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RESEARCH ARTICLE

The amount of undisturbed forest in proximity of severe disturbance patches enhances their recovery in temperate Europe

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Abstract

Context Forest recovery following disturbances is essential for maintaining ecosystem services, especially after large-scale events where regeneration is limited by seed availability. Understanding how environmental and biotic factors influence regeneration across spatial scales is fundamental for landscape-scale management, yet the importance and spatial extent of landscape-scale effects on local recovery remains uncertain.

Objectives We aimed to assess the relative influence of recovery drivers at plot, patch, and landscape scales on post-disturbance forest regeneration. Specifically, we investigated how local topography,

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disturbance characteristics, and the spatial arrangement of undisturbed forests affect tree regeneration after severe disturbances, namely windthrows, fires, and bark beetle outbreaks.

Methods Our study combines a comprehensive ground-based dataset of post-disturbance regeneration from temperate European forests with Landsat-derived maps of forest cover. We applied a distance-weighted regression approach to evaluate the effect of landscape (i.e., undisturbed forest in proximity of disturbance patches) on recovery, improving upon traditional buffer-based approaches.

Results We found that ¾ of the landscape influence on forest regeneration occurred within 112 m from plot centers, with undisturbed forests nearby positively enhancing regeneration, likely due to increased seed availability. In contrast, plot-level factors, namely disturbance severity and elevation, negatively impacted regeneration, suggesting that regeneration success can be hindered by severe disturbances reducing living biological legacies, as well as harsher local climatic conditions, associated with higher elevations.

Conclusions Our findings underline the importance of integrating landscape-scale management with targeted local interventions to promote post-disturbance forest recovery. Management strategies should consider spatially explicit planning to enhance seed source availability and mitigate severe disturbance impacts.

Keywords Post-disturbance regeneration · Ground-based inventories · Landsat-based disturbance map · Recovery drivers · Landscape effect · Distance-weighted regression

Introduction

Natural disturbances are a major driver of forest ecosystem dynamics (Turner 2010). Anthropogenic climate change is predicted to alter disturbance regimes (Seidl et al. 2017), particularly the size and severity of disturbances, threatening forests' ability to carry out their functions and provide related ecosystem services (Thom and Seidl 2016). The process of forest recovery after disturbances (i.e., restoring the essential structures and processes of a forest ecosystem) is therefore of importance for the continuous provision of ecosystem services over time (Stritih et al. 2023). Tree regeneration

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represents a prominent indicator of post-disturbance recovery, both in terms of structure and species composition, as it can shape the future development of the forest stand (Seidl and Turner 2022). We use the term regeneration referring to all tree seedlings and saplings that are not yet large enough to be classified as trees (i.e., in this study, individuals with a DBH < 7 cm). It can be further categorized into three processes: advanced regeneration (seedlings that germinated before the disturbance), post-disturbance regeneration (seedlings that germinated from seed after the disturbance), and vegetative regrowth (resprouts from trees following the disturbance). Regeneration success is mediated by both environmental and biotic drivers, acting at various spatial scales, from local to landscape, and on different developmental stages of regeneration (i.e., seed production and dispersal, germination, seedling survival and growth) (Dey et al. 2019). Furthermore, the agent, magnitude, and spatio-temporal characteristics of the disturbance directly determine the starting point of the recovery process, by affecting the type, quantity, and spatial distribution of biological legacies (i.e., all organisms and physical patterns carrying over after a disturbance) (Johnstone et al. 2016). These include living legacies, such as advanced regeneration, which can give an early boost to forest recovery, and surviving mature trees, which can act as a direct seed source and create favorable microclimates for the establishment and growth of regeneration (Jõgiste et al. 2017; Taeroe et al. 2019).

Forest recovery has been extensively studied using both retrospective methods, by the means of ground-based and remote sensing approaches, and prospective ones, including simulations with models of forest dynamics. Ground-based methods include plot-based inventories that assess structural and compositional aspects of regeneration (e.g., Cerioni et al. (2024); Rodman et al. (2022)), as well as dendrochronological techniques to assess growth recovery (Lloret et al. 2011). Remote sensing approaches have enabled large-scale assessments of recovery, utilizing temporal trends in spectral indices (e.g., White et al. (2022)) and structural metrics such as canopy height or cover derived from lidar and satellite imagery (e.g., Senf et al. (2019); Stritih et al. (2023)). Forest cover metrics have also been derived using advanced techniques such as machine learning and spectral unmixing ((Mandl et al. 2024); Senf et al. (2020)). Simulation models of forest dynamics have been employed to project recovery trajectories under various scenarios, assessing metrics such as regeneration density, carbon stocks, structural complexity, and species composition (e.g., Hansen et al. (2018); Hlásny et al. (2021).

