



Same, but different: similar states of forest structure in temperate mountain regions of Europe despite different social-ecological forest disturbance regimes

Ana Stritih · Cornelius Senf · Tobias Kuemmerle · Catalina Munteanu · Lasha Dzadzamia · Jernej Stritih · Dragan Matijašić · Owen Cortner · Rupert Seidl

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Abstract

Context Ecosystem services provided by mountain forests are critically linked to forest structure. Social-ecological disturbance regimes (i.e., the rate, frequency, and patch size distribution of disturbances driven by interacting natural and anthropogenic processes) and land use affect forest structure, but their specific impacts are not fully understood.

Objectives We examine how differences in disturbance regimes affect patterns of forest structure across three European mountain ranges with similar vegetation types but different land-use histories: the European Alps, the Carpathians, and the Caucasus.

Methods We related data on horizontal and vertical forest structure, measured by spaceborne lidar (GEDI), with Landsat-derived information on forest disturbances (1986–2020) and topographic, climatic, and anthropogenic predictors.

Results We found similar social-ecological disturbance regimes in the Alps and Carpathians (average annual disturbance rates of 0.34% and 0.39%,

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A. Stritih (✉) · R. Seidl
Chair of Ecosystem Dynamics and Forest Management,
TUM School of Life Sciences, Department of Life
Science Systems, Technical University of Munich,
Hans-Carl-Von-Carlowitz-Platz 2, 85354 Freising,
Germany
e-mail: ana.stritih@tum.de

A. Stritih · R. Seidl
Berchtesgaden National Park, Doktorberg 6,
83471 Berchtesgaden, Germany

C. Senf
School of Life Sciences, Earth Observation for Ecosystem
Management, Technical University of Munich,
Hans-Carl-Von-Carlowitz-Platz 2, 85354 Freising,
Germany

T. Kuemmerle
Geography Department, Humboldt University, Berlin,
Germany

T. Kuemmerle
Integrative Research Institute On Transformations
of Human-Environment Systems (IRI THESys),
Humboldt-University, Berlin, Germany

C. Munteanu
Chair of Wildlife Ecology and Management, Faculty
of Environment and Natural Resources, University
of Freiburg, 79106 Freiburg, Germany

L. Dzadzamia
Deutsche Gesellschaft Für Internationale Zusammenarbeit
(GIZ) GmbH, Tbilisi, Georgia

J. Stritih
Eco-Corridors Fund for the Southern Caucasus, Tbilisi,
Georgia

D. Matijašić
National Forestry Agency of Georgia, 6 Dimitry Gulia St,
Tbilisi, Georgia

respectively, and median patch size < 0.5 ha), yet much lower disturbance rates and patch sizes in the Caucasus (0.08% yr⁻¹ and < 0.2 ha). Despite different disturbance regimes, we found similar patterns of forest structure. Two alternative states emerged consistently across all mountain ranges: a tall and closed-canopy state in 74–80% of forests and a low and open-canopy state (< 50% canopy cover) in the rest. While forest structure responded consistently to abiotic drivers such as topography and climate, its association with anthropogenic pressures differed between mountain ranges. Stand-replacing disturbances played an important role in the Carpathians, while forest structure in the Caucasus was related to proximity to settlements, reflecting local forest use.

Conclusions Different social-ecological contexts in mountain regions can produce markedly different forest disturbance regimes. Despite these differences, similar states of forest structures emerge, suggesting strong attractors of structure in temperate mountain forests.

Keywords Alternative structural states · Disturbance regimes · Forest management · GEDI · Land-use history · Landsat

Introduction

Forests are essential for sustaining life in mountain regions by providing people with protection from natural hazards, fuelwood, and construction materials (Grêt-Regamey and Weibel 2020); as well as providing habitat to many species (Rahbek et al. 2019). The capacity of forests to provide these services and to host high biodiversity strongly depends on their structure (e.g., canopy density, tree height, and biomass) (Stritih et al. 2021a). Forest structure is partly determined by natural processes (e.g., tree growth and mortality), but it is also influenced in major ways by the humans who manage forests (Kulakowski et al. 2011; Garbarino et al. 2013; Mitchell et al. 2023). Both sets of factors, natural and anthropogenic, are currently changing in mountain regions as climate change leads to changes in

tree mortality and growth (McDowell et al. 2020), and as socio-economic change leads to rural out-migration, farmland abandonment and changes in forest management (Rudel et al. 2005; Birdsey and Pan 2015). Understanding how these changes impact forest structure is important for sustaining the many ecosystem services provided by mountain forests in the future.

A key process influencing forest structure is disturbance. Forest disturbances are pulses of tree mortality that abruptly change forest structure and resource availability across spatial scales, from individual patches to landscapes (Turner 2010). They can be caused by natural agents (e.g., windthrows, bark beetle outbreaks, or forest fires, among others) or by humans (e.g., logging). Disturbances can change forest structure and composition (Seidl and Turner 2022) or even cause a transition from a closed-canopy forest to an alternative state, such as shrubland (Tepley et al. 2017; Miller et al. 2019). Anthropogenic disturbances often have a particularly strong impact on forest structure (Roebroek et al. 2023). For example, clearcuts cause stand-replacing disturbances, and subsequent re-planting often leads to accelerated forest recovery, but it also homogenizes forest structures (Senf et al. 2019), which in turn alters natural disturbance regimes (Schurman et al. 2018). At the landscape level, disturbances create patchiness, fostering heterogeneity (Turner 2010; Senf et al. 2020) and biodiversity (Thom and Seidl 2016), but they can also have negative impacts on the provision of ecosystem services (Thom and Seidl 2016; Stritih et al. 2021a). The impact of disturbances depends on their frequency, return interval, severity, and size, which together characterize the disturbance regime of a region (Turner 2010; Turner and Seidl 2023). In many parts of the world, disturbance regimes are driven by the interactions between human activity and natural processes, shaping a social-ecological forest disturbance regime (Gordijn and O'Connor 2023).

In addition to disturbances, forest structure is also shaped by current forest management (Li et al. 2022; Roebroek et al. 2023) and the legacies of past land use (Munteanu et al. 2015; Bürgi et al. 2017). For example, selective logging and thinning often aim to stimulate the growth of individual trees or promote specific tree species, but generally reduce forest biomass (Zhou et al. 2013; Cazzolla Gatti et al. 2015), while livestock grazing inside forests can impede tree regeneration (Etchebarne and Brazeiro 2016). Current

O. Cortner
Environmental Policy Lab, Department of Environmental
Systems Science, ETH Zürich, Zürich, Switzerland

O. Cortner
Yale School of the Environment, New Haven, CT, USA

forest structure, species composition, and disturbance dynamics are often strongly influenced by historical land use, including past forest management (Munteanu et al. 2015; Conedera et al. 2017; Knight et al. 2022; Morales-Molino et al. 2022; Kaim et al. 2023; Lestienne et al. 2023). For example, forests that have regrown or were afforested on previous agricultural land tend to be more structurally homogeneous (Foster et al. 2003; Kulakowski et al. 2011) and are thus more susceptible to natural disturbances (Mantero et al. 2020; Stritih et al. 2021b). Furthermore, historical developments in land management can create lock-ins through institutions, social norms or economic conditions that can constrain current forest management decisions (Wilson 2014; Tappeiner et al. 2021). Understanding such legacies and path dependencies is essential for interpreting the current changes observed in forests (Tappeiner et al. 2021).

