températures estivales étaient plus élevées qu'aujourd'hui (document 4), comme cela a également été observé dans les Carpates (Carter et al. 2018). L'insensibilité de *P. abies* aux températures estivales peut simplement signifier que la température n'a pas dépassé la plage de tolérance climatique de l'espèce. En outre, comme *P. abies* est particulièrement sensible au stress de la sécheresse en fin d'été en raison de son système racinaire peu profond (Henne et al. 2011), notamment dans les latitudes méridionales et à basse altitude (Spiecker 1995 ; Büntgen et al. 2006 ; Castagneri et al. 2014 ; Bosela et al. 2021), il est plausible d'affirmer que la disponibilité de l'humidité n'était pas un facteur limitant pour les populations d'épicéas dans le Durmitor. Dans cette optique, la croissance de l'épicéa est positivement corrélée aux températures estivales si l'humidité du printemps est assurée (Schurman et al. 2019).

Le comportement de *P. abies* face au feu n'est pas bien compris. D'une part, l'espèce présente des traits favorisant le feu, comme l'accumulation de débris inflammables et de litière sur le sol forestier, une teneur élevée en résine, une structure de canopée avec des branches très proches du sol (Feurdean et al. 2019). D'autre part, *P. abies* est considéré comme une espèce intolérante au feu en raison de son écorce mince, de son incapacité à repousser, de son cycle de vie relativement long et de ses racines peu profondes, qui sont facilement détruites par le feu (Feurdean et al. 2019). De plus, bien que *P. abies* a une régénération post-incendie vigoureuse (Bobek et al. 2018b), il ne survit pas après des feux de grande intensité et montre une réponse négative à l'augmentation de la fréquence des feux (Niklasson et al.

2010; Feurdean et al. 2019; Spînu et al. 2020). À Biogradska Gora, *P. abies* a fortement décliné au cours du Moyen Âge en raison d'incendies de haute sévérité et de haute fréquence associés à l'utilisation du sol (pâturage et culture) (documents 2 et 3). Cependant, ni l'impact humain ni le feu n'ont influencé de manière significative *P. abies* dans le Durmitor. Une insensibilité similaire de *P. abies* à le feu a été trouvée par Carter et al. (2018) dans les reconstructions écologiques à long terme des Carpates. La présence constante sur le long terme de *P. abies* pendant tout l'Holocène est en accord avec les études montrant que *P. abies* peut persister même avec un FRI aussi bas que 200-300 ans (Brown and Giesecke 2014; Feurdean et al. 2017a, b; Finsinger et al. 2018). Enfin, sa population bien établie dans les environs de Zminje jezero soutient l'idée que les incendies de forte intensité n'affectent pas les populations de *P. abies*, s'ils restent rares (FRI > 350 ans).

Bien que d'autres recherches sur les forêts mixtes européennes d'épicéa-hêtre-sapin soient nécessaires pour valider les réponses des espèces au feu, au climat et à l'impact humain qui sont présentées dans le document 4, les informations obtenues dans cette étude pourraient aider à établir des priorités sylvicoles et à guider les stratégies de gestion (par exemple, les mesures de conservation, la foresterie adaptative) pour garantir la fourniture de services écosystémiques de ces forêts mixtes européennes de montagne à l'avenir (Bolte et al. 2009; Temperli et al. 2012; Conedera et al. 2017). Compte tenu des projections climatiques futures, les stratégies de gestion forestière devraient chercher à réduire le risque d'incendie et à augmenter la résistance et la résilience des peuplements à la sécheresse et aux incendies. À la lumière de nos observations, le maintien ou le rétablissement d'une composition mixte dans les forêts de montagne pourrait être un bon choix à différents points de vue. La présence simultanée d'épicéas, de sapins et de hêtres offre la possibilité de tirer parti des différentes caractéristiques de chaque espèce. *A. alba* pourrait être mieux adapté aux futures températures, plus élevées et plus tolérant à la sécheresse comparé à *P. abies* et *F. sylvatica* (Ellenberg 2009; Henne et al. 2011). *F. sylvatica* pourrait agir comme un élément coupe-feu (Feurdean et al. 2017b; Carter et al. 2018; Bobek et al. 2018a). *P. abies* pourrait être utilisé grâce à sa régénération vigoureuse après les incendies (Bobek et al. 2018a) et sa persistance dans un intervalle de retour du feu aussi bas que 200-300 ans. Les stratégies de gestion forestière adaptative (Bolte et al. 2009) ont déjà permis de transformer des peuplements secondaires monospécifiques d'épicéas en forêts de montagne mixtes irrégulières plus stables (Hilmers et al. 2020). Un nombre plus élevé d'espèces d'arbres dans les forêts mixtes améliore la résilience des forêts aux événements climatiques extrêmes en atténuant leurs effets sur les performances de croissance, la résistance et la récupération des arbres (Metz et al. 2016; Gazol and Camarero 2016). En outre, un plus grand nombre d'espèces peut réduire le risque d'incendie en augmentant l'hétérogénéité de la forêt et en créant des points de discontinuité dans la biomasse, ce qui rend la dispersion du feu plus difficile (Feurdean et al. 2019). Enfin, la diversité des espèces, en plus de maintenir un niveau élevé de biodiversité, a également un effet positif sur la productivité des forêts (augmentation du volume des

arbres) et donc sur l'adsorption du carbone par les forêts, ce qui est particulièrement important pour l'atténuation du changement climatique (Zhang et al. 2012; Toïgo et al. 2015; Liang et al. 2016).