Poorly developed forest regeneration processes (i.e., due to few legacy trees in the disturbed patch, absence of trees capable of vegetative regrowth, and scarce advanced and post-disturbance regeneration) can impair recovery (Taeroe et al. 2019). Low seed availability, resulting from both a lack of seed producing legacy trees and contiguous forest, is a major factor impairing regeneration, often in connection with the occurrence of extreme post-disturbance climatic conditions (Donato et al. 2016; Hansen et al. 2018). However, there is evidence that temperate European forests show sufficient recovery even after large and severe disturbances (Senf and Seidl 2022; Cerioni et al. 2024; Mandl et al. 2024). Studies have shown that post-disturbance recovery is strongly influenced by a combination of local environmental and biotic factors, as well as the characteristics of the forest stand prior to disturbance (Diaci et al. 2017;Taeroe et al. 2019; Szwagrzyk et al. 2021). A continental-scale synthesis showed that elevation and post-disturbance salvage logging were the main drivers negatively affecting regeneration after large and severe windthrows (Cerioni et al. 2024). Few studies directly highlighted low seed availability as a major factor affecting post-disturbance regeneration, in particular related to dispersal limitation of species with heavy seeds (Lässig et al. 1995; Rozman et al. 2015; Szwagrzyk et al. 2021). How seed tree availability at a disturbance site and within the close neighborhood affects recovery is yet to be fully resolved (but see Mantero et al. (2023); Mejstřík et al. (2024).

Recovery studies assessing seed availability have used proxies at both the local and patch scale, such as disturbance severity or basal area of surviving trees, to account for seed sources from within a disturbed patch (e.g., Szwagrzyk et al. (2021)), or distance to the nearest forest edge or patch size to account for seed dispersal from the surrounding undisturbed forest (e.g., Donato et al. (2016); Hansen et al. (2018); Rozman et al. (2015). However, both of these metrics rely on the assumption that a precise forest edge can be identified, separating the disturbed patch

from intact forest, which is, in practice, unrealistic with natural disturbances, where a gradual transition between patch and undisturbed forest is more common (Franklin et al. 2021). Furthermore, the potential seed source availability from the undisturbed forest varies spatially across the patch, due to differences in patch shape and maximum seed dispersal, which are not accounted for by patch size. Moreover, ground-based distance to forest edge only accounts for the minimum distance to the undisturbed forest and not for the overall seed potential, to which trees farther from the forest edge could still contribute. A spatially-explicit measure of landscape composition in terms of undisturbed forest in proximity of a disturbed patch can therefore provide a more robust assessment of potential seed availability.

The importance of landscape composition and configuration for regeneration is often neglected (but see Arroyo-Rodríguez et al. (2023)), though landscape effects are considered major drivers of various forest ecosystem processes, including forest degradation and biodiversity (Seidl et al. (2016); Senf et al. (2017; Bourgoin et al. (2021); López-Baucells et al. (2022)). When landscape effects are assessed, they are usually investigated within arbitrary distance thresholds, often in multiple overlapping buffers. However, a primary limitation of this approach is the high degree of spatial autocorrelation, leading to the estimation of similar effect sizes across buffers (Miguet et al. 2016). Furthermore, assuming that landscape elements within a buffer have an equal impact on the response variable, while landscape elements outside have none, is ecologically unrealistic, as we expect the impact of landscape to decrease continuously with distance from the focal site, rather than abruptly dropping to zero at the buffer's edge (Aue et al. 2012; Chandler and Hepinstall-Cymerman 2016; Miguet et al. 2017). This pattern also holds true for potential seed availability, which tends to exponentially decrease at increasing distances from the seed source (e.g., Applestein et al. (2022)).

Here we leveraged an already established ground-based continental-scale dataset of forest regeneration after large and severe disturbances across temperate European forests (Cerioni et al. 2024), together with Landsat-derived map products (Senf and Seidl 2021), to assess drivers of post-disturbance recovery. By combining the complementary strengths of ground inventories and remote sensing approaches, we investigated the relative impact of environmental and disturbance-related drivers at local, patch, and landscape scale on tree regeneration. In order to properly assess the spatial extent and influence of the landscape effect, in terms of seed availability from undisturbed forest, we adopted a novel distance-weighted regression approach, which addresses the limitations of traditional buffer-based techniques. Thus, we were able to answer the following research questions: i) How strongly does undisturbed forest in the landscape impact forest recovery at the local scale, and how far does its effect extend? ii) What are the main drivers of post-disturbance forest recovery, and iii) does the landscape effect overcome drivers at local and patch scale?

Material and methods

Variable description and computation

Ground-based response variable

A ground-based dataset of forest recovery following severe disturbances was compiled from studies across temperate European forests, including regeneration density, size, and species composition (Cerioni et al. 2024). We applied the disturbance definition from ground-based inventories by Cerioni et al. (2024), who classified events with at least 70 % canopy cover loss over contiguous patches larger than 1 ha as severe disturbances. Accordingly, our analysis includes windthrows, fires, and spruce bark beetle outbreaks, which are the predominant natural disturbance agents in European forests (Sommerfeld et al. 2018; Patacca et al. 2023). Only observations that intersect with our multi-decadal (i.e., 1986–2020) remote sensing products, further explained in the following paragraph, were retained for analysis, ensuring consistency between ground-based inventories and remote sensing-derived variables. This resulted in 719 plots of variable size (typically 10×10 m, but ranging from 16 to 5000 m^2) arranged in 41 patches, with one inventory per patch carried out between 8 to 27 years post-disturbance (Fig. 1a-b; Table S1). In order to account for the variability in environmental conditions between areas across Europe, we grouped them into four geographical clusters (i.e., Hemiboreal, Central European, Alpine, and sub-Mediterranean region)

