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Alternative states in the structure of mountain forests across the Alps and the role of disturbance and recovery

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Abstract

Context Structure is a central dimension of forest ecosystems that is closely linked to their capacity to provide ecosystem services. Drivers such as changing disturbance regimes are increasingly altering forest structure, but large-scale characterizations of forest structure and disturbance-mediated structural dynamics remain rare.

Objectives Here, we characterize large-scale patterns in the horizontal and vertical structure of mountain forests and test for the presence of alternative structural states. We investigate factors determining the occurrence of structural states and the role of disturbance and recovery in transitions between states.

Methods We used spaceborne lidar (GEDI) to characterize forest structure across the European Alps. We combined GEDI-derived structural metrics with Landsat-based disturbance maps and related structure to topography, climate, landscape configuration, and past disturbances.

Results We found two alternative states of forest structure that emerged consistently across all forest types of the Alps: short, open-canopy forests (24%) and tall, closed-canopy forests (76%). In the absence of disturbance, open-canopy forests occurred at high elevations, forest edges, and warm, dry sites. Disturbances caused a transition to open-canopy conditions in approximately 50% of cases. Within 35 years after disturbance, 72% of forests recovered to a closed-canopy state, except in submediterranean forests, where recovery is slow and long-lasting transitions to open-canopy conditions are more likely.

Conclusions As climate warming increases disturbances and causes thermophilization of vegetation, transitions to open-canopy conditions could become more likely in the future. Such restructuring could pose a challenge for forest management, as open-canopy forests have lower capacities for providing important ecosystem services.

Keywords Mountain forests · GEDI · Disturbance · Basins of attraction · Recovery

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Introduction

There is emerging evidence that mountain forests in the European Alps are experiencing accelerating

changes in structure and composition due to climate and land-use change (Thom and Seidl 2022), as well as an increasing frequency of natural disturbances (Senf et al. 2021). The ecological resilience of forests to disturbances, i.e. the ability to recover their structure and functions after disturbances, is therefore of growing concern in forest management (Nikinmaa et al. 2020). In theory, ecological resilience is often described through the concept of alternative stable states or domains of attraction (Holling 1973; Miller et al. 2019), where resilience is the capacity of a system to return to its previous basin of attraction after a disturbance rather than shift to an alternative stable state (Carpenter et al. 2001). However, the limited availability of information on horizontal and vertical forest structure and dynamics across large spatial scales makes it difficult to characterize basins of attraction and recovery trajectories in practice.

Evidence for the existence of alternative stable states has been reported for forest-shrubland mosaics (Cramer et al. 2019; Miller et al. 2019; Falk et al. 2022) and in tropical forest-grassland-savanna systems, where the distribution of tree cover shows three distinct modes (Hirota et al. 2011). The alternative states are thought to be in stable equilibrium, determined by climate (Hirota et al. 2011) and stabilized by positive feedbacks, such as frequent fires in savannas and soil development in forests (Murphy and Bowman 2012; Van Nes et al. 2014; Cramer et al. 2019). However, changes in climate and disturbance regimes could cause transitions from closed forest to more open systems such as open forests or shrubland states (Tepley et al. 2017; Miller et al. 2019; Falk et al. 2022). Transitions from closed to open forests could leave long-lasting imprints on forest structure and function (McDowell et al. 2020). For example, a simulation study in mountain forests in the European Alps demonstrated that climate warming could lead to an irreversible transition to an alternative stable state with smaller trees (Albrich et al. 2020). However, observational evidence for such transitions in temperate mountain forests is rare.

The mountain forests of the Alps are characterized by complex structures that are shaped by strong topographic and climatic gradients, as well as land use, natural disturbances, and their interactions (Kulakowski et al. 2011; Bebi et al. 2017; Conedera et al. 2017). To date, assessments of mountain forest structures and dynamics often focused on individual sites

or landscapes, using field surveys or airborne lidar data (Winter et al. 2015; Wohlgemuth et al. 2017; Senf et al. 2019). Such studies have shown that disturbances, including windthrow and bark beetle outbreaks, can modify the structure and functions of mountain forests over long time periods (Bottero et al. 2013; Wohlgemuth et al. 2017; Caduff et al. 2022). A few decades after large disturbances, many mountain forests are on track towards recovering a closed canopy (Senf and Seidl 2022), but have not yet fully recovered their functions, e.g., the capacity to provide protection from natural hazards (Wohlgemuth et al. 2017; Baggio et al. 2022; Caduff et al. 2022). Post-disturbance recovery may become more challenging as disturbance regimes change (Senf et al. 2021). If, for instance, disturbance intervals become shorter than the time forests need to reach maturity, forest regeneration could be hampered, which may lead to a transition to alternative states (Johnstone et al. 2016). However, the high spatial variability of mountain forest structure and the stochastic nature of disturbances make it difficult to generalize findings from individual disturbed sites or landscapes to larger ecological regions. To identify patterns of alternative states or evaluate the probability that disturbances cause a transition between these states, consistent information on forest structure is therefore needed across a wider spatial extent.

In recent years, significant progress has been made in observing forest dynamics across large scales by detecting changes in canopy cover from optical remote sensing (Hansen et al. 2013; Seidl et al. 2020; Senf 2022). Based on such observations, large forest areas in Europe have been found to be rather resilient to disturbances, recovering their pre-disturbance canopy cover in ca. 20 years, i.e., a time period much shorter than the return interval of disturbances (Senf and Seidl 2022). However, optical observations of canopy cover do not capture changes in vertical structure, tree height or amount of biomass (Bolton et al. 2017), which are needed to differentiate forests from shrubland (Rüetschi et al. 2021), and which determine the capacity to provide important forest ecosystem services (Stritih et al. 2021). To address this gap and improve global biomass estimates, NASA launched a new spaceborne lidar system in 2018, called the Global Ecosystem Dynamic Investigation (GEDI). GEDI is a laser remote sensing system, specifically designed to provide information about

vertical vegetation structure across the temperate and tropical zones (Dubayah et al. 2020). With the launch of GEDI, consistent information about forest structure is now available across large spatial scales (Schneider et al. 2020).

Here, we use spaceborne lidar data from GEDI to analyze forest structure across all forests of the European Alps (10′ 563′ 360 ha) to identify patterns of forest structure. Specifically, we test for the presence of alternative states in mountain forest structure and investigate how climate, topography, landscape configuration, and disturbance history influence the prevalence of particular states. We hypothesize that disturbance and recovery are major drivers causing transitions between states. To test this hypothesis, we combine GEDI-derived forest structure with Landsat-based disturbance maps to examine post-disturbance forest dynamics.

Methods

Study area

Our study area covers the full European Alps as defined by the Alpine Convention, i.e. a total land area of 19 Mill. ha with 10.5 Mill. ha of forests (see Fig. 1). The European Alps are characterized by steep elevational gradients (from near sea level to above 4000 m a.s.l.), are situated between different climatic zones (i.e., temperate-Atlantic, temperate-continental, Mediterranean, Pannonian), have a long and varied history of human land use (Conedera et al. 2017), and feature a high diversity of vegetation and forest types. The most widespread potential natural vegetation type is deciduous broadleaf forest (Bohn et al. 2004), mainly dominated by European beech (*Fagus sylvatica* L.), although forest composition has been modified by past land use, with forest management promoting Norway spruce (*Picea abies* (L.) Karst.). At higher elevations, broadleaved forests give way to conifers, including Norway spruce, European larch (*Larix decidua* L.), and pines (mainly Swiss stone pine *Pinus cembra* L., and mountain pine *Pinus mugo* Turra) as well as shrubs such as green alder (*Alnus viridis* (Chaix) D.C.) (Rüetschi et al. 2021). The tree-line in the Alps varies between around 1800 m a.s.l. in the northern and southern Alps to up to 2400 m a.s.l. in the central Alps, although the actual treeline

is frequently below the potential treeline because of land use (Gehrig-Fasel et al. 2007). On dry, south-facing slopes and in the south-western Alps near the Mediterranean Sea, submediterranean forests dominate, characterized by species such as downy oak (*Quercus pubescens* Willd.) (Bohn et al. 2004). During the last decades, the forests of the Alps have expanded due to land abandonment (Bebi et al. 2017). They have also experienced an increasing frequency of natural disturbances such as windthrows, bark beetle outbreaks, and forest fires (Sebald et al. 2021; Senf et al. 2021). These developments are of pressing concern for forest management, as many mountain communities in the Alps rely on forests to provide essential ecosystem services, such as protection from natural hazards (Sebald et al. 2019; Stritih et al. 2021).