References

- Adámek M, Bobek P, Hadincová V, et al (2015) Forest fires within a temperate landscape: A decadal and millennial perspective from a sandstone region in Central Europe. *Forest Ecology and Management* 336:81–90
- Allevato E, Saulino L, Cesarano G, et al (2019) Canopy damage by spring frost in European beech along the Apennines: effect of latitude, altitude and aspect. *Remote Sensing of Environment* 225:431–440. <https://doi.org/10.1016/j.rse.2019.03.023>
- Ammann B, van der Knaap WO, Lang G, et al (2014) The potential of stomata analysis in conifers to estimate presence of conifer trees: examples from the Alps. *Veget Hist Archaeobot* 23:249–264. <https://doi.org/10.1007/s00334-014-0431-9>
- Auer I, Böhm R, Jurkovic A, et al (2007) HISTALP—historical instrumental climatological surface time series of the Greater Alpine Region. *Int J Climatol* 27:17–46. <https://doi.org/10.1002/joc.1377>
- Badalamenti E, Battipaglia G, Gristina L, et al (2019) Carbon stock increases up to old growth forest along a secondary succession in Mediterranean island ecosystems. *PLoS ONE* 14:e0220194. <https://doi.org/10.1371/journal.pone.0220194>
- Baker AG, Bhagwat SA, Willis KJ (2013) Do dung fungal spores make a good proxy for past distribution of large herbivores? *Quaternary Science Reviews* 62:21–31. <https://doi.org/10.1016/j.quascirev.2012.11.018>
- Barredo JI, Brailescu C, Teller A, et al (2021) Mapping and assessment of primary and old-growth forests in Europe. Publications Office of the European Union, Luxembourg
- Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. *Forest Ecology and Management* 258:525–537. <https://doi.org/10.1016/j.foreco.2009.01.053>
- Bebi P, Seidl R, Motta R, et al (2017) Changes of forest cover and disturbance regimes in the mountain forests of the Alps. *Forest Ecology and Management* 388:43–56. <https://doi.org/10.1016/j.foreco.2016.10.028>
- Bircher N, Cailleret M, Zingg A, Bugmann H (2016) Potenzielle Grundflächenveränderungen auf Bestandesebene im Klimawandel. In: Pluess AR, Augustin S, Brang P (eds) *Wald im Klimawandel - Grundlagen für Adaptionsstrategien*. Haupt, pp 157–171
- Birks HH (2017) Plant macrofossil introduction. In: *Reference Module in Earth Systems and Environmental Sciences*. Elsevier
- Birks HH (2002) Plant Macrofossils. In: Smol JP, Birks HJB, Last WM, et al. (eds) *Tracking Environmental Change Using Lake Sediments*. Springer Netherlands, Dordrecht, pp 49–74
- Birks HJB (2019) Contributions of Quaternary botany to modern ecology and biogeography. *Plant Ecology & Diversity* 12:189–385. <https://doi.org/10.1080/17550874.2019.1646831>
- Birks HJB, Tinner W (2016) Past forests of Europe. In: San-Miguel-Ayán J, de Rigo D, Caudullo G, et al. (eds) *Past forests of Europe. European Atlas of Forest Tree Species*. Publication Office of the European Union, Luxembourg, pp 36–39
- Bobek P, Šamonil P, Jamrichová E (2018a) Biotic controls on Holocene fire frequency in a temperate mountain forest, Czech Republic. *J Quaternary Sci* 33:892–904. <https://doi.org/10.1002/jqs.3067>

- Bobek P, Svobodová HS, Werchan B, et al (2018b) Human-induced changes in fire regime and subsequent alteration of the sandstone landscape of Northern Bohemia (Czech Republic). *The Holocene* 28:427–443. <https://doi.org/10.1177/0959683617729443>
- Bobek P, Svobodová-Svitavská H, Pokorný P, et al (2019) Divergent fire history trajectories in Central European temperate forests revealed a pronounced influence of broadleaved trees on fire dynamics. *Quaternary Science Reviews* 222:105865. <https://doi.org/10.1016/j.quascirev.2019.105865>
- Bolte A, Ammer C, Löf M, et al (2009) Adaptive forest management in central Europe: Climate change impacts, strategies and integrative concept. *Scandinavian Journal of Forest Research* 24:473–482. <https://doi.org/10.1080/02827580903418224>
- Bolte A, Hilbrig L, Grundmann BM, Roloff A (2014) Understory dynamics after disturbance accelerate succession from spruce to beech-dominated forest—the Siggaboda case study. *Annals of Forest Science* 71:139–147. <https://doi.org/10.1007/s13595-013-0283-y>
- Boncina A (2011) History, current status and future prospects of uneven-aged forest management in the Dinaric region: an overview. *Forestry* 84:467–478. <https://doi.org/10.1093/forestry/cpr023>
- Bosela M, Lukac M, Castagneri D, et al (2018) Contrasting effects of environmental change on the radial growth of co-occurring beech and fir trees across Europe. *Science of the Total Environment* 615:1460–1469
- Bosela M, Štefančík I, Petráš R, Vacek S (2016) The effects of climate warming on the growth of European beech forests depend critically on thinning strategy and site productivity. *Agricultural and Forest Meteorology* 222:21–31. <https://doi.org/10.1016/j.agrformet.2016.03.005>
- Bosela M, Tumajer J, Cienciala E, et al (2021) Climate warming induced synchronous growth decline in Norway spruce populations across biogeographical gradients since 2000. *Science of The Total Environment* 752:141794. <https://doi.org/10.1016/j.scitotenv.2020.141794>
- Bradshaw RHW, Lindbladh M (2005) Regional spread and stand-scale establishment of *Fagus sylvatica* and *Picea abies* in Scandinavia. *Ecology* 86:1679–1686. <https://doi.org/10.1890/03-0785>
- Branch NP (2013) Early–Middle Holocene vegetation history, climate change and human activities at Lago Riane (Ligurian Apennines, NW Italy). *Veget Hist Archaeobot* 22:315–334. <https://doi.org/10.1007/s00334-012-0384-9>
- Branch NP, Marini NAF (2014) Mid-Late Holocene environmental change and human activities in the northern Apennines, Italy. *Quaternary International* 353:34–51. <https://doi.org/10.1016/j.quaint.2013.07.053>
- Brandt JS, Kuemmerle T, Li H, et al (2012) Using Landsat imagery to map forest change in southwest China in response to the national logging ban and ecotourism development. *Remote Sensing of Environment* 121:358–369. <https://doi.org/10.1016/j.rse.2012.02.010>
- Brokaw NVL (1982a) Treefalls: frequency, timing, and consequences. In: Leigh EG, Rand AS, Windsor DM (eds) *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*. Smithsonian Institution Press, Washington, D.C, pp 101–108
- Brokaw NVL (1982b) The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14:158–160
- Brown KJ, Giesecke T (2014) Holocene fire disturbance in the boreal forest of central Sweden: Holocene fire disturbance in the boreal forest, central Sweden. *Boreas* 43:639–651. <https://doi.org/10.1111/bor.12056>
- Buchwald E (2005) A hierarchical terminology for more or less natural forests in relation to sustainable management and biodiversity conservation. In: *Third expert meeting on harmonizing forest-related definitions for use by various stakeholders* Food and Agriculture Organization of the United Nations. Rome, pp 111–127