European mountain landscapes harbor many of Europe's last primary forests (Sabatini et al. 2018) and are hotspots of biodiversity (Myers et al. 2000; Olson and Dinerstein 2002; Večeřa et al. 2019). For example, the Carpathian mountains sustain populations of large mammals, including brown bear, wolf, European bison, and lynx (UNEP 2007), and the Caucasus is also home to the Caucasian leopard, Caucasian tur, and Bezoar goats (Zazanashvili et al. 2020). At the same time, European mountain landscapes have a long history of land use and have recently experienced substantial social-ecological transformations (Schirpke et al. 2021). For example, many forests of the Alps have been logged since the early industrial era (Johann 2007), and this region has experienced pronounced human depopulation and an increase in forest area since the 19th century (Bebi et al. 2017). In the Carpathians, many forests were intensively managed for timber during the socialist era in the 20th century (Munteanu et al. 2016), while forests in the Caucasus were largely protected (UNECE/FAO 2019). After the collapse of socialism, changes in land use, forest ownership and management have led to concerns about forest loss and degradation in both regions (Griffiths et al. 2012; Knorn et al. 2012; Chen et al. 2021; Cortner et al. 2024). At the same time, the forests of Eastern Europe are frequently identified as an important space for European policies, from biodiversity conservation to a bioeconomy transition (European Commission 2021). How these ongoing social-ecological changes affect forest disturbance regimes and forest structure is

incompletely understood. Comparing mountain ranges with similar bioclimatic and biogeographic conditions yet different land-use histories has the potential to insights into the relationship between disturbance, social-ecological context, and forest structure.

There has been substantial progress in observing changes in canopy cover over large spatial scales from optical satellite data (Hansen et al. 2013; Zhu 2017; Senf 2022). Using the Landsat archive, forest disturbances have been mapped for Europe going back to 1986 (Senf and Seidl 2021). Such observations allow for quantifying the characteristics of disturbance regimes. However, as optical satellite data does not penetrate deep into the forest canopy, it has limitations in quantifying the vertical structure of forests (Bolton et al. 2017). To address this gap, the Global Ecosystem Dynamics Investigation (GEDI) spaceborne lidar, launched in 2019 (Dubayah et al. 2020), has generated the first consistent data about the vertical structure of vegetation across large spatial extents. In previous work, we used GEDI data to analyze forest structure across the European Alps, finding two alternative states of forest structure (Stritih et al. 2023). Such patterns have important implications for forest functions, yet it remains unclear whether they can be generalized to other temperate mountain regions with different forest management and land-use histories.

Here, we characterize social-ecological disturbance regimes (i.e., the rate, frequency, and patch size distribution of disturbances driven by interacting natural and anthropogenic processes) and forest structure across three European mountain ranges with different land-use histories: the European Alps, the Carpathian mountains, and the Caucasus mountains. At the same time, these three mountain ranges have similar forest types in terms of potential natural vegetation, providing a natural experiment to assess the importance of land-use histories. Specifically, we ask the following questions:

- (1) Are there differences in social-ecological forest disturbance regimes across the three mountain ranges?
- (2) Do differences in disturbance regimes result in different patterns of forest structure?
- (3) How are patterns in forest structure related to different groups of drivers (disturbances, anthropogenic pressures, topographic and climatic factors), and are these relationships consistent across mountain ranges?

We hypothesize that differences in land-use history and current forest management result in different social-ecological disturbance regimes in the three mountain ranges. Since we expect disturbance dynamics to be a key driver of forest structure, we also hypothesize that different disturbance regimes will lead to distinct patterns of forest structure in the mountain forests of temperate Europe. In addition, we expect that forest structure relates similarly to climate and topography across the three mountain ranges, while the associations between anthropogenic pressures and forest structures should reflect differences in land-use histories.

Methods

Study areas

We used the spatial extents for the three mountain ranges, the European Alps, the Carpathian and the Caucasus mountains, as defined by the Global Mountain Biodiversity Assessment (GMBA) mountain inventory v2 (Snethlage et al. 2022). The mountain ranges span elevations from near sea level to >2600 m a.s.l. in the Carpathians, >4800 m in the Alps and >5600 m in the Caucasus (Table 1). The most widespread potential natural vegetation types across all three mountain ranges are mesophytic deciduous and coniferous forests (Fig. 1), with dominant species including European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst.), and silver fir (*Abies alba* Mill.) in the Alps and Carpathians, and Oriental beech (*F. orientalis* Lipsky), European hornbeam (*Carpinus betulus* L.), Oriental spruce (*P.*

orientalis (L.) Link), and Caucasian fir (*Abies nordmanniana* (Steven) Spach) in the Caucasus. In the Alps and Carpathians, subalpine forests are dominated by conifers, such as European larch (*Larix decidua* L.), Swiss stone pine (*Pinus cembra* L.), and mountain pine (*P. mugo* Turra), while broadleaves (such as Oriental beech and birch (*Betula litwinowii* Doluch.) form the subalpine forests of the Caucasus (Zazanashvili et al. 2000). Submediterranean and subcontinental forests at warmer sites consist of thermophilous broadleaved species such as oaks (*Quercus pubescens* Willd., *Q. petraea* (Matt.) Liebl.) and Oriental hornbeam (*Carpinus orientalis* Mill.) (Bohn et al. 2007). The Caucasus, which includes the Greater and Lesser Caucasus ranges, has a particularly pronounced climatic gradient and includes forest types that are not present in the other mountain ranges, such as Colchic temperate rainforests on the coast of the Black sea or semiarid forest steppes in the Eastern Caucasus (Bohn et al. 2007), but these range-specific forests were not included in our comparative analysis.

All three mountain ranges share a long history of human land use, with their landscapes shaped by mountain agriculture for millennia (Feurdean et al. 2016; Conedera et al. 2017). However, their forests have experienced different trajectories of human use in the recent past. In the Alps, forests have been intensively logged since the beginning of the early industrial period to produce energy and construction materials, with management favoring Norway spruce over other tree species and with restrictions on other forest uses such as livestock grazing (Johann 2007). Since the nineteenth century, regulations on forest use, out-migration from rural areas, and structural changes in

Table 1 Characteristics of the mountain ranges (defined according to the GMBA mountain inventory v2 (Snethlage et al. 2022) and their social-ecological forest disturbance

regimes (based on Landsat data, Senf and Seidl 2021). Disturbance patches are defined as connected pixels disturbed in the same years, with a minimum size of two pixels (0.18 ha)

Mountain range	Alps	Carpathians	Caucasus
Elevation range [m a.s.l.]	0 – 4809	41 – 2655	0 – 5642
Approximate upper treeline elevation [m a.s.l.]	1800 – 2300	1400 – 1800	2200 – 2700
Area [km ²]	175'902	121'834	157'586
Forest cover [%]	57	75	47
Mean annual disturbance rate [%]	0.34	0.39	0.08
Annual disturbance frequency [no. patches per km ²]	0.50	0.29	0.11
Median (5 th - 95 th percentile) patch size of disturbances [ha]	0.45 (0.18 – 2.16)	0.36 (0.18 – 2.79)	0.18 (0.18 – 0.99)

