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Recovery and resilience of European temperate forests after large and severe disturbances

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Abstract

Recent observations of tree regeneration failures following large and severe disturbances, particularly under warm and dry conditions, have raised concerns about the resilience of forest ecosystems and their recovery dynamics in the face of climate change. We investigated the recovery of temperate forests in Europe after large and severe disturbance events (i.e., resulting in more than 70% canopy loss in patches larger than 1 ha), with a range of one to five decades since the disturbance occurred. The study included 143 sites of different forest types and management practices that had experienced 28 disturbance events, including windthrow (132 sites), fire (six sites), and bark beetle outbreaks (five sites). We focused on assessing post-disturbance tree density, structure, and composition as key indicators of forest resilience. We compared post-disturbance height-weighted densities with site-specific pre-disturbance densities to qualitatively assess the potential for structural and compositional recovery, overall and for dominant tree species, respectively. Additionally, we analyzed the ecological drivers of post-windthrow tree density, such as forest management,

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topography, and post-disturbance aridity, using a series of generalized additive models. The descriptive results show that European temperate forests have been resilient to past large and severe disturbances and concurrent climate conditions, albeit with lower resilience to high-severity fire compared with other disturbance agents. Across sites and disturbance agents, the potential for structural recovery was greater than that of compositional recovery, with a large proportion of plots becoming dominated by early-successional species after disturbance. The models showed that increasing elevation and salvage logging negatively affect post-windthrow regeneration, particularly for late-successional species, while pioneer species are negatively affected by increasing summer aridity. These findings provide a key baseline for assessing future recovery and resilience following the recent occurrence of widespread disturbance in the region and in anticipation of future conditions characterized by increasing heat and drought stress.

KEYWORDS
environmental filtering, forest reorganization, ground-based inventories, post-disturbance regeneration, recovery drivers, salvage logging

1 | INTRODUCTION

Anthropogenic climate change is causing widespread changes in forest ecosystems, both directly through changes in temperature and precipitation, and indirectly by altering natural disturbance regimes (Anderson-Teixeira et al., 2013; McDowell et al., 2020). Changes in disturbance regimes, particularly increases in the frequency, size, or severity of disturbances, pose a threat to the resilience of forests and their ability to maintain ecosystem functions and related services over time (Forzieri et al., 2022; Millar & Stephenson, 2015; Seidl et al., 2017; Thom & Seidl, 2016). Specifically, disturbances that are both large in scale and severe can impair the process of recovery (i.e., the restoration of forest structure, composition, and function), which is a central component of resilience (Nikinmaa et al., 2020), by triggering successional shifts toward altered forest types or non-forested ecosystems (Coop et al., 2020; Donato et al., 2016; Martínez-Vilalta & Lloret, 2016; Young et al., 2019).

Impaired forest recovery is primarily attributed to a combination of limited seed supply and other legacies resulting from large and severe disturbances, as well as a challenging environment, particularly drought accompanied by high temperatures, which can hinder the successful establishment and growth of tree regeneration, especially in the case of fire (Davis et al., 2019; Hansen et al., 2018; Harvey et al., 2016). In addition to these environmental filters, a variety of biotic factors can influence recovering forests, including interactions with other plants and animals, and anthropogenic disturbances (Dey et al., 2019; Diaci et al., 2017; Szwagrzyk et al., 2021). In particular, historical land use and forest management practices can affect disturbance legacies, that is, organisms and biologically derived patterns that persist following a disturbance (Johnstone et al., 2016; Seidl & Rammer, 2014). For example, salvage logging is routinely conducted following disturbances, although it is a controversial practice in the context of forest recovery because it can inadvertently damage advanced regeneration and remove legacies such as deadwood and surviving trees and shrubs that together contribute to recovery via seed sources, erosion control, and microclimate amelioration (Leverkus et al., 2021; Lindenmayer et al., 2017; Marangon et al., 2022; Taeroe et al., 2019; cf. Konôpka, Šebeň, & Merganičová, 2021). Many of the factors that affect recovery processes are linked to a specific disturbance agent. For example, wind and insect outbreaks, even of high severity, tend to leave the forest understory intact, whereas high-severity fires typically remove understory vegetation and surface litter and alter forest soil conditions (Frelich & Reich, 1999).

The erosion of resilience caused by regeneration failures after large and severe disturbances has been reported in temperate forests around the world (Bowd et al., 2023; Moser et al., 2010; Stevens-Rumann & Morgan, 2019; Turner et al., 2019). In European temperate forests, the regeneration of dominant tree species is well adapted to the historical range of disturbance variability, which is generally characterized by frequent, low-severity gap-scale events and periodic intermediate- and high-severity disturbances caused by wind, insect outbreaks, fire, and other agents (Adámek et al., 2016; Čada et al., 2016; Frankovič et al., 2021; Nagel et al., 2021; Schurman et al., 2018; Svoboda et al., 2014). However, there are concerns that a changing climate and increasing disturbance impacts may push European temperate forest dynamics beyond their historical range of variability (Patacca et al., 2023; Senf & Seidl, 2018, 2021b; Sommerfeld et al., 2018), potentially impacting recovery processes. In order to implement appropriate management responses, it is crucial to understand whether European temperate forests are capable of recovering in terms of structure and composition after large and severe disturbances and to identify the driving factors that influence this process.

A widely used approach to study forest recovery, particularly after large-scale disturbances, is remote sensing (Guz et al., 2022; Rodman et al., 2021; White et al., 2022). Post-disturbance recovery has been assessed in European forests using satellite imagery (e.g. Landsat, Modis) and active sensors (e.g. Lidar), showing that the majority of forests are resilient and are recovering following disturbances documented over the past few decades (Dobrowolska et al., 2022; Nolè et al., 2022; Senf et al., 2019; Senf & Seidl, 2022). Although remote sensing provides valuable information over large regions, its resolution is relatively coarse, and its temporal extent is limited to a few decades (Senf, 2022). To complement remote sensing, empirical ground-based studies of post-disturbance regeneration should be conducted, as they cover a longer temporal extent compared with continuous satellite records and provide structural and compositional information at a much finer resolution (Senf & Seidl, 2022).

Recent empirical ground-based studies conducted in European forests have confirmed adequate regeneration following disturbances caused by different agents and of different severity (Macek et al., 2017; Moris et al., 2017; Taeroe et al., 2019). Regeneration processes, including post-disturbance regeneration, advanced regeneration, surviving trees, and vegetative sprouting, can all contribute to forest recovery. For example, following wind disturbance, post-disturbance regeneration is generally considered the most important of these four mechanisms, although their relative importance also depends on species life-history traits, whereby advanced regeneration may play an important role for shade-tolerant species (Taeroe et al., 2019). The initial post-disturbance reorganization phase is widely recognized as an important window for future forest dynamics (Seidl & Turner, 2022). However, ecosystem trajectories may become more unpredictable when disturbances are compounded, as in the case of salvage logging (Buma, 2015; Gill et al., 2017). Therefore, long-term inventories are needed to assess forest recovery after large and severe disturbances. Such information is needed to inform forest management decisions, as well as for modeling ecosystem dynamics, including carbon balance (Goetz et al., 2012; Harris et al., 2022).

