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ORIGINAL ARTICLE

Natural Disturbances are Essential Determinants of Tree-Related Microhabitat Availability in Temperate Forests

Veronika Zemlerová,[1] Daniel Kozák,[1]* Martin Mikoláš,[1] Marek Svitok,[1,2] Radek Bače,[1] Marie Smyčková,[1] Arne Buechling,[1] Maxence Martin,[3] Laurent Larrieu,[4,5] Yoan Paillet,[6] Catalin-Constantin Roibu,[7] Ion Catalin Petritan,[8] Vojtěch Čada,[1] Matej Ferenčík,[1] Michal Frankovič,[1] Rhiannon Gloor,[1] Jeňýk Hofmeister,[1] Pavel Janda,[1] Ondrej Kameniar,[1] Linda Majdanová,[1] Katka Markuljaková,[1] Radim Matula,[1] Marek Mejstřík,[1] Miloš Rydval,[1] Ondřej Vostarek,[1] and Miroslav Svoboda[1]

[1]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 21 Praha 6 – Suchdol, Czech Republic; [2]Department of Biology and General Ecology, Faculty of Ecology and Environmental Sciences, Technical University in Zvolen, Masaryka 24, 960 01 Zvolen, Slovakia; [3]Département des Sciences Fondamentales, Université du Québec à Chicoutimi, 555 boul. de l'Université, Chicoutimi, Quebec G7H2B1, Canada; [4]Université de Toulouse, INRAE, UMR DYNAFOR, Castanet-Tolosan, France; [5]CNPF-CRPF Occitanie, Toulouse, France; [6]Univ. Grenoble Alpes, INRAE, UR Lessem, 2 rue de la Papeterie, BP76, 38402 Saint-Martin-d'Heres, France; [7]Forest Biometrics Laboratory–Faculty of Forestry, 'Stefan Cel Mare', University of Suceava, Universităii Street, No. 13, 720229 Suceava, Romania; [8]Department of Forest Engineering, Forest Management Planning and Terrestrial Measurements, Faculty of Silviculture and Forest Engineering, Transilvania University of Braş ov, 500123 Braş ov, Romania

Abstract

Assessing the impacts of natural disturbance on the functioning of complex forest systems are imperative in the context of global change. The unprecedented rate of contemporary species extirpations, coupled with widely held expectations that future disturbance intensity will increase with warming, highlights a need to better understand how natural processes structure habitat availability in forest ecosystems. Standardised typologies of tree-related microhabitats (TreMs) have been developed to facilitate assessments of resource availability for multiple taxa. However, natural disturbance effects on TreM diversity have never been assessed. We amassed a comprehensive dataset of TreM occurrences and a concomitant 300-year disturbance history reconstruction that spanned large environmental gradients in temperate primary forests. We used nonlinear analyses to quantify relations between past disturbance parameters and contemporary patterns of TreM occurrence. Our results reveal that natural forest dynamics, characterised

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*Corresponding author; e-mail: kozakd@fld.czu.cz

by fluctuating disturbance intervals and variable severity levels, maintained structurally complex landscapes rich in TreMs. Different microhabitat types developed over time in response to divergent disturbance histories. The relative abundance of alternate TreMs was maximised by unique interactions between past disturbance severity and elapsed time. Despite an unequal distribution of individual TreMs, total microhabitat diversity was maintained at constant levels, suggesting that spatially heterogeneous disturbances maintained a shifting mosaic of habitat types over the region as a whole. Our findings underscore the fundamental role of natural processes in promoting conditions that maximise biodiversity potential. Strict conservation and management systems that preserve natural disturbance outcomes, including associated biological legacies, may therefore safeguard biodiversity at large scales.

Key words: TreM; disturbance history; primary forests; dendroecology; biodiversity; carpathians.

