



Cite this article: Mikoláš M *et al.* 2021 Natural disturbance impacts on trade-offs and co-benefits of forest biodiversity and carbon. *Proc. R. Soc. B* **288**: 20211631. <https://doi.org/10.1098/rspb.2021.1631>

Received: 20 July 2021
Accepted: 27 September 2021

Subject Category:
Global change and conservation

Subject Areas:
ecology, ecosystems, biological applications

Keywords:
biodiversity conservation, carbon sequestration, carbon storage, climate change, historical disturbance, primary forest

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Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5666862>.

Natural disturbance impacts on trade-offs and co-benefits of forest biodiversity and carbon

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With accelerating environmental change, understanding forest disturbance impacts on trade-offs between biodiversity and carbon dynamics is of high socio-economic importance. Most studies, however, have assessed immediate or short-term effects of disturbance, while long-term impacts remain poorly understood. Using a tree-ring-based approach, we analysed the effect of 250 years of disturbances on present-day biodiversity indicators and carbon dynamics in primary forests. Disturbance legacies spanning centuries shaped contemporary forest co-benefits and trade-offs, with contrasting, local-scale effects. Disturbances enhanced carbon sequestration,

reaching maximum rates within a comparatively narrow post-disturbance window (up to 50 years). Concurrently, disturbance diminished aboveground carbon storage, which gradually returned to peak levels over centuries. Temporal patterns in biodiversity potential were bimodal; the first maximum coincided with the short-term post-disturbance carbon sequestration peak, and the second occurred during periods of maximum carbon storage in complex old-growth forest. Despite fluctuating local-scale trade-offs, forest biodiversity and carbon storage remained stable across the broader study region, and our data support a positive relationship between carbon stocks and biodiversity potential. These findings underscore the interdependencies of forest processes, and highlight the necessity of large-scale conservation programmes to effectively promote both biodiversity and long-term carbon storage, particularly given the accelerating global biodiversity and climate crises.

1. Introduction

Carbon storage and habitat provisioning for biodiversity are two of the most important ecosystem services provided by forests [1,2]. Forest ecosystems are large terrestrial carbon pools, sequestering approximately 34% of annual anthropogenic carbon emissions [3]. As such, forest management aimed at increasing carbon storage is a major component of natural climate solutions (NCS). Over the next decade, NCS have the potential to cost-effectively provide 37% of carbon mitigation needed to limit global warming to 2°C with a 66% chance [4]. Yet, the effectiveness of carbon storage for climate mitigation depends on long-term forest functionality and integrity, which critically depends on biodiversity [5]. However, abrupt biodiversity declines have been observed in natural forests worldwide, as a result of widespread habitat degradation or fragmentation owing to human impacts on intact forest landscapes [6]. Rapid global climate change and the biodiversity crisis necessitate adaptive policies and strategies, in which forests will play a key role [7,8].

Carbon storage and biodiversity are related to the dynamic nature of forest ecosystems. Disturbance is a primary driver of forest structure, and while disturbance events typically generate the structural variability required to sustain high biodiversity, large pulses of tree mortality and subsequent decomposition can reduce forest carbon stocks [9]. For these reasons, it is extremely difficult to determine whether forests can simultaneously sustain both high carbon and high biodiversity, with previous research from a variety of forest types either demonstrating trade-offs [10] or synergies (i.e. ‘co-benefits’ [11]).

Recent studies suggest a positive relationship between total carbon storage (i.e. ‘stocks’) and biodiversity in tropical forests [11,12]. Similarly, there is a positive relationship between carbon stocks and both bird and tree species diversity at landscape scales across Europe and North America [11,13]. Crucially, more detailed stand-scale analyses from temperate regions suggest the opposite pattern [10], and results differ widely depending on the scale of analysis, biogeographic regions or taxonomic groups [10,14–16]. These uncertainties in our understanding of possible trade-offs between forest carbon storage and biodiversity conservation challenge policy development aiming to optimize both objectives, particularly in response to abrupt changes as climate warming alters natural disturbance regimes [9,17,18]. Harnessing the potential of forests to tackle

the climate and biodiversity crises requires improved understanding of natural disturbance processes and their long-term effects on forest carbon dynamics and biodiversity [7,19,20].

Disturbances like wind, insect outbreaks and forest fire can rapidly kill trees over a range of extents, re-shaping forest structure at both stand (e.g. tree age class distribution and seral condition) and landscape (e.g. vegetation pattern and patch mosaics) scales [21]. Because disturbances influence the successional development of recovering vegetation for decades or even centuries, they can have long-lasting effects on forest biodiversity and carbon [19]. Variation in the spatial and temporal scale of disturbances raises many challenges when trying to quantify disturbance effects on forest functions, especially with short-term data. Large-scale studies on the effects of historical disturbances on present day forest functions and biodiversity are rare, however, largely because of the difficulties in reconstructing detailed, long-term histories of natural disturbances and stand development [22]. Only a large-scale and long-term perspective can provide insight on the effects of past disturbances on present-day forest functions [23]. This broad perspective is crucially needed for assessing the vulnerability of forest ecosystems to changing conditions and for developing policy options to simultaneously tackle biodiversity conservation and climate change mitigation [24].

A significant proportion of Earth’s forest cover still exists free of direct human intervention in locations known as primary forests (approx. 27%) [25]. Primary forests are the result of complex natural disturbance histories, and are typically highly heterogeneous, both within and among stands that include the range in seral stages as well as old-growth forest [26,27]. Their structural heterogeneity translates into high spatial variability in carbon storage and biodiversity, although primary forests generally maintain high levels of both [28]. Being less influenced by humans compared to managed or secondary forests, primary forests represent natural laboratories for investigating interactions among biodiversity, carbon and disturbance dynamics [29].