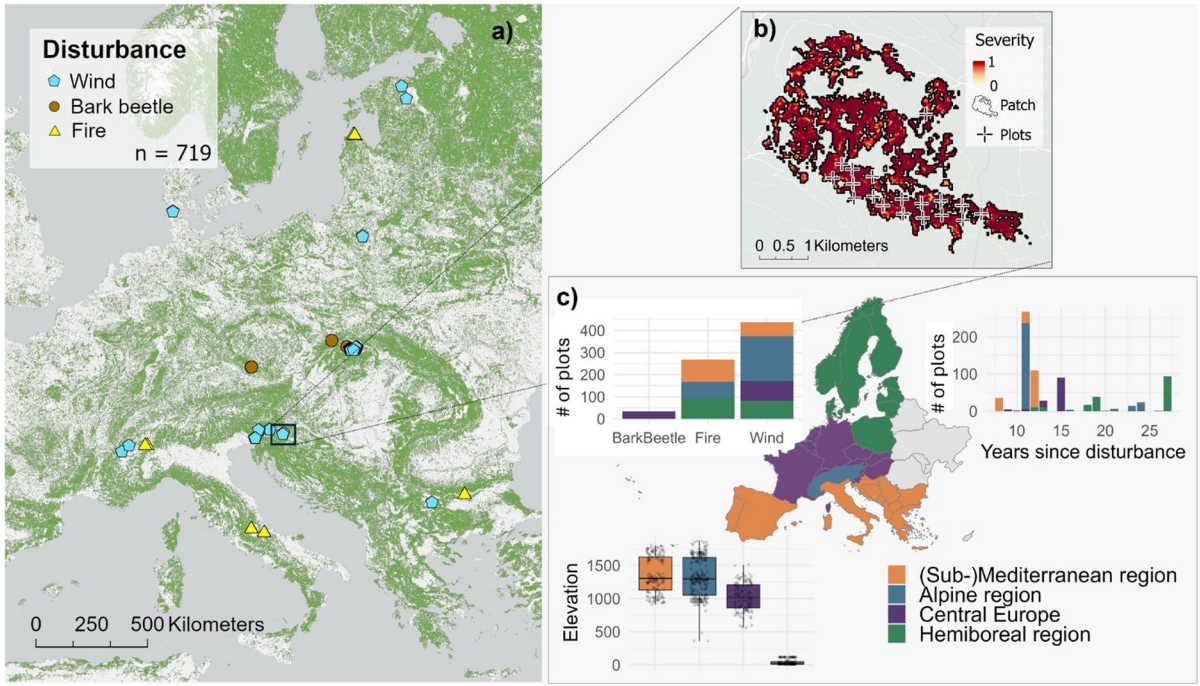


Fig. 1 **a** Map of plot locations within the study site, indicating the respective disturbance agents. **b** The disturbance patch in the top right highlights disturbance severity and provides an example of how plots (i.e. focal sites) are distributed within a patch. **c** The bar plot, the histogram and the scatter plot display the distribution of disturbance agents, years since disturbance, and elevation for each geocluster, corresponding to the map inset in the center

(Fig. 1c). Furthermore, we used a height-weighted regeneration density index, normalized per hectare (hereafter *weighted regeneration density*, or WRD), to standardize regeneration densities across areas with varying time since disturbance, following the methodology of Cerioni et al. (2024). Since WRD exhibited a skewed distribution of regeneration density data, we applied a square-root transformation to stabilize variance and improve the normality of model residuals. By combining regeneration height and density, this index provides a more accurate assessment of forest recovery and future stand development than density alone (Harris et al. 2022).

Remote sensing-derived predictors

We utilized a remote sensing-based pan-European forest disturbance map from Senf and Seidl (2021) which employs the LandTrendr algorithm (Kennedy et al. 2010) to analyze annual Landsat time series for pixel-wise detection of forest disturbances as a foundation for our analysis. Based on spectral change segmentation, each pixel was classified as no forest, forest, or disturbed forest, in case that at least one disturbance event during the study period was captured. To derive spatially coherent disturbance units, we defined disturbance patches as contiguous groups of disturbed pixels (using an 8-neighbour connectivity rule) that shared the same year of disturbance. The year of disturbance onset was assigned based on expert knowledge, as in Cerioni et al. (2024). In the following, we introduce the predictor variables that characterize post-disturbance recovery across three hierarchical levels: (1) plot-scale predictors describing local site conditions, (2) patch-scale predictors summarizing the disturbance characteristics of the surrounding patch, and (3) landscape-scale predictors quantifying the spatial context and seed source availability in the surrounding forest matrix. Table 1 provides a detailed overview of the predictors, their summary statistics, the expected effects and the scale on which the predictors were considered.