- Buckley R (1991) Environmental impacts of recreation in parks and reserves. In: Perspectives in Environmental Management. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 243–258
- Büntgen U, Frank DC, Schmidhalter M, et al (2006) Growth/climate response shift in a long subalpine spruce chronology. *Trees* 20:99–110. <https://doi.org/10.1007/s00468-005-0017-3>
- Büntgen U, Tegel W, Kaplan JO, et al (2014) Placing unprecedented recent fir growth in a European-wide and Holocene-long context. *Frontiers in Ecology and the Environment* 12:100–106. <https://doi.org/10.1890/130089>
- Burrascano S, Keeton WS, Sabatini FM, Blasi C (2013) Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. *Forest Ecology and Management* 291:458–479. <https://doi.org/10.1016/j.foreco.2012.11.020>
- Calcote R (1995) Pollen Source Area and Pollen Productivity: Evidence from Forest Hollows. *The Journal of Ecology* 83:591. <https://doi.org/10.2307/2261627>
- Calcote R (1998) Identifying forest stand types using pollen from forest hollows. *The Holocene* 8:423–432. <https://doi.org/10.1191/095968398670894847>
- Carrer M, Castagneri D, Popa I, et al (2018) Tree spatial patterns and stand attributes in temperate forests: The importance of plot size, sampling design, and null model. *Forest Ecology and Management* 407:125–134. <https://doi.org/10.1016/j.foreco.2017.10.041>
- Carter VA, Bobek P, Moravcová A, et al (2020) The role of climate-fuel feedbacks on Holocene biomass burning in upper-montane Carpathian forests. *Global and Planetary Change* 193:103264. <https://doi.org/10.1016/j.gloplacha.2020.103264>
- Carter VA, Moravcová A, Chiverrell RC, et al (2018) Holocene-scale fire dynamics of central European temperate spruce-beech forests. *Quaternary Science Reviews* 191:15–30. <https://doi.org/10.1016/j.quascirev.2018.05.001>
- Castagneri D, Nola P, Motta R, Carrer M (2014) Summer climate variability over the last 250 years differently affected tree species radial growth in a mesic *Fagus–Abies–Picea* old-growth forest. *Forest Ecology and Management* 320:21–29. <https://doi.org/10.1016/j.foreco.2014.02.023>
- Cateau E, Larrieu L, Vallauri D, et al (2015) Ancienneté et maturité : deux qualités complémentaires d'un écosystème forestier. *Comptes Rendus Biologies* 338:58–73. <https://doi.org/10.1016/j.crv.2014.10.004>
- Cheddadi R, Araújo MB, Maiorano L, et al (2016) Temperature range shifts for three European tree species over the last 10,000 years. *Front Plant Sci* 7:1581. <https://doi.org/10.3389/fpls.2016.01581>
- Christensen JH, Hewitson B, Busuioc A, et al (2007) Regional Climate Projections. In: Solomon S, Qin D, Manning M, et al. (eds) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press. Cambridge UK and New York USA
- Colombaroli D, Henne PD, Kaltenrieder P, et al (2010) Species responses to fire, climate and human impact at tree line in the Alps as evidenced by palaeo-environmental records and a dynamic simulation model. *Journal of Ecology* 98:1346–1357. <https://doi.org/10.1111/j.1365-2745.2010.01723.x>
- Conedera M, Colombaroli D, Tinner W, et al (2017) Insights about past forest dynamics as a tool for present and future forest management in Switzerland. *Forest Ecology and Management* 388:100–112
- Davis OK (1987) Spores of the dung fungus *Sporormiella*: Increased abundance in historic sediments and before Pleistocene megafaunal extinction. *Quaternary Research* 28:290–294. [https://doi.org/10.1016/0033-5894\(87\)90067-6](https://doi.org/10.1016/0033-5894(87)90067-6)

- Deza-Araujo M, Morales-Molino C, Tinner W, et al (2020) A critical assessment of human-impact indices based on anthropogenic pollen indicators. *Quaternary Science Reviews* 236:106291. <https://doi.org/10.1016/j.quascirev.2020.106291>
- Diaci J (ed) (1999) Virgin forests and forest reserves in Central and East European countries: history, present status and future development. Proceedings of the invited lecturers' reports presented at the COST E4 management committee and working groups meeting in Ljubljana, Slovenia, 25-28 April, 1998. Dept. of Forestry and Renewable Forest Resources, Ljubljana, Slovenia
- Diaci J, Rozenbergar D, Anic I, et al (2011) Structural dynamics and synchronous silver fir decline in mixed old-growth mountain forests in Eastern and Southeastern Europe. *Forestry* 84:479–491. <https://doi.org/10.1093/forestry/cpr030>
- Di Pasquale G, Allevato E, Cocchiararo A, et al (2014) Late Holocene persistence of *Abies alba* in low-mid altitude deciduous forests of central and southern Italy: new perspectives from charcoal data. *J Veg Sci* 25:1299–1310. <https://doi.org/10.1111/jvs.12196>
- Dittmar C, Zech W, Elling W (2003) Growth variations of Common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe - a dendroecological study. *Forest Ecology and Management* 173:63–78
- Dörfler W (2013) Prokoško Jezero: An environmental record from a subalpine lake in Bosnia-Herzegovina. In: Müller J, Rassmann K, Hofmann R (eds) *Okolište 1 – Untersuchungen Einer Spätneolithischen Siedlungskammer in Zentralbosnien*, Universitätsforschungen Zur Prähistorischen Archäologie. Habelt Verlag, Bonn, pp 311–340
- Drößler L, von Lüpke B (2005) Canopy gaps in two virgin beech forest reserves in Slovakia. *J For Sci* 51:446–457. <https://doi.org/10.17221/4578-JFS>
- Ellenberg H (2009) *Vegetation Ecology of Central Europe*, Fourth Edition. Cambridge University Press
- Euforgen (2009) Distribution map of European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*), and Silver fir (*Abies alba*). <http://www.euforgen.org>
- European Environment Agency (2016) *European forest ecosystems: state and trends*. Publications Office, Luxembourg
- European Environment Agency L (2007) *European Forest Types. Categories and types for sustainable forest management reporting and policy*. Copenhagen
- Fajardo A, de Graaf R (2004) Tree dynamics in canopy gaps in old-growth forests of *Nothofagus pumilio* in Southern Chile. *Plant Ecology* 173:95–105. <https://doi.org/10.1023/B:VEGE.0000026333.54741.97>
- FAO (2015) *Forest resources Assessment Working Paper 180*. In: *Global Forest Resources Assessment 2015. Terms and definitions*. Rome, p 36
- FAO (2011) *Mountain forests in a changing world: realizing values, addressing challenges*. FAO, Rome
- Feurdean A, Florescu G, Vannière B, et al (2017a) Fire has been an important driver of forest dynamics in the Carpathian Mountains during the Holocene. *Forest Ecology and Management* 389:15–26. <https://doi.org/10.1016/j.foreco.2016.11.046>
- Feurdean A, Tonkov S, Pfeiffer M, et al (2019) Fire frequency and intensity associated with functional traits of dominant forest type in the Balkans during the Holocene. *Eur J Forest Res* 138:1049–1066. <https://doi.org/10.1007/s10342-019-01223-0>
- Feurdean A, Veski S, Florescu G, et al (2017b) Broadleaf deciduous forest counterbalanced the direct effect of climate on Holocene fire regime in hemiboreal/boreal region (NE Europe). *Quaternary Science Reviews* 169:378–390. <https://doi.org/10.1016/j.quascirev.2017.05.024>