Here, we investigated the long-term response of biodiversity indicators (biodiversity potential index and occurrence of an umbrella species, the capercaillie (*Tetrao urogallus* L.)), and forest carbon dynamics (sequestration and total storage) to 250 years of disturbance history across a gradient of disturbance severity and timing. To reconstruct disturbance histories, we collected 7725 tree cores in 30 of the best-preserved primary Norway spruce (*Picea abies* (L.) Karst.) forest stands in temperate Europe. We addressed three main research questions:

- (i) how does variation in past disturbance history affect contemporary patterns of biodiversity indicators, carbon storage, and carbon sequestration?
- (ii) what is the relative importance of disturbance severity and timing in determining contemporary biodiversity indicators and carbon storage and sequestration? and
- (iii) under which disturbance conditions are there co-benefits versus trade-offs between forest biodiversity, carbon storage and sequestration?

2. Material and methods

(a) Study area

We conducted this study in one of the largest remaining contiguous forest ecosystems in Europe—the Carpathian Mountain ecoregion (figure 1), which encompasses the majority of extant

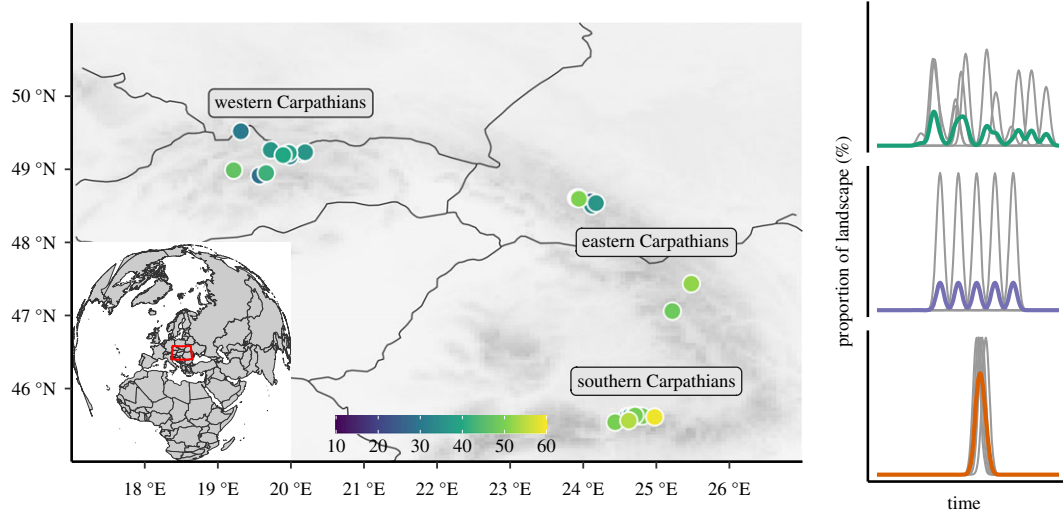


Figure 1. Study area and plot locations. Data collection was based on a hierarchical stratified random sampling design. Forest stands (circles) were randomly distributed within remnant primary forest patches and across broad environmental gradients. The colour gradient indicates the maximum severity of historical disturbance of the studied stands. The reconstructed disturbance history for all studied stands is based on the tree ring analyses of 25 trees per plot. Examples of hypothetical disturbance histories (three panels on the right) show moderate (green), low (violet) and high severity (orange) disturbance regimes (the grey line represents the tree level signals, while the coloured line represents the plot-level disturbance signal). The y-axis corresponds to the proportion of forest where a disturbance event caused the removal of the tree canopy, as inferred from tree-rings. (Online version in colour.)

temperate primary spruce forests in Europe [29]. We combined datasets used in previous analyses of disturbance history [21]. The respective field sampling procedures are summarized in the project REMOTE [30]. Thirty primary forest stands with no signs of human management were selected in the subalpine zone of the Carpathian Mountains. Stands with no evidence of direct human influence, such as logging or livestock grazing, were selected with the help of local experts or primary forest inventories [31]. The studied forests occupy altitudes ranging from 1150 to 1700 m.a.s.l. Mean annual temperature varies between 1.5 and 4°C, with mean growing season (May to October) temperature ranges of 7.5 to 10°C, and an annual precipitation of about 800 to 2000 mm. Bedrock and soils are variable, with Podzols, Cambisols and Leptosols making up the predominant soil types [32]. Norway spruce is the dominant tree species, mixed with minor components (less than 5%) of rowan (*Sorbus aucuparia* L.) and stone pine (*Pinus cembra* L.). The understory is dominated by bilberry (*Vaccinium myrtillus* L.), hairy reed grass (*Calamagrostis villosa* (Chaix) J. F. Gmelin), greater wood-rush (*Luzula sylvatica* Huds.) and wavy hair-grass (*Avenella flexuosa* (L.) Trin.). In these forests, disturbance is primarily caused by wind and the European spruce bark beetle, *Ips typographus* (L.) [21].

(b) Forest structure and dendrochronological data

We used a hierarchical sampling framework to analyse the effect of historical disturbances on biodiversity and carbon dynamics. During the years 2011–2014, within each landscape (eastern, western, southern Carpathians) we studied 10–12 stands and established a series of 1000 m² sample plots using a stratified random design. The approximate size of the sampled landscape was roughly 10 000 km², and each stand was approximately 100 ha in size. We used a regular grid with cells of two hectares and randomly placed a circular plot within each grid cell. In total, we sampled 309 plots, representing an average of 12 plots per stand.

Within each plot, we measured the composition and structure of living and dead standing trees. We recorded the diameter of each live and dead standing tree (diameter at breast height (DBH) ≥ 10 cm) and assigned a decay class to each dead tree

[33]. The line intersect method [33] was used to measure the amount of downed dead wood. All fallen trees or branch fragments greater than or equal to 10 cm in diameter encountered along each transect were measured and identified by species and decay class, using a total transect length of 100 m per plot, split into five sub-transects of 20 m each, evenly radiating from the plot centre. We computed the volume of downed dead wood after Harmon & Sexton [33]. We collected increment cores from 25 trees selected randomly from the non-suppressed living trees with DBH ≥ 10 cm in each plot. Each increment core was collected 1 m above the ground and was processed for laboratory analysis.