We characterized *topography* using plot-level elevation, which was derived from the Forest and

Table 1 Overview of the predictors included in the main analysis, their median and standard deviation/levels, expected effects and the scale level

Predictor	Median; standard deviation / levels	Hypothesized influence on WRD		Scale level	References
		Sign	Hypothesis		
Disturbance severity (plot)	0.90; 0.17	-	Plot-scale disturbance severity affects ecosystem disruption, with higher severity causing greater structural and microclimatic changes by removing all biomass and fully opening the canopy	Plot	Mandl et al. (2024)
Elevation	1200; 582 m a.s.l	-	Higher elevation reduces temperature, shortens the growing season, and limits recovery, while lower elevations show less impact	Plot	Cerioni et al. (2024); Szwagrzyk et al. (2021)
Disturbance agent	Two levels: Wind/Bark beetle (baseline), Fire	-	Wind and beetle disturbances preserve parts of vegetation and soil, aiding higher recovery densities, while fires remove the understory and degrade soil, slowing recovery	Patch	Frelich (2002); Kern et al. 2019
Disturbance severity (patch)	0.84; 0.16	-	Lower severity within a patch supports better recovery, even within generally high-severity plots, explaining spatial heterogeneity in recovery within the patch	Patch	Mandl et al. (2024)
Edge density	0.023; 0.015	±	Higher edge density boosts seed dispersal and biodiversity but also increases exposure to wind and invasive species, affecting resilience	Patch	García-Romero et al. (2019)
Years since disturbance	13: 6	+	Regeneration density increases with time since disturbance, as pioneers colonize first, followed by shade-tolerant species, aiding recovery	Patch	Fei et al. (2006)
Undisturbed forest	Raster: 0 (absence), 1 (presence)	+	Proximity to undisturbed forest facilitates regeneration by providing stable seed sources	Landscape	Applestein et al. (2022)

Buildings removed Copernicus DEM (FABDEM; 30 m; Hawker et al. (2022)). *Disturbance severity* at the plot-level was quantified as the magnitude of spectral change in the 30 × 30 m pixel overlapping the plot center, derived from the disturbance map of Senf and Seidl (2021). At the patch-level, *severity* was summarized as the median across all pixels within a disturbance patch, providing a broader

representation of the overall disturbance impact. *Edge density*, representing the amount of interface between disturbed and undisturbed areas, was calculated by dividing the total length of edges by the disturbance patch area (McGarigal and Marks 1995) using the R package *landscapemetrics (*Hesselbarth et al. 2019*)*. Since the metric is standardized by area, it enables comparisons across patches of different sizes. All continuous plot- and patch-scale predictors were z-transformed (i.e., standardized to a mean of zero and standard deviation of one) prior to model fitting, except for the categorical variable disturbance agent. This transformation ensures comparability of effect sizes and supports model convergence by reducing differences in predictor scales.

Moving beyond local conditions, we defined the landscape predictor *undisturbed forest* as all the forested areas where no disturbance happened since 1986, based on the European disturbance map (Senf and Seidl 2021). We expected only undisturbed forests to influence recovery, via increased seed availability, and made the assumption that such forests, undisturbed for the length of the Landsat-derived map (i.e., 1986–2020), were already old enough to produce seeds. To assess how our spatially-explicit landscape predictor compares to conventionally calculated metrics in capturing the variability in WRD, we further computed the distance to the nearest forest edge, a commonly used proxy for seed availability (e.g., Donato et al. (2016); Hansen et al. (2018)), as the Euclidean distance from each plot center to the centroid of the nearest undisturbed forest pixel, with the expectation that the spatially-explicit landscape predictor would better capture the variability in WRD. The final set of predictors did not include any management-related variables. Managed areas after the disturbance were associated with higher values of plot-scale disturbance severity (Fig. S1), which thus, serves as a proxy of the combined effect of disturbance severity and post-disturbance management in our study, with higher severity indicating higher removal of biological legacies through post-disturbance management (i.e., removal of deadwood, residual trees and in some instances likely also advanced regeneration due to the use of heavy machinery).

Modeling distance-based effects on post-disturbance forest recovery

To investigate the landscape-scale effect on post-disturbance recovery, we implemented a distance-weighted optimization model approach using the R package (i.e. *scalescape* (Lowe et al. 2022). In this framework, the landscape predictor (i.e., undisturbed forest) is weighted according to its distance from the plot center, with areas closer to the plot exerting a stronger influence that gradually diminishes for more distant areas, following a Gaussian decay function. Compared to traditional buffer-based methods, which assume equal importance for all areas within a fixed radius and disregard areas beyond it, the distance-weighted approach provides a more ecologically realistic representation of spatial processes (Fig. S2).