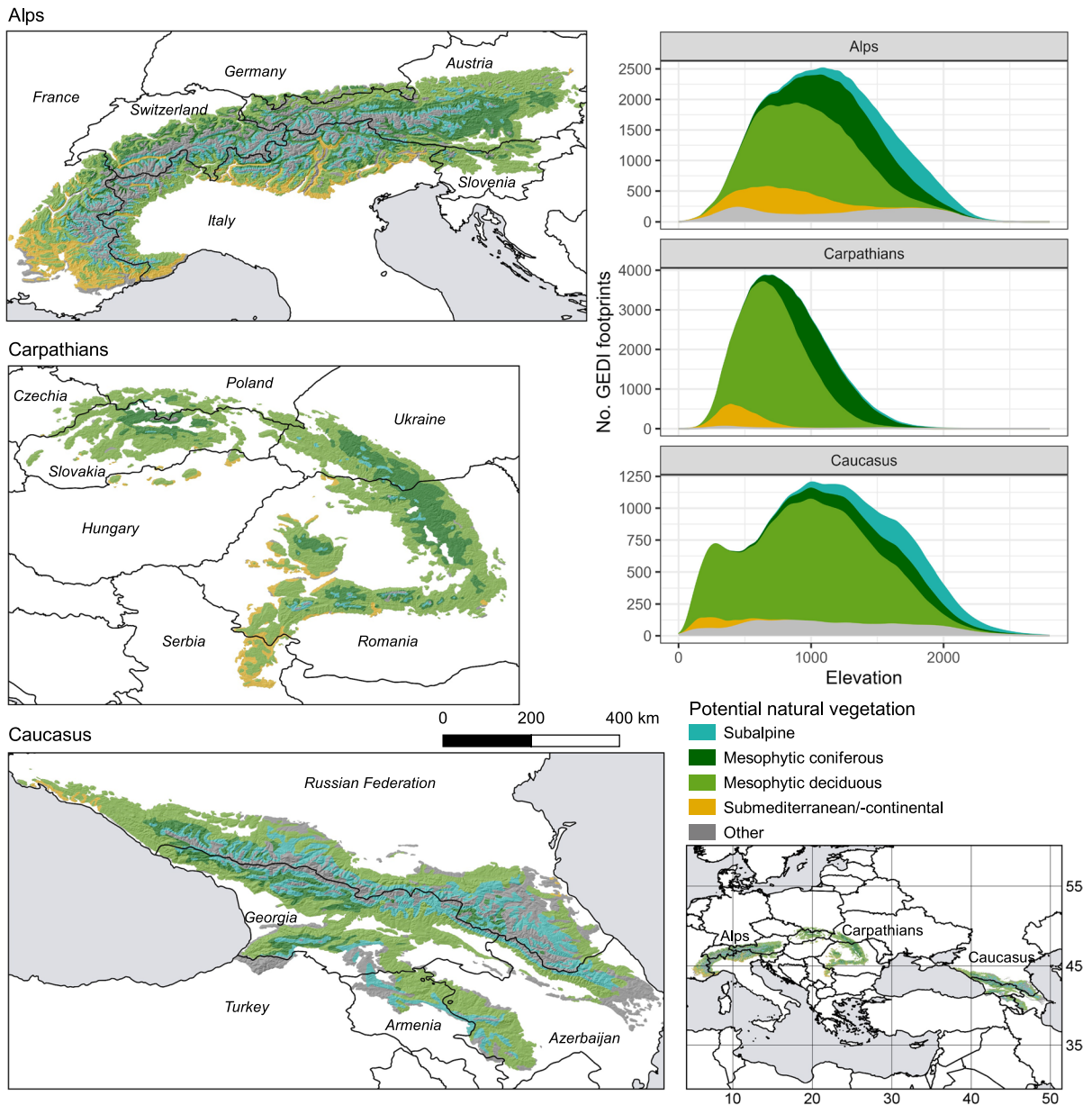


Fig. 1 Potential natural vegetation in the Alps, Carpathians and Caucasus (according to Bohn et al. 2004, 2007; mountain range definitions according to GMBA (Snehlage et al. 2022)). Histograms show the distribution of forested GEDI footprints

across elevation in each mountain range. The four main vegetation types that occur across all three mountain ranges (shown here in colour) were included in the analysis

agriculture have contributed to land abandonment and the expansion and densification of forests (Bebi et al. 2017; Garbarino et al. 2020). Today, both private and publicly-owned forests in the Alps are primarily managed for timber production and for sustaining their protective effect (Maroschek et al. 2015; Temperli

et al. 2017). Especially in the northern Alps, management is supported by high road density and cable yarding technology that allows harvesting in difficult terrain (Enache et al. 2016).

In the Carpathians, a similar process of farmland abandonment and forest transition has been ongoing

since the beginning of the 20th century and accelerated after the end of socialism in the 1990s (Munteanu et al. 2014). During the socialist era in the second half of the 20th century, forests were nationalized and intensively managed in many areas. This included heavy logging to fund reparation payments after World War II (Nita et al. 2018) and was characterized by clearcuts and plantations of fast-growing species (Munteanu et al. 2016). Today, most countries in the Carpathians are members of the European Union and are net exporters of timber (ForestEurope 2020).

In contrast to the Alps and the Carpathians, mountain forests in the Caucasus were strictly protected during most of 20th century due to the recognition of their importance for protection against soil erosion and natural hazards, and due to the timber imports to the Caucasus region from other parts of the Soviet Union (UNECE/FAO 2019). Forest management was thus mostly limited to small-scale use (Metreveli 2002). Agricultural abandonment and forest expansion have also been less pronounced in the Caucasus than in the other two mountain ranges (Buchner et al. 2020), and many forests are still used for forest grazing (UNECE/FAO 2019). Forests remain state-owned (ForestEurope 2020) and lack a history of industrialized timber harvesting, with most of the harvested wood used locally as fuelwood (Garforth et al. 2016; UNECE/FAO 2019), especially during the economic crises that followed the collapse of the Soviet Union (Torchinava 2016). Rural poverty remains high in the Caucasus region in comparison to the other two mountain ranges (World Bank 2023).

Further details about anthropogenic and natural disturbances in the three mountain regions are provided in the Supplementary material (Table S2).

Social-ecological forest disturbance data

To characterize forest disturbance regimes, we used a satellite-based pan-European disturbance map (Senf and Seidl 2021), which was extended to include the Caucasus region for this study. The disturbance map is based on Landsat data and includes stand-replacing disturbances of both human and natural causes that occurred in the years between 1986 and 2020, with 30 m spatial resolution and annual temporal resolution. We defined disturbance patches as connected pixels (using an eight-neighbor rule) that were disturbed in the same year, with a minimum mapping

unit of two pixels (0.18 ha). We used the disturbance map to quantify disturbance rates (% forest area disturbed annually), frequencies (number of forest disturbance patches per year), and patch size distributions in each mountain range, as well as to identify trends in disturbed forest area over time.