(c) Disturbance history

We used disturbance chronologies from a published, approximately 250 year long record of disturbance history encompassing our study plots [21]. The chronologies delineate plot-scale past disturbance occurrences with high temporal resolution and estimate the magnitude of associated events.

These chronologies were derived from analyses of temporal patterns in inter-annual tree growth. Growth variation was quantified from measurements of annual radial increment in tree core samples, which were collected from the same survey plots used in this study. Statistically anomalous tree growth variation exceeding site-specific thresholds and sustained over minimum pre-defined temporal intervals were attributed to disturbance-driven canopy openings [21]. Disturbance severity was defined in terms of the proportional area of tree canopy removed [34]. These growth surges also defined the timing of event occurrence. Years since the main disturbance were calculated as the year of data collection minus the year of maximum severity. For recently disturbed plots, where the current canopy area disturbed was larger than dendrochronologically detected maximum disturbance severities, the severity was expressed by current canopy openness. Current canopy openness was calculated as the difference between mean canopy closure of the whole dataset and current canopy closure of a given plot. Reconstructions of individual disturbance events, based on these canopy area models, were subsequently aggregated into temporal and spatial chronologies of historical disturbance [21].

(d) Biodiversity indicator data

Because complete biodiversity inventories are usually not feasible in forest stands, most research on the relationships between biodiversity and ecosystem functioning relies on indicators, either based on forest structural features (i.e. habitat-based), or on the diversity of one or more species (i.e. taxa-based) [35]. Here, we used both approaches employing a biodiversity potential index (BPI) based on forest structure [36] and presence/absence data of a key umbrella bird species for the study region—the capercaillie [37].

(i) Biodiversity potential

The BPI is a proxy of the suitability of a given stand to sustain biodiversity and is based on a set of five basic structural attributes: (1) standing dead trees, (2) downed logs, (3) large old trees, (4) diversity of understory vegetation, and (5) light availability at the ground floor, which are equally weighted to compose a summary index [36]. Several studies have shown these attributes to be strongly predictive of some elements of biodiversity [38]. They relate, for instance, to saproxylic beetles, wood-inhabiting fungi, lichens and mosses, understory vascular plants and light demanding species of true bugs. BPI varies between 0 and 5, with a high BPI representing a highly heterogeneous and diverse stand structure. A detailed description of the BPI calculation procedure is presented in the electronic supplementary material, figures S1 and S2.

In order to evaluate the effectiveness of BPI as a proxy for biodiversity, we selected a subset of 58 plots with available data [39] on lichens and wood-inhabiting fungi that are both considered important indicators of forest continuity and naturalness [40]. Generalized linear mixed models with gamma distributions revealed a significant positive relationship between BPI and both diversity of red-listed lichen ($z = 3.75$, $p = 0.0002$) and fungi species ($z = 1.97$, $p = 0.0494$). Using the BPI to predict the diversity of those groups on new data provided highly accurate estimates with a cross-validated mean absolute percentage prediction error of 4.8 and 16.3%, respectively. Thus, we consider the BPI a useful proxy for biodiversity in primary spruce forests in the Carpathians. For further details see the electronic supplementary material and Bače *et al.* [36].

(ii) Umbrella species data

We investigated the occurrence of the umbrella species capercaillie, a species of high conservation concern in Europe [37]. A capercaillie is a ground-dwelling bird species that inhabits forest habitats characterized by open canopy (40–60%), structural heterogeneity, and rich ground vegetation [41]. Capercaillies typically inhabit primary forests in the study region [42], although habitat associations may differ in other parts of Europe. We thoroughly searched the study plots for signs of capercaillie occurrence (e.g. feathers, droppings, tracks in the snow) for 15 mins, both in summer and winter seasons (one visit per season). Only presence (at least one presence, recorded during at least one visit) and absence (no sign recorded during both seasons) data were used in the analyses [39].

(e) Carbon data

(i) Carbon storage (aboveground carbon stocks in tree biomass)

We calculated contemporary carbon storage in different aboveground tree biomass pools using published allometric models based on DBH [39]. Specifically, aboveground living biomass, composed of stem, branch, and foliage tissue, was calculated using species-specific equations for 14 tree species [43]. Species-specific allometric equations are shown in the electronic supplementary material, table S1. Biomass of standing dead trees was determined using models from Kublin & Breidenbach [44].

Finally, the volume of forest floor deadwood was computed according to Harmon & Sexton [33] and converted to biomass using estimates of wood density that account for decay stage [45]. We subsequently summed all biomass components and approximated total aboveground carbon storage as 50% of total biomass [46].

(ii) Carbon sequestration

Using the tree ring dataset [21], we also estimated contemporary carbon sequestration (mean rates of change in forest carbon stocks) based on total plot-level aboveground biomass increment (AGBI) averaged over the last 10 years [47]. Based on allometric models [43] (see the electronic supplementary material, table S1), we used annual DBH increases to estimate AGBI for all living plot trees for each year in the most recent 10 year interval preceding field surveys. Inter-annual DBH increases for the 10 year window were computed from measures of annually resolved radial growth obtained from tree core samples. Radial growth rates and associated DBH variation in unsampled plot trees were approximated with data from neighbouring trees in congruent size classes. Decadal mean biomass increments of individual trees were then aggregated to produce estimates of contemporary plot-scale AGBI [48].