Global ecosystem dynamics investigation (GEDI)

GEDI is a spaceborne lidar (light detection and ranging) mission, installed on the International Space Station in 2018 and providing data since March 2019. Being an active remote sensing system, GEDI uses 4 laser beams to scan the Earth's surface across temperate and tropical regions in eight transects along its orbital track, sampling locations every 60 m along each transect, and aiming to sample around 4% of the Earths surface during its mission (Dubayah et al. 2020). For each sample footprint of 25 m diameter, GEDI sends out a waveform and measures its return, reflected from the ground and vegetation. After separating vegetation and ground returns, vegetation structural metrics such as percentiles of canopy height, fraction of canopy cover, plant area index, and foliage height diversity can be derived (Schneider et al. 2020). These metrics are freely available online in the GEDI Level 2A and 2B products.

To characterize mountain forests of the Europe Alps, we focused on two ecologically relevant metrics: tree cover and the 75th percentile of relative height (i.e. the canopy height below which 75% of the waveform energy is reflected). While a large array of additional metrics are available, our exploratory analyses showed that many metrics from GEDI are highly correlated, with cover and height capturing most of the variability (see Supporting information). The 75th percentile of relative heights (RH75) was chosen over other height percentiles because it is
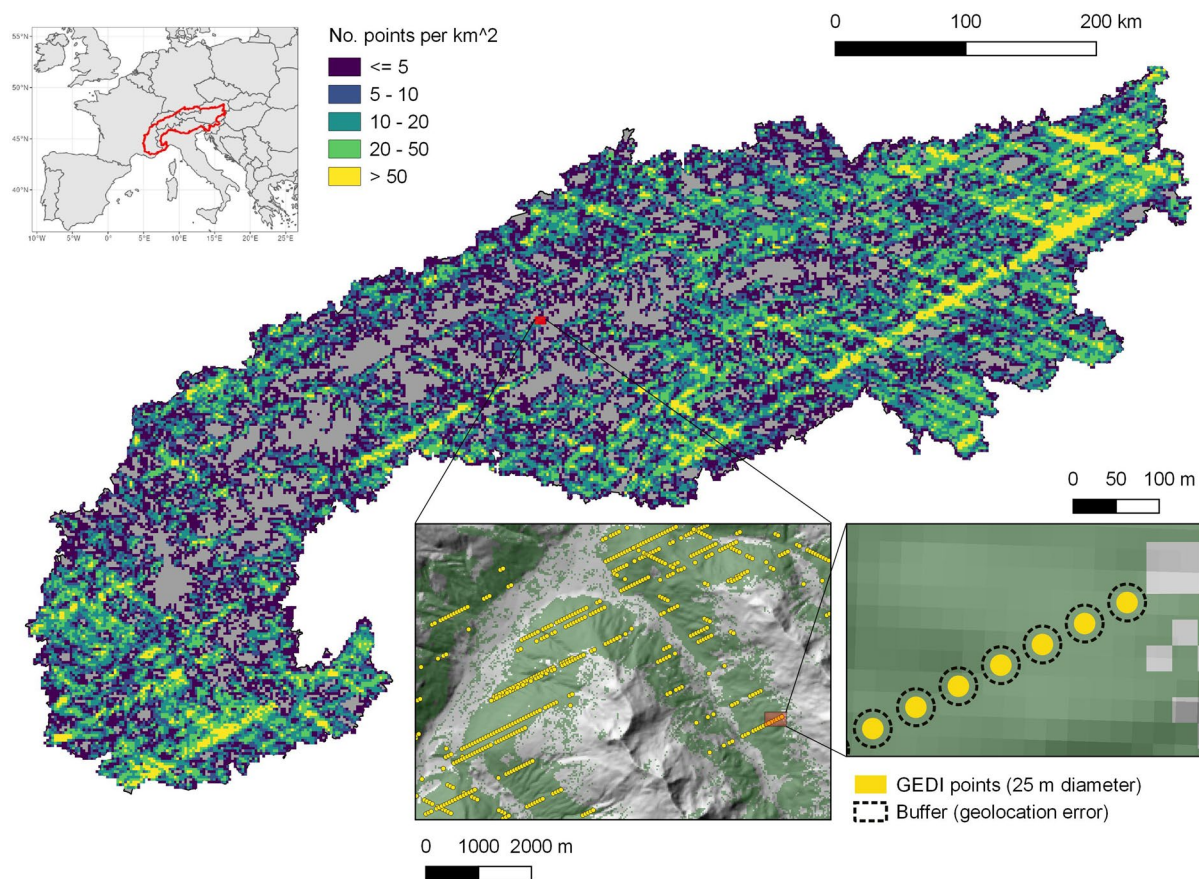
Fig. 1 Map of the Alps (defined by the borders of the Alpine convention) with the number of available GEDI footprints in forests in each 4 km² grid cell. Only the footprints measured during June–August 2019–2021, filtered by slope and quality flag were used. The inset maps show the distribution of GEDI footprints in a mountain landscape in the Swiss Alps. To select only footprints located in forests while accounting for possible geolocation errors, we used a buffer of 9 m around the 25-m-diameter GEDI footprints

expected to best reflect stand dynamics while simultaneously being less sensitive to individual tall or residual trees (Bolton et al. 2015). To include only leaf-on measurements in our analyses (Potapov et al. 2021), we used GEDI data acquired during the period from June to August in the years 2019 to 2021. In addition, we filtered the measurements based on quality flags and only included footprints fully covered by forest according to a remote sensing-based forest cover map (Senf and Seidl 2021). To avoid edge effects stemming from possible geolocation errors (Dubayah et al. 2020), we buffered each GEDI footprint by 9 m before intersection with the forest mask (see Fig. 1). GEDI data were processed using the rGEDI package (Silva et al. 2020).

Steep slopes have been found to affect the accuracy of spaceborne lidar measurements (Schneider et al. 2020; Fayad et al. 2021; Liu et al. 2021). In a preliminary assessment of data quality, we found higher values of GEDI metrics (including cover and height) on steeper slopes. To address artefacts related to topography, we tested two approaches (i.e., the selection of ground-detection algorithms Tang et al. 2014; Tang and Armston 2019) and slope-adaptive metrics (Wang et al. 2019; Fayad et al. 2021)), and compared them with a reference dataset from the German Alps derived by means of airborne laser scanning (Mandl et al. in prep). None of the tested alternative approaches consistently improved the correspondence to our reference dataset. Hence, we continued to use default GEDI metrics, but excluded footprints above

40° of slope from our analysis (corresponding to 7.8% of all forested GEDI footprints; see detailed description in the Supporting information). After filtering, over 2.7 million GEDI footprints were available across the Alps. In many of the densely forested areas of the southern and eastern Alps, more than 50 footprints per square kilometer were measured (see Fig. 1), although the distribution of GEDI tracks in space is uneven due to variations in the orbital tracks of the International Space Station (Dubayah et al. 2020).