- Feurdean A, Willis KJ (2008) Long-term variability of *Abies alba* in NW Romania: implications for its conservation management. *Diversity and Distributions* 14:1004–1017. <https://doi.org/10.1111/j.1472-4642.2008.00514.x>
- Finsinger W, Fevre J, Orbán I, et al (2018) Holocene fire-regime changes near the treeline in the Retezat Mts. (Southern Carpathians, Romania). *Quaternary International* 477:94–105. <https://doi.org/10.1016/j.quaint.2016.04.029>
- Finsinger W, Morales-Molino C, Gálka M, et al (2017) Holocene vegetation and fire dynamics at Crveni Potok, a small mire in the Dinaric Alps (Tara National Park, Serbia). *Quaternary Science Reviews* 167:63–77. <https://doi.org/10.1016/j.quascirev.2017.04.032>
- Finsinger W, Vanel Q, Ribolini A, Tinner W (2021) Early to late Holocene vegetation and fire dynamics at the treeline in the Maritime Alps. *Veget Hist Archaeobot* 30:507–524. <https://doi.org/10.1007/s00334-020-00795-x>
- Fordham DA, Saltré F, Haythorne S, et al (2017) PaleoView: a tool for generating continuous climate projections spanning the last 21 000 years at regional and global scales. *Ecography* 40:1348–1358. <https://doi.org/10.1111/ecog.03031>
- Foster DR, Orwig DA, McLachlan JS (1996) Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Trends in Ecology & Evolution* 11:419–424
- Foster DR, Schoonmaker PK, Pickett STA (1990) Insights from Paleoecology to Community Ecology. *TREE* 5:119–122
- Frankovič M, Janda P, Mikoláš M, et al (2021) Natural dynamics of temperate mountain beech-dominated primary forests in Central Europe. *Forest Ecology and Management* 479:118522. <https://doi.org/10.1016/j.foreco.2020.118522>
- Frelich L (2016) Forest dynamics. *F1000Res* 5:183. <https://doi.org/10.12688/f1000research.7412.1>
- Fyfe RM, Woodbridge J, Roberts N (2015) From forest to farmland: pollen-inferred land cover change across Europe using the pseudobiomization approach. *Glob Change Biol* 21:1197–1212. <https://doi.org/10.1111/gcb.12776>
- Garbarino M, Borgogno Mondino E, Lingua E, et al (2012) Gap disturbances and regeneration patterns in a Bosnian old-growth forest: a multispectral remote sensing and ground-based approach. *Annals of Forest Science* 69:617–625. <https://doi.org/10.1007/s13595-011-0177-9>
- Gazol A, Camarero JJ (2016) Functional diversity enhances silver fir growth resilience to an extreme drought. *J Ecol* 104:1063–1075. <https://doi.org/10.1111/1365-2745.12575>
- Gazol A, Camarero JJ, Gutiérrez E, et al (2015) Distinct effects of climate warming on populations of silver fir (*Abies alba*) across Europe. *J Biogeogr* 42:1150–1162. <https://doi.org/10.1111/jbi.12512>
- Giesecke T, Hickler T, Kunkel T, et al (2007) Towards an understanding of the Holocene distribution of *Fagus sylvatica* L. *Journal of Biogeography* 34:118–131. <https://doi.org/10.1111/j.1365-2699.2006.01580.x>
- Gratzer G, Keeton WS (2017) Mountain Forests and Sustainable Development: The Potential for Achieving the United Nations' 2030 Agenda. *Mountain Research and Development* 37:246–253. <https://doi.org/10.1659/MRD-JOURNAL-D-17-00093.1>
- Green DG (1981) Time series and postglacial forest ecology. *Quat res* 15:265–277. [https://doi.org/10.1016/0033-5894\(81\)90030-2](https://doi.org/10.1016/0033-5894(81)90030-2)
- Grindean R, Tanțău I, Feurdean A (2019) Linking vegetation dynamics and stability in the old-growth forests of Central Eastern Europe: Implications for forest conservation and management. *Biological Conservation* 229:160–169. <https://doi.org/10.1016/j.biocon.2018.11.019>