We initially fitted a null model that only included plot- and patch-scale predictors, but not the landscape predictor, in order to establish a baseline for assessing the effect of undisturbed forest on regeneration. The null model was formulated as a linear mixed-effects model with random effects for patches nested within geographical clusters to account for the spatial autocorrelation of the data, as follows:

$$\begin{aligned} sqrt\left(WRD_{ijk}\right) = {} & \beta 0 + \beta 1 \cdot plot.severity_{ijk} \\ & + \beta 2 \cdot patch.severity_{jk} \\ & + \beta 3 \cdot elevation_{ijk} \\ & + \beta 4 \cdot years.since.disturbance_{jk} \\ & + \beta 5 \cdot edge.density_{jk} \\ & + \beta 6 \cdot agent_{jk} + u_k + v_{jk} + \int_{ijk} \end{aligned}$$

where WRD_{ijk} is the weighted regeneration density for plot i within patch j within cluster k, β_0 is the overall intercept, β_1, β_2,... β_6 are the fixed effect coefficients for the z-transformed predictors listed in Table 1. The random effects are modeled as: $u_k \sim N(0,\sigma^2_u)$ as the random intercept for each geographical cluster k, $v_{jk} \sim N(0,\sigma^2_v)$ as the random intercept for each patch j within cluster k, and $\epsilon_{ijk} \sim N(0,\sigma^2_\epsilon)$ as the residual error for each observation, i.e., the variability in the response variable that cannot be explained by the predictors included in the model.

The full model extended the null model by including the distance-weighted landscape predictor (i.e.,

undisturbed forest). To estimate the optimal spatial extent of the landscape predictor, we iteratively tested different range parameter values, representing the spatial scale at which the influence of undisturbed forest tapers off. For each value, the full model was refitted, and its log-likelihood was calculated. The range parameter that maximized the log-likelihood was selected as the optimal value, indicating the distance threshold beyond which the contribution of the landscape predictor becomes marginal. When using a Gaussian decay function to weight the landscape predictor, this range corresponds to one standard deviation of the Gaussian kernel. As a result, approximately 75.8 % of the total weight is accumulated within this distance, reflecting a theoretical property of the kernel rather than an empirical estimate derived from the data.

To test the significance of the landscape predictor, we applied a parametric bootstrapping likelihood ratio test, following the recommendations by Lowe et al. (2022). This approach accounts for the co-dependence between the regression coefficient and the distance parameter, which can bias standard likelihood ratio tests. We simulated 3,000 datasets under the null hypothesis of no landscape effect, refitted the null and full model for each, and calculated their log likelihood ratio (LLR). The proportion of simulated LLRs greater than or equal to the observed LLR, derived from the original dataset, provided the robust p-value, quantifying the statistical significance of the landscape predictor's effect on WRD. This approach allowed us to assess the role of undisturbed forest as a scale-dependent driver of post-disturbance recovery, accounting for the hierarchical structure of the data and the spatially-explicit influence of landscape. We further tested the goodness of commonly used proxies of seed availability (i.e., distance to the nearest forest edge, and patch size), by separately adding such proxies to the null model and comparing its performance (i.e., marginal and conditional R^2 as well as the Akaike Information Criterion) to the full model. All statistical analyses were conducted in R (version 4.4.3; R Core Team (2024)), along with the scalescape and lme4 packages (Bates et al. 2015; Lowe et al. 2022).

Results

Environmental and disturbance-related drivers had varying impacts on regeneration across the different spatial scales. However, plot- and patch-scale predictors showed similar results in both the null and the full model (i.e., the model including the variable *undisturbed forest* as landscape-scale predictor) (Fig. 2). At the plot-scale, we found a clear negative effect of both elevation and disturbance severity on regeneration (-21.42 ± 3.03 and -1.53 ± 0.63, respectively; all model results are given for z-transformed predictors as effect size ± st. error for the full model, except when specified differently), indicating that more severe disturbances and increasing elevation may hamper the recovery process. Conversely, the impact of patch-scale predictors on regeneration remained uncertain. We found a positive effect of

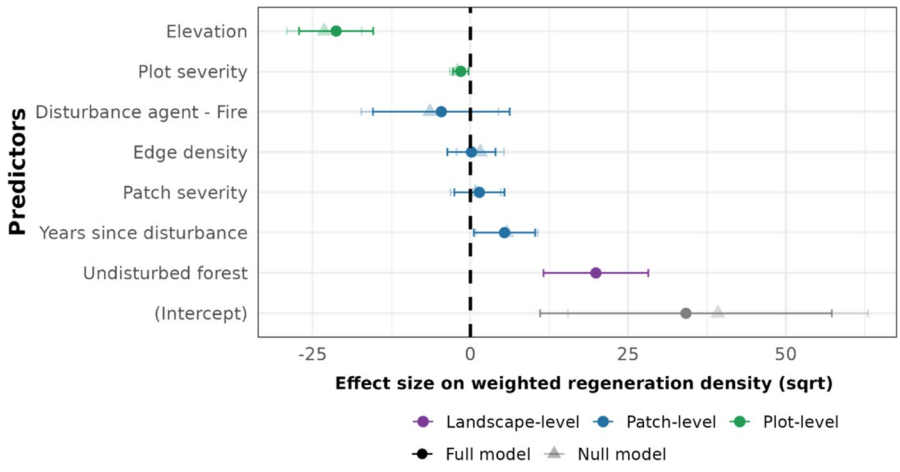


Fig. 2 Effect of recovery drivers at various spatial scales on weighted regeneration density, for both the full and null models. All plot- and patch-scale predictors, except Disturbance agent, are z-transformed. Error bars represent the 95 % confidence intervals for the estimated parameters