Identifying potential alternative structural states and their drivers

We used a gaussian mixture model (Scrucca et al. 2016) to distinguish potential alternative states in forest structures based on canopy cover and the 75th percentile of height. Gaussian mixture models are probabilistic models where the data is represented as a combination of Gaussian distributions (components), with each component corresponding to a cluster in the data. As such, Gaussian mixture models are particularly well suited for modelling data with multimodal distributions. The optimal number of components was selected based on the Bayes Information Criterion (Fraley and Raftery 1998), and the membership (i.e. probability of belonging to each cluster) was calculated for each GEDI footprint.

To investigate how environmental conditions determine a forests' likelihood of being in any given state, we modelled the probability of membership in each cluster based on a set of four predictor groups: (1) topography, (2) climate, (3) forest composition and configuration and (4) disturbance history. Topographic predictors included elevation, slope and terrain roughness, all derived from the Copernicus 25 m European digital elevation model (EU-DEM v1.1 2016). Slope aspect (northerness and easterness) and terrain position were also included in a preliminary analysis, but did not improve the performance of the model, and were omitted from subsequent analyses. Climate predictors included mean annual temperature, mean annual precipitation, and mean annual temperature seasonality, all derived from CHELSA V2.1 (Karger et al. 2017). Forest composition and configuration were described through the potential natural vegetation type (Bohn et al. 2004) and the distance to the closest forest edge. We specifically focused our analysis on the four main potential natural vegetation types of the Alps according

to Bohn et al. (2004): subalpine, mesophytic coniferous (including montane and altimontane spruce- and fir-dominated forests), mesophytic deciduous (mainly colline to montane beech forests, with some oak forests) and submediterranean forests. Together, these four types account for 88% of the forest area of the Alps. For a detailed description of the major vegetation types occurring in the Alps, see the Supporting information. Disturbance history predictors were derived from an existing remote sensing-based forest disturbance map covering the time period 1986 to 2020 (Senf and Seidl 2021) and included the time since the last stand-replacing disturbance, the proportion of the GEDI footprint disturbed (including a 9-m buffer to account for geolocation error) and the size of the disturbance patch. The disturbance product used includes both natural disturbances and human disturbances (e.g., timber harvesting). To capture potential nonlinear and interacting effects of the environmental predictors on the membership in a given state, we used a non-parametric random forest model (Breiman 2001), using equal sampling across states. We calculated the permutation-based importance of the predictor variables (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 in each iteration.

Among all the forested GEDI footprints, 24% overlapped at least partly with disturbances that occurred since 1986, while only 117′174 (4.3%) were located entirely inside a disturbance patch. To further investigate the specific role of disturbances in transitions between alterative states, fully disturbed GEDI footprints (i.e., those where > 95% of the area was disturbed) were analyzed in a space-for-time approach. The distributions of structural metrics were plotted over time since disturbance in 5-year time steps, and the mean cluster membership was calculated as a function of time since disturbance for the main types of potential natural vegetation, as this classification captures the broad-scale variability of site conditions across the Alps, from subalpine to submediterranean forests.

Results

Alternative states of forest structure

We found a bimodal distribution of height and cover across all the main potential natural vegetation types

in the Alps (Fig. 2). Both modes separated well into two distinct clusters in the gaussian mixture modelling. The two-cluster solution was more likely than any other number of clusters or no clustering at all, suggesting strong evidence for two alternate states in forest structure across the European Alps. Most footprints belong to the first cluster of tall, closed-canopy forests, with cover above ca. 0.75 and RH75 above ca. 10 m. We refer to this cluster as closed-canopy state in the following. The proportion of forests in the closed-canopy state is highest in mesophytic deciduous forests (81%) as well as in mesophytic coniferous forests (77%), and lower in subalpine (72%) and submediterranean (67%) forests. The second cluster was characterized by short and open forests and is referred to as open-canopy state in the following. Open-canopy states appear most frequently in the south-western Alps, as well as in inner-Alpine forests at high elevations (Fig. 3). Zooming in to the landscape scale, we can observe open-canopy forests near forest edges, i.e., close to the upper treeline as well as at the bottom of mountain valleys (Fig. 3).

The random forest model fitted to predict the membership of forests in either the closed- or open-canopy state had an overall predictive accuracy of 70%, with an area under the receiver-operator curve (AUC) value of 0.75, indicating acceptable model performance (Hosmer and Lemeshow 2000). The most important predictors of the open-canopy state were elevation, time since disturbance, distance to forest edge, slope, and mean annual temperature (Fig. 4). Both elevation and temperature have two local maxima, where open-canopy states are more likely to occur at high elevations and low temperatures, but also at low elevations and high temperatures. Footprints located near forest edges (< 100 m) are more likely to be in the open-canopy state. The probability of being in an open-canopy state decreases with time since disturbance (Fig. 4), although the open-canopy state can also be found in 21% of forests that have not been disturbed since 1986.
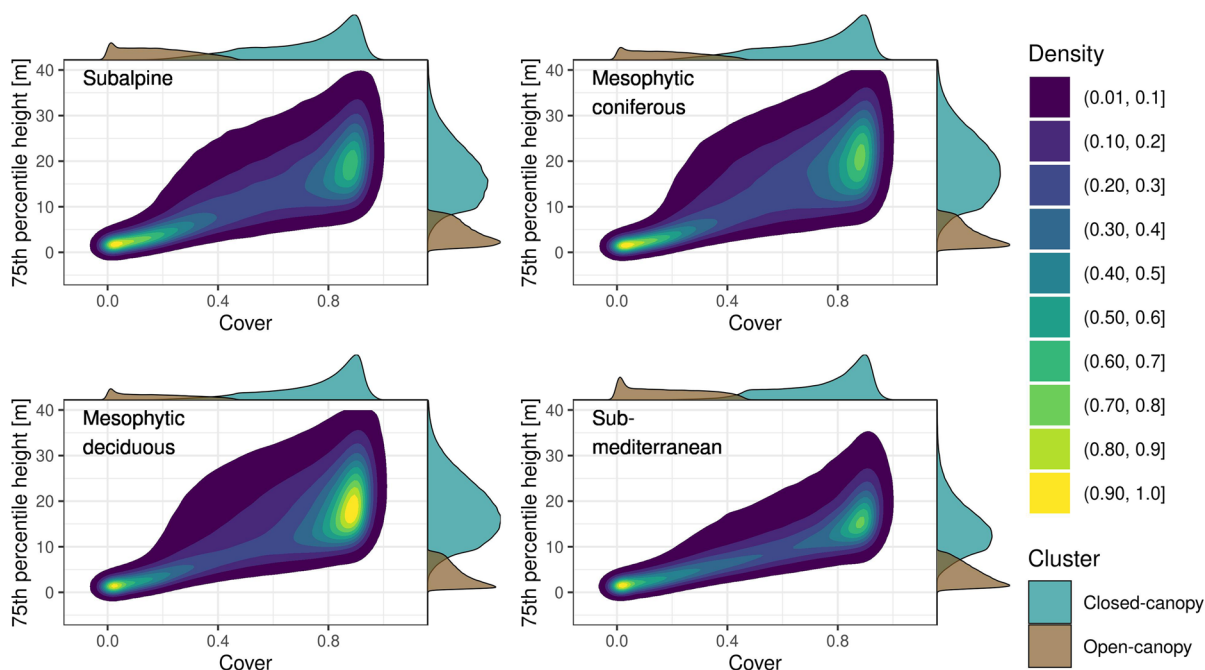