(f) Data analysis

Generalized additive mixed models (GAMM, [49]) with restricted maximum likelihood were used to estimate optimal disturbance conditions that support the highest biodiversity potential, the highest probability of umbrella bird species occurrence, maximum carbon sequestration and maximum carbon storage while accounting for a hierarchical structure of sampling design (plots nested within stands). Based on detailed dendrochronological measurements [21], disturbance conditions were defined as the time since the most severe disturbance and its severity per plot. Separate models were built for biodiversity and carbon dynamics data [39]. Capercaillie occurrence was fitted by binomial GAMM with a logit link function. Characteristics of carbon stocks (total biomass carbon, living biomass carbon, dead standing biomass carbon, downed dead biomass carbon and biomass carbon increment) were fitted by GAMMs with a normal error distribution and an identity link function. The fixed effects component of the GAMMs contained thin plate regression spline smoothers for year and severity of the strongest disturbance. We set the upper limit on the smooth terms to four degrees of freedom and implemented an extra penalty to allow for shrinking the effective degrees of freedom towards zero, i.e. to perform variable selection [50]. The random effect structure involved identity of stands, while landscape-level hierarchy was not formally treated in statistical modelling owing to a low number of replicates (three landscapes only). We built the random effects part of the GAMMs sequentially, first specifying models with complex random effect structure involving factor smoothers, the nonlinear counterpart to the combination of random intercepts and random slopes [51]. The models were subsequently simplified to the random intercepts and random slopes. The most parsimonious random effect structure was selected using χ^2 tests on the differences in the restricted maximum-likelihood scores [52]. We assessed model performance using diagnostic plots and square-root transformed data on standing dead wood to meet the assumptions of normality and homogeneity of variance. Because the sampling design was spatially structured, we constructed correlograms of residuals to check for autocorrelation [53] but did not find significant spatial autocorrelation.

To assess the influence of disturbances at the stand level, the plot-level disturbance and carbon data were averaged per stand, and the capercaillie occurrences were summarized per stand. The

Table 1. Results of GAMMs at plot (patch) scale and GAMs at stand scale testing for the effect of time since the strongest disturbance and its severity on capercaillie occurrence, biodiversity potential and characteristics of carbon stocks in primary forests. (Effective degrees of freedom (edf), test statistics (χ^2/F) and probabilities (p) are displayed along with adjusted determination coefficients (R^2) for each model. Results significant at $\alpha = 5\%$ are highlighted in italics.)

scale	variable	time since maximum disturbance			maximum disturbance severity			
		edf	χ^2/F	p	edf	χ^2/F	p -value	R^2
plot (patch)	capercaillie occurrence	<0.1	<0.1	0.759	1.5	7.3	0.034	0.13
	biodiversity potential	3.9	3.7	<0.001	1.0	3.8	<0.001	0.27
	carbon stock	2.9	10.4	<0.001	1.6	0.7	0.082	0.37
	carbon sequestration	7.4	30.1	<0.001	0.8	0.7	0.038	0.51
stand	capercaillie occurrence	<0.1	<0.1	0.658	0.6	0.5	0.113	0.06
	biodiversity potential	0.8	0.4	0.248	1.4	2.4	0.013	0.24
	carbon stock	1.0	2.3	0.139	1	<0.1	0.981	<0.01
	carbon sequestration	<0.1	<0.1	0.484	0.4	0.2	0.289	0.02

stand-level data were fitted using generalized additive models (GAM, [49]) with the same settings as the GAMMs above. The performance of plot-level GAMMs and stand-level GAMs was compared using adjusted determination coefficients (R^2). The R^2 was defined as the proportion of variance explained, where original variance and residual variance are both estimated using unbiased estimators penalizing for number of predictors [54].

To investigate variability of forest co-benefits over multiple spatial scales, we calculated coefficients of variation of the observed values among plots (patches), stands and landscapes and plotted the estimates for each forest function.

The analyses were performed in R [55] using the libraries *itsadug* [52], *mgcv* [49] and *ncf* [53].

3. Results

Our results revealed that past disturbances had significant and century-long effects on contemporary forest functions (carbon storage, carbon sequestration, capercaillie occurrence, and structure-based biodiversity potential) (table 1 and figure 2; electronic supplementary material, figure S3).

At the plot (patch) scale, total carbon storage was highest in sites that were strongly disturbed (*ca* 30–70% canopy removed) a century or two ago. By contrast, the highest rates of carbon sequestration occurred in more recently (*ca* 50 years ago) disturbed sites that experienced a broad range of disturbance severity (optimum from *ca* 20 to 80% canopy removed) (figure 2; electronic supplementary material, figure S3). Biodiversity potential in primary forests showed a bimodal, U-shaped response on disturbance severity and was high under a broad variety of disturbance conditions. Specifically, the BPI was highest in recently disturbed forests and those disturbed two centuries ago, covering a wide range of disturbance severities (*ca* 15–75%). Finally, moderate severity disturbances (*ca* 25–40% canopy removed) increase the probability of capercaillie presence irrespective of disturbance timing (figure 2; electronic supplementary material, figure S3). Aboveground carbon storage reached maximum values under different disturbance conditions than carbon sequestration, probability of capercaillie occurrence, and biodiversity potential (figure 2; electronic supplementary material, figure S3).

At the stand level, the influence of disturbance characteristics was less pronounced, and the GAMs exhibited

considerably lower explanatory power than the corresponding plot-level GAMMs (table 1). Similarly, variability of all forest functions decreased with increasing spatial scale (figure 3), demonstrating that natural disturbance regimes generate fluctuating trade-offs in ecosystem services at local scales but maintain an overall homeostasis or stability of co-benefits over large regions.

4. Discussion

Carbon storage and biodiversity are interrelated ecosystem functions [56], which fluctuate over time under natural disturbance regimes. Different seral conditions and variable successional pathways create a diversity of ecosystem functions. Here, while biodiversity potential had a U-shaped response to time since disturbance in these unmanaged spruce stands, being highest early after disturbance and then in later stages of forest development, carbon sequestration and stocks peaked in early-successional and old-growth stages, respectively. Recent disturbances increased light and deadwood availability, conditions known to benefit many elements of forest biodiversity [57]. As soon as the forest canopy closed, reduced light availability and more homogeneous forest structure resulted in decreased biodiversity potential. Meanwhile, carbon sequestration was highest immediately following disturbance, bolstered by the rapid growth of younger trees already in the understory owing to advanced regeneration [47]. By contrast, aboveground carbon storage was higher in old-growth forest development stages, particularly in large stems and dead wood [58,59]. Our results indicate that the later stages of forest development after disturbance again increased the biodiversity potential associated with complex forest structures (figure 2).