Although numerous ground-based case studies have examined regeneration following various disturbance events (e.g. Marcolin et al., 2019; Vodde et al., 2015; Wild et al., 2014), to our knowledge, no previous efforts have conducted a continental-scale synthesis of forest recovery from long-term ground-based studies after stand-replacing disturbances caused by different disturbance agents in Europe. Such an approach can provide additional insights into the common drivers of post-disturbance regeneration, whereas case studies may reveal more idiosyncratic successional pathways. Therefore, we compiled both newly collected and previously published data on forest regeneration after large and severe disturbances occurring between 1962 and 2012, in combination with spatially explicit environmental datasets, to investigate the post-disturbance resilience of European temperate forests (Cerioni et al., 2024). The dataset serves as a benchmark of post-disturbance forest recovery over the past five decades, providing a basis for comparing future assessments of forest regeneration following large and severe disturbances under a warmer and more drought-prone climate. We address the following questions: (1) Are European temperate forests capable of recovering in terms of both structure and tree species composition after large and severe disturbances caused by different agents? (2) What are the climatic, topographic, and management factors that affect post-disturbance regeneration, and is there a difference in forest recovery between different post-disturbance management treatments?

2 | MATERIALS AND METHODS

2.1 | Data collection and calculation of variables

We carried out ground-based inventories of forest recovery across European temperate forests (defined according to climatological classification by Rivas-Martínez et al., 2004), following large and severe disturbances (Figure 1). These disturbances were defined as those resulting in a loss of canopy cover of at least 70% in a contiguous patch larger than 1 ha, which equals the average disturbance patch size in Europe quantified from a time series of Landsat images (Senf & Seidl, 2021a). We combined data from 143 sites, including 1475 field plots. The recovery data were collected for three disturbance agents: wind (17 events, 132 sites, and 1129 plots), fire (6 events, 6 sites, and 305 plots), and bark beetles (*Ips typographus* L.) (5 events, 5 sites, and 41 plots). These disturbance agents are the most important natural disturbance agents in European forests (Patacca et al., 2023; Sommerfeld et al., 2018) (Table 1). We did not include recently disturbed sites (<5 years post-disturbance), as short post-disturbance periods may not capture the recovery process. Our dataset includes inventories ranging from 7 to 52 years after disturbance. In cases where multiple plot-level censuses were performed at the same site, only the most recent inventory was included. Field procedures, including sampling design, plot sizes, and parameters assessed, varied among sites (Table S1). However, each inventory included common parameters such as the density and species composition of regeneration, defined as tree species older than 1 year and with diameter at breast height (DBH) < 7 cm (either aggregated in height classes or with individually recorded heights), trees (defined as tree species with DBH ≥7 cm), information on forest management before and after the disturbance, and GPS coordinates of plot centers.

Post-disturbance density of tree species, including regeneration and trees, was used as an indicator of forest resilience and the response variable in the statistical models with recovery drivers. In order to make post-disturbance densities comparable across sites with different times since disturbance, we standardized them by calculating a height-weighted density index following the approach of Vickers et al. (2019), which is based on the concept of aggregate height (i.e., the sum of the individual heights of a species or group of species) (Fei et al., 2006). This index accounts for the different survival rates of individuals of different heights and provides

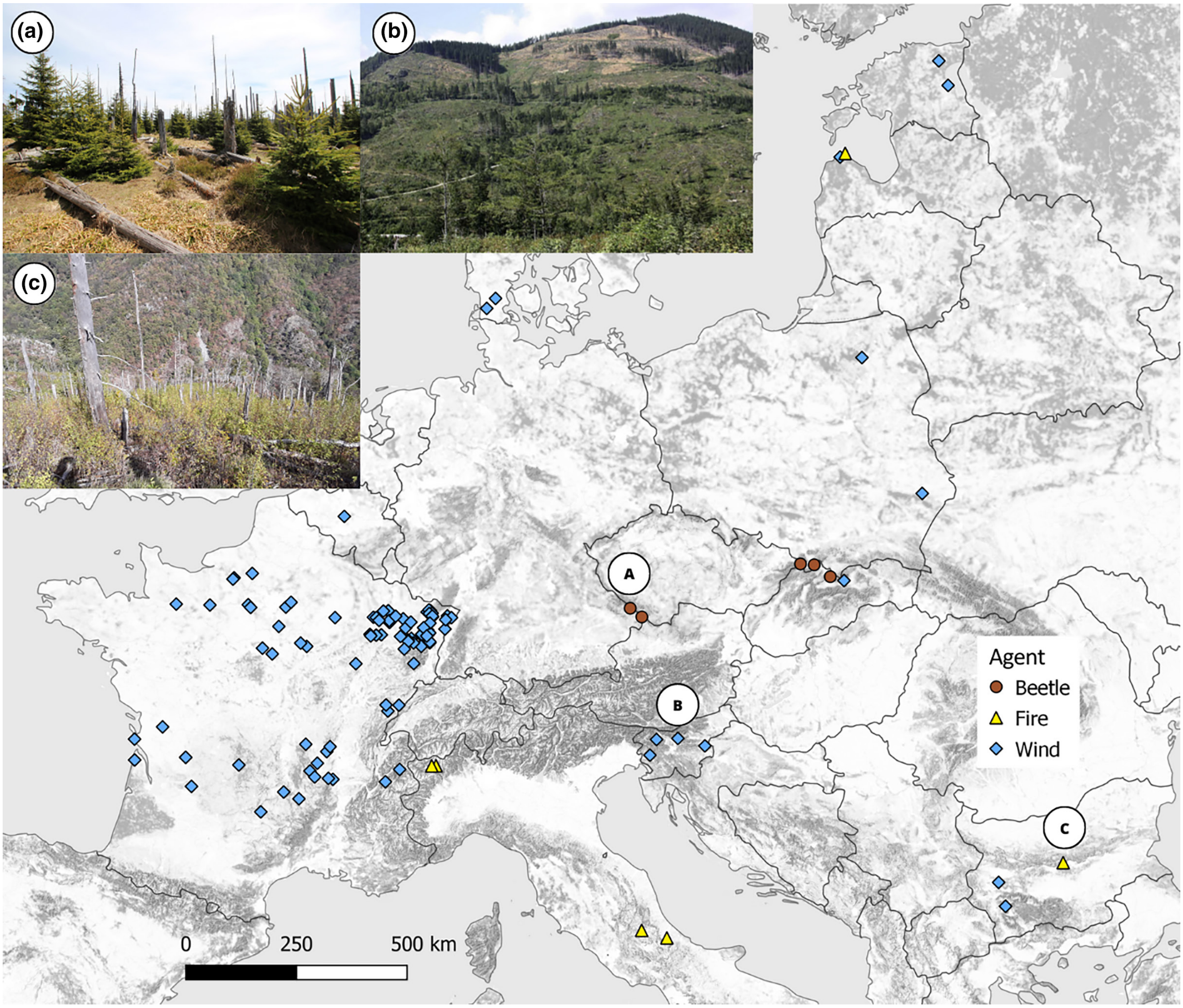

FIGURE 1 Location of the study sites and respective disturbance agents. The pictures show forests recovering after bark beetles in Czechia (a), wind in Slovenia (b), and fire in Bulgaria (c). The background map is a grayscale version of Stamen Terrain Background (Map tiles by Stamen Design, under CC BY 4.0. Data by OpenStreetMap, under ODbL). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