Fig. 2 Distribution of GEDI footprints in a space defined by canopy cover [0,1] and the 75th percentile of relative height (m) for four of the main potential natural vegetation types in the Alps (following Bohn et al. 2004). Marginal distributions show the distributions of each variable for the two clusters identified with a Gaussian mixture model, where one cluster represents tall, closed-canopy forests and the second cluster represents short, open-canopy forests. The same figure including only undisturbed forests is shown in the Supporting information (Fig. S7)
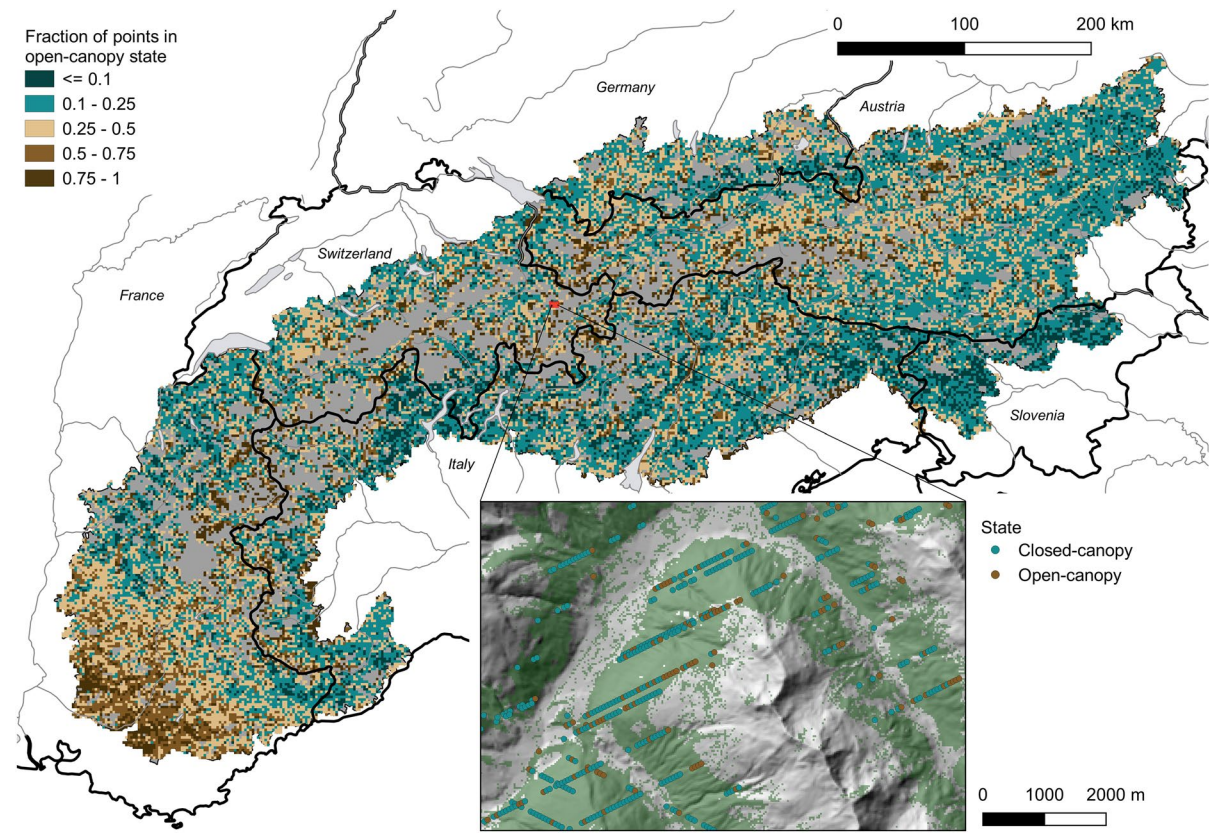
Fig. 3 Map of the proportion of GEDI footprints classified as open-canopy forest across the Alps. Country borders are shown in black, and major rivers and lakes in grey. In the zoom-in on a Swiss mountain landscape, open-canopy forests mostly occur near forest edges, i.e. close to the upper treeline or at the valley bottom

The role of disturbances in transitions between alternative states

Disturbances are an important driver of transitions between alternative structural states in mountain forest ecosystems. When analyzing only footprints that have been disturbed within the last 35 years, we observe a clear shift from the open-canopy state towards the closed-canopy state over time since disturbance (Fig. 5; see Figure S6 for changes in individual structural metrics). The observed recovery pattern is consistent across subalpine and mesophytic forest types, although it is partly modified by temperature, with slower recovery at high elevations and low temperatures, as well as at sites with high mean annual temperatures (see interactions between time since disturbance and other variables in Figure S9). In subalpine and mesophytic coniferous forests, the probability of forests being in a closed-canopy state 35 years after a disturbance is similar to that of undisturbed forests (Fig. 6). In the potential natural vegetation zone of mesophytic deciduous forests, recovery accelerates 15 years after disturbance. Yet, after 35 years, disturbed forests are still more likely to be in an open-canopy state than undisturbed forests in this forest type (see Fig. 6). A much slower recovery rate was observed in submediterranean forests (Fig. 5), where the majority of forests remain in an open-canopy state even 35 years after disturbance (Fig. 6).

Discussion

In this study, we used novel spaceborne lidar data to characterize spatial and temporal patterns in vertical forest structure across the European Alps. From low-elevation deciduous forests to subalpine coniferous forests, we found a consistent bimodal distribution of
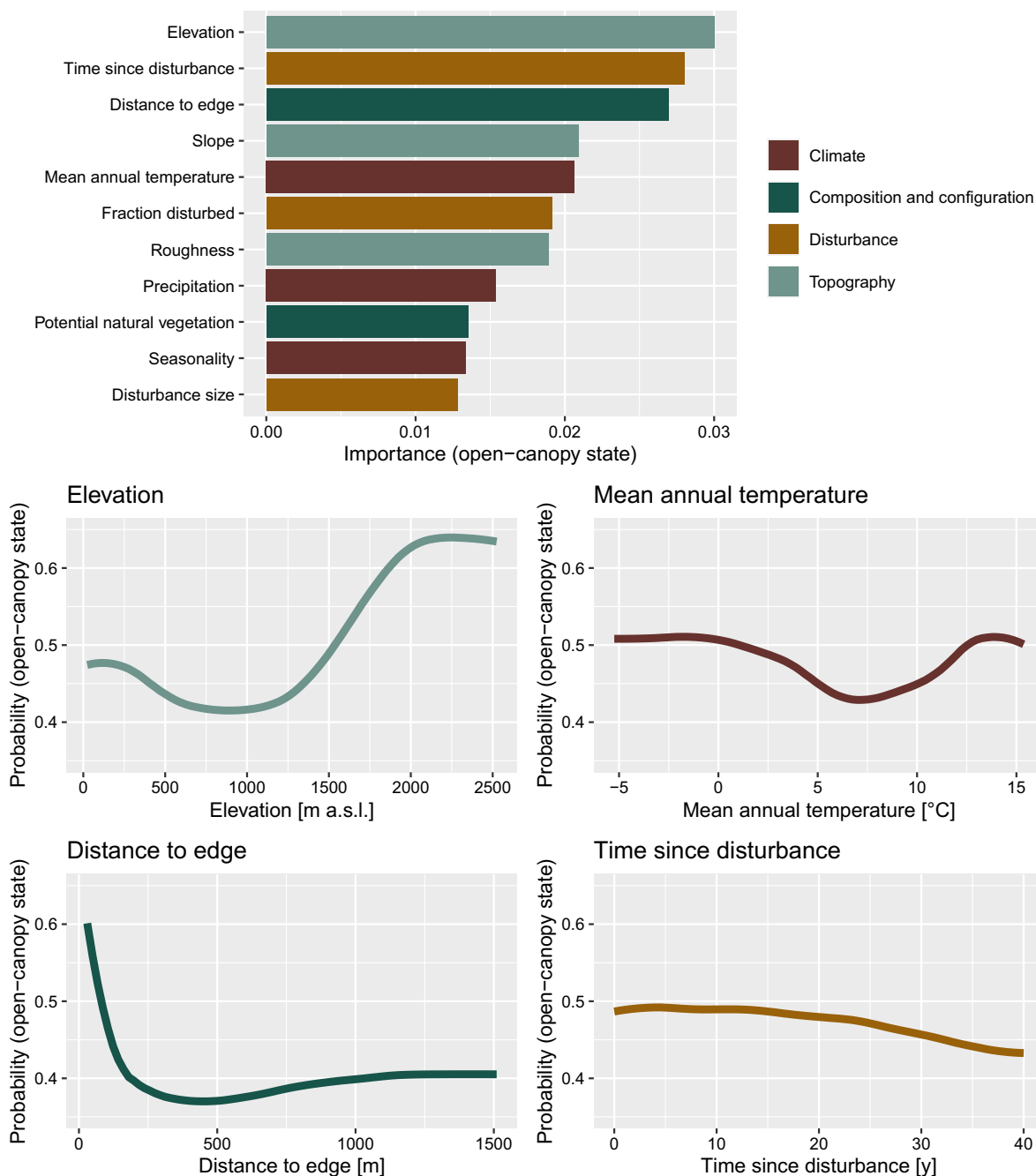
Fig. 4 Variable importance (top) for the random forest model predicting the two alternative states of forest structure, and partial dependence plots (bottom) showing the probability of open-canopy forests based on the most important variables from each group of predictors. See Supporting information for partial dependence plots of all predictors (Fig. S8), and the interactions between time since disturbance with other predictors (Fig. S9)