GEDI data on forest structure

We used GEDI data to assess forest structure across the three mountain ranges. GEDI is a spaceborne LiDAR (Light Detection And Ranging) system installed on the International Space Station and providing data since 2019. GEDI emits laser pulses and measures their reflected returns for sample footprints 25 m in diameter (Dubayah et al. 2020). Based on the returned waveforms, vegetation structural metrics can be derived (see e.g. Mandl et al. (2023); Tang et al. (2012) for details). We used GEDI level 2A and 2B products, which include profiles of canopy height and derived structural metrics (including canopy cover, plant area index, and foliage height diversity), and processed them using the rGEDI package (Silva et al. 2020). We included data from 2019 to 2021, using footprints acquired between June and August to include only leaf-on data (Potapov et al. 2021). We filtered GEDI data to include only high-quality footprints fully located within forests as defined by a satellite-based forest-cover map (Senf and Seidl (2021) for the Alps and Carpathians and by Hansen et al. (2013) for the Caucasus), with a buffer of 9 m around the footprint locations to account for possible geolocation errors (Dubayah et al. 2020). We also excluded footprints on slopes steeper than 40°, as GEDI accuracy can be impaired by steep terrain (Mandl et al. 2023). This resulted in 3,053,500 GEDI footprints available for analysis in the Alps, 3,074,088 in the Carpathians, and 1,751,049 in the Caucasus.

We focused on two metrics of forest structure, the fraction of canopy cover and the 75th percentile of relative heights (RH75). Based on these metrics, we fitted a Gaussian mixture model (Scrucca et al. 2016) for each mountain range to describe forest structure following the approach described in Strith et al. (2023). Gaussian mixture models are well-suited to identifying clusters in multi-modal distributions because they use a combination of Gaussian distributions to represent clusters in the data. We used this feature of Gaussian mixture models to identify clusters in the 2D-space

defined by tree height and cover. These clusters potentially represented different states of forest structure (e.g., open and short vs. closed and tall).

Potential drivers of forest structure

We investigated the relationship between states of forest structure and their potential drivers by fitting a random forest model (Breiman 2001) for each mountain range to predict the occurrence of each state based on predictors describing topography, climate, social-ecological forest disturbance history, and other anthropogenic pressures. *Topographic* predictors included elevation, slope, and terrain roughness, derived from the shuttle radar topography mission terrain model (NASA SRTM 2013). We obtained *climate* predictors from the CHELSA V2.1 dataset (Karger et al. 2017), including mean annual temperature, total annual precipitation, and mean annual temperature seasonality. Based on the *disturbance* map described in Section “[Social-ecological forest disturbance data](#)”, we derived the time since the last stand-replacing disturbance, the proportion of the GEDI footprint disturbed and the size of the disturbance patch in which the GEDI footprint was located. Predictors describing *anthropogenic pressure* included the distance to settlements, population density within a 10-km radius (both derived from the GHS population grid (Schiavina et al. 2022)), and distance to roads (derived from a combination of the GRIP dataset (Meijer et al. 2018) and OpenStreetMap (OSM 2022)).

We used a random forest model to relate forest structural characteristics identified from GEDI to the potential predictor variables because this model can capture potentially nonlinear relations and interactions between predictors (Breiman 2001). For each of the 300 trees in the random forest, we selected a random sample of 10,000 GEDI footprints from each of the alternative states to ensure a balanced sample. We calculated the permutation-based importance of each predictor variable (Breiman 2001; Genuer et al. 2015) and performed a ten-fold cross-validation, where 90% of the footprints were used for training and 10% for validation. We included only forests within the potential natural vegetation types that occur across all three mountain ranges (subalpine, mesophytic coniferous and deciduous, and submediterranean/-continental) according to Bohn et al. (2007, 2004), which correspond to 89% of all forested GEDI footprints in the Alps and Caucasus, and 99% in the Carpathians.

Results

Social-ecological forest disturbance regimes

We found similar disturbance rates in the Alps and the Carpathians, with 0.34% of forests disturbed annually in the Alps, and 0.39% in the Carpathians, corresponding to average return intervals (i.e., mean time between two disturbance events) of 294 and 256 years, respectively. In both these mountain ranges, the disturbed area increased between 1986 and 2020 (Fig. 2), with a Sen’s slope of 692 ha/year (95% confidence interval 330–991 ha/year) in the Alps and 691 ha/year (confidence interval 267 – 1,138 ha/year) in the Carpathians. The area disturbed during the 2010s was approximately 70% larger than during the 1990s. We observed particularly high disturbance rates in years following severe windthrow events, such as storm Uschi in 2002 and storm Vaia in 2018 in the Alps, and storm Elisabeth in 2004 in the Carpathians. In contrast, the rate of disturbance was considerably lower in the Caucasus, with a mean annual disturbance rate of 0.08%, corresponding to a disturbance return interval of 1250 years. The disturbed area was larger in the 1990s and had a weakly decreasing trend over the 35-year observation period (Sen’s slope -78 ha/year, with a confidence interval between -158 and -22 ha/year).

In all three mountain ranges, the majority of disturbed patches were smaller than 0.5 ha (60% in the Alps, 59% in the Carpathians, and 85% in the Caucasus), with median patch sizes of 0.45, 0.36 ha, and 0.18 ha, respectively (Fig. 2, Table 1). Only 5% of disturbed patches were larger than 1 ha in the Caucasus, compared to 16% in the Alps and 19% in the Carpathians. The largest observed disturbance patches were 190 ha in the Caucasus, 2,080 ha in the Alps and 5,700 ha in the Carpathians.

Forest structure

Across all three mountain ranges and forest types, we found consistent bimodal distributions of canopy cover and height based on GEDI data (Fig. 3; see also Supplementary material, Figure 9). We identified two distinct clusters of forest structure using Gaussian mixture models: tall, closed-canopy forests and short, open-canopy forests (henceforth referred to as closed-canopy and open-canopy forests,