Highlights

- Natural disturbances generate TreMs, enhancing habitat availability
- TreM diversity did not change in time, alive vs. dead trees show contrasting trends
- Occurrence frequencies of TreM groups differ with disturbance timings and severity

Introduction

Disturbances in Forest Ecosystems

Forest ecosystems that harbour a high proportion of global terrestrial biodiversity are strongly influenced by natural disturbances, local site conditions, and climate (WCSFD 1999; Gustafsson and others 2012). Over the last decades, our understanding of the environmental and short-term effects of natural disturbances has greatly improved (Sousa 1984; Swanson and others 2010; Thorn and others 2017). However, the long-term impact of natural disturbance history of varying frequency and severity in shaping habitat structures for forest biodiversity has rarely been assessed (Mori 2011; Yeboah and Chen 2016). The frequency, size and severity of disturbances are expected to increase with climate change (Seidl and others 2014). The intensification and potential interaction of future disturbance processes highlights an essential need to better understand the impacts of long-term natural disturbance dynamics on habitat availability for forest biodiversity.

TreMs, and Why to Study Their Relationship with Disturbances

The biodiversity of several taxa cannot be easily measured because taxonomic inventories are time consuming and involve specialists; therefore, different indirect approaches and indicators have been developed (Larsson and others 2001) such as ''tree-related microhabitats (TreMs) which are distinct, well delineated structures occurring on living or dead standing trees, that form a particular and essential substrate or habitat for a great number of species from various taxa'' (Larrieu and others 2018). TreMs are gaining increasing attention in forest management, conservation and research and have been widely recognised as important biodiversity indicators in both protected and commercial forests (Bütler and others 2004; Larrieu and others 2018). Although more evidence is needed to describe their relationships with species from many taxonomic groups, in general, a positive correlation between TreMs and local biodiversity has been observed (Larrieu and others 2019; Asbeck and others 2021b). TreMs are generally more abundant and diverse in unmanaged than in managed forests (Winter and Möller 2008; Larrieu and others 2011; Paillet and others 2017; Asbeck and others 2021a) and the main drivers for the occurrence of TreMs at the tree level are diameter (Paillet and others 2017; Kozák and others 2018; Paillet and others 2019), tree status (dead or alive) and tree species (Larrieu and Cabanettes 2012; Kozák and others 2018; Paillet and others 2019; Courbaud and others 2021). In primary forests, tree demography, diameter distribution and mortality are driven by natural disturbance regimes; thus, they might have profound effect on TreM density and diversity. However, this relationship has not yet been well documented (Martin and others 2021).

The Effect of Natural Disturbances on TreMs

Natural disturbances play a key role in shaping the structural heterogeneity of forest ecosystems and habitat provisioning for biodiversity. Standing deadwood and deadwood density formed by disturbances are crucial for the presence of TreMs (Donato and others 2012; Meigs and others 2017). TreMs can be formed by a direct injury (bark loss)

or injuries formed over longer time periods (decay cavities), by both abiotic (fractures in the trunk, fractures of branches, cracks caused by windstorms or in rare cases by lightning strikes) and biotic factors (insect galleries formed by bark–beetles) (Larrieu and others 2018). These injuries can immediately provide habitat opportunities for a great number of species from various taxa (Larrieu and others 2018; Bütler and others 2020). Other TreM types, such as cavities, need more time for development; rot-holes in particular require several decades to several hundreds of years to form (Bütler and others 2020). The presence of dead trees facilitates the occurrence of cavities as well as bark shelters, bark pockets or fungi. Moreover, disturbances also affect forest structure. The time since disturbance and severity of disturbance are good predictors of DBH (diameter at breast height) distribution (Janda and others 2017; Rodrigo and others 2022). Considering the positive correlation of TreM abundance with DBH (Kozák and others 2018; Paillet and others 2019), we hypothesise that disturbance dynamics affect TreM diversity, and that occurrence frequencies of individual TreM groups would respond differently to disturbance characteristics, as the forest provides different conditions (DBH and age distribution, proportion of snags and deadwood) after a disturbance event.