structural characteristics that indicate two alternative states in forest structure across a wide range of environmental conditions. While most GEDI footprints represented closed-canopy forests, open-canopy forests are more prevalent at high elevations, at very cold or very warm sites, and near forest edges. Notably,
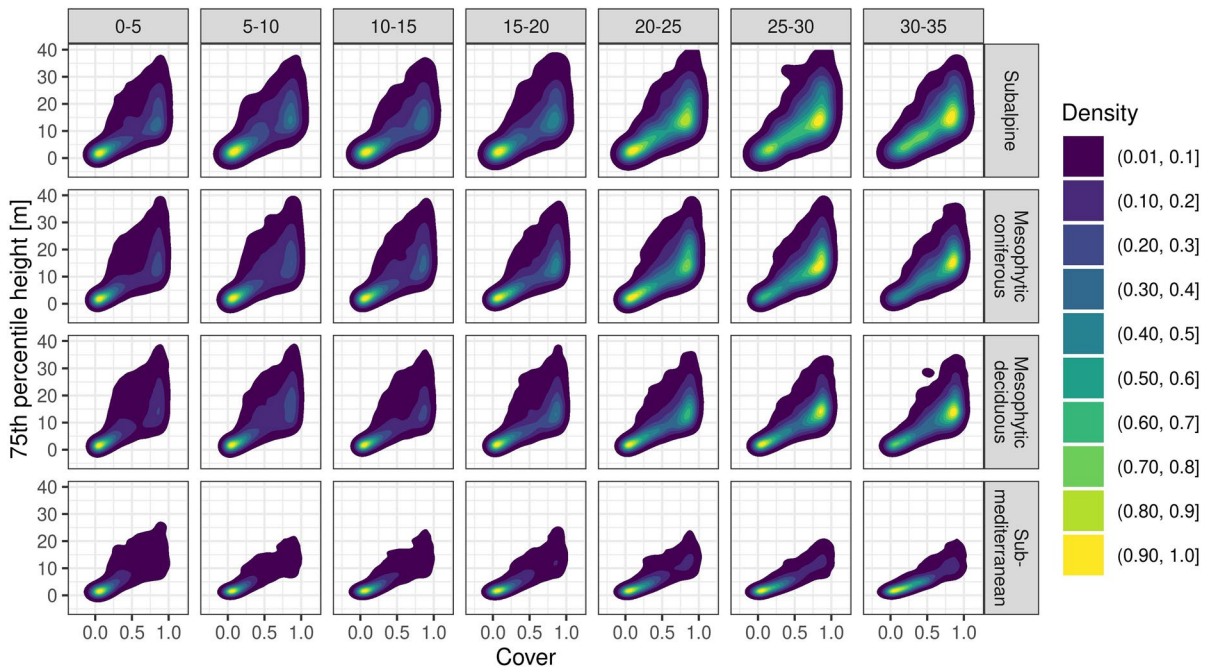
Fig. 5 Distribution of disturbed GEDI points in a space defined by canopy cover and relative height (75th percentile) over time after disturbance for four of the main potential natural vegetation types in the Alps

Fig. 6 Mean probability of points belonging to the closed-canopy cluster over time after disturbance for four of the main PNV types in the Alps. The ribbon indicates the 95% interval of the mean probability obtained by 500-fold bootstrap resampling of the points (with replacement). The dotted line shows the mean probability of points belonging to the closed-canopy cluster in undisturbed forests
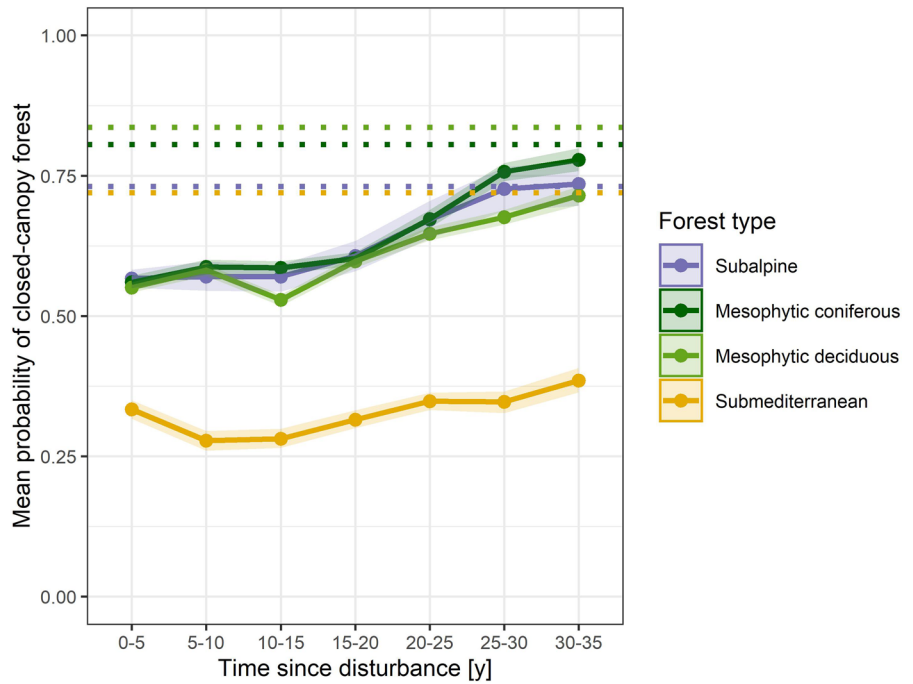
these alternative states were also observed in the absence of recent disturbance; they thus do not only represent a transient effect of disturbance and recovery, but rather are likely to be true alternative states of forest vegetation. At the upper treeline, for instance, low temperatures and harsh winter conditions limit tree recruitment and growth (Frei et al. 2018). In open areas, seedlings are more likely to by damaged by wind and frost (Presas et al. 2009), which inhibits tree establishment, representing a stabilizing feedback for keeping forests in an open-canopy state near the timber line (D'Odorico et al. 2013). A further stabilizing feedback of open forests is the encroachment of light-demanding shrubs such as green alder and mountain pine in open areas, including avalanche tracks and abandoned pastures (Anthelme et al. 2001; Dullinger et al. 2003), which may inhibit the recruitment of spruce and larch (Dullinger et al. 2005; Lingua et al. 2008; Šenfeldr et al. 2014). However, transitions are possible: Once some level of tree cover is established, it creates a more suitable microclimate for new seedlings, leading to a positive feedback on establishment and eventually resulting in canopy closure (Lingua et al. 2008; Presas et al. 2009; D'Odorico et al. 2013; Bader et al. 2021). Besides the upper treeline, forest edges occur at the interface with other land uses, mainly pastures or meadows, and permanently open areas such as streams or frequent avalanche tracks. In fact, over 70% of the GEDI footprints in the Alps are within 200 m of a forest edge. At the forest edge, trees are more exposed to wind disturbance due to reduced sheltering from other trees (Seidl et al. 2014), and the microclimate is drier than inside the forest (De Frenne et al. 2021), which may limit tree regeneration at dry sites (Harvey et al. 2016). Our findings of increased propensity of open forests close to forest edges are in line with a recent empirical analysis from the northern Alps, finding a significant reduction of tree basal area in close proximity to an edge (Pöpperl and Seidl 2021).