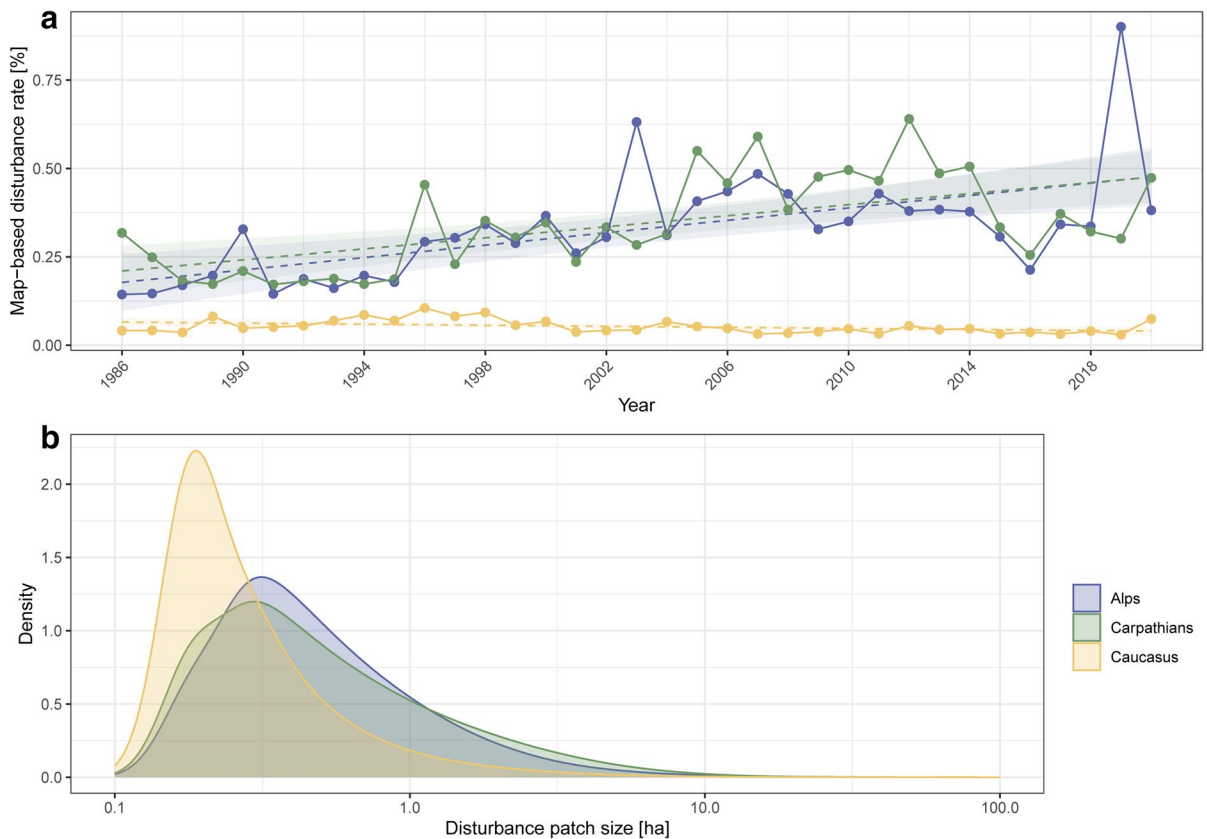


Fig. 2 Disturbed area per year as percentage of the current forest area in the Alps, Carpathians, and Caucasus (**a**) and patch size distribution of disturbances (**b**). The Alps and Carpathians experienced an increase in disturbance rates since the mid-1980s, with peaks in the Alps in 2003 and 2019 (after storms Uschi in 2002 and Vaia in 2018). The Caucasus Mountains experienced more forest disturbances in the late 1980s and 1990s, with a decrease after 2000. The dotted lines show

linear trends – increasing in the Alps and Carpathians, and slightly decreasing in the Caucasus Mountains. The patch size distributions include all annual patches of at least two Landsat pixels (0.18 ha). We note that patch size distributions are shown on a log scale with a cut-off at 100 ha for better visibility. Maximum disturbance patch sizes reached 190 ha in the Caucasus Mountains, 2080 ha in the Alps, and 5700 ha in the Carpathians

respectively). The two clusters occurred over overlapping ranges of climatic and topographic conditions, even in the absence of disturbance (see Supplementary material, Figure 9). Most forests belonged to the closed-canopy cluster, which represented 80% of the GEDI footprints in the Carpathians, 76% in the Alps, and 74% in the Caucasus Mountains (Fig. 3). These clusters had largely similar characteristics in all three mountain ranges, with some small yet notable differences. For example, submediterranean forests in the Alps had a more open structure than those in other mountain ranges, while forests in the mesophytic coniferous zone in the Caucasus Mountains reached greater heights than similar forests in the other mountain ranges.

Based on variables for topography, climate, disturbances, and other anthropogenic pressures, our random forest models were able to predict the occurrence of open- vs. closed-canopy forests moderately well, with area under the receiver-operator curve (AUC) values of 0.79 in the Caucasus Mountains, 0.74 in the Alps and 0.73 in the Carpathians. Topographic predictors had a similar effect on the occurrence of open-canopy forests across all three mountain ranges. Among them, elevation was most important, with open-canopy forests generally occurring at higher elevations. In the Caucasus Mountains, precipitation was the most important climatic factor (Fig. 4), as open-canopy forests occurred more often at drier sites, particularly in the eastern Caucasus. Temperature had a

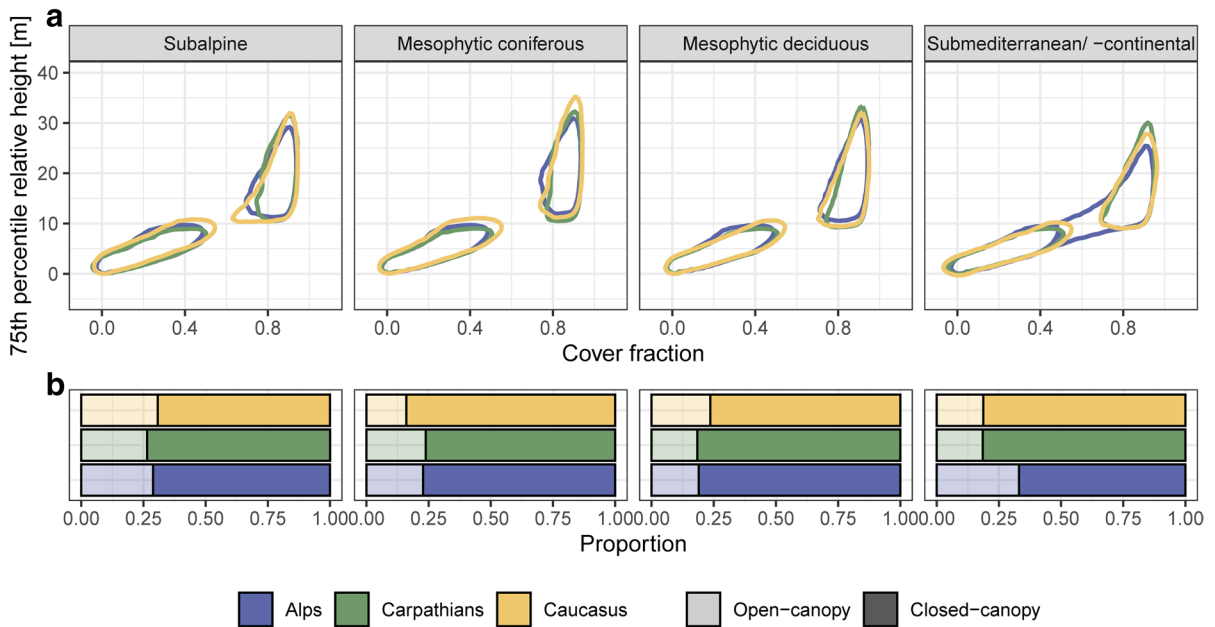


Fig. 3 Based on the observed bimodal distributions of canopy cover and height from GEDI, two distinct clusters of forest structure were identified: tall, closed-canopy forests and short, open-canopy forests. The contours show the area that contains