- Guido MA, Menozzi BI, Bellini C, et al (2013) A palynological contribution to the environmental archaeology of a Mediterranean mountain wetland (North West Apennines, Italy). *The Holocene* 23:1517–1527. <https://doi.org/10.1177/0959683613496294>
- Hall D (2004) Rural tourism development in southeastern Europe: transition and the search for sustainability. *Int J Tourism Res* 6:165–176. <https://doi.org/10.1002/jtr.482>
- Hanewinkel M, Cullmann DA, Schelhaas M-J, et al (2013) Climate change may cause severe loss in the economic value of European forest land. *Nature Clim Change* 3:203–207. <https://doi.org/10.1038/nclimate1687>
- Hansen AJ, Neilson RP, Dale VH, et al (2001) Global Change in Forests: Responses of Species, Communities, and Biomes. *BioScience* 51:765. [https://doi.org/10.1641/0006-3568\(2001\)051\[0765:GCIFRO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0765:GCIFRO]2.0.CO;2)
- Hastie T, Tibshirani R (1986) Generalized Additive Models. *Statistical Science* 1:297–318
- Henne PD, Elkin C, Colombaroli D, et al (2013) Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modeling. *Landscape Ecol* 28:819–833. <https://doi.org/10.1007/s10980-012-9782-8>
- Henne PD, Elkin C, Franke J, et al (2015) Reviving extinct Mediterranean forest communities may improve ecosystem potential in a warmer future. *Frontiers in Ecology and the Environment* 13:356–362. <https://doi.org/10.1890/150027>
- Henne PD, Elkin CM, Reineking B, et al (2011) Did soil development limit spruce (*Picea abies*) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model: Soil depth limits spruce expansion in the Alps. *Journal of Biogeography* 38:933–949. <https://doi.org/10.1111/j.1365-2699.2010.02460.x>
- Higuera P, Peters M, Brubaker L, Gavin D (2007) Understanding the origin and analysis of sediment-charcoal records with a simulation model. *Quaternary Science Reviews* 26:1790–1809. <https://doi.org/10.1016/j.quascirev.2007.03.010>
- Higuera PE, Gavin DG, Bartlein PJ, Hallett DJ (2010) Peak detection in sediment - charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *Int J Wildland Fire* 19:996–1014. <https://doi.org/10.1071/WF09134>
- Hilmers T, Avdagić A, Bartkowicz L, et al (2019) The productivity of mixed mountain forests comprised of *Fagus sylvatica*, *Picea abies*, and *Abies alba* across Europe. *Forestry: An International Journal of Forest Research* 92:512–522. <https://doi.org/10.1093/forestry/cpz035>
- Hilmers T, Biber P, Knoke T, Pretzsch H (2020a) Assessing transformation scenarios from pure Norway spruce to mixed uneven-aged forests in mountain areas. *Eur J Forest Res* 139:567–584. <https://doi.org/10.1007/s10342-020-01270-y>
- Hilmers T, Biber P, Knoke T, Pretzsch H (2020b) Assessing transformation scenarios from pure Norway spruce to mixed uneven-aged forests in mountain areas. *Eur J Forest Res* 139:567–584. <https://doi.org/10.1007/s10342-020-01270-y>
- Hofstetter S, Tinner W, Valsecchi V, et al (2006) Lateglacial and Holocene vegetation history in the Insubrian Southern Alps—New indications from a small-scale site. *Veget Hist Archaeobot* 15:87–98. <https://doi.org/10.1007/s00334-005-0005-y>
- Horvat I, Glavač V, Ellenberg H (1974) *Vegetation of Southeast Europe*. Gustav Fischer Verlag, Stuttgart
- Huo L-Z, Boschetti L, Sparks A (2019) Object-based classification of forest disturbance types in the Conterminous United States. *Remote Sensing* 11:477. <https://doi.org/10.3390/rs11050477>

- IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland
- IPCC (2021) Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press
- Jovanovic B, Jovanovic R, Zupancic M (1986) Natural Potential Vegetation of Yugoslavia. Scientific Council of Vegetation Map of Yugoslavia, Ljubljana
- Kaplan JO, Krumhardt KM, Zimmermann N (2009) The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews* 28:3016–3034. <https://doi.org/10.1016/j.quascirev.2009.09.028>
- Klopčič M, Mina M, Bugmann H, Boncina A (2017) The prospects of silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst) in mixed mountain forests under various management strategies, climate change and high browsing pressure. *European Journal of Forest Research* 136:1071–1090. [https://doi.org/DOI 10.1007/s10342-017-1052-5](https://doi.org/DOI%2010.1007/s10342-017-1052-5)
- Knorn J, Kuemmerle T, Radeloff VC, et al (2013) Continued loss of temperate old-growth forests in the Romanian Carpathians despite an increasing protected area network. *Envir Conserv* 40:182–193. <https://doi.org/10.1017/S0376892912000355>
- Kovats RS, Valentini R, Bouwer LM, et al (2014) Europe. In: Barros VR, Field CB, Dokken DJ, et al. (eds) *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, USA, pp 1267–1326.
- Kranjc A (2009) History of deforestation and reforestation in the Dinaric karst. *Geographical Research* 47:15–23. <https://doi.org/10.1111/j.1745-5871.2008.00552.x>
- Kulkarni C, Peteet D, Boger R, Heusser L (2016) Exploring the role of humans and climate over the Balkan landscape: 500 years of vegetational history of Serbia. *Quaternary Science Reviews* 144:83–94. <https://doi.org/10.1016/j.quascirev.2016.05.021>
- Kuneš P, Svobodová-Svitavská H, Kolář J, et al (2015) The origin of grasslands in the temperate forest zone of east-central Europe: long-term legacy of climate and human impact. *Quaternary Science Reviews* 116:15–27. <https://doi.org/10.1016/j.quascirev.2015.03.014>
- Liang J, Crowther TW, Picard N, et al (2016) Positive biodiversity-productivity relationship predominant in global forests. *Science* 354:aaf8957. <https://doi.org/10.1126/science.aaf8957>
- Linares JC, Camarero JJ (2012) From pattern to process: linking intrinsic water-use efficiency to drought-induced forest decline. *Glob Change Biol* 18:1000–1015. <https://doi.org/10.1111/j.1365-2486.2011.02566.x>
- Maringer J, Conedera M, Ascoli D, et al (2016) Resilience of European beech forests (*Fagus sylvatica* L.) after fire in a global change context. *Int J Wildland Fire* 25:699–710. <https://doi.org/10.1071/WF15127>
- Mazziotta A, Heilmann-Clausen J, Bruun HH, et al (2016) Restoring hydrology and old-growth structures in a former production forest: Modelling the long-term effects on biodiversity. *Forest Ecology and Management* 381:125–133
- McMullin RT, Wiersma YF (2019) Out with OLD growth, in with ecological continNEWity: new perspectives on forest conservation. *Front Ecol Environ* 17:176–181. <https://doi.org/10.1002/fee.2016>
- Messier C, Puettmann K, Coates D (2013) *Managing forests as complex adaptive systems: Building resilience to the challenge of global change*. NY: Routledge, New York