Disturbances are major agents of change in forests and can cause a shift from closed-canopy forests to open-canopy forests. However, we find that disturbances frequently do not lead to such a transition between alternative structural states in the Alps. In fact, over 50% of disturbed forests remain in the closed-canopy cluster also after disturbances (Fig. 6), indicating that most disturbances in the Alps are of a low or intermediate severity. It is important to note that disturbances in the Alps are small relative to the grain of the disturbance product used herein (Landsat-based, 30 m grain). Many disturbance patches detected by Landsat will thus be composed only of pixels containing the edge of the disturbance perimeter, leading to a mixture of disturbance severities at the patch scale. That is, even if disturbance severity is high (i.e., removal of large parts of the canopy), edges and residual live trees will be detected by GEDI, leading to a mixed disturbance severity signal. In addition, GEDI does not differentiate between live and dead trees, so standing dead wood after disturbance will contribute to the detected forest structure. Nonetheless, both residual live and dead trees can help maintain forest ecosystem services after disturbance, such as providing protection from avalanches (Wohlgemuth et al. 2017; Teich et al. 2019; Stritih et al. 2021).

In forests that do shift to the alternate state of open-canopy forest after a disturbance, this transition is mostly temporary. The recovery of mountain forests is slow during the first years post disturbance (Fig. 6). This corresponds to field surveys in protective forests after bark beetle outbreaks (Caduff et al. 2022) and windthrows (Baggio et al. 2022), which have shown that forests' capacity to provide protection against avalanches is at a low point 10–15 years after a disturbance, when dead wood decays and regeneration is still limited. However, within 35 years, the large majority of disturbed forests have recovered most of their canopy cover relative to undisturbed conditions, and have transitioned back to a closed-canopy state. The recovery times observed here are slower than the recovery times of ca. 20 years estimated from optical satellite data across diverse forest systems in Europe (Senf and Seidl 2022; White et al. 2022), yet they are in line with other lidar-based observations of structural recovery of central European forests (Senf et al. 2019). While lidar is sensitive to changes in vertical structure, optical satellites mainly capture changes in horizontal canopy closure (Bolton et al. 2017). Integrating both long-term optical remote sensing information and recent large-scale active sensors such as GEDI can therefore help to better quantify forest structural dynamics across large spatial and long temporal extents. Nonetheless, even when considering vertical structure, observed recovery times are still considerably shorter than disturbance intervals

of > 200 years observed for most parts of the European Alps (Senf and Seidl 2022).

The only exceptions to the pattern of fast post-disturbance recovery are submediterranean forests, which show a much higher propensity for remaining in an open-canopy state after disturbance, and recover considerably slower than other forest types. These forests occur at warm and dry sites, especially in the south-western Alps, and the potential natural vegetation consists of thermophilous species such as downy oak (Bohn et al. 2004). They have a distinctly different disturbance regime (i.e., dominated by wildfire and drought) compared to the other forest types of the Alps (i.e., dominated by wind, avalanches and bark beetles) (Bebi et al. 2017), which may contribute to a higher disturbance severity and slower recovery in these forests. After the canopy is opened by disturbance, microclimate is altered, creating a positive feedback and resulting in strong drought limitation on tree regeneration (Harvey et al. 2016). Disturbances are thus most likely to result in permanent shifts to open-canopy forests in these forest types. This has important implications for the future of protective forests in the Alps, as downy oak is expected to become more dominant in the Alps with climate warming (Rigling et al. 2013; Vacchiano and Motta 2015). Given the reduced capacity of these forests to provide protection from natural hazards (Moos et al. 2021), and their slower recovery after disturbance, the protective capacity of mountain forests at the dry and warm edge could be jeopardized in the future. This will mean increased risks to infrastructure and people living in these areas (Teich and Bebi 2009).

The moderate predictive power of the drivers investigated in our analysis (AUC = 0.75) indicates that other factors, such as land-use legacies and undetected or older disturbances, play an important role in determining forest structure in the Alps. Since the Neolithic, the Alps were extensively used for agriculture, with many forests cleared for meadows and pastures (Bebi et al. 2017; Conedera et al. 2017). Furthermore, grazing in subalpine forests created forest pastures with sparse tree cover (Garbarino et al. 2009). Although grazing in forests declined during the twentieth century (Bebi et al. 2017), the legacies of such land use still influence forest structure today (Garbarino et al. 2013). Open-canopy forests can also be a result of small-scale disturbances, which might not be detected in the satellite-based disturbance map used here (Senf and Seidl 2021). In addition, disturbances that occurred before 1986 might still affect current forest structure, but could not be considered in our study. However, given that three out of four forest types (representing 78% of the forest area of the Alps) recovered to pre-disturbance canopy cover within 35 years (Fig. 6), we expect that older disturbances have a limited effect on our finding of alternative structural states of forest structure in the Alps.

Mountainous areas are particularly challenging for spaceborne lidar, as ground returns from steep slopes or terrain features such as boulders are difficult to distinguish from vegetation returns (Schneider et al. 2020). Although the small footprint size of GEDI was designed to limit slope effects (Duncanson et al. 2022), we still observe higher estimates of tree height and canopy cover on steeper slopes, an effect that we at least partly attribute to the positive slope bias in GEDI data (Liu et al. 2021; Lang et al. 2022). Because of a possible overestimation of height and cover, using absolute height thresholds to evaluate recovery after disturbance or calculating recovery rates (e.g. in meters of height per year) can be problematic (Milenković et al. 2022). In addition, due to the high correlation between structural metrics measured with GEDI (see Supporting information, Fig. S13) it is difficult to differentiate open forests from low but dense shrub forests within the open-canopy cluster identified here. These limitations highlight the need for caution when interpreting observations from spaceborne lidar data in an ecological context. Nonetheless, the large amount of data points available from GEDI means that in spite of these inaccuracies, robust signals related to ecosystem dynamics can be obtained. More broadly, an important limitation of the data analyzed is that it does not allow any inferences regarding changes in species composition. Future work should thus investigate whether the alternative states identified here are related to the occurrence of particular species, and whether post-disturbance recovery leads to self-replacement of prevailing tree species or to reassembly (Seidl and Turner 2022). Finally, our analyses across large spatial scales remain necessarily descriptive. Future work should focus on identifying the mechanisms that result in the emergence of alternative structural states, e.g. by experimentally altering important drivers that induce

stabilizing feedbacks (Kueppers et al. 2017; Hagedorn et al. 2019).