a better assessment of recruitment and future stand development than when only raw post-disturbance density is considered (Harris et al., 2022). Each tallied individual was given a weight according to the ratio of its height to that of a reference height (i.e., the height of a theoretical individual with DBH = 7 cm, which was assigned a weight of 1; see Supporting Information 1 for further details on the model we used to estimate the reference height), summed up at the plot-level and scaled up to a hectare. All individuals taller than the reference height or with DBH larger than 7 cm were weighted as 1. When individual tree height was not recorded during the inventory, we estimated it according to DBH-height curves for each site or group of sites (Supporting Information 1). When only the aggregated density in height classes was available, each class was given a weight according to the ratio of its height midpoint to the reference height. For the purpose of analyses, tree species were grouped according to their life-history traits into (1) pioneer, (2) early-successional, and (3) late-successional tree species (using light values from Landolt et al. (2010) and expert knowledge) (Table S2).

To assess the influence of different recovery drivers on post-disturbance density, we used spatially explicit European-scale datasets to derive harmonized predictors across the study sites. These predictors included environmental and management variables that are documented to have an effect on forest recovery (Table 2). Topographic variables, including elevation, slope steepness, aspect, and heat load index (HLI), were calculated at the plot level (using the plot center coordinates) using QGIS (version 3.22.9; QGIS.org, 2022) with the Forest and Buildings removed Copernicus DEM (FABDEM) with a spatial resolution of 30 m (Hawker & Neal, 2021) (accessed on 10 February 2022). Slope steepness and aspect

TABLE 1 Characteristics of the large and severe disturbance patches across the study region.

Agent type	Site	Country	Patch(es) size (ha)	Year of event	Reference
Bark beetle	Istebna	POL	2.91	2011	S. Keren & J. Socha (unpublished data)
Bark beetle	Kotlov zlab	SLK	40	1993–1999	Pittner et al. (2020)
Bark beetle	Pilsko	SLK	5.7	2007	M. Saniga, S. Kucbel, J. Vencurik, J. Pittner, & P. Jaloviar (unpublished data)
Bark beetle	Šumava	CZE	2000	1997–1999	Wild et al. (2014)
Bark beetle	Trojmezná	CZE	550	2008	Bače et al. (2015); Červenka et al. (2016, 2020)
Fire	Antey	ITA	5	1990	Garbarino MSc thesis
Fire	Aquila	ITA	125	2007	Morresi et al. (2019)
Fire	Bazi mire	LAT	1022	1992	Kitenberga et al. (2020)
Fire	Bourra	ITA	160	2005	Marcolin et al. (2019); Marzano et al. (2013)
Fire	Lettomanoppello	ITA	83	2007	Morresi et al. (2019)
Fire	Sokolna	BUL	196	2012	M. Panayotov & M. Cerioni (unpublished data)
Wind	Arvillard, Cuvy	FRA	5, 16	1990	Fuhr et al. (2015)
Wind	Bistrishko	BUL	60	2001	Tsvetanov et al. (2018)
Wind	Bohor	SLO	1.5–3	2008	Cerioni et al. (2022); Fidej et al. (2018)
Wind	Črnivec	SLO	16–87	2008	Cerioni et al. (2022); Fidej et al. (2018)
Wind	Halliku	EST	2.5–5	2002	Ilisson et al. (2007); Vodde et al. (2010, 2015)
Wind	High Tatras	SLK	10,000	2004	Konôpka et al. (2019)
Wind	Jelovica	SLO	125	2006	Ščap et al. (2013)
Wind	Lovrup Skov, Stursbøl Hegn	DEN	15,000	1999	J. H. C. de Koning & M. Hart (unpublished data)
Wind	Parangalitsa	BUL	4	1983	Tsvetanov et al. (2018)
Wind	Parangalitsa	BUL	22	1962	Tsvetanov et al. (2018)
Wind	Piska/Szast	POL	460	2002	Dobrowolska (2015); Szwagrzyk et al. (2017); Szwagrzyk, Gazda, et al. (2018)
Wind	Roztocze	POL	2.50	2008	Szwagrzyk, Maciejewski, et al. (2018)
Wind	Slitere	LAT	1.1–25.6	1969	Bāders et al. (2017); Bāders et al. (2021)
Wind	Trnovski gozd	SLO	7–16	2008	Cerioni et al. (2022); Fidej et al. (2018)
Wind	Tudu	EST	2.5–5	2001	Ilisson et al. (2007); Vodde et al. (2010, 2015)
Wind (Lothar / Martin)	France	FRA	1.4–556	1999	Dietz et al. (2020)
Wind (Vivian/ Wiebke)	Sonian forest—Kersselaerspleyn	BEL	1.1	1990	Vandekerkhove et al. (2018)

were calculated from the FABDEM using third-order polynomials (Haralick, 1983), and plot-level values were calculated using bilinear interpolation for each of the above-mentioned variables. HLI was calculated based on plot latitude, slope steepness, and aspect, using Equation (1) from McCune and Keon (2002). To characterize post-disturbance climate, we used the most recent European Centre for Medium-Range Weather Forecasts (ECMWF) ERA5-Land re-analysis data, which has a spatial resolution of 0.1° (~9 km) and is available from 1950 to the present (Muñoz-Sabater et al., 2021). We extracted the monthly averaged gridded data for potential evaporation (pev) and total precipitation (P) for the summer months (JJA) from 1950 to 2019 (accessed on 25 July 2022). Yearly aridity index (AI) was calculated as the average of monthly JJA aridity indices, which were computed as $1 - P/\text{pev}$ (Allen et al., 1998). Aridity change was calculated as the difference between the mean AI of the 7 post-disturbance years and the aridity baseline, calculated as the average of the index for the years between 1950 and 1980. Data wrangling, preliminary analyses, and visualization were done using R (R Core Team, 2022), primarily relying on the "tidyverse" package (Wickham et al., 2019).

TABLE 2 Description of the variables explored in the analyses of post-disturbance recovery drivers.