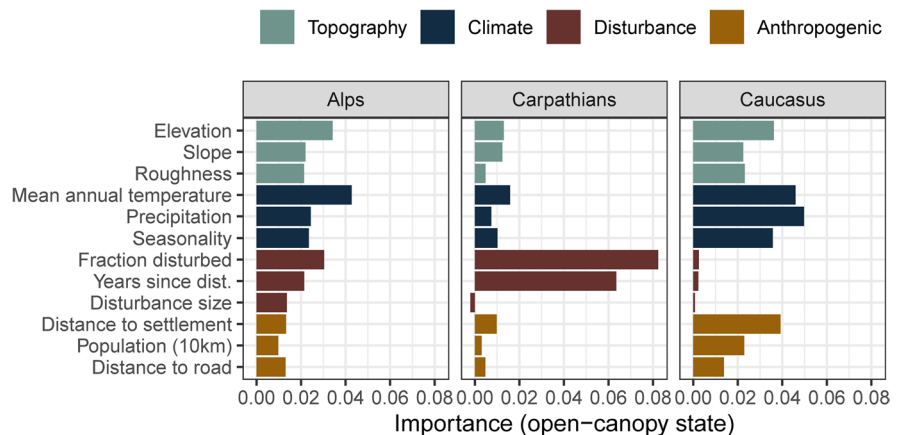
90% of all GEDI footprints in each cluster (a), with bar plots showing the proportion of forests in each cluster per mountain range and vegetation type (b)

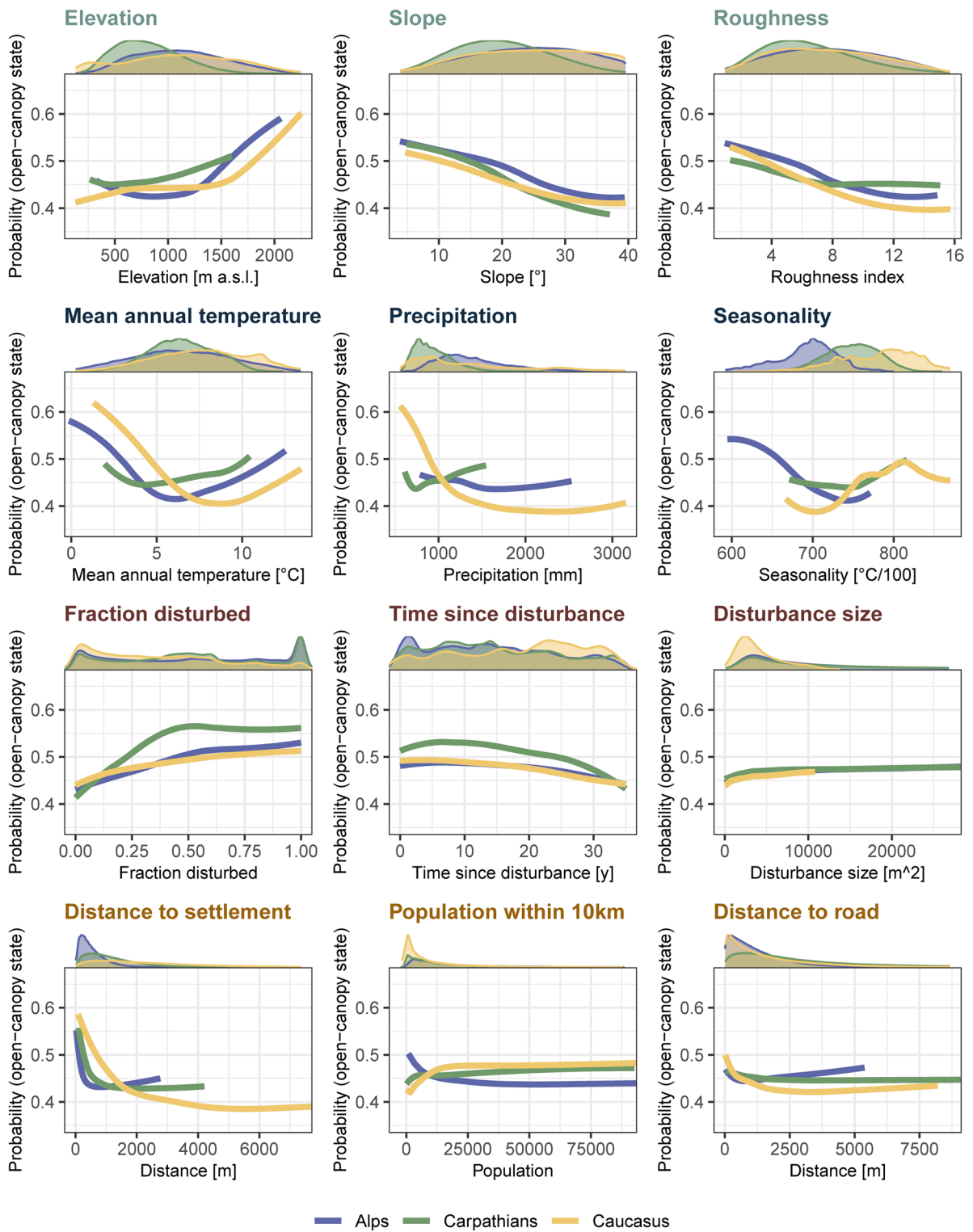
similar effect in the Alps and Caucasus, with open-canopy forests occurring more at both very cold and very warm sites. This effect was less pronounced in the Carpathians, where the temperature gradient is smaller (Fig. 5).

Variables related to disturbances were particularly important predictors of forest structure in the Carpathians (Fig. 4), and their effect was more pronounced than in the other two mountain ranges. This

was related to a higher disturbance severity: 65% of GEDI footprints in the Carpathians were in an open-canopy state in the first five years after a disturbance, compared to 51% in the Caucasus and 47% in the Alps. The effect of disturbances decreased with time since disturbance; 35 years after a disturbance, most forests had returned to a closed-canopy state (69% in the Alps, 77% in the Carpathians and 83% in the Caucasus). Disturbance patch size did not have a strong

Fig. 4 Importance of factors related to topography, climate, social-ecological forest disturbance and other anthropogenic pressure for predicting the occurrence of open-canopy forests in the three mountain ranges by means of random forest models





◀**Fig. 5** Partial dependence plots showing the probability of open-canopy forests in relation to individual drivers in the random forest models. Marginal plots at the top of the figures show the distributions of the drivers in each mountain range. Partial dependences were calculated for the interval between the 1st and 99th percentile of each variable. For disturbance size, distance to settlements, population, and distance to road, the figures are cut off at the 95th percentile for better visibility

effect on forest structure in any of three mountain ranges. We found other anthropogenic pressures to be more important in the Caucasus than in the Alps and Carpathians. Forests within 2.5 km of settlements were more likely to have an open-canopy structure, as were forests close to roads and in areas with higher population densities.

Discussion

Forest disturbances shape forest structure and via structure influence forest biodiversity and the provisioning of ecosystem services. This makes it important to understand how different disturbance regimes impact structure. Here, we make use of the natural experiment provided by the European mountain ranges with similar climate and biogeography yet highly different social-ecological conditions. We find distinctly different disturbance regimes between these mountain ranges, with the Caucasus differing strongly from the Alps and the Carpathians. We suggest that these differences reflect the combined impact of differences in current management intensities as well as different land-use legacies, which result in different social-ecological disturbance regimes. Remarkably, despite these differences, we found highly consistent patterns of forest structure across all three mountain ranges, with the emergence of two alternative states of forest cover and height, suggesting strong attractors of mountain forest structure despite differences in social-ecological drivers.