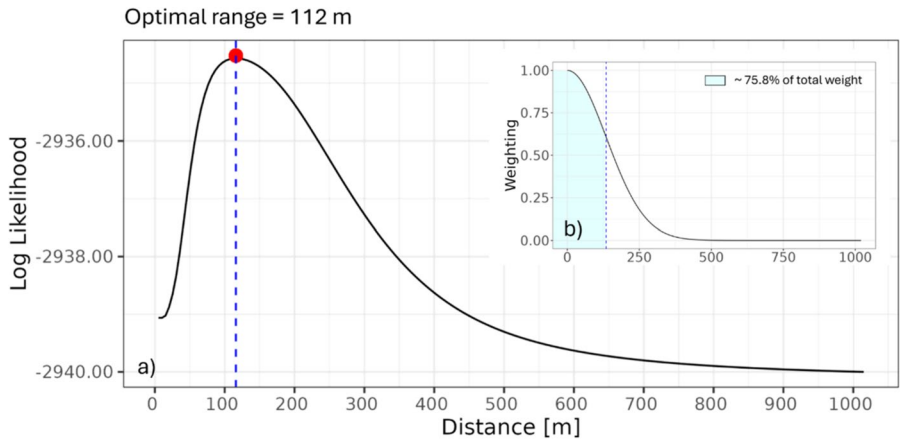


Fig. 3 Estimation of the distance within which our landscape predictor (i.e., undisturbed forests) effectively influenced the response variable weighted regeneration density. Panel a) shows the log-likelihood profile across tested distances, with the optimal range (red circle) identified through parameter optimization. Panel b) illustrates the corresponding Gaussian decay weighting curve, indicating that ~ 75.8 % of the total weight is accumulated within this distance

time since disturbance (5.40 ± 2.49), suggesting that, as time progressed, the weighted regeneration density tended to increase. Other patch-scale drivers (i.e., disturbance agent, patch severity, and edge density) were accompanied by substantial uncertainty, indicating high variability in their impact.

At the landscape-scale, we found that undisturbed forest had the largest positive effect among all tested variables (19.88 ± 4.23) (Fig. 2), as weighted regeneration density increased with increasing amounts of undisturbed forest in the close surroundings. Notably, our distance-weighting approach pinpointed 112 m from the plot centres as the maximum effective distance for the influence of undisturbed forest (Fig. 3a). The optimal range was determined by a sharp peak in the log-likelihood profile, indicating the best model fit. This range corresponds, when using a Gaussian decay function to weight the landscape predictor, to the distance at which ¾ of the effect of undisturbed forest on weighted regeneration density occurred (Fig. 3b). When assessing the effect of more commonly used proxies of seed availability on regeneration, instead of the landscape predictor, we found that distance to the nearest forest edge negatively affected weighted regeneration density (-2.2329 ± 0.722), while the effect of patch size was largely uncertain (3.3773 ± 3.833). In both cases the effect of plot- and patch-scale predictors on regeneration were in line with both the full and original null models (Table S2).

Table 2 Metrics of model fit for different null models and full model (values between parentheses are from bootstrapped model)

	Conditional R^2	Marginal R^2	AIC
Null model	0.862	0.533	5897
Full model	0.853 (0.892)	0.521 (0.543)	5880 (5689)
Null (+ patch size)	0.854	0.541	5894
Null (+ distance to nearest forest edge)	0.832	0.517	5888

We used the Akaike Information Criterion (AIC) to assess model fit and found that the full model provided a better fit to the data compared to the null model, thus supporting the inclusion of the landscape predictor (Table 2). This was further confirmed by the parametric bootstrap likelihood ratio test, which indicated that the landscape predictor significantly improved model performance ($p = 0.034$). However, both models performed similarly, in terms of explained variance by the fixed effects alone, or by combined fixed and random effects (i.e., marginal and conditional R^2, respectively). When compared with null models including commonly used proxies of seed availability, the full model proved to be superior in terms of quality, although on a similar level in terms of explained variance (Table 2).