- Metz J, Annighöfer P, Schall P, et al (2016) Site-adapted admixed tree species reduce drought susceptibility of mature European beech. *Glob Change Biol* 22:903–920. <https://doi.org/10.1111/gcb.13113>
- Mihevc A, Prelovšek M, Hajna NZ (eds) (2010) Introduction to the Dinaric karst. Inštitut za raziskovanje krasa ZRC SAZU
- Mikoláš M, Ujházy K, Jasík M, et al (2019) Primary forest distribution and representation in a Central European landscape: Results of a large-scale field-based census. *Forest Ecology and Management* 449:117466. <https://doi.org/10.1016/j.foreco.2019.117466>
- Millar CI, Stephenson NL (2015) Temperate forest health in an era of emerging megadisturbance. *Science* 349:823–826. <https://doi.org/10.1126/science.aaa9933>
- Mina M, Bugmann H, Cordonnier T, et al (2017) Future ecosystem services from European mountain forests under climate change. *J Appl Ecol* 54:389–401. <https://doi.org/10.1111/1365-2664.12772>
- Morales-Molino C, Steffen M, Samartin S, et al (2020) Long-Term responses of Mediterranean mountain forests to climate change, fire and human activities in the Northern Apennines (Italy). *Ecosystems*. <https://doi.org/10.1007/s10021-020-00587-4>
- Motta R (1996) Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the Western Italian Alps. *Forest Ecology and Management* 88:93–98. [https://doi.org/10.1016/S0378-1127\(96\)03814-5](https://doi.org/10.1016/S0378-1127(96)03814-5)
- Motta R, Berretti R, Castagneri D, et al (2011) Toward a definition of the range of variability of central European mixed *Fagus* – *Abies* – *Picea* forests: the nearly steady-state forest of Lom (Bosnia and Herzegovina). *Can J For Res* 41:1871–1884. <https://doi.org/10.1139/x11-098>
- Motta R, Garbarino M, Berretti R, et al (2015) Structure, spatio-temporal dynamics and disturbance regime of the mixed beech–silver fir–Norway spruce old-growth forest of Biogradska Gora (Montenegro). *Plant Biosystems* 149:966–975. <https://doi.org/10.1080/11263504.2014.945978>
- Mountain Research Initiative EDW Working Group (2015) Elevation-dependent warming in mountain regions of the world. *Nature Clim Change* 5:424–430. <https://doi.org/10.1038/nclimate2563>
- Muscolo A, Bagnato S, Sidari M, Mercurio R (2014) A review of the roles of forest canopy gaps. *Journal of Forestry Research* 25:725–736. <https://doi.org/10.1007/s11676-014-0521-7>
- Nagel TA, Levanic T, Diaci J (2007) A dendroecological reconstruction of disturbance in an old-growth *Fagus-Abies* forest in Slovenia. *Ann For Sci* 64:891–897. <https://doi.org/10.1051/forest:2007067>
- Nagel TA, Mikac S, Dolinar M, et al (2017) The natural disturbance regime in forests of the Dinaric Mountains: A synthesis of evidence. *Forest Ecology and Management* 388:29–42. <https://doi.org/10.1016/j.foreco.2016.07.047>
- Nagel TA, Svoboda M (2008) Gap disturbance regime in an old-growth *Fagus* – *Abies* forest in the Dinaric Mountains, Bosnia-Herzegovina. *Canadian Journal of Forest Research* 38:2728–2737. <https://doi.org/10.1139/X08-110>
- Nagel TA, Svoboda M, Rugani T, Diaci J (2010) Gap regeneration and replacement patterns in an old-growth *Fagus* – *Abies* forest of Bosnia–Herzegovina. *Plant Ecol* 208:307–318. <https://doi.org/10.1007/s11258-009-9707-z>
- Niklasson M, Zin E, Zielonka T, et al (2010) A 350-year tree-ring fire record from Białowieża Primeval Forest, Poland: implications for Central European lowland fire history. *Journal of Ecology* 98:1319–1329. <https://doi.org/10.1111/j.1365-2745.2010.01710.x>

- Paillet Y, Pernot C, Boulanger V, et al (2015) Quantifying the recovery of old-growth attributes in forest reserves: A first reference for France. *Forest Ecology and Management* 346:51–64. <https://doi.org/10.1016/j.foreco.2015.02.037>
- Parviainen J (2005) Virgin and natural forests in the temperate zone of Europe. *For Snow Landsc Res* 79:9–18
- Peterken GF (1996) *Natural woodland: ecology and conservation in northern temperate regions*. Cambridge University Press, Cambridge UK
- Piovesan G, Biondi F, Filippo AD, et al (2008) Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Global Change Biology* 14:1–17. <https://doi.org/10.1111/j.1365-2486.2008.01570.x>
- Potapov P, Hansen MC, Laestadius L, et al (2017) The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. *Sci Adv* 3:e1600821. <https://doi.org/10.1126/sciadv.1600821>
- Pretzsch H, Schütze G (2005) Crown allometry and growing space efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed stands. *Plant Biology* 7:628–639. <https://doi.org/10.1055/s-2005-865965>
- Rajczak J, Pall P, Schär C (2013) Projections of extreme precipitation events in regional climate simulations for Europe and the Alpine Region: Projection of extreme precipitation. *J Geophys Res Atmos* 118:3610–3626. <https://doi.org/10.1002/jgrd.50297>
- Reif A, Walentowski H (2008) The assessment of naturalness and its role for nature conservation and forestry in Europe. *Waldökologie, Landschaftsforschung u 64 nd Naturschutz* 6:63–76
- Roberts N (2014) The first farmers. In: *The Holocene: An Environmental History*. John Wiley & Sons, Ltd.
- Rull V (2010) Ecology and Palaeoecology: Two Approaches, One Objective. *TOECOLJ* 3:1–5. <https://doi.org/10.2174/1874213001003020001>
- Runkle JR (1982) Patterns of Disturbance in Some Old-Growth Mesic Forests of Eastern North America. *Ecology* 63:1533–1546. <https://doi.org/10.2307/1938878>
- Sabatini FM (2014) Causes and determinants of plant biodiversity in Southern European old-growth forests. Structural heterogeneity, dispersal limitation and abiotic resources. Sapienza Università di Roma. Facoltà di Scienze Matematiche, Fisiche e Naturali Dottorato in Sc. Ecologiche
- Sabatini FM, Burrascano S, Keeton WS, et al (2018) Where are Europe's last primary forests? Diversity and Distributions 24:1426–1439. <https://doi.org/10.1111/ddi.12778>
- Sabatini FM, Keeton WS, Lindner M, et al (2020) Protection gaps and restoration opportunities for primary forests in Europe. *Divers Distrib* 26:1646–1662. <https://doi.org/10.1111/ddi.13158>
- Sadori L, Giardini M, Gliozzi E, et al (2015) Vegetation, climate and environmental history of the last 4500 years at lake Shkodra (Albania/Montenegro). *The Holocene* 25:435–444. <https://doi.org/10.1177/0959683614561891>
- Samartin S, Heiri O, Joos F, et al (2017) Warm Mediterranean mid-Holocene summers inferred from fossil midge assemblages. *Nature Geosci* 10:207–212. <https://doi.org/10.1038/ngeo2891>
- Schliemann SA, Bockheim JG (2011) Methods for studying treefall gaps: A review. *Forest Ecology and Management* 261:1143–1151. <https://doi.org/10.1016/j.foreco.2011.01.011>
- Schmuck G, San-Miguel-Ayanz J, Durrant T, et al (2015) *Forest Fires in Europe, Middle East and North Africa 2014*. Publications Office of the European Union, Luxembourg