Interestingly, rather than timing, severity was the most important disturbance feature for capercaillies. The probability of capercaillie occurrence was high across the full range of time since disturbance, as long as the disturbance severity was moderate. This contrasts with a study from the Bavarian forest that found increasing habitat suitability with time since disturbance and a positive effect of high severity disturbances [60]. The contrasting results might depend on regional differences that influence successional

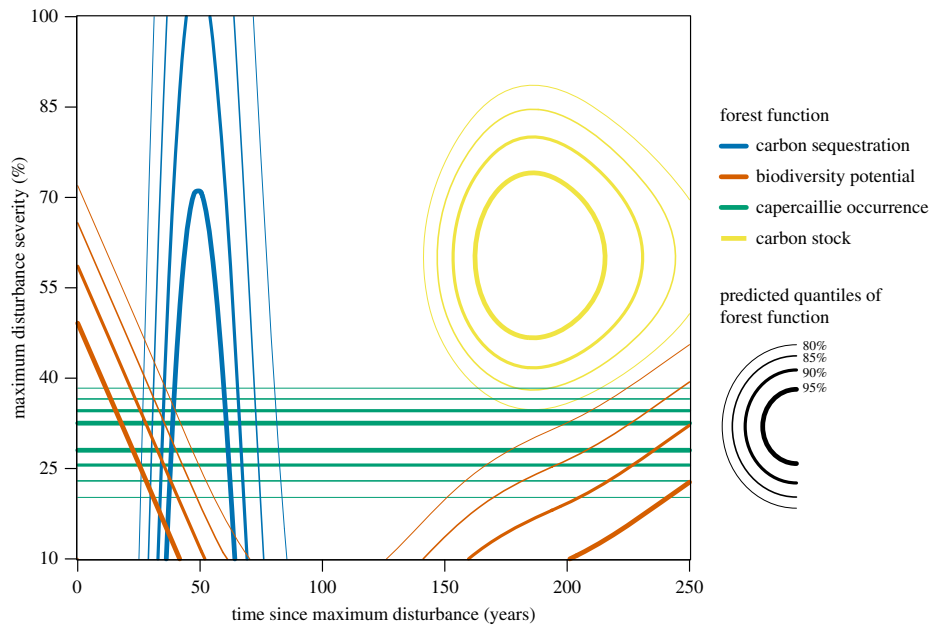


Figure 2. Maxima of forest functions along the gradients of maximum disturbance severity and time since that event. Isolines represent upper percentiles (greater than 80%) of GMM-predicted values of the forest functions.

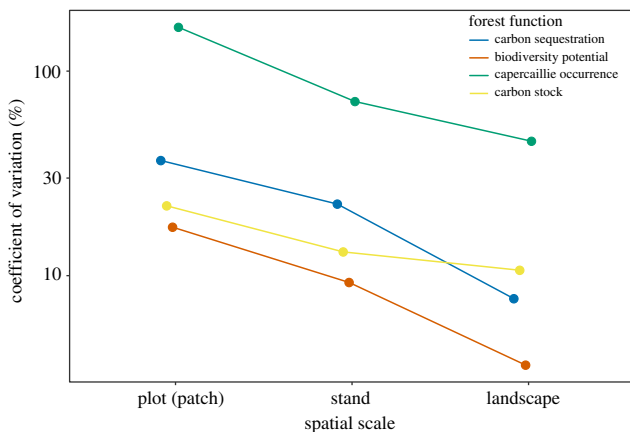


Figure 3. Coefficient of variation of forest functions calculated among plots (patches), stands and landscapes. Note that the ordinate is logarithmically scaled.

pathways, or they may be attributable to Kortmann *et al.* [60] only investigating dynamics over two decades following disturbance, a limited timeframe that could correspond to short-term post-disturbance reproductive success. The preference of capercaillies to moderately disturbed plots independently of disturbance timing as found here may also be explained by the fact that moderate severity disturbances—both recent and further in the past—generally lead to high structural complexity in the studied primary forests [26]. In general, moderate severity disturbance could result in an optimal balance, under which several forest functions can reach relatively high levels (see the overlaps in figure 2).

Whether forests and forest management for carbon storage can jointly achieve climate change mitigation goals and sufficient quantity and quality habitat for rare species and biodiversity is a key topic in conservation research and policy [10]. Our results highlight the importance of spatial and temporal scales when accounting for relationships between forest biodiversity and carbon functions [61]. Although it may prove challenging to simultaneously

maximize total carbon storage, sequestration and biodiversity maintenance at small spatial scales, our results show that natural disturbance regimes can maintain relatively high levels of all functions in Carpathian spruce-dominated landscapes not subject to forest management [62].

As such, primary forests represent both important carbon stores and biodiversity hotspots [29]. Although optimal site conditions for carbon and biodiversity may be associated with different disturbance histories, it is important to highlight the positive relationship between carbon stocks and biodiversity potential and the lack of a significant difference between carbon stocks on plots with and without capercaillie occurrence (electronic supplementary material, figure S4). In general, carbon storage values are significantly higher in primary forests compared to mature managed forests under the same site conditions (elevation, soil etc.) [63]. Thus, despite the local fluctuation caused by natural disturbance, our study supports the conservation of unmanaged forest landscapes as an effective tool to promote both biodiversity and carbon co-benefits.

5. Study caveats

While our statistical model and covariation analyses relied on established approaches, our study has some limitations that warrant discussion. First, it only focused on aboveground tree carbon without considering soil, which can form a considerable proportion of total forest carbon [56]. An intensive soil sampling of the study area would address this issue but was beyond the scope and capacity of the current study [62]. Therefore, the peak in carbon values 200 years after natural disturbance should be interpreted with caution because including soil data could show longer-term increases in total carbon. Second, we used two biodiversity indicators as a proxy of biodiversity. While we concede that a multi-taxon approach could provide more appropriate results, the biodiversity potential index was a reliable predictor of species richness of wood-inhabiting fungi and lichens (see §2d(i);

electronic supplementary material). Moreover, capercaillies have been widely used in conservation planning and shown to be a suitable umbrella species for rare forest bird species occurrence [37]. Thus, we believe that our analyses produced results with a high degree of generality.