Discussion

Our study provides significant evidence that the amount of undisturbed forest in close proximity of disturbance patches significantly enhances recovery after large and severe disturbances in temperate European forests. By combining ground-based regeneration data with a remote-sensing derived disturbance map, we show that undisturbed forests mostly influence post-disturbance recovery within a radius of ≈ 100 m from the plot centres. Some local drivers, namely plot-scale disturbance severity and elevation significantly hinder regeneration processes, while patch-scale drivers show more mixed and uncertain effects, underscoring the importance of scale-sensitive approaches in assessing forest recovery. To our knowledge, no previous study has assessed forest recovery at the continental scale by combining ground-based and remote sensing data. Furthermore, landscape-scale effects, which are often neglected or generally assessed using buffer-based methods, were analysed with a more ecologically realistic distance-weighting approach. Such an approach advances beyond traditional proxies for seed availability, such as patch size or distance to the nearest forest edge, while mitigating spatial autocorrelation and reducing pseudoreplication compared with buffer-based methods, thus ensuring more robust statistical inference (Dormann et al. 2007; Holland et al. 2004). By integrating distance-weighting within a multi-scale modelling framework, our method enables the simultaneous assessment of recovery drivers at different spatial scales, distinguishing between plot-, patch-, and landscape-scale effects (Dey et al. 2019; Moll et al. 2020).

Effects of plot-, patch-, and landscape-scale drivers of post-disturbance recovery

A key finding from our study is that the landscape effect operates in parallel with plot- and patch-scale drivers rather than overriding them, as the effects of the latter were not substantially altered when accounting for the effect of undisturbed forest in the landscape. Local factors such as elevation and plot-scale disturbance severity emerged as negative drivers of weighted regeneration density. This finding is consistent with previous studies highlighting constraints imposed by environmental gradients (Szwagrzyk et al. 2021). Higher altitudes may impose harsher climatic conditions, shorter growing seasons and lower temperatures (Lamprecht et al. 2018; Pepin et al. 2022), limiting recovery success. For instance, a network of monitoring plots in the High Tatra Mountains (Slovakia) showed that post-disturbance forest regeneration at higher altitudes had fewer and smaller trees, as well as lower species diversity, compared to lower-altitude locations (Konôpka et al. 2019). Similarly, high-severity disturbances, which were often connected with subsequent salvage logging, result in soil degradation and removal of biological legacies, including seed sources and microsites that facilitate seedling establishment (Johnstone et al. 2016; Taeroe et al. 2019; Zehetgruber et al. 2017). Such a pattern was not evident for patch-scale severity, possibly because we initially selected only relatively high-severity disturbance patches, therefore having on average a very low amount of surviving mature trees, which could positively affect regeneration. Furthermore, we did not find any significant difference in weighted regeneration density after fire compared to other disturbances, i.e., windthrow and beetle outbreak. Wind and beetle disturbances tend to leave living biological legacies in the understory, such as advanced regeneration, which can provide a kickstart to the recovery process, in contrast with stand-replacing fires (Frelich 2002). Potential explanations for our result might be related to the low amount of replication for fire-disturbed patches or to the negative effects of compound salvage logging on advanced regeneration, which could have partially hidden the differences between disturbance agents. Years since disturbance proved to be the only significant patch-scale driver, with a positive influence on weighted regeneration density. Although such a pattern may be expected for simple density, as more regeneration establishes over the initial years since disturbance, this was not true for post-windthrow weighted density alone (Cerioni et al. 2024), as weighting individual post-windthrow regeneration by height removed the trend of time since disturbance, contrary to post-fire regeneration. The inclusion of fire disturbances to the statistical analyses might, therefore, represent a partial explanation for our different result.

The positive impact of undisturbed forest in proximity of disturbance patches on regeneration highlights their crucial role in supporting recovery processes even in areas far from the forest edge, likely through mechanisms of seed dispersal and the

provision of habitat for seed dispersers (e.g., birds) (Molina et al. 2023). Our results suggest that patches with a minimum radius larger than 112 m, which represented the distance at which undisturbed forest in proximity to the patch had already exerted three quarters of its effect, could experience difficulties in regenerating. This optimal distance is consistent with the seed dispersal ability of common species in European temperate forests (i.e., *Picea abies* (L.) H. Karst., *Fagus sylvatica* L., *Pinus sylvestris* L., *Abies alba* Mill.) (Amm et al. 2012; Kramer et al. 2006; Wang and Hattemer 2001). At the same time, the fact that a quarter of the effect originates from beyond 112 m acknowledges the importance of fat tails in tree seed rain distribution, in which most seeds fall close to the parent tree, but a smaller proportion can disperse farther due to factors such as strong winds or animal movement (Clark et al. 1999). We emphasize that our spatially-explicit landscape variable proved to be a superior proxy for seed availability compared to the more commonly used patch size and distance to the nearest forest edge. While the strong negative effect of distance to the nearest forest edge was expected, as disturbed areas are further from potential seed sources, patch size did not exhibit a clear effect on regeneration. This may be due to variations in patch shape and irregularities in the forest edge, which are only captured by the spatially-explicit *undisturbed forest* variable. Contrary to our findings, patch size was an important driver of post-disturbance reorganization in Central European forests, where regeneration structure and species composition diverged from that of undisturbed areas, with increasing size of disturbance patches, likely due to more climate extremes in larger patches that negatively affected regeneration survival (Seidl et al. 2024). However, the disturbance patches analyzed by Seidl et al. (2024) were generally smaller (mostly under 1 ha) than those in our study. This difference suggests that, beyond a certain threshold in patch size, seed availability, as reflected in our landscape variable, starts playing a stronger positive role on regeneration.