Variable (unit measure)	Values range/levels	Expected effect	Reference
Disturbance agent	Beetle, Fire, Wind	Advanced regeneration surviving after wind or beetle could boost the recovery process compared with severe fires, which remove the understory vegetation and may have a detrimental effect on soil. Analogously, late-successional species will be proportionally more present than pioneer species after wind or beetle, compared with fire	Frelich and Reich (1999); Taeroe et al. (2019)
Time since disturbance (years)[a]	7 to 52	Pioneer species will decrease with time since disturbance, while later-successional species will proportionally increase. Overall weighted density is deemed to peak at the onset of self-thinning stage	Fei et al. (2006)
Elevation (m a.s.l.)[a]	5 to 1951	With increasing elevation, growing season gets shorter and climate more extreme, reducing density and size of regeneration. At low altitudes, changes in elevation will not play a large role	Cunningham et al. (2006); Szwagrzyk et al. (2021)
Slope steepness (°)	0 to 70	Steeper slopes are more conducive to processes such as erosion and surface water runoff, which hamper plant establishment and growth, resulting in lower post-disturbance densities and size	Baier et al. (2007)
Slope aspect (°)	0 to 360	Southerly exposed sites are more exposed to droughts, while north-facing slopes may lack direct radiation. Aspect will interact with elevation in affecting regeneration	Brang (1998)
Topographic wetness index	−8.05 to 3.67	Can be considered a proxy for soil moisture and soil drought, incorporates specific catchment area and slope steepness. Low levels of this index will result in lower plant establishment and post-disturbance densities	Beven and Kirkby (1979); Kopecký et al. (2021)
Heat load index[a]	0.13 to 1.07	Can be considered a proxy for topographically driven potential heat load, incorporates latitude, slope steepness, and aspect. Extreme levels of solar radiation will negatively affect regeneration density, depending on site elevation and microclimate	McCune and Keon (2002)
Aridity change[a]	−0.099 to 0.146	Post-disturbance droughts have a negative impact on plant establishment. An increase in aridity in the first years post-disturbance, compared with the historical baseline, will result in lower regeneration densities and size	Stevens-Rumann and Morgan (2019)
Pre-disturbance management[a]	None, Light (<50 years since management stopped), Managed	Unmanaged sites tend to have a more irregular uneven-aged structure, therefore a larger share of legacies (i.e., organisms and matter carrying over the disturbances), also in the form of advanced regeneration, compared with managed sites, which will favor the recovery process	Johnstone et al. (2016)
Post-disturbance management[a]	None, Only salvage logging, Intensive (Logging + planting/thinning)	Salvage logging can damage legacies such as advanced regeneration and be detrimental to the ecosystem recovery process. As such, pioneer species will be relatively more common after salvage treatments, compared with unmanaged or planted sites	Lindenmayer et al. (2017); Taeroe et al. (2019)

[a] Included in the final models.

2.2 | Analyses

2.2.1 | Assessment of structural and compositional recovery potential

Recovery was qualitatively evaluated with regard to restoring pre-disturbance forest structure (i.e., structural recovery potential, sensu Rodman et al., 2022) and tree species composition (i.e., compositional recovery potential, sensu Andrus et al., 2020). For structural recovery potential, post-disturbance weighted density was compared with its respective site-specific pre-disturbance tree density (i.e., structural recovery target; conceptually akin to engineering resilience, sensu Nikinmaa et al., 2020). Pre-disturbance tree density was either calculated based on pre-disturbance inventories or estimated from density values in undisturbed stands of similar composition in the surroundings of the damaged area (Table S3). We inferred that sites having a high share of plots with a post-disturbance weighted density below their structural recovery target are at high risk of regeneration failure.

For compositional recovery potential, site-specific recovery targets were set for the density of the respective pre-disturbance dominant tree species (defined as the species accounting for more than half of the overall composition or as the two most common species if none had a share above 50%) as a proportion of the structural recovery target (i.e., 50% of the structural recovery target in the case of a single dominant species or 25% for each dominant species in the case of two dominant species) (Table S3). A plot was considered to show compositional recovery potential if the weighted densities of the dominant species were at least equal to the corresponding target value(s). Both structural and compositional recovery potential were computed at the plot level and summarized for each site as the share of recovered plots. Values in the results section are presented as averages of the site-level shares (overall, and for each disturbance agent). Unlike the results of the statistical models, which can be generalized beyond our study sites, caution must be taken in drawing conclusions from these recovery assessments, as they summarize the investigated areas without accounting for the spatial dependencies and adjustment for heterogeneity with respect to external covariates among sites or sampling effort imbalances.

2.2.2 | Modeling of post-disturbance recovery drivers

To account for spatial autocorrelation among plots (i.e., pseudoreplication) in our dataset and potential non-linearities between predictors and response variables, we developed a series of Generalized Additive Mixed Models (GAMMs) to examine the influence of various drivers on the post-disturbance weighted density of different species groups. The GAMM models were computed using the R package "mgcv" (version 1.8-38; Wood, 2017). Because both raw and post-disturbance weighted densities were highly right-skewed, we took their natural logarithm and modelled this transformed variable as Gaussian. After fitting exploratory models that included all observations with disturbance agent as a three-level categorical variable, and three separate models for each disturbance agent, we focused solely on the wind-disturbed sites for the formal statistical analyses (data points = 1129; sites = 132), because of the uneven spatial distribution and low replication of fire and beetle-disturbed sites. This approach was adopted to minimize bias and uncertainty related to the model results. Based on a priori ecological information, the explanatory variables included random site effect, elevation, pre-disturbance-management, post-disturbance management, time since disturbance, aridity change, and HLI. Prior to conducting the formal statistical analyses, we decided to include HLI as a predictor instead of slope steepness, aspect, or topographic wetness index because of potential multi-collinearity between these related DEM-derived variables.

To enable the comparison of covariate effects across different responses, we employed the same model structure for all the response variables investigated in this study, including overall weighted density, pioneer species weighted density, early-successional species weighted density, and late-successional species weighted density. The models were fitted independently for each response variable, allowing for distinct parameter estimates for each response. Specifically, the model structure for a response variable Y at the j-th plot within the i-th site is as follows:

$$\begin{aligned}\log(Y_{ij}+1) &= \beta_0 + b_i + s(\text{elevation}_{ij}) \\ &+ \sum_k \gamma_k \cdot I(\text{pre-disturbance management of the } ij\text{-th plot is } k) \\ &+ \sum_k \delta_k \cdot I(\text{post-disturbance management of the } ij\text{-th plot is } k) \\ &+ \beta_{\text{years}} \cdot \text{years\_since\_disturbance}_i + \beta_{\text{aridity\_change}} \cdot \text{aridity\_change}_i \\ &+ \beta_{\text{HLI}} \cdot \text{HLI}_i + \varepsilon_{ij},\end{aligned} \tag{1}$$

where β_0 is the overall intercept; $I(.)$ is the indicator function (assuming the value of 1 when its argument is true and the value of 0 otherwise); γ_k is the effect of the k-th level of pre-disturbance management (with the usual baseline-type restriction for identifiability as in ANOVA, or general linear models, Graybill, 1976); δ_k is the effect of the k-th level of post-disturbance management (with the usual baseline-type restriction for identifiability); β_{years} is the slope of the linear trend on time since disturbance (measured in years); $\beta_{\text{aridity\_change}}$ is the slope on the linear effect of summer aridity change; β_{HLI} is the slope on the linear effect of HLI index; b_i is the random site effect (assuming $b_i \sim N(0, \sigma_b^2)$), included as a random intercept; $s(.)$ is the smooth effect of elevation, implemented as a penalized spline (De Boor, 1978; Wood, 2017); ε_{ij} is the error term with a Gaussian distribution ($\varepsilon_{ij} \sim N(0, \sigma^2)$).