TreMs in Primary Forests

Primary forests, defined as a forest without direct human impacts (Sabatini and others 2018; Mikoláš and others 2019), are of outstanding biological and cultural value (Watson and others 2018). They provide optimal conditions for many endangered and rare species, and they enable us to gain crucial insight into the complex interrelationships between biodiversity and the evolutionary pressures of natural disturbances (Sabatini and others 2018). Recent studies show that primary forests host a greater total richness of TreMs and abundance of some specific types than their managed counterparts (Winter and Möller 2008; Paillet and others 2017; Asbeck and others 2021a). Higher richness of TreMs in primary forests may be explained by the higher occurrence of large and old living trees with crown deadwood and snags, as these habitat trees bear large amounts of TreMs and do not occur in such high numbers in managed forests. Further, primary forests typically consist of heterogeneous conditions as they have high variation in DBH and tree age, which are the result of natural disturbances (Stokland and others 2012). As such, primary forests remain the only places that enable us to gain crucial insight into the complex interrelations between TreMs and long-term natural disturbance histories. In contrast, in managed forest, the constant removal of trees or parts of trees that show ''defects,'' such as exposed sap- and heartwood or crown deadwood created by natural disturbances, provides a hindrance to disentangling the long-term natural disturbance effects on TreMs (Martin and Raymond 2019).

The study settings allowed us to assess a full range of diverse disturbance histories on TreMs occurrence. Using a unique dendroecological disturbance history reconstruction (Schurman and others 2018) from European temperate primary spruce forests across the Carpathian Mts., we examine the relative importance of natural historical disturbance regimes in shaping TreMs occurrence and diversity. For the Carpathian Norway spruce [*Picea abies* (L.) Karst.] forests, mixed-severity disturbance regimes with high variability of severities and frequencies have been identified as the dominant driver of forest dynamics (Svoboda and others 2014; Janda and others 2017; Trotsiuk and others 2014; Schurman and others 2018). The main disturbance agents in temperate Europe are wind and bark–beetle (*Ips typographus*) outbreaks (Temperli and others 2013; Čada and others 2016; Holeksa and others 2017). We addressed three main research questions: (1) How does the disturbance severity and time since the most severe disturbance on a plot level affect TreM diversity? (2) In which development phase (early-seral, mid-seral, late-seral) does TreM diversity reach its peak? (3) Are there any differences in how disturbance severity and time since the most severe disturbance affect occurrence frequencies of individual TreM groups?

Material and Methods

Study Sites

Our study was conducted in primary temperate forests in the Slovak and Romanian part of the Carpathian Mountains, which are amongst the countries with the highest extent of primary forests in continental Europe (Sabatini and others 2018; Mikoláš and others 2019). These forests developed under natural disturbance dynamics and have not been affected by human management over the last century at least, mainly due to montane topography and remote location (Sabatini and others 2018). Primary forests of the Carpathian Mountains are dominated by Norway spruce [*Picea abies* (L.) Karst.]. Admixed tree species, such as fir (*Abies*

alba Mill.), rowan (*Sorbus aucuparia* L.), pine (*Pinus cembra*), beech (*Fagus sylvatica*) and birch (*Betula* spp.) were present only on some plots. The climate of the Carpathians is broadly classified as cool-humid, with mean precipitation of 1100 mm and mid-altitude (1000 m a.s.l.) annual temperatures of 4.5°C over the past half a century (Spinoni and others 2015).

We conducted our research in 13 forest stands in Slovakia and 13 stands in Romania (Table 1; Figure 1). We collected data from 297 permanent circular research plots with an area of 1000 m^2 (17.84 m radius from the plot centre). The plots were established in selected polygons of primary forests using a stratified random design (Svoboda and others 2014). All the plots are part of a long-term research network studying natural forest dynamics in primary forests (Remote Primary Forest 2021). Within each plot, positions of all living and dead trees > 60 mm in diameter at breast height (DBH) were recorded using a laser rangefinder with compass and customised software Field-Map (Field-Map; Monitoring and Mapping Solutions, Jílové u Prahy, Czech Republic).

TreM Survey

We visually inspected every standing dead or live tree on a plot with DBH greater than 60 mm for TreM presence based on typology by Larrieu and others (2018) which consists of 15 groups (for example, woodpecker breeding cavities) and 45 types (Table 2). In further analysis, we worked only on a group level to have sufficient statistical power. In total, we inspected 22,108 trees and quantified TreM diversity and abundance for each plot. Diversity was defined as TreM richness, that is, the number of TreM groups occurring in a plot. Abundance was recorded for every TreM group individually and was defined as a number of trees on a plot bearing a given TreM group.