- Schurman JS, Babst F, Björklund J, et al (2019) The climatic drivers of primary *Picea* forest growth along the Carpathian arc are changing under rising temperatures. *Glob Change Biol* 25:3136–3150. <https://doi.org/10.1111/gcb.14721>
- Schütz J-P, Saniga M, Diaci J, Vrška T (2016) Comparing close-to-nature silviculture with processes in pristine forests: lessons from Central Europe. *Annals of Forest Science* 73:911–921. <https://doi.org/10.1007/s13595-016-0579-9>
- Seidl R, Thom D, Kautz M, et al (2017) Forest disturbances under climate change. *Nature Clim Change* 7:395–402. <https://doi.org/10.1038/nclimate3303>
- Seneviratne SI, Nicholls N, Easterling D, et al (2012) Changes in Climate Extremes and their Impacts on the Natural Physical Environment. In: Field CB, Barros V, Stocker TF, Dahe Q (eds) *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation*. Cambridge University Press, Cambridge, pp 109–230
- Seppä H (2013) Pollen Analysis, Principles. In: Elias SA (ed) *The Encyclopedia of Quaternary Science*. Elsevier, Amsterdam, pp 794–804
- Sirotkovic J (1987) *Enciklopedija Jugoslavije*. Jugoslovenski leksikografski zavod Miroslav Krleža, Zagreb, Croatia,
- Song X-P, Hansen MC, Stehman SV, et al (2018) Global land change from 1982 to 2016. *Nature* 560:639–643. <https://doi.org/10.1038/s41586-018-0411-9>
- Spiecker H (1995) Growth dynamics in a changing environment - long-term observations. *Plant and Soil* 168:555–561
- Spies TA (2004) Ecological concepts and diversity of old-growth forests. *Journal of Forestry* 102:14–20
- Spies TA, Franklin JF, Klopsch M (1990) Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can J For Res* 20:649–658. <https://doi.org/10.1139/x90-087>
- Spînu AP, Niklasson M, Zin E (2020) Mesophication in temperate Europe: A dendrochronological reconstruction of tree succession and fires in a mixed deciduous stand in Białowieża Forest. *Ecol Evol* 10:1029–1041. <https://doi.org/10.1002/ece3.5966>
- Stancioiu PT, O'Hara KL (2006) Morphological plasticity of regeneration subject to different levels of canopy cover in mixed-species, multiaged forests of the Romanian Carpathians. *Trees* 20:196–209. <https://doi.org/10.1007/s00468-005-0026-2>
- Sugita S (1994) Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *The Journal of Ecology* 82:881–897. <https://doi.org/10.2307/2261452>
- Swetnam TW, Allen CD, Betancourt JL (1999) Applied historical ecology: using the past to manage for the future. *Ecological Applications* 9:1189–1206. [https://doi.org/10.1890/1051-0761\(1999\)009\[1189:AHEUTP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[1189:AHEUTP]2.0.CO;2)
- Temperli C, Bugmann H, Elkin C (2012) Adaptive management for competing forest goods and services under climate change. *Ecological Applications* 22:2065–2077. <https://doi.org/10.1890/12-0210.1>
- Tinner W, Colombaroli D, Heiri O, et al (2013) The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. *Ecological Monographs* 83:419–439. <https://doi.org/10.1890/12-2231.1>
- Tinner W, Conedera M, Ammann B, Lotter AF (2005) Fire ecology north and south of the Alps since the last ice age. *The Holocene* 15:1214–1226. <https://doi.org/10.1191/0959683605hl892rp>