In summary, the model allows for estimation of slopes with respect to several ecological gradients, such as time since disturbance, aridity change, and HLI. It also enables a detailed examination of the (potentially nonlinear) effect of elevation, while accounting for random site variability and the ANOVA-like effects of pre- and post-disturbance management types. It is important to note that the additive structure of the model (1) for logarithmically transformed responses implies that, on the original scale, the model is multiplicative.

Additionally, assumed gaussianity on the log-scale implies a lognormal distribution (Crow & Shimizu, 1988) on the scale of the original recovery measurements. The unknown model parameters, including the nonparametric estimate of function as a "functional parameter," were estimated using an optimization of the penalized likelihood with penalty coefficients kept at the values previously estimated by the generalized cross-validation procedure (Wood et al., 2016).

3 | RESULTS

3.1 | Post-disturbance forest structure and composition

The 143 sites featured in the recovery analyses were sampled, on average, 19 ± 4 years after a large and severe disturbance, with minor differences among agents: 13 ± 6, 15 ± 8, and 19 ± 4 years for beetles, fire, and wind, respectively (descriptive values are given as site-level mean ± standard deviation without accounting for differences in sampling effort among sites). Post-disturbance density (i.e., including both regeneration and trees) following large and severe disturbances varied widely across European temperate forests and disturbance agents, with an overall mean of 6274 ± 4665 individuals/ha. Post-beetle density was on average greater than that after wind or fire, with 9240 ± 3124, 6275 ± 4703, and 3615 ± 3495 individuals/ha, respectively (but note that the number of sites was highly unbalanced among the agents) (Figure 2a; Figure S1a). A complete lack of regeneration or trees only occurred in 3.5% of the plots across 25 sites, on average 15 years after the disturbance and more commonly after fire events than wind (6.6% vs. 2.8% of plots, respectively). When incorporating tree height in the density index (i.e., weighted density), the relative rankings between disturbances changed: 3339 ± 2546 theoretical individuals (i.e., trees with DBH equal to 7 cm)/ha were present after wind, compared with 1482 ± 885 and 810 ± 1153 individuals/ha, respectively, after beetle and fire disturbances (Figure 2a; Figure S1a).

Post-disturbance raw and height-weighted densities showed different trends over time since disturbance for the different agents (Figure S2). For windthrow, raw density decreased as the time since disturbance increased, while the weighted density was relatively stable over time (cf. Fei et al., 2006). Weighted density correlated with time since disturbance only in the case of fire (Figure S2). When comparing post-disturbance weighted densities with pre-disturbance density values, European temperate forests showed adequate structural recovery potential (Figure 2b; Figure S1b). On average, 86.2% of the investigated sites exhibited structural recovery potential, but there were differences among disturbance agents; a larger proportion of the wind and beetle-disturbed sites met the recovery target compared with fire-disturbed sites (88.7%, 82.2%, and 33.6%, respectively).

A lower proportion of the sites exhibited compositional recovery potential, with an average of 52.3% (Figure 2b; Figure S1b). Beetle and wind-disturbed sites tended to show greater compositional recovery potential than fire-disturbed sites, at 84.4%, 52.5%, and 19.1%, respectively. Pre-disturbance stands were primarily composed of late-successional species, which were dominant at 66% of the sites, while the overall proportion of early-successional and pioneer species largely increased after disturbance (43.3% and 12.9%, respectively). The proportion of late-successional species decreased to 43.8% following disturbance. Compared with wind and beetle-disturbed areas, which were analogous to the overall patterns, post-fire stands were mainly comprised of early-successional (60.2%) and pioneer species (26.7%). Across all sites, beech (*Fagus sylvatica* L.) was the most common post-disturbance species, with an average density per site of 1487 ± 2879 individuals/ha, followed by spruce (*Picea abies* (L.) H. Karst) with 681 ± 1588 individuals/ha. Beech and spruce were also the most prevalent forest types among the investigated areas, as they were either the dominant or co-dominant species at 43 sites each. Beech-dominated sites tended to show greater compositional recovery potential compared with spruce-dominated sites, with an average of 82.5% and 54.1% of plots per site, respectively.

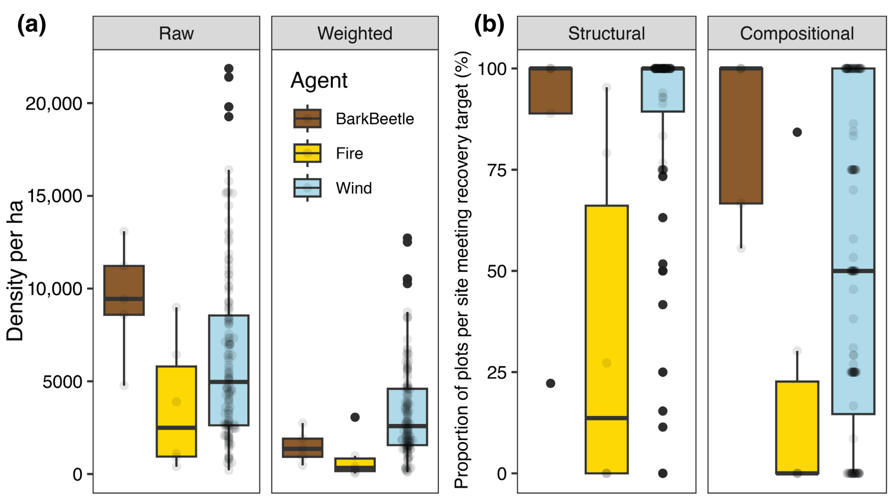

FIGURE 2 Site-level post-disturbance raw and weighted density distribution (a); share of plots per site structurally and compositionally recovering (b) across different disturbance agents (n sites = 5 beetle; 6 fire; 132 wind). Boxes bound the interquartile ranges (IQR), black lines show the median values, and whiskers extend to a maximum of 1.5 × IQR beyond the box. Small diamonds are site-level data points (transparent, or in black for outliers).

3.2 | Management and environmental drivers of post-windthrow recovery

The influence of forest management and environmental variables on post-windthrow weighted density varied (Tables 3 and 4; Table S4). For all species combined, post-windthrow salvage logging (109 sites, 632 plots) had a negative influence on post-windthrow weighted density (−0.55 ± 0.20) (model results are given as effect size ± standard error; note that the response variables, that is, weighted densities, were log-transformed), compared with no post-windthrow management (28 sites, 354 plots) and intensive management (i.e., logging followed by planting/tending; 5 sites, 143 plots). In other words, in salvaged sites we expect the median value of the overall post-windthrow weighted density to be 58% (with a confidence interval of 47%–70%) of that in unmanaged sites, holding other variables constant. The same result was found for the late-successional species model (−1.16 ± 0.33), while there was no significant effect for early-successional or pioneer species (Figure 3). Pre-disturbance management was not significant in any of the weighted density models.