Table 1. Characteristics of the Study Area

Country	Location	Stand	*n* plots	Mean *n* of trees per plot	TreMs		Time since (years)			Severity (% CA)		
					Mean richness	Mean abundance	Min	Max	Mean	Min	Max	Mean
Romania	Fagaras	1	12	85.2	7.9	106.2	42	227	120.2	21	74	41.3
		2	12	89.1	8.3	169.9	47	227	147.7	23	94	48.8
		3	12	86.1	9.2	171.8	52	200	142.3	22	72	48.3
		4	12	88.2	9.3	159.2	4	236	141.1	19	76	34.9
		5	12	66.2	7.8	121.3	98	215	152.1	35	100	53.0
		6	13	93.8	8.2	118.6	36	187	124.3	20	91	40.0
		7	12	58.7	8.7	105.0	1	191	147.0	17	49	36.7
		8	11	74.4	7.7	105.0	6	120	90.3	23	80	49.8
		9	12	91.3	8.2	151.8	81	141	103.3	27	73	48.0
		10	12	75.8	8.3	157.3	104	252	148.6	22	92	55.3
	Giumalau	11	11	97.1	8.6	128.2	39	258	153.7	23	60	38.6
		12	22	91.5	8.0	91.1	2	315	113.0	22	83	48.2
		13	13	81.7	8.8	142.0	2	202	131.3	24	97	56.4
Slovakia	High Tatras	14	5	89.2	8.8	133.0	3	170	69.6	17	97	62.6
		15	9	60.9	9.0	113.8	3	84	13.2	29	98	68.4
		16	8	74	10.0	178.8	3	196	66.4	24	100	58.1
		17	7	83.1	7.6	101.3	3	151	83.4	19	96	36.9
		18	7	65.4	9.1	173.3	7	194	111.6	23	85	42.4
		19	14	60.2	7.6	93.6	2	217	101.1	21	98	40.1
		20	10	96.5	8.8	109.2	8	139	67.8	31	62	49.4
	Low Tatras	21	10	55.2	9.5	64.5	3	149	75.4	24	72	37.5
		22	15	61.1	8.5	86.8	3	195	140.5	21	67	40.5
	Great Fatra	23	25	43.9	8.6	55.8	3	269	123.9	18	92	41.0
		24	5	34.6	9.8	69.0	1	147	59.2	32	93	66.2
	Orava Beskids	25	6	35	9.7	74.3	3	198	91.2	17	93	42.3
	Polana	26	5	81.6	10.4	229.0	99	154	127.8	32	95	58.2

CA: canopy area removed by disturbance as a percent of the total canopy area of the stand.