Conclusions

We found evidence for two alternative states of forest structure (i.e., tall, closed-canopy and short, open-canopy) in mountain forests of the European Alps. The occurrence of both states is largely determined by topography and landscape configuration, and stabilizing feedbacks exist that maintain these states also in the absence of disturbance. The large majority of forests are in the closed-canopy state, while open-canopy forests occur particularly at high elevations, near forest edges, and at warm sites. Disturbance and recovery are major agents of transition between the two structural states. Disturbance causes a transition from the closed-canopy to the open-canopy attractor in approximately 50% of the cases. In most cases, this disturbance-induced shift is temporary: Within 35 years, the majority of forests recover to a structure similar to undisturbed forests, shifting back to the closed-canopy attractor. However, we observed higher disturbance severities and reduced recovery in submediterranean forest types, which could indicate a more permanent shift of these forests to open-canopy conditions after disturbance. Such transitions may pose an important challenge for mountain forest management in the future, as submediterranean forests are likely to become more prevalent in the Alps under climate warming, and as open-canopy forests have lower capacities for providing important ecosystem services such as protection against natural hazards.

Data Availability All of the data used in this study are publicly available. 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 European disturbance map is available at https://doi.org/10.5281/zenodo.3924381. The CHELSA climate data is available at www.chelsa-climate.org, and the Copernicus DEM can be downloaded from https://land.copernicus.eu/imagery-in-situ/eu-dem/eu-dem-v1.1. The Map of the Natural Vegetation of Europe (Bohn et al. 2004) can be accessed through https://www.synbiosys.alterra.nl/eurovegmap. The R-scripts used for data processing and analysis is available at https://doi.org/10.5281/zenodo.7562291.

Declarations

Competing interests The authors declare no conflict of interest.

Ethical approval An ethical approval is not applicable.

References

Albrich K, Rammer W, Seidl R (2020) Climate change causes critical transitions and irreversible alterations of mountain forests. Glob Change Biol 26:4013–4027

Anthelme F, Grossi JL, Brun JJ, Didier L (2001) Consequences of green alder expansion on vegetation changes and arthropod communities removal in the northern French Alps. For Ecol Manage 145:57–65

Bader MY, Llambí LD, Case BS et al (2021) A global framework for linking alpine-treeline ecotone patterns to underlying processes. Ecography 44:265–292

Baggio T, Brožová N, Bast A et al (2022) Novel indices for snow avalanche protection assessment and monitoring of wind-disturbed forests. Ecol Eng. https://doi.org/10.1016/j.ecoleng.2022.106677

Bebi P, Seidl R, Motta R et al (2017) Changes of forest cover and disturbance regimes in the mountain forests of the Alps. For Ecol Manage 388:43–56

Bohn U, Neuhäusl R, Gollub G, et al (2004) Karte der natürlichen Vegetation Europas / Map of the Natural vegetation

of Europe. Scale 1: 2 500 000. Federal Agency for Nature Conservation 530

Bolton DK, Coops NC, Wulder MA (2015) Characterizing residual structure and forest recovery following high-severity fire in the western boreal of Canada using Landsat time-series and airborne lidar data. Remote Sens Environ 163:48–60

Bolton DK, Coops NC, Hermosilla T et al (2017) Assessing variability in post-fire forest structure along gradients of productivity in the Canadian boreal using multi-source remote sensing. J Biogeogr 44:1294–1305

Bottero A, Garbarino M, Long JN, Motta R (2013) The interacting ecological effects of large-scale disturbances and salvage logging on montane spruce forest regeneration in the western European Alps. For Ecol Manage 292:19–28

Breiman L (2001) Random forests. Mach Learn 45:5–32

Caduff ME, Brožová N, Kupferschmid AD et al (2022) How large-scale bark beetle infestations influence the protective effects of forest stands against avalanches: a case study in the Swiss Alps. For Ecol Manag. https://doi.org/10.1016/j.foreco.2022.120201

Carpenter S, Walker B, Anderies JM, Abel N (2001) From metaphor to measurement: resilience of what to what? Ecosystems 4:765–781

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 Manage 388:100–112

Cramer MD, Power SC, Belev A et al (2019) Are forest-shrubland mosaics of the Cape Floristic Region an example of alternate stable states? Ecography 42:717–729

D'Odorico P, He Y, Collins S et al (2013) Vegetation-microclimate feedbacks in woodland-grassland ecotones. Glob Ecol Biogeogr 22:364–379

De Frenne P, Lenoir J, Luoto M et al (2021) Forest microclimates and climate change: importance, drivers and future research agenda. Glob Change Biol 27:2279–2297

Dubayah R, Blair JB, Goetz S et al (2020) The global ecosystem dynamics investigation: high-resolution laser ranging of the Earth's forests and topography. Sci Remote Sens 1:100002

Dullinger S, Dirnböck T, Grabherr G (2003) Patterns of shrub invasion into high mountain Grasslands of the Northern Calcareous Alps, Austria. Arct Antarct Alp Res 35:434–441

Dullinger S, Dirnböck T, Köck R et al (2005) Interactions among tree-line conifers: differential effects of pine on spruce and larch. J Ecol 93:948–957

Duncanson L, Kellner JR, Armston J et al (2022) Aboveground biomass density models for NASA's Global Ecosystem Dynamics Investigation (GEDI) lidar mission. Remote Sens Environ 270:112845

EU-DEM v1.1 (2016) Copernicus Land Monitoring Service

Falk DA, van Mantgem PJ, Keeley JE et al (2022) Mechanisms of forest resilience. For Ecol Manag 512:120129

Fayad I, Baghdadi N, Alvares CA et al (2021) Terrain slope effect on forest height and wood volume estimation from gedi data. Remote Sens. https://doi.org/10.3390/rs13112136

Fraley C, Raftery AE (1998) How many clusters? Which clustering method? Answers via model-based cluster analysis. Computer Journal 41:586–588

Frei ER, Bianchi E, Bernareggi G et al (2018) Biotic and abiotic drivers of tree seedling recruitment across an alpine treeline ecotone. Sci Rep 8:1–12

Garbarino M, Weisberg PJ, Motta R (2009) Interacting effects of physical environment and anthropogenic disturbances on the structure of European larch (*Larix decidua* Mill.) forests. For Ecol Manage 257:1794–1802

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

Gehrig-Fasel J, Guisan A, Zimmermann NE (2007) Tree line shifts in the Swiss Alps: climate change or land abandonment? J Veg Sci 18:571–582

Genuer R, Poggi JM, Tuleau-Malot C (2015) VSURF: an R package for variable selection using random forests. R J 7:19–33

Hagedorn F, Gavazov K, Alexander JM (2019) Above- and belowground linkages shape responses of mountain vegetation to climate change. Science 1123:1119–1123

Hansen MC, Potapov PV, Moore R et al (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850–853

Harvey BJ, Donato DC, Turner MG (2016) High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Glob Ecol Biogeogr 25:655–669

Hirota M, Holmgren M, van Nes EH, Scheffer M (2011) Global resilience of tropical forest. Science 334:232–235

Holling C (1973) Resilience and stability of ecological systems. Annual review of ecology and systematics

Hosmer DW, Lemeshow S (2000) Assessing the fit of the model applied logistic regression. Wiley, Hoboken pp 143–202

Johnstone JF, Allen CD, Franklin JF et al (2016) Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ 14:369–378

Karger DN, Conrad O, Böhner J et al (2017) Climatologies at high resolution for the earth's land surface areas. Scientific Data 4:1–20