The effect of elevation on post-windthrow weighted density was complex, but generally negative for all successional groups, with some differences in the weighted density patterns with increasing elevation (Figure 4; Table 4). The negative effect of elevation was more pronounced at high elevations (i.e., above 1000 m a.s.l., but note the larger confidence intervals above 1500 m a.s.l.), except for early-successional species, which showed a marked decrease at low elevation, followed by a relatively stable pattern above 500 m a.s.l. HLI was negatively associated with post-windthrow weighted densities, but was significant only for pioneer and early-successional species (−1.71 ± 0.50 and −1.18 ± 0.50, respectively). Pioneer species decreased with increasing time since disturbance and with greater aridity change (−0.097 ± 0.048 and −14.85 ± 6.28, respectively). Raw density models showed overall similar patterns to the weighted models (i.e., the same predictors were significant), with minor differences in effect sizes (Table S5).

4 | DISCUSSION

As anthropogenic climate change continues to alter disturbance regimes, there is growing concern regarding the resilience of forests and their ability to recover their functions and provide ecosystem services after large and severe disturbances (McDowell et al., 2020). In this study, we conducted field surveys and analyzed bioclimatic and topographic datasets to provide the first continental-scale quantitative analyses of European temperate forest recovery after large and severe disturbances. By assessing post-disturbance forest structure and composition and comparing them to pre-disturbance stand characteristics, we found evidence for the overall resilience of European temperate forests to such disturbances. These findings are consistent with several previous studies that have assessed forest recovery after a variety of disturbance severities using both remote

TABLE 3 Summary of parametric effects from the Generalized Additive Mixed Model analyses of post-windthrow weighted densities of different successional groups (log-transformed), predicted by environmental and management drivers.

Response variable	Overall w. density		Pioneer w. density		Early-successional w. density		Late-successional w. density	
Predictor	Estimate	Standard error	Estimate	Standard error	Estimate	Standard error	Estimate	Standard error
Intercept	6.76***	1.11	8.83***	2.30	5.49*	2.37	4.65*	2.19
Pre-dist. mgmt: managed versus none	0.74	0.86	−1.96	1.79	0.70	1.87	−0.98	1.71
Pre-dist. mgmt: light versus none	−1.35	1.17	−3.81	2.49	−1.17	2.55	−0.69	2.38
Post-dist. mgmt: only salvage log. versus none	−0.55**	0.20	−0.27	0.36	−0.27	0.35	−1.16***	0.33
Post-dist. mgmt: intensive versus none	−0.11	0.25	0.32	0.42	−0.037	0.40	−0.41	0.39
Years since disturbance	0.027	0.024	−0.097*	0.048	−0.045	0.049	0.089†	0.046
Aridity change	−2.41	3.05	−14.85*	6.28	3.64	6.49	2.26	5.98
Heat load index	−0.57†	0.31	−1.71***	0.50	−1.18*	0.50	−0.068	0.47

Note: Signif. codes: "***" 0, "***" .001, "**" .01, "*" .05, "†" .1 " " 1.

TABLE 4 Results of the Generalized Additive Mixed Model analyses of post-windthrow weighted densities of different successional groups (log-transformed), showing effective degrees of freedom (edf) as measures of effect complexity/nonlinearity, and significance (*p*-value) of smooth terms.

Response variable	Overall w. density		Pioneer w. density		Early-successional w. density		Late-successional w. density	
Predictor	edf	*p*-Value	edf	*p*-Value	edf	*p*-Value	edf	*p*-Value
Elevation	7.22	4.74e-05	4.98	2.14e-05	8.31	2.65e-05	4.90	0.000934
Site	90.70	<2e-16	106.96	<2e-16	106.80	<2e-16	108.32	<2e-16

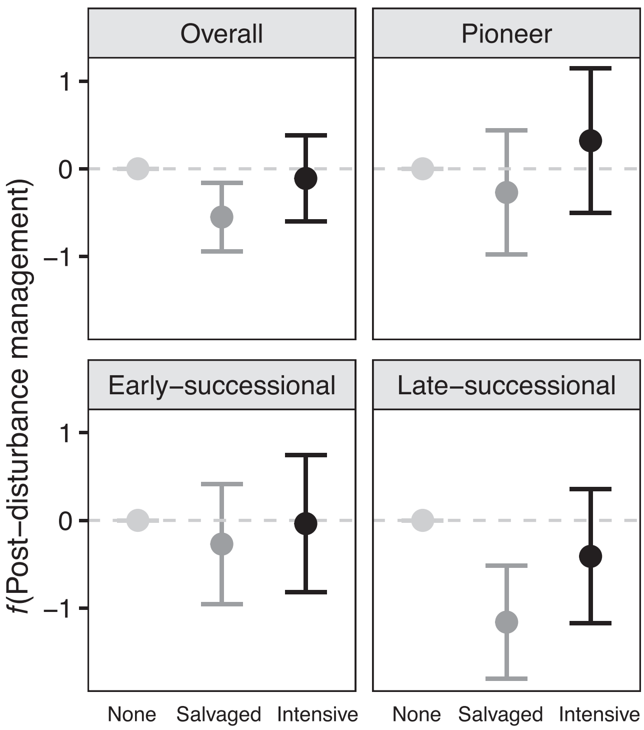

FIGURE 3 Effect of post-disturbance management on post-windthrow weighted density of different successional groups, based on results of Generalized Additive Mixed Model analyses (the "Unmanaged" category is the baseline). Note that "Salvaged" category refers to plots where only salvage logging was carried out. Error bars represent the 95% confidence intervals for the estimated parameters.

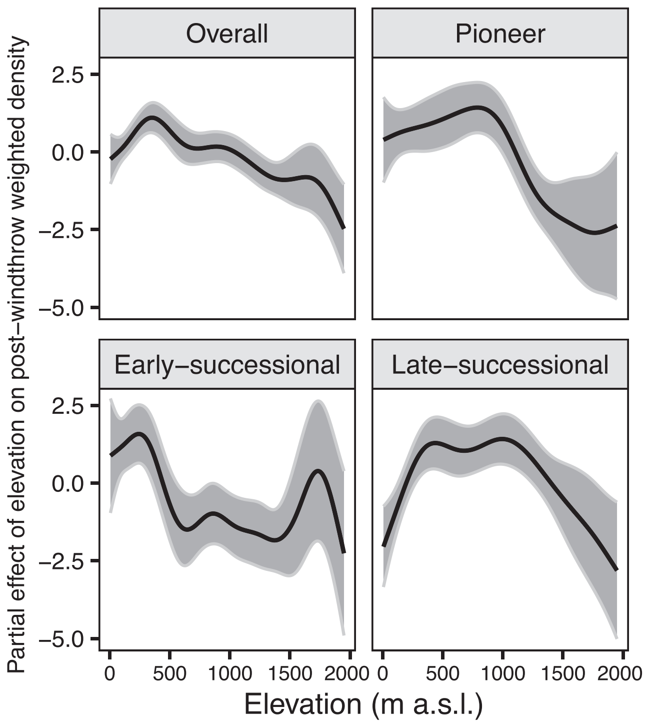

FIGURE 4 Effect of elevation on post-windthrow weighted density of different successional groups shown with partial dependence plots derived from the results of Generalized Additive Mixed Models. Gray bands represent the 95% confidence intervals for the regression lines.