- Tinner W, Conedera M, Gobet E, et al (2000) A palaeoecological attempt to classify fire sensitivity of trees in the southern Alps. *The Holocene* 10:565–574. <https://doi.org/10.1191/095968300674242447>
- Tinner W, Hubschmid P, Wehrli M, et al (1999) Long-term forest fire ecology and dynamics in southern Switzerland. *Journal of Ecology* 87:273–289. <https://doi.org/10.1046/j.1365-2745.1999.00346.x>
- Tinner W, Lotter A (2006) Holocene expansions of *Fagus sylvatica* and *Abies alba* in Central Europe: where are we after eight decades of debate? *Quaternary Science Reviews* 25:526–549. <https://doi.org/10.1016/j.quascirev.2005.03.017>
- Tognetti R, Lombardi F, Lasserre B, et al (2014) Tree-Ring Stable Isotopes Reveal Twentieth-Century Increases in Water-Use Efficiency of *Fagus sylvatica* and *Nothofagus* spp. in Italian and Chilean Mountains. *PLoS ONE* 9:e113136. <https://doi.org/10.1371/journal.pone.0113136>
- Toïgo M, Vallet P, Perot T, et al (2015) Overyielding in mixed forests decreases with site productivity. *J Ecol* 103:502–512. <https://doi.org/10.1111/1365-2745.12353>
- Tyrrell LE, Crow TR (1994) Structural Characteristics of Old-Growth Hemlock-Hardwood Forests in Relation to Age. *Ecology* 75:370–386. <https://doi.org/10.2307/1939541>
- UN General Assembly (2015) Transforming our world : the 2030 Agenda for Sustainable Development
- UNEP/CBD/SBSTTA (2001) Main Theme: Forest Biological Diversity. Report of the Ad Hoc Technical Expert Group on Forest Biological Diversity. Seventh Meeting Montreal
- Vacek Z, Prokúpková A, Vacek S, et al (2021) Mixed vs. monospecific mountain forests in response to climate change: structural and growth perspectives of Norway spruce and European beech. *Forest Ecology and Management* 488:119019. <https://doi.org/10.1016/j.foreco.2021.119019>
- Valsecchi V, Finsinger W, Tinner W, Ammann B (2008) Testing the influence of climate, human impact and fire on the Holocene population expansion of *Fagus sylvatica* in the southern Prealps (Italy). *The Holocene* 18:603–614. <https://doi.org/10.1177/0959683608089213>
- Vescovi E, Ammann B, Ravazzi C, Tinner W (2010a) A new Late-glacial and Holocene record of vegetation and fire history from Lago del Greppo, northern Apennines, Italy. *Veget Hist Archaeobot* 19:219–233. <https://doi.org/10.1007/s00334-010-0243-5>
- Vescovi E, Kaltenrieder P, Tinner W (2010b) Late-Glacial and Holocene vegetation history of Pavullo nel Frignano (Northern Apennines, Italy). *Review of Palaeobotany and Palynology* 160:32–45. <https://doi.org/10.1016/j.revpalbo.2010.01.002>
- Wagner FH, Ferreira MP, Sanchez A, et al (2018) Individual tree crown delineation in a highly diverse tropical forest using very high resolution satellite images. *ISPRS Journal of Photogrammetry and Remote Sensing* 145:362–377. <https://doi.org/10.1016/j.isprsjprs.2018.09.013>
- Walker M, Johnsen S, Rasmussen SO, et al (2009) Formal definition and dating of the GSSP (Global Stratotype Section and Point) for the base of the Holocene using the Greenland NGRIP ice core, and selected auxiliary records. *J Quaternary Sci* 24:3–17. <https://doi.org/10.1002/jqs.1227>
- Watson JEM, Evans T, Venter O, et al (2018) The exceptional value of intact forest ecosystems. *Nat Ecol Evol* 2:599–610. <https://doi.org/10.1038/s41559-018-0490-x>
- Watson JEM, Shanahan DF, Di Marco M, et al (2016) Catastrophic Declines in Wilderness Areas Undermine Global Environment Targets. *Current Biology* 26:2929–2934. <https://doi.org/10.1016/j.cub.2016.08.049>
- Whitlock C, Colombaroli D, Conedera M, Tinner W (2018) Land-use history as a guide for forest conservation and management. *Conservation Biology* 32:84–97. <https://doi.org/10.1111/cobi.12960>

- Whitlock C, Larsen C (2001) Charcoal as a fire proxy. In: Smol JP, Birks HJB, Last WM, et al. (eds) Tracking Environmental Change Using Lake Sediments. Springer Netherlands, Dordrecht, pp 75–97
- Wick L, Möhl A (2006) The mid-Holocene extinction of silver fir (*Abies alba*) in the Southern Alps: a consequence of forest fires? Palaeobotanical records and forest simulations. *Veget Hist Archaeobot* 15:435–444. <https://doi.org/10.1007/s00334-006-0051-0>
- Wirth C, Gleixner G, Heimann M (eds) (2009) Old-growth forests: function, fate, and value. Springer, Berlin
- Wolters S, Enters D, Bittmann F (2010) Landscape history and land-use dependent soil erosion in central Bosnia from the Bronze Age to Medieval Times. In: EGU General Assembly Conference Abstracts. p 11200
- Wu M, Knorr W, Thonicke K, et al (2015) Sensitivity of burned area in Europe to climate change, atmospheric CO₂ levels, and demography: A comparison of two fire-vegetation models. *J Geophys Res Biogeosci* 120:2256–2272. <https://doi.org/10.1002/2015JG003036>
- Wymann Von Dach S, Bracher CP, Peralvo M, et al (2018) Leaving no one in mountains behind: Localizing the SDGs for resilience of mountain people and ecosystems. <https://doi.org/10.7892/BORIS.120130>
- Zhang Y, Chen HYH, Reich PB (2012) Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *Journal of Ecology* 100:742–749. <https://doi.org/10.1111/j.1365-2745.2011.01944.x>

Thank you

During the time I developed this PhD project, many people encouraged and helped me.

Firstly, I would like to express my gratitude to my thesis supervisors, whose intellectual guidance, patience, and availability enabled me to keep up my motivation during this Balkan adventure.

Walter, without your supervision this work would not have been possible: you have consistently helped and guided me through a process of scientific and personal growth. I thank you for your scientific rigour and high level of expertise, your creative approach and your broad and critical eye in interpreting data. I learned so much from you and I am grateful for our countless scientific discussions.

Emanuele, thank you for your great responsiveness and willingness to take me under your supervision at a very delicate time, for giving me great freedom and autonomy and for pushing me to seek new skills. I greatly appreciated your precious help in critical phases and your enriching inputs throughout my research work.

Ilham, thanks for your great availability and support (also on week-ends), for your decisive character that I greatly admire and for your scientific and personal advice.

Alan, thank you for sharing part of the journey with me (unfortunately a little short!).

Next, I would like to thank you all my collaborators, co-authors and thesis committee members for contributing to the progress of my research, for their insightful comments and for raising important questions that guided me to improve my work.

My sincere thanks also go to all the colleagues at ISEM for having always created a stimulating and sunny atmosphere: Sandrine, Sylvie, Isabelle, Laurent, Marie-Pierre, Bertrand, Thierry, Sarah, Jérôme, Laure. Many thanks also to the Italian LAB meeting group for stimulating discussions and updates.

I would like also to express my gratitude to the referees and to the member of the jury for bringing their knowledge and experience in evaluating and improve this work.

Moreover, I would like to thank the University of Padova for the financial support provided during these three years and also to the TESAF Department for providing a partial scholarship to accomplish the final stage of this PhD. I also thank the University of Montpellier and the ISEM for welcoming me during my French stay.

I warmly thank old and new friends for having been supportive, kind, helpful and funny: Paula C., Elisa, Veronica, Nagham, Febrina, Mary, Olga, Ginevra, Katherine, Claudia, Daniely, Carmen, Marion, Camilla, Florine, Luke, Paula R., Giada, Giacomo, Paola, Francesca.

Lastly, I would like to thank my family for their encouragement and support and I am very grateful to my partner Dario who was very patient and helpful, making my life colorful and happy and the graphs fancier.

“I don't really feel it's necessary to know exactly what I am. The most important thing in life and work is to become something different from what you were at the beginning. If, starting a book, one knew from the beginning what one would come to say at the end, who would find the courage to write it?” (Paul-Michel Foucault)