Management implications

Our results offer valuable insights into the forest recovery process, which can inform forest managers in addressing disturbance impacts, and emphasize the importance of spatially optimized strategies. Managers should carefully evaluate the convenience of interventions in disturbance patches, balancing both ecological and economic benefits and costs. Within a patch, regeneration next to the forest edge could take advantage of the more favourable microclimate compared to the rest of the patch (Baker et al. 2014). In areas further from the edge we showed that recovery could effectively benefit from seed dispersal until an average distance of approximately 100 m, although this is likely dependent on the dominant forest species in the surrounding forest. Post-disturbance management should, therefore, account for the spatial configuration of undisturbed forest in proximity to a disturbance patch and, possibly, postpone planned harvesting in the neighboring forest until sufficient regeneration is established. Costly measures such as planting could be prioritized in severely disturbed and high-elevation areas, especially when they are far from the forest edge. When such plantings are carried out, incorporating structurally complex and species-rich regeneration can reduce the susceptibility of the future forest stands to disturbances.

Further management recommendations reflect a balanced consideration of relevant research in disturbance ecology and forest management. Since salvage logging can act as a compound disturbance, leading to a higher severity of damage and potentially harming advanced regeneration (Taeroe et al. 2019), we recommend limiting its application to areas that are more vulnerable to potential post-disturbance beetle outbreaks and where activities can be conducted with marginal damage to advanced regeneration (i.e., spatially optimized salvaging sensu Augustynczik et al. (2021)). It must also be considered that undisturbed forest stands at the edge of disturbed patches may be more vulnerable to further disturbances, such as storms or pest outbreaks (Kautz et al. 2013; Ruck et al. 2012; Zeng et al. 2009). Forest managers should aim to minimize this risk, by retaining healthy trees along exposed edges, and preserve resilient forests at the landscape scale, possibly by increasing forest structural and species diversity (Barrere et al. 2024). Overall, we highlight the need for management strategies that integrate both landscape conservation and localized interventions to enhance post-disturbance recovery. In fact, forest management is not limited to the extremes of intensive commercial exploitation and complete protection. A range of

management intensities and silvicultural approaches can be applied, tailored to local ecological conditions and human needs. For instance, varying the intensity of wood removal (or leaving deadwood in situ) can positively affect the diversity of forest regeneration, contributing to the resilience of future forest stands (Šebeň et al. 2024).

Limitations and prospects for future research

Our study emphasizes the importance of investigating scale-specific drivers of post-disturbance forest recovery and shows that combining ground-based and remote sensing datasets represents a powerful way to achieve this. However, one major challenge in such an approach is the discrepancy in spatial resolution between field plots (typically 10 × 10 m in our dataset) and remote sensing products (e.g., Landsat-based disturbance maps with 30 × 30 m pixels), which often misaligns with the scale at which ecological processes operate (Senf 2022). This spatial mismatch can complicate the linkage between field-based observations and remote sensing-derived metrics (e.g., disturbance severity). Furthermore, while our study draws upon a large, ground-based dataset spanning multiple disturbance areas across Europe, which enhances the generalizability of our findings, our dataset remains subject to potential biases due to the limited representation of some disturbance types (e.g., fire) and geographical regions (e.g., German-speaking countries in central Europe, Balkan countries). Lastly, seed dispersal distribution varies across different modes of dispersal and individual species over their life stages, whereas our study assessed the effect of undisturbed forest regardless of the dominant species, nor explicitly accounting for the age of undisturbed stands. A key reason for this generalization is the lack of a harmonized, Europe-wide dataset on tree species composition at the spatial resolution of our analysis, which prevented a consistent, species-level application of dispersal functions across the entire study area. As emerging pan-European datasets on tree species composition become progressively available, future research efforts should aim to incorporate species-specific dispersal processes more explicitly, while capturing underrepresented disturbance agents and geographical areas, thereby refining large-scale assessments of post-disturbance recovery.

Conclusions

Our study advances the understanding of landscape-scale influence on post-disturbance recovery, showing that the presence of undisturbed forests in proximity of disturbance patches distinctively enhances recovery. By integrating ground-based measures of recovery with remote sensing-derived disturbance maps, we provide a robust and spatially explicit framework for assessing recovery drivers across multiple scales. Our findings highlight the importance of considering landscape context in forest management strategies and underscore the need for spatially adaptive forest planning to support post-disturbance forest resilience.

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Author Contribution L.M. and M.C. conceived the study, designed the methodology, led data analysis and wrote the first draft. T.A.N. and C.S. contributed to the conceptual development of the study and provided guidance on the ecological interpretation of results. All remaining authors, including M.C., and T.A.N. collected the post-disturbance regeneration data. All authors provided critical feedback on the manuscript and approved the final submitted version.

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Data availability The pan-European disturbance map used in this study is available at: https://zenodo.org/records/7080016. The field dataset can be accessed at: https://doi.org/10.5061/dryad.ncjsxkt0z.

Declarations

Competing interests The authors declare no competing interests.

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