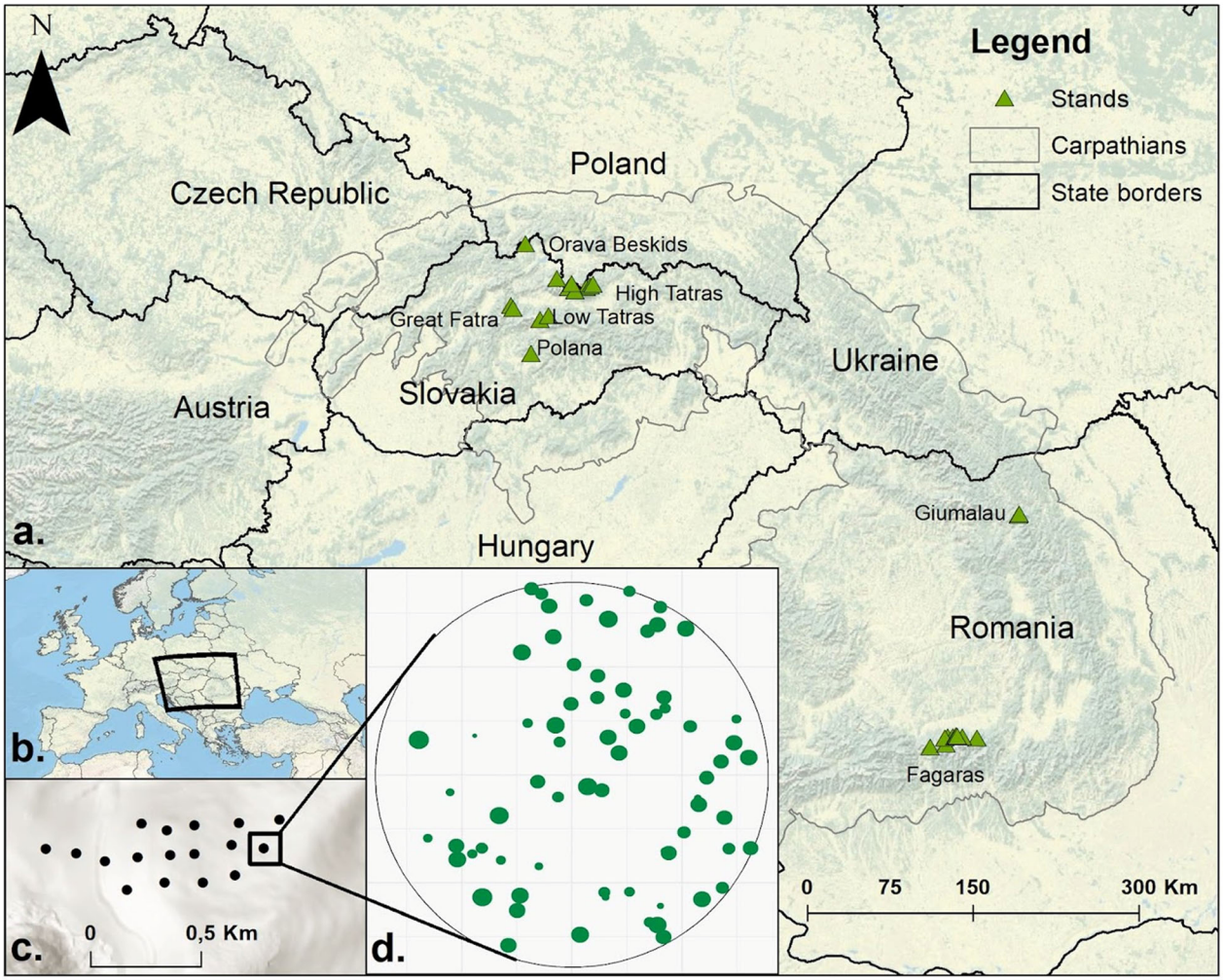


Figure 1. **a** Map of the research area indicating the location of the study sites. Stands are represented by *green triangles*. **b** Inset map shows a study region within Europe represented by a *black bounding box*. **c** Example arrangement of plots within one stand. **d** Example arrangement of trees within one plot.

Disturbance Characteristics

Disturbance history was reconstructed using increment cores collected from the permanent study plot network. The derived chronologies provided data for approximately the last 250 years. The increment cores were collected from 25 trees selected randomly from the non-suppressed living trees with DBH at least 10 cm in each plot, 1 m above the ground and processed for laboratory analysis. The tree-ring widths were measured with the LintabTM sliding-stage measuring device (Rinntech, Heidelberg) with a resolution of 0.01 mm. Cores were visually cross-dated and verified using COFECHA (Holmes 1983). The reconstruction of disturbance events was based on the assumption that disturbance processes affect levels of neighbourhood competition and resource supply, and hence, growth responses in extant individuals (Svoboda and others 2014). Statistically anomalous tree growth variation exceeding site-specific thresholds and sustained over minimum pre-defined temporal intervals was attributed to disturbance-driven gap formation events (Frelich 2002; Trotsiuk and others 2014). Severity of the disturbance event was then defined in terms of the proportional area of tree canopy removed. An estimate of the canopy area removed was calculated using regression methods and allometric equations relating the aggregate present-day size of tree responders (individuals with a disturbance signal) to the original extent of the disturbance-induced canopy gap (Lorimer and Frelich 1989). For each plot we, identified the main disturbance as the event with the maximum severity (proportion of canopy area disturbed). Number of years since

Table 2. TreM Typology Used in This Study Based on Larrieu and Others (2018)