sensing (Senf et al., 2019; Senf & Seidl, 2022) and ground-based data (Taeroe et al., 2019). However, our study also identified high-risk sites (≈14%) that would require additional tree establishment to achieve structural recovery (i.e., imminent failure, sensu Vickers et al., 2019). Furthermore, we observed considerable heterogeneity among sites and disturbance agents, with fire-disturbed sites generally exhibiting lower recovery potential compared with that after other disturbance agents. In contrast to wind disturbances, which typically leave advanced regeneration intact (Taeroe et al., 2019), and bark beetle outbreaks, in which both advanced regeneration and regeneration that establishes during protracted outbreaks play a significant role (Andrus et al., 2020; Macek et al., 2017), stand-replacing fires tend to leave very few living legacies in temperate forest ecosystems (Gill et al., 2017; Guz et al., 2021; Moser et al., 2010). Overall, we found that nearly 70% of the fire-disturbed areas had not structurally recovered at the time of observation. However, it is important to note that this does not necessarily indicate a change to a non-forested ecosystem, as new trees could still establish, and the recovery interval may still be shorter than the disturbance interval (i.e., not in a critical state, sensu Senf & Seidl, 2022). For instance, Scots pine (*Pinus sylvestris* L.) forests in the northern Czech Republic took about 140 years to recover to pre-fire conditions, while the average wildfire frequency in that region is once every 200 years (Adámek et al., 2016). It is important to also point out that none of the forest types that experienced fire in this study (forests dominated by either beech, black pine (*Pinus nigra* Arn.), Scots pine, or spruce) are known to recover from canopy (i.e., serotinous cones) or soil seed banks (Habrouk et al., 1999), such that regeneration after fire will largely depend on arrival of seeds from outside the disturbance area, prolonging the recovery process.

Throughout European temperate forests, the potential for structural recovery was more likely than compositional recovery, with approximately half of the areas showing compositional recovery potential. We observed that plots not meeting the compositional recovery objective displayed different species mixtures compared with the pre-disturbance stand, with a greater proportion of early-successional and pioneer species. This pattern is consistent with findings from studies examining a variety of sites and disturbance agents (Andrus et al., 2020; Bisbing et al., 2019; Moser et al., 2010; Rodman et al., 2022; Scherrer et al., 2021; Szwagrzyk et al., 2021; Vickers et al., 2019). However, these findings alone are not sufficient evidence of a persistent change in ecosystem composition in response to climate change (i.e., reassembly). Establishing such evidence would require a characterization of the historical range of variability and evidence of a significant departure from that range (Seidl & Turner, 2022). It should be noted that our assessment of compositional recovery potential only considered the maintenance of absolute dominance for the main pre-disturbance tree species, which is a less stringent criterion than the maintenance of the pre-disturbance relative proportion. This difference in assessment criteria may explain the differences in the proportion of compositional recovery found in other studies (Cerioni et al., 2022; Rodman et al., 2022; Vickers et al., 2019).

While rapid compositional recovery may be beneficial for timber production, the failure to recover pre-disturbance tree species composition is not necessarily undesirable. In the context of a changing climate, disturbances can create opportunities for the establishment of better-adapted species, especially in the case of monoculture forests whose composition has been altered in the past (Dietz et al., 2020; Scherrer et al., 2021; Thom et al., 2017). Furthermore, early-seral communities play an important role in biodiversity and the creation of wildlife habitat (Swanson et al., 2011). Early-seral patches may also prevent homogenization of the forested landscape, thus reducing susceptibility to future disturbances (Bače et al., 2023). As the time since disturbance increased in our study, pioneer species decreased and were replaced by later-successional species. Therefore, allowing natural succession after large and severe disturbances, rather than resorting to salvage logging and planting, may be a viable option for forest managers, even in intensively managed forest areas such as Europe (Kulakowski et al., 2017; Sommerfeld et al., 2021).

Some environmental factors influenced forest recovery after large-scale, severe windthrow events. Higher elevation negatively affected all types of regeneration, which is consistent with our expectations and findings from other studies (Macek et al., 2017; Szwagrzyk et al., 2021; cf. Kramer et al., 2014). This result has important implications in the context of global warming. Future warming may ease climate constraints and increase growing season length at high elevations (Pretzsch et al., 2020), potentially reversing the relationship between elevation and post-disturbance recovery. Such post-disturbance recovery patterns, in which higher elevation is positively related to seedling density and forests at low elevation are at risk of regime shift, have already been documented, particularly in the case of wildfires (Guz et al., 2021; Moser et al., 2010; Rodman et al., 2022; Stevens-Rumann & Morgan, 2019). Surprisingly, the HLI, an indicator of solar radiation derived from topographic variables and latitude, was negatively associated with post-windthrow densities of early-seral species, suggesting that cooler slopes tended to recover better than warmer slopes. In contrast to our findings, topographic variables were not a significant driver of juvenile densities following bark beetle disturbances in the Rocky Mountains (Andrus et al., 2020), while potential solar radiation was found to positively affect *Sorbus aucuparia* L., which we classified as an early-successional species, in mountain forests of Poland after wind and beetle disturbances (Szwagrzyk et al., 2021). We found that changes in post-disturbance aridity compared with the historical baseline had little effect on post-windthrow densities, except in the case of pioneer species, which were negatively affected by an increase in aridity compared with the historical baseline. This is not surprising given that pioneer species in European forests (e.g. *Betula*, *Populus*, and *Salix* species) are characterized as drought intolerant (Leuschner & Meier, 2018). In conifer forests in northwestern United States, post-disturbance drought and temperature had an important impact on post-fire regeneration densities, establishment, and growth (Davis et al., 2019; Guz et al., 2021; Hankin et al., 2019). A potential explanation for this difference may be that the role of post-disturbance drought likely differs across sites and disturbance agents, and is relevant in more arid locations and particularly after fire disturbances, where young seedlings established from seed have poorly developed root systems.