6. Conclusion

Our results significantly enhance our understanding of the effects of historical disturbance on contemporary ecosystem co-benefits and trade-offs. In particular, they emphasize that accounting for long-term variation of past disturbance could improve current policies aimed at mitigating climate change and biodiversity loss. Disturbances have long-lasting effects on forest functions and post-disturbance successional pathways [26]. Clearly, accounting for long time scales and alternative post-disturbance development trajectories poses a significant challenge to designing effective conservation and mitigation strategies, particularly given projected changes in disturbance regimes. Our results suggest that these challenges can be addressed by embracing a landscape perspective. While carbon sequestration and storage or biodiversity cannot be maximized everywhere on small spatial scales, a larger landscape has the capacity to deliver optimal levels of biodiversity and carbon co-benefits. A variety of disturbance spatial scales and temporal frequencies are needed to foster both carbon sequestration and stocks, and to maintain high levels of biodiversity. Because all three objectives cannot be simultaneously maximized in small reserves, it is important to delineate large tracts of strictly protected forest landscapes to maintain a range of seral stages under a

regime of natural disturbances. The size of such protected areas could be guided by the minimum dynamic area framework, which would help to determine the minimum reserve size required to incorporate natural disturbance regimes and maintain ecological processes [64]. Furthermore, forests must be allowed to attain older ages if they are to reach their biodiversity and carbon storage potential [65,66]. Thus, protecting existing primary forests and increasing the size of strictly protected forest landscapes (e.g. rewilding) is necessary to encompass shifting patch mosaics driven by a wide range of disturbances. These strategies would help maintain a range of ecosystem functions in times of accelerating environmental change.

Data accessibility. Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.0k6djh13> [39].

Authors' contributions. M.M.: conceptualization, data curation, investigation, methodology, writing—original draft; M.Svi.: formal analysis, investigation, writing—review and editing; R.B.: data curation, methodology, writing—review and editing; W.S.K.: conceptualization, writing—review and editing; V.T.: conceptualization, writing—review and editing; G.W.M., H.K., A.B., D.K., K.Bol., K.Beg., V.C., O.C., D.R., M.D., M.Fer., M.Fra., R.G., J.H., P.J., O.K., J.L., L.M., T.N., J.P., J.L.P., R.R., C.C.R., M.R., F.S., J.S., M.Syn., O.V., V.Z.: writing—review and editing; M.Svo.: funding acquisition, resources, supervision. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

Funding. Funding for this research was provided by the Czech Science Foundation (grant GACR no. 21–27454S) and the institutional project no. CZ.02.1.01/0.0/0.0/16_019/0000803. M.S. was supported by the Operational Programme Integrated Infrastructure (OPII) funded by the ERDF (ITMS313011T721).

References

- Luyssaert S, Schulze ED, Börner A, Knohl A, Hessenmöller D, Law BE, Ciais P, Grace J. 2008 Old-growth forests as global carbon sinks. *Nature* **455**, 213–215. (doi:10.1038/nature07276)
- Howard C, Flather CH, Stephens PA. 2020 A global assessment of the drivers of threatened terrestrial species richness. *Nat. Commun.* **11**, 1–10. (doi:10.1038/s41467-020-14771-6)
- Friedlingstein P *et al.* 2019 Global carbon budget 2019. *Earth Syst. Sci. Data* **11**, 1783–1838. (doi:10.5194/essd-11-1783-2019)
- Griscom BW *et al.* 2017 Natural climate solutions. *Proc. Natl Acad. Sci. USA* **114**, 11 645–11 650. (doi:10.1073/pnas.1710465114)
- Parrish JD, Braun D, Unnasch RS. 2003 Are we conserving what we say we are? Measuring ecological integrity within protected areas. *BioScience* **53**, 851–860. (doi:10.1641/0006-3568(2003)053[0851:AWCWWS]2.0.CO;2)
- Betts MG, Wolf C, Ripple WJ, Phalan B, Millers KA, Duarte A, Butchart SHM, Levi T. 2017 Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* **547**, 441–444. (doi:10.1038/nature23285)
- Buotte PC, Law BE, Ripple WJ, Berner TL. 2020 Carbon sequestration and biodiversity co-benefits of preserving forests in the western United States. *Ecol. Appl.* **30**, 1–11. (doi:10.1002/eap.2039)
- Mammola S, Riccardi N, Prié V, Correia R, Cardoso P, Lopes-Lima M, Sousa R. 2020 Towards a taxonomically unbiased European Union biodiversity strategy for 2030. *Proc. R. Soc. B* **287**, 20202166. (doi:10.1098/rspb.2020.2166)
- Thom D, Seidl R. 2016 Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biol. Rev.* **91**, 760–781. (doi:10.1111/brv.12193)
- Sabatini FM *et al.* 2019 Trade-offs between carbon stocks and biodiversity in European temperate forests. *Glob. Change Biol.* **25**, 536–548. (doi:10.1111/gcb.14503)
- Thom D, Golivets M, Edling L, Meigs GW, Gourevitch JD, Sonter L, Galford GL, Keeton WS. 2019 The climate sensitivity of carbon, timber, and species richness covaries with forest age in boreal–temperate North America. *Glob. Change Biol.* **25**, 2446–2458. (doi:10.1111/gcb.14656)
- Lennox GD *et al.* 2018 Second rate or a second chance? Assessing biomass and biodiversity recovery in regenerating Amazonian forests. *Glob. Change Biol.* **24**, 5680–5694. (doi:10.1111/gcb.14443)
- Lecina-Diaz J, Alvarez A, Regos A, Drapeau P, Paquette A, Messier C, Javier R. 2018 The positive carbon stocks–biodiversity relationship in forests: co-occurrence and drivers across five sub-climates. *Ecol. Appl.* **28**, 1481–1493. (doi:10.1002/eap.1749)
- Di Marco M, Watson JE, Currie DJ, Possingham HP, Venter O. 2018 The extent and predictability of the biodiversity–carbon correlation. *Ecol. Lett.* **21**, 365–375. (doi:10.1111/ele.12903)
- Ferreira J *et al.* 2018 Carbon-focused conservation may fail to protect the most biodiverse tropical forests. *Nat. Clim. Change* **8**, 744–749. (doi:10.1038/s41558-018-0225-7)
- Asbeck T, Sabatini F, Augustynczyk ALD, Basile M, Helbach J, Jonker M, Knuff A, Bauhus J. 2021 Biodiversity response to forest management intensity, carbon stocks and net primary production in temperate montane forests. *Sci. Rep.* **11**, 1625. (doi:10.1038/s41598-020-80499-4)
- Seidl R *et al.* 2017 Forest disturbances under climate change. *Nat. Clim. Change* **7**, 395–402. (doi:10.1038/NCLIMATE3303)
- Kurz WA, Stinson G, Rampley G. 2008 Could increased boreal forest ecosystem productivity offset carbon losses from increased disturbances? *Phil. Trans. R. Soc. B* **363**, 2259–2268. (doi:10.1098/rstb.2007.2198)
- Turner MG *et al.* 2020 Climate change, ecosystems and abrupt change: science priorities. *Phil.*