Kueppers LM, Conlisk E, Castanha C et al (2017) Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. Glob Change Biol 23:2383–2395

Kulakowski D, Bebi P, Rixen C (2011) The interacting effects of land use change, climate change and suppression of natural disturbances on landscape forest structure in the Swiss Alps. Oikos 120:216–225

Lang N, Kalischek N, Armston J et al (2022) Global canopy height regression and uncertainty estimation from GEDI LIDAR waveforms with deep ensembles. Remote Sens Environ 268:112760

Lingua E, Cherubini P, Motta R, Nola P (2008) Spatial structure along an altitudinal gradient in the Italian central Alps suggests competition and facilitation among coniferous species. J Veg Sci 19:425–436

Liu A, Cheng X, Chen Z (2021) Performance evaluation of GEDI and ICESat-2 laser altimeter data for terrain and

canopy height retrievals. Remote Sens Environ. https://doi.org/10.1016/j.rse.2021.112571

McDowell NG, Allen CD, Anderson-Teixeira K et al (2020) Pervasive shifts in forest dynamics in a changing world. Science. https://doi.org/10.1126/science.aaz9463

Milenković M, Reiche J, Armston J et al (2022) Assessing amazon rainforest regrowth with GEDI and ICESat-2 data. Sci Remote Sens. https://doi.org/10.1016/j.srs.2022.100051

Miller AD, Thompson JR, Tepley AJ, Anderson-Teixeira KJ (2019) Alternative stable equilibria and critical thresholds created by fire regimes and plant responses in a fire-prone community. Ecography 42:55–66

Moos C, Guisan A, Randin CF, Lischke H (2021) Climate change impacts the protective effect of forests: a case study in Switzerland. Front for Glob Change 4:1–15

Murphy BP, Bowman DMJS (2012) What controls the distribution of tropical forest and savanna? Ecol Lett 15:748–758

Nikinmaa L, Lindner M, Cantarello E et al (2020) Reviewing the use of resilience concepts in forest sciences. Curr for Rep 6:61–80

Pöpperl F, Seidl R (2021) Effects of stand edges on the structure, functioning, and diversity of a temperate mountain forest landscape. Ecosphere. https://doi.org/10.1002/ecs2.3692

Potapov P, Li X, Hernandez-Serna A et al (2021) Mapping global forest canopy height through integration of GEDI and Landsat data. Remote Sens Environ 253:112165

Presas EB, Camarero JJ, Ninot JM, Gutiérrez E (2009) Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming. Glob Ecol Biogeogr 18:460–472

Rigling A, Bigler C, Eilmann B et al (2013) Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. Glob Change Biol 19:229–240

Rüetschi M, Weber D, Koch TL et al (2021) Countrywide mapping of shrub forest using multi-sensor data and bias correction techniques. Int J Appl Earth Observ Geoinf. https://doi.org/10.1016/j.jag.2021.102613

Schneider FD, Ferraz A, Hancock S et al (2020) Towards mapping the diversity of canopy structure from space with GEDI. Environ Res Lett. https://doi.org/10.1088/1748-9326/ab9e99

Scrucca L, Fop M, Murphy TB, Raftery AE (2016) Mclust 5: clustering, classification and density estimation using Gaussian finite mixture models. R J 8:289–317

Sebald J, Senf C, Heiser M et al (2019) The effects of forest cover and disturbance on torrential hazards: large-scale evidence from the Eastern Alps. Environ Res Lett. https://doi.org/10.1088/1748-9326/ab4937

Sebald J, Senf C, Seidl R (2021) Human or natural? Landscape context improves the attribution of forest disturbances mapped from Landsat in Central Europe. Remote Sens Environ 262:112502

Seidl R, Turner MG (2022) Post-disturbance reorganization of forest ecosystems in a changing world. Proc Natl Acad Sci 119:1–10

Seidl R, Rammer W, Blennow K (2014) Simulating wind disturbance impacts on forest landscapes: tree-level heterogeneity matters. Environ Model Softw 51:1–11

Seidl R, Honkaniemi J, Aakala T et al (2020) Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems. Ecography 43:967–978

Senf C (2022) Seeing the system from above—the use and potential of remote sensing for studying ecosystem dynamics. Ecosystems. https://doi.org/10.1007/s10021-022-00777-2

Senf C, Seidl R (2021) Mapping the forest disturbance regimes of Europe. Nature 4:63–70

Senf C, Seidl R (2022) Post-disturbance canopy recovery and the resilience of Europe's forests. Glob Ecol Biogeogr. https://doi.org/10.1111/geb.13406

Senf C, Müller J, Seidl R (2019) Post-disturbance recovery of forest cover and tree height differ with management in Central Europe. Landsc Ecol. https://doi.org/10.1007/s10980-019-00921-9

Senf C, Sebald J, Seidl R (2021) Increasing canopy mortality affects the future demographic structure of Europe's forests. One Earth 4:749–755

Šenfeldr M, Treml V, Maděra P, Volařík D (2014) Effects of prostrate Dwarf Pine on Norway spruce clonal groups in the treeline ecotone of the Hrubý Jeseník Mountains, Czech Republic. Arct Antarct Alp Res 46:430–440

Silva CA, Hamamura C, Valbuena R, et al (2020) rGEDI: An R Package for NASA's Global Ecosystem Dynamics Investigation (GEDI) Data Visualizing and Processing. v0.1.9. https://github.com/carlos-alberto-silva/rGEDI

Stritih A, Bebi P, Rossi C, Grêt-Regamey A (2021) Addressing disturbance risk to mountain forest ecosystem services. J Environ Manag 296:113188

Tang H, Armston J (2019) Algorithm Theoretical Basis Document (ATBD) for GEDI L2B Footprint Canopy Cover and Vertical Profile Metrics

Tang H, Brolly M, Zhao F et al (2014) Deriving and validating Leaf Area Index (LAI) at multiple spatial scales through lidar remote sensing: a case study in Sierra National Forest, CA. Remote Sens Environ 143:131–141

Teich M, Bebi P (2009) Evaluating the benefit of avalanche protection forest with GIS-based risk analyses—a case study in Switzerland. For Ecol Manage 257:1910–1919

Teich M, Giunta AD, Hagenmuller P et al (2019) Effects of bark beetle attacks on forest snowpack and avalanche formation—implications for protection forest management. For Ecol Manage 438:186–203

Tepley AJ, Thompson JR, Epstein HE, Anderson-Teixeira KJ (2017) Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. Glob Change Biol 23:4117–4132

Thom D, Seidl R (2022) Accelerating mountain forest dynamics in the Alps. Ecosystems 25:603–617

Vacchiano G, Motta R (2015) An improved species distribution model for Scots pine and downy oak under future climate change in the NW Italian Alps. Ann for Sci 72:321–334

Van Nes EH, Hirota M, Holmgren M, Scheffer M (2014) Tipping points in tropical tree cover: linking theory to data. Glob Change Biol 20:1016–1021

Wang Y, Ni W, Sun G et al (2019) Slope-adaptive waveform metrics of large footprint lidar for estimation of forest aboveground biomass. Remote Sens Environ 224:386–400

White JC, Hermosilla T, Wulder MA, Coops NC (2022) Mapping, validating, and interpreting spatio-temporal trends in post-disturbance forest recovery. Remote Sens Environ 271:112904

Winter MB, Baier R, Ammer C (2015) Regeneration dynamics and resilience of unmanaged mountain forests in the Northern Limestone Alps following bark beetle-induced spruce dieback. Eur J Forest Res 134:949–968

Wohlgemuth T, Schwitter R, Bebi P et al (2017) Post-windthrow management in protection forests of the Swiss Alps. Eur J Forest Res 136:1029–1040