Our study provides valuable insights into the role of management in driving recovery after large-scale severe windthrows. We found that intensively managed areas, whether managed before or after the disturbance (i.e., salvage logging followed by planting or tending), did not consistently show better recovery than unmanaged areas. However, it is important to note that this could be a consequence of not having enough power in the statistical tests (i.e., type II error). It is worth mentioning that sites that were only salvaged and left to natural regeneration performed worse than those that were planted after logging or without any post-windthrow management. This negative effect was evident for shade-tolerant species, which was expected, as these species are typically planted, and their advanced regeneration could have been damaged by logging activities. Although salvage logging is often carried out for economic reasons, it is known to cause direct harm to regeneration and can thus negatively affect forest recovery (Bowd et al., 2021; Royo et al., 2016; Taeroe et al., 2019). Furthermore, the deadwood being removed could otherwise act as a regeneration substrate, especially for spruce, when sufficiently decayed (Bače et al., 2012; Priewasser et al., 2013; Tsvetanov et al., 2018), a microsite that protects seedlings from climate stress (Marangon et al., 2022), or as an obstacle for herbivores (Hagge et al., 2019; Kramer et al., 2014; Marangon et al., 2022). However, a meta-analysis by Leverkus et al. (2021) found that post-disturbance salvage logging does not generally hinder forest regeneration, and in some cases, the soil perturbation caused by logging can promote the regeneration of pioneer species by reducing competition with ground vegetation (Ilisson et al., 2007). In general, our results are consistent with a previous remote sensing-based study indicating that both managed and unmanaged forests in central Europe recover well after disturbances (Senf et al., 2019), although that study found lower rates of recovery in the case of unmanaged forests (i.e., lower engineering resilience).

This study synthesizes forest recovery after large and severe disturbances over the past five decades, which can be considered a baseline period when climate change impacts were comparatively low. Consequently, these findings provide a benchmark for assessing how future forest recovery will be influenced by altered disturbance regimes under a changing climate (Seidl et al., 2017; Seidl & Rammer, 2017). Although European temperate forests have demonstrated resilience to large-scale, high-severity disturbances and concurrent climate conditions during this period, there are still a number of research directions that warrant further attention. We assessed a wide range of disturbance sizes and severities (i.e., removing between 70% and 100% of canopy cover in patches ranging in size from 1 to 100s of hectares). However, even small differences in these parameters may have important implications, particularly with respect to severity, which has been found to be a more important driver of recovery than disturbance size (Senf & Seidl, 2022). Future work should explicitly account for differences in disturbance severity and size by combining field data on recovery with remote sensing of disturbance characteristics (e.g. patch size, shape, and severity). Moreover, we did not account for demographic processes such as future tree mortality and establishment. Previous research in subalpine forests of the Rocky Mountains has shown that initial post-disturbance regeneration is not always indicative of long-term successional trajectories, particularly after large and severe wildfires and compounded disturbances (Gill et al., 2017). Therefore, it is important to continue to monitor long-term recovery in plot networks such as those used in this study. Additionally, we did not quantify the role of biotic interactions in forest recovery due to a lack of consistent data, such as competition or facilitation when herbaceous vegetation and shrubs are present, which are expected to vary across a stress gradient (Käber et al., 2023), and ungulate browsing, which has strong negative effects on palatable tree species (Andrus et al., 2020; Cerioni et al., 2022; Vickers et al., 2019) and often leads to reduced species richness (Bernes et al., 2018; Konôpka, Šebeň, Pajtík, et al., 2021). We emphasize the need for continued monitoring of forest recovery following both past and future disturbances to improve our understanding of the complex process of forest recovery under climate change.

AUTHOR CONTRIBUTIONS

Matteo Cerioni: Conceptualization, data curation, formal analysis, investigation, methodology, visualization, and writing—original draft. **Marek Brabec:** Formal analysis, methodology, software, and writing—review & editing. **Thomas A. Nagel:** Conceptualization, funding acquisition, methodology, project administration, supervision, and writing—original draft. **Radek Bače:** Investigation, data curation, and writing—review & editing. **Endijs Bāders:** Investigation, data curation, and writing—review & editing. **Andrej Bončina:** Investigation, data curation, and writing—review & editing. **Josef Brůna:** Investigation, data curation, and writing—review & editing. **Ewa Chećko:** Investigation, data curation, and writing—review & editing. **Thomas Cordonnier:** Investigation, data curation, and writing—review & editing. **Johannes H. C. de Koning:** Investigation, data curation, methodology, and writing—review & editing. **Jurij Diaci:** Investigation, data curation, and writing—review & editing. **Dorota Dobrowolska:** Investigation, data curation, and writing—review & editing. **Alexander Dountchev:** Investigation, data curation, and writing—review & editing. **Jeroen Engelhart:** Investigation, data curation, and writing—review & editing. **Gal Fidej:** Investigation, data curation, and writing—review & editing. **Marc Fuhr:** Investigation, data curation, and writing—review & editing. **Matteo Garbarino:** Investigation, data curation, and writing—review & editing. **Āris Jansons:** Investigation, data curation, and writing—review & editing. **Srdjan Keren:** Investigation, data curation, and writing—review & editing. **Māra Kitenberga:** Investigation, data curation, and writing—review & editing. **Matija Klopčič:** Investigation, data curation, and writing—review & editing. **Bohdan Konôpka:** Investigation, data curation, and writing—review & editing. **Martin Kopecký:** Investigation, data curation, methodology, and writing—review & editing. **Kajar Köster:** Investigation, data curation, and writing—review & editing. **Stanislav Kucbel:** Investigation, data curation, and writing—review & editing. **Eric Lacombe:** Investigation, data curation, and writing—review & editing. **Lisa Laurent:** Investigation, data curation, and writing—review & editing. **Anja Leyman:** Investigation, data curation, and writing—review & editing. **Emanuele Lingua:** Investigation, data curation, and writing—review & editing. **Martin Macek:** Investigation, data curation, and writing—review & editing. **Zbigniew Maciejewski:** Investigation, data curation, and writing—review & editing. **Francesco Malandra:** Investigation, data curation, and writing—review & editing. **Raffaella Marzano:** Investigation, data curation, and writing—review & editing. **Marek Metslaid:** Investigation, data curation, and writing—review & editing. **Donato Morresi:** Investigation, data curation, and writing—review & editing. **Momchil Panayotov:** Investigation, data curation, and writing—review & editing. **Bogdan Pawlak:** Investigation, data curation, and writing—review & editing. **Ján Pittner:** Investigation, data curation, and writing—review & editing. **Vladimír Šebeň:** Investigation, data curation, and writing—review & editing. **Jarosław Socha:** Investigation, data curation, and writing—review & editing. **Miroslav Svoboda:** Investigation, data curation, and writing—review & editing. **Jerzy Szwagrzyk:** Investigation, data curation, and writing—review & editing. **Nickolay Tsvetanov:** Investigation, data curation, and writing—review & editing. **Carlo Urbinati:** Investigation, data curation, and writing—review & editing. **Patrick Vallet:** Investigation, data curation, methodology, and writing—review & editing. **Peter Van de Kerckhove:** Investigation, data curation, and writing—review & editing. **Kris Vandekerkhove:** Investigation, data curation, and writing—review & editing. **Jaroslav Vencurik:** Investigation, data curation, and writing—review & editing. **Alessandro Vitali:** Investigation, data curation, and writing—review & editing. **Floortje Vodde:** Investigation, data curation, and writing—review & editing. **Jan Wild:** Investigation, data curation, and writing—review & editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare they have no conflict of interest.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.ncjsxkt0z. The R code generated for the data analysis for the study is available from Github at https://github.com/MatteoCerioni93/Recovery_analyses.git.

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