- Trans. R. Soc. B* **375**, 20190105. (doi:10.1098/rstb.2019.0105)
20. Case MJ, Johnson BG, Bartowitz KJ, Hudiburg TW. 2021 Forests of the future: climate change impacts and implications for carbon storage in the Pacific Northwest, USA. *For. Ecol. Manag.* **482**, 118886. (doi:10.1016/j.foreco.2020.118886)
 21. Schurman JS *et al.* 2018 Large-scale disturbance legacies and the climate sensitivity of primary *Picea abies* forests. *Glob. Change Biol.* **24**, 2169–2181. (doi:10.1111/gcb.14041)
 22. Mori AS. 2011 Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. *J. Appl. Ecol.* **48**, 280–292. (doi:10.1111/j.1365-2664.2010.01956.x)
 23. Harmon ME, Pabst RJ. 2015 Testing predictions of forest succession using long-term measurements: 100 yrs of observations in the Oregon Cascades. *J. Veg. Sci.* **26**, 722–732. (doi:10.1111/jvs.12273)
 24. Druckenbrod DL, Martin-Benito D, Orwig DA, Pederson N, Poulter B, Renwick KM, Shugart HH. 2019 Redefining temperate forest responses to climate and disturbance in the eastern United States: new insights at the mesoscale. *Glob. Ecol. Biogeogr.* **28**, 557–575. (doi:10.1111/geb.12876)
 25. Food and Agricultural Organization (FAO). 2020 Global Forest Resource Assessment 2020 – key findings. Rome. Published online May 2020. See <https://doi.org/10.4060/ca8753en> (retrieved in June 2021).
 26. Meigs R *et al.* 2017 More ways than one: mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. *For. Ecol. Manag.* **406**, 410–426. (doi:10.1016/j.foreco.2017.07.051)
 27. IUCN. 2020 Policy statement on primary forests including intact forest landscapes. See https://www.iucn.org/sites/dev/files/content/documents/iucn_pfi-ifl_policy_2020_approved_version.pdf.
 28. Keeton WS. 2018 Source or sink? Carbon dynamics in old-growth forests and their role in climate change mitigation. In *Ecology and recovery of eastern old-growth forests* (eds A Barton, WS Keeton), pp. 267–288. Washington, DC: Island Press.
 29. Sabatini FM *et al.* 2018 Where are Europe's last primary forests? *Divers. Distrib.* **24**, 1426–1439. (doi:10.1111/ddi.12778)
 30. Remote Primary Forests. 2021 *REMOTE primary forests: research on mountain temperate primary forests*. Prague, Czech Republic: Remote Primary Forests. See www.remoteforests.org/.
 31. Mikoláš M *et al.* 2019 Primary forest distribution and representation in a Central European landscape: results of a large-scale field-based census. *For. Ecol. Manag.* **449**, 117466. (doi:10.1016/j.foreco.2019.117466)
 32. Čada V *et al.* 2020 Quantifying natural disturbances using a large-scale dendrochronological reconstruction to guide forest management. *Ecol. Appl.* **30**, e02189. (doi:10.1002/eap.2189)
 33. Harmon ME, Sexton J. 1996 *Guidelines for measurements of woody detritus in forest ecosystems*, 73p. Seattle, WA: LTER Network Office, University of Washington.
 34. Lorimer CG, Frelich LE. 1989 A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Can. J. For. Res.* **19**, 651–663. (doi:10.1139/x89-102)
 35. Burrascano S *et al.* 2018 Congruence across taxa and spatial scales: are we asking too much of species data? *Glob. Ecol. Biogeogr.* **27**, 980–990. (doi:10.1111/geb.12766)
 36. Bače R *et al.* Submitted. Long-term response of habitat quality to disturbance of varying time and severity across the European spruce forests.
 37. Suter W, Graf RF, Hess R. 2002 Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. *Conserv. Biol.* **16**, 778–788. (doi:10.1046/j.1523-1739.2002.01129.x)
 38. Gao T, Nielsen A, Hedblom M. 2015 Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecol. Indic.* **57**, 420–434. (doi:10.1016/j.ecolind.2015.05.028)
 39. Mikoláš M *et al.* 2021 Data from: Natural disturbance impacts on trade-offs and co-benefits of forest biodiversity and carbon. Dryad Digital Repository. (doi:10.5061/dryad.0k6djhb13)
 40. Hillmers T, Nicolas Friess N, Bässler C, Heurich M, Brandl R, Pretzsch H, Seidl R, Müller J. 2018 Biodiversity along temperate forest succession. *J. Appl. Ecol.* **55**, 2756–2766. (doi:10.1111/1365-2664.13238)
 41. Wegge P, Rolstad J. 2017 Climate change and bird reproduction: warmer springs benefit breeding success in boreal forest grouse. *Proc. R. Soc. B* **284**, 20171528. (doi:10.1098/rspb.2017.1528)
 42. Mikoláš M *et al.* 2017 Mixed-severity natural disturbances promote the occurrence of an endangered umbrella species in primary forests. *For. Ecol. Manag.* **405**, 210–218. (doi:10.1016/j.foreco.2017.09.006)
 43. Forrester DI *et al.* 2017 Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. *For. Ecol. Manag.* **396**, 160–175. (doi:10.1016/j.foreco.2017.04.011)