Differences in social-ecological forest disturbance regimes

We found contrasting disturbance regimes between the mountain forests of the Alps and Carpathians on the one hand, and the Caucasus on the other, with much lower disturbance rates and smaller disturbance sizes in the Caucasus. These differences are

likely related to both anthropogenic and natural disturbances, which are often closely interrelated. For example, windthrows and bark beetle outbreaks are often followed by salvage logging (Falt'an et al. 2021; Hlásny et al. 2021), while management interventions such as thinning can result in a short-term increase in susceptibility to windthrow (Stritih et al. 2021b). The lower disturbance rates in the Caucasus are thus likely related to both fewer natural disturbances and to differences in forest management practices.

The majority of observed disturbances are likely driven by human activities in all three mountain ranges (Potapov et al. 2015). In both the Carpathians and the Caucasus, the socioeconomic transition that these areas have experienced since the 1990s has raised concerns about forest loss and degradation (Chen et al. 2021; Albulescu et al. 2022; Vasile 2022; Vasile and Iordăchescu 2022; Cortner et al. 2024). However, there are key differences between these mountain ranges. Forests in the Caucasus have remained state-owned and are largely protected. In Georgia, for example, the main management objective for nearly 80% of forests is to maintain their protective effect against erosion and natural hazards, while only 20% of forests are designated for timber production (UNECE/FAO 2019). This is reflected in the low rate of stand-replacing disturbances (Fig. 2). In contrast, Carpathian forests were in many cases restituted to private owners after the end of socialism in eastern Europe. Private ownership and access to European timber markets have contributed to high logging rates (Griffiths et al. 2012; Potapov et al. 2015; Alix-Garcia et al. 2016). Interestingly, our results indicate that the social-ecological disturbance regime in the Carpathians was very similar to that of the Alps, where forest management is thought to have changed less and to have been more sustainable.

Natural disturbances also play an important role in the disturbance regimes of temperate mountain forests in Europe (Kulakowski et al. 2017). This is particularly visible in the case of large windthrow events, such as storm Vaia in the Alps in 2018 or storm Elisabeth in the Slovak Tatra in the Carpathians in 2004 (see Fig. 2). Most cyclone-induced windstorms reach Europe from the west and are therefore less impactful in Eastern Europe, although they can still affect forests in the Carpathians (Pettit et al. 2021). Large windthrows are commonly followed by bark beetle outbreaks (Stadelmann et al. 2014), and such pulses

of natural disturbance cascades are a key part of the natural dynamics of conifer-dominated mountain forests (Janda et al. 2017; Kameniar et al. 2023). Natural disturbances are likely exacerbated by climate change (Seidl et al. 2014), with extreme wind events becoming more common in Europe (Schemm et al. 2017; Pettit et al. 2021), and spruce becoming more susceptible to bark beetle attacks under warmer and drier conditions (Temperli et al. 2013; Netherer et al. 2015). Climate change may thus partly explain the increasing disturbance rates in the Alps and Carpathians since the 1980s (Fig. 2).

The fact that disturbance rates are increasing in the Alps and Carpathians, but not the Caucasus, can be in part explained by differences in land-use legacies. Dense spruce monocultures, which were planted after clear-cuts or established on abandoned farmland, are particularly susceptible to natural disturbances (Munteanu et al. 2016; Stritih et al. 2021b; Scherrer et al. 2023). In the Alps and Carpathians, many such forests were established during the 20th century, and large parts of these forests are now in a development stage where trees are increasingly susceptible to disturbance agents such as wind or bark beetles (Stritih et al. 2021b) and are reaching harvestable age (Munteanu et al. 2015). In contrast, due to the lower intensity of forest management in the past, forests in the Caucasus have retained predominantly natural tree species composition and structure, with a higher dominance of broadleaved trees and higher structural diversity (Martin-Benito et al. 2020; Ministry of Environmental Protection and Agriculture of Georgia 2022), and they are therefore less susceptible to large-scale natural disturbances. The disturbance regime of these forests is dominated by small-scale events (Fig. 2b), similar to those of primary beech forests of the Carpathians (Hobi et al. 2015). In summary, we found considerable support for our hypothesis that differences in current management and land-use history result in distinct disturbance regimes of the three mountain ranges.

Convergent states of forest structure among mountain ranges

Despite the differences in social-ecological disturbance regimes, our results point to surprisingly similar patterns of forest structure across the three mountain ranges. Specifically, we found that the bimodal

distributions of forest canopy height and cover reported previously for the Alps (Stritih et al. 2023) are also present in the Carpathians and Caucasus. The two distinct clusters we found (i.e., short, open-canopy forests and tall, closed-canopy forests) co-occur in similar topographic and climatic conditions suggesting a prevalence of two alternative states of forest structure across mountain forests in temperate Europe. Consequently, we did not find support for our hypothesis that different disturbance regimes lead to different forest structural states across the Alps, Carpathians, and Caucasus.

Multi-modal distributions of tree cover have previously been used to characterize alternative states of vegetation characterized in forest-shrubland and forest-savanna-grassland systems (Hirota et al. 2011), where the states are stabilized by positive feedbacks (Miller et al. 2019; Pausas and Bond 2020). For example, frequent fires or grazing maintain open-canopy vegetation in regions otherwise suitable for the development of closed forests (Pausas and Bond 2020). The convergence towards two consistent, alternative states of forest structure across the different mountain ranges in our study might be evidence for similar common stabilizing mechanisms in these temperate forests. Open-canopy forests are more likely to occur at the edges of suitable conditions for forests, such as at the upper tree line in all three mountain ranges, or at the transition to steppe vegetation in the drier Eastern Caucasus. At these edges, seedlings established in the open are more likely to be damaged by harsh conditions, such as wind and frost at the upper tree line (Presas et al. 2009) or drought at the lower tree line (Gómez-Aparicio et al. 2005). Once the canopy is sufficiently dense, however, it buffers extreme temperatures and wind and increases humidity (De Frenne et al. 2021), creating a more suitable microclimate for seedling survival (D'Odorico et al. 2013) resulting in a positive feedback loop that helps maintain closed forest canopies.

In all three mountain ranges, disturbances can trigger transitions from closed-canopy to open-canopy forests, although we also observed the open-canopy state in undisturbed forests. Disturbances were an important predictor of forest structure in the Carpathians, where the climatic gradient is narrower than in the Alps and Caucasus and where disturbance severity was higher. However, if disturbances were the only driver of open-canopy forests, we would expect

only 6% of forests to be in this state in the Carpathians, 5% in the Alps, and less than 1% in the Caucasus given the observed rates of disturbance and recovery. Disturbance-driven transitions to open-canopy forests are mostly temporary, as most disturbed forests recover to a closed-canopy state within 35 years after disturbance in all three mountain ranges. Recovery is facilitated by the intermediate severity and small patch sizes of disturbances that prevail throughout the mountain forests of temperate Europe. These factors result in sufficient seed supplies and favorable microclimatic conditions for tree establishment (Jonášová et al. 2010; Winter et al. 2015). Furthermore, the disturbance return interval we found is much longer than the recovery time, suggesting that permanent shifts to open-canopy states due to disturbance are unlikely (Janda et al. 2017; Senf and Seidl 2022). However, in some cases, recovery may be hampered by dry conditions (e.g., in submediterranean forests in the Alps; Stritih et al. 2023) or by a high density of grazing ungulates (Hlásny et al. 2021). Furthermore, while structural features such as canopy cover recover relatively quickly, other features, especially those typical for old-growth forests, such as structural diversity and the presence of very large trees (Burrascano et al. 2013), only recover over much longer time periods (Albrich et al. 2021).