 44. Kublin E, Breidenbach J, Kändler G. 2015 TapeR: flexible tree taper curves based on semiparametric mixed models. R package version 0.3.3. See <https://CRAN.R-project.org/package=TapeR>.
 45. Teodosiu M, Bouriaud OB. 2012 Deadwood specific density and its influential factors: a case study from a pure Norway spruce old-growth forest in the Eastern Carpathians. *For. Ecol. Manag.* **283**, 77–85. (doi:10.1016/j.foreco.2012.06.050)
 46. Kobler J, Zehetgruber B, Dirnböck T, Jandl R, Mirtl M, Schindlbacher A. 2019 Effects of aspect and altitude on carbon cycling processes in a temperate mountain forest catchment. *Landsc. Ecol.* **34**, 325–340. (doi:10.1007/s10980-019-00769-z)
 47. Trotsiuk V *et al.* 2016 The legacy of disturbance on individual tree and stand-level aboveground biomass accumulation and stocks in primary mountain *Picea abies* forests. *Forest Ecol. Manag.* **373**, 108–115. (doi:10.1016/j.foreco.2016.04.038)
 48. Woodwell G, Whittaker RH. 1968 Primary production in terrestrial ecosystems. *Am. Zool.* **8**, 19–30. (doi:10.1093/icb/8.1.19)
 49. Wood SN. 2017 *Generalized additive models: an introduction with R*, 2nd edn, 496p. Boca Raton: Chapman and Hall/CRC.
 50. Marra G, Wood SN. 2011 Practical variable selection for generalized additive models. *Comput. Stat. Data Anal.* **55**, 2372–2387. (doi:10.1016/j.csda.2011.02.004)
 51. Baayen H, Vasissth S, Kliegl R, Bates D. 2017 The cave of shadows: addressing the human factor with generalized additive mixed models. *J. Mem. Lang.* **94**, 206–234. (doi:10.1016/j.jml.2016.11.006)
 52. Van Rij J, Wieling M, Baayen R, Van Rijn H. 2017 itsadug: Interpreting time series and autocorrelated data using GAMMs. R package version 2, 3. See <https://CRAN.R-project.org/package=itsadug>.
 53. Bjørnstad ON, Falck W. 2001 Nonparametric spatial covariance functions: estimation and testing. *Environ. Ecol. Stat.* **8**, 53–70. (doi:10.1023/A:1009601932481)
 54. Wherry RJ. 1931 A new formula for predicting the shrinkage of the coefficient of multiple correlation. *Ann. Mathem. Stat.* **2**, 440–457. (doi:10.1214/aoms/1177732951)
 55. R Core Team. 2019 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <http://www.r-project.org>.
 56. Keith H, Vardon M, Obst C, Young V, Houghton RA, Mackey B. 2021 Evaluating nature-based solutions for climate mitigation and conservation requires comprehensive carbon accounting. *Sci. Total Environ.* **769**, 144341. (doi:10.1016/j.scitotenv.2020.144341)
 57. Beudert B, Bässler C, Thorn S, Noss R, Schröder B, Dieffenbach-Fries H, Foullois N, Müller J. 2015 Bark beetles increase biodiversity while maintaining drinking water quality. *Conserv. Lett.* **8**, 272–281. (doi:10.1111/conl.12153)
 58. Keith H, Mackey BG, Lindenmayer DB. 2009 Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proc. Natl Acad. Sci. USA* **106**, 11 635–11 640. (doi:10.1073/pnas.0901970106)
 59. Magnani F *et al.* 2007 The human footprint in the carbon cycle of temperate and boreal forests. *Nature* **447**, 849–851. (doi:10.1038/nature05847)
 60. Kortmann M, Heurich M, Latifi H, Rösner S, Seidl R, Müller J, Thorn S. 2018 Forest structure following natural disturbances and early succession provides habitat for two avian flagship species, capercaillie (*Tetrao urogallus*) and hazel grouse (*Tetrastes bonasia*). *Biol. Conserv.* **226**, 81–91. (doi:10.1016/j.biocon.2018.07.014)
 61. Thompson PL, Kéfi S, Zelnik YR, Dee LE, Wang S, De Mazancourt C, Loreau M, Gonzalez A. 2021 Scaling up biodiversity ecosystem functioning relationships: the role of environmental heterogeneity in space and time. *Proc. R. Soc. B* **288**, 20202779. (doi:10.1098/rspb.2020.2779)
 62. Pregitzer KS, Euskirchen ES. 2004 Carbon cycling and storage in world forests: biome patterns related

- to forest age. *Glob. Change Biol.* **10**, 2052–2077. (doi:10.1111/j.1365-2486.2004.00866.x)
63. Keeton WS, Chernyavskyy M, Gratz G, Main-Knorn M, Shpylchak M, Bihun Y. 2010 Structural characteristics and aboveground biomass of old-growth spruce-fir stands in the eastern Carpathian mountains, Ukraine. *Plant Biosyst.* **144**, 1–12. (doi:10.1080/11263500903560512)
64. Leroux SJ, Schmiegelow FK, Lessard RB, Cumming SG. 2007 Minimum dynamic reserves: a framework for determining reserve size in ecosystems structured by large disturbances. *Biol. Conserv.* **138**, 464–473. (doi:10.1016/j.biocon.2007.05.012)
65. Franklin JF *et al.* 2002 Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manag.* **155**, 399–423. (doi:10.1016/S0378-1127(01)00575-8)
66. Moomaw WR, Masino SA, Faison EK. 2019 Intact forests in the United States: proforestation mitigates climate change and serves the greatest good. *Front. Forests Global Change* **2**, 27. (doi:10.3389/ffgc.2019.00027)