While the influence of stand-replacing disturbances was less important in the Caucasus, forest structure was more closely linked to other anthropogenic pressures, with forests in areas with higher human population densities and closer to roads more likely to have an open-canopy structure. This pattern reflects both the reliance of local communities on forests for the provisioning of ecosystem services, including (often illegal or unrecorded) logging for fuelwood and livestock grazing (Torchinava 2016; UNECE/FAO 2019), and the limited technological and institutional capacity for forest management in more remote areas farther from roads and settlements (Garforth et al. 2016; UNECE/FAO 2019). Livestock grazing near settlements can impede the natural regeneration of trees (Shakeri et al. 2012; Etchebarne and Brazeiro 2016). Such open-canopy forests are therefore often referred to as “degraded” from the perspective of carbon storage or timber production (Ministry of Environmental Protection and Agriculture of Georgia 2022). At the same time, open-canopy forests, such as wood pastures, are increasingly

recognized for their high biodiversity and cultural values (Plieninger et al. 2015; Öllerer et al. 2019). Wood pastures also used to be common in the Alps (Garbarino et al. 2011) but have declined due to grazing restrictions in forests (Johann 2007; Bebi et al. 2017) and to the intensification of agriculture and resulting abandonment of mountain pastures (Garbarino et al. 2011; Plieninger et al. 2015).

In summary, our third hypothesis was largely supported by our data. The mountain forest ecosystems of temperate Europe responded fairly consistently to abiotic drivers such as topography and climate, with open-canopy forests more likely to occur at cold and dry sites. In contrast, the importance and effects of anthropogenic pressures differed between mountain ranges. Despite these differences, the emerging structural patterns are similar across the Alps, Carpathians, and Caucasus, underlining that different suites of drivers can lead to similar ecosystem patterns.

Methodological considerations

This study demonstrates how combining remote sensing tools can yield insights into forest disturbances and structure across large spatial extents. GEDI enabled the characterization of vertical forest structure across three mountain ranges for one point in time, while the Landsat-based disturbance map provided a dynamic perspective on changes in canopy cover and disturbances over three decades. However, the inherent limitations of the approaches combined here need to be considered. The accuracy of GEDI is limited in complex, mountainous terrain (Fayad et al. 2021; Mandl et al. 2023), and the high correlations between different structural variables (see Supplementary material, Figure 12) may mask more nuanced differences in forest structure (Stritih et al. 2023), such as those found in structurally complex old-growth forests. In addition, the Landsat-based disturbance map used here primarily provided information on stand-replacing disturbances and disregarded low-severity disturbances or disturbances affecting trees only in the subcanopy and understory (Senf and Seidl 2021), such as those caused by selective logging or thinning as well as uses such as firewood collecting and forest grazing. Such disturbances are more evident in the patterns of forest structure derived from spaceborne lidar, highlighting the complementarity of the two different remote sensing products combined here.

Broad-scale analyses like ours enable the detection of general patterns across administrative boundaries and facilitate analyses of non-linear and interacting relationships between ecological and social drivers. However, we note that an understanding of the regional context is essential for interpreting the observed patterns (Wyborn and Evans 2021; Tubbure et al. 2022). Necessarily, an analysis at the scale of entire mountain ranges masks local variability in forest ecosystems and their human uses (Bebi et al. 2017), including cross-border differences in current and historical institutions related to forest management (Munteanu et al. 2014). Our analysis included a range of environmental and anthropogenic variables, and their potential effects on forest structure are largely consistent with current understanding of social-ecological processes; yet these relationships are correlative in nature and do not necessarily represent causality. The effects of specific drivers need to be addressed in more detail to increase process understanding. For example, matching methods could be used to assess the effects of specific drivers across otherwise comparable landscapes (Baumann et al. 2015; Butsic et al. 2017), controlled experiments could test the role of stabilizing feedbacks on alternative states (Kueppers et al. 2017), and/or the knowledge of local communities about their current and past land management practices could be integrated into spatial analyses (Joa et al. 2018).

Conclusions

Comparing forest disturbances and structure across three European mountain forests with similar environmental conditions and different social-ecological conditions and land-use histories yielded two major insights. First, we found distinct differences in social-ecological forest disturbance regimes, with increasing disturbance rates over time in the Alps and Carpathians, yet much lower disturbance rates and smaller disturbance patches in the Caucasus. These regime differences can be attributed to differences in current forest management and legacies of past land-use. Second, despite the pronounced differences in disturbance regimes, we found that forests in the Alps, Carpathians and Caucasus show surprisingly similar patterns of forest structure, converging at two distinct, alternative states of forest structure (tall,

closed-canopy forests and short, open-canopy forests) in all mountain ranges. Open-canopy forests consistently occurred at the upper and lower tree line in cold and snow-dominated sites as well as dry, warm sites, but the influence of other drivers of forest structure differs between mountain ranges. The effect of stand-replacing disturbances was particularly important in the Carpathians, while other anthropogenic drivers were more important in the Caucasus, with local use of fuelwood and grazing likely contributing to the prevalence of open-canopy structures near settlements.

Our results indicate that both current management and past land use play important roles in shaping the dynamics and structure of mountain forests, but also highlight that similar alternative states emerge consistently across a wide range of conditions. This suggests generalities in the drivers of mountain forest dynamics and indicates strong attractors of forest development that should be investigated further. Finally, our findings caution against a simplistic understanding of the relationship between prominent variables of forest change (e.g., disturbance, land use) with forest structure and underline that forest states are emergent properties of complex social-ecological systems.

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Author contributions AS: Conceptualization, Formal analysis, Visualization, Writing – Original draft. CS: Conceptualization, Data curation, Writing – review & editing, Funding acquisition. TK: Conceptualization, Writing – review & editing. CM: Writing – review & editing. LD: Writing – review & editing. JS: Writing – review & editing. DM: Writing – review & editing. OC: Writing – review & editing. RS: Conceptualization, Writing – review & editing, Funding acquisition.

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Data availability The data used in this study are publicly available. Definitions of the mountain ranges are available

from the GMBA Mountain Inventory v2 (<https://doi.org/10.48601/earthenv-t9k2-1407>). The GEDI Level 2A and 2B products can be downloaded at https://lpdaac.usgs.gov/products/gedi02_av002/ and https://lpdaac.usgs.gov/products/gedi02_bv002/, respectively. The CHELSA climate data is available at www.chelsa-climate.org, and the NASA SRTM DEM can be downloaded from <https://doi.org/10.5069/G9445JDF>. The Map of the Natural Vegetation of Europe (Bohn et al. 2004) can be accessed through <https://www.synbiosys.alterra.nl/eurovegmap>. The GHS population data is available at <https://doi.org/10.2905/D6D86A90-4351-4508-99C1-CB074B022C4A>, while data on roads was retrieved from OSM (<http://download.geofabrik.de/>) and the GRIP dataset (www.globio.info/download-grip-dataset). The European disturbance map including the Alps and Carpathians is available at <https://doi.org/10.5281/zenodo.3924381>. The disturbance map for the Caucasus as well as the R-scripts used for data processing and analysis are available here: <https://doi.org/10.5281/zenodo.11259592>.

Declarations

Competing interests The authors declare no competing interests.

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