TreM group	Type
Woodpecker breeding cavities	Small, medium, large woodpecker breeding cavities and woodpecker flute
Rot-holes	Trunk base rot-hole, trunk rot-hole, semi-open trunk rot-hole, chimney trunk base rot-hole, chimney trunk rot-hole and hollow branch
Insect galleries	Insect galleries and bore holes
Concavities	Dendrotelm, woodpecker foraging excavation, trunk bark-lined concavity and root-buttress
Exposed sapwood only	Bark loss, fire scars, bark shelter and bark pockets
Exposed sapwood and heartwood	Stem breakage, limb breakage, crack, lightning scar and fork split at insertion
Remaining broken limb	Remaining broken limb
Twig tangles	Witch broom, epicormic shoots
Burrs and cankers	Burr, canker
Perennial fungal fruiting bodies	Perennial polypore
Ephemeral fungal fruiting bodies and slime moulds	Annual polypore, pulpy agaric, large pyrenomycetes and myxomycetes
Epiphytic and parasitic crypto- and phanerogams	Bryophytes, lichens, ivy and lianas, ferns, mistletoe
Nests	Vertebrate and invertebrate nest
Microsoils	Bark and crown microsoil
Exudates	Sap run and heavy resinosis

the main disturbance was calculated by subtracting the year of this event from the year of data collection. 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. Relative current canopy openness was calculated as the difference between mean canopy closure of the whole dataset and current canopy closure of a given plot (Bače and others 2017). Time since these recent disturbances was calculated based on the decay stage (Aakala and others 2006) of the majority of standing dead trees on a plot as an average estimated time since death for individual stages as the year of the measurement minus 1 year for trees with status 1 (recently dead, there are small twigs with leaves), 3 years for trees with status 2 (recently dead, there are small twigs without leaves) or 5 years for trees with status 3 (small twigs not visible, but big branches are present) (unpublished data, Bače). We defined disturbance events as ''low severity'' (characterised by events severity below 40%), ''moderate severity'' (between 40 and 60%) and ''high severity'' (affecting more than 60% of canopy trees) (Janda and others 2017). For detailed disturbance characteristic descriptions and calculations, we refer readers to Appendix 1 and Čada and others (2020).

Data Analysis

Generalised additive mixed models (GAMMs, Wood 2017) were used to test the effect of time since maximum disturbance and severity on the TreM profile (TreM diversity and TreM occurrence frequencies of individual TreM groups) in the forest plots. We treated stand identity as a random effect in the models to account for the hierarchical design of the study (that is, plots nested within stands). The TreM diversity (number of TreM groups occurring on a plot for total, alive and dead trees) was used as a response variable in GAMM with gaussian error distribution and logarithmic link function. The occurrence of individual TreM groups was modelled as binomial frequencies (proportion of trees bearing a given group out of all trees sampled in a plot) with a logit link function. Thin plate regression splines were used as base smoothers in the GAMMs (Wood 2003). We examined diagnostic plots of residuals to check the performance of the models. Because the dispersion parameters of some binomial GAMMs deviated from one, the standard errors of these models were estimated by a quasi-likelihood procedure. The analysis was performed in R v. 3.6.1 (R Core Team 2019) using the libraries DHARMa (Hartig 2022) and mgcv (Wood 2017).

Results

TreM Diversity

The diversity of TreM groups was significantly influenced by time since the maximum disturbance for both live and standing dead trees. Alive trees showed contrasting trend compared to dead trees. Whilst total TreM occurrence on living trees had a U-shaped response to time since disturbance, being highest early after a disturbance and then in late-seral development phases, TreMs diversity on standing dead trees increased after a disturbance event and subsequently fluctuated in the mid development phases. The total number of TreM groups did not significantly change through (Table 3; Figure 2). Recently disturbed plots showed diversity comparable to those disturbed later than 150 years ago. We found a significant relationship with disturbance severity and number of TreM groups for live trees; diversity increased marginally with severity. For total and dead trees, the relationship with severity was not significant (Table 3; Figure 2).

Occurrence Frequencies of Individual TreM Groups

Amongst the 15 investigated TreM groups, the probability of the occurrence of ten groups was significantly influenced by time since maximum severity disturbance and/or severity of that event (Table 3). The highest occurrence frequencies were more or less evenly distributed in the disturbance space (Figure 3). Only insect galleries and exposed sapwood followed a similar pattern with severity, reaching the highest occurrence frequencies in strongly disturbed forest plots. For insect galleries, time was also significant, and the highest occurrence frequencies was reached either in recently disturbed plots, or plots disturbed around 250 years ago. Ephemeral and perennial fungal fruiting bodies followed a similar pattern with time; they had higher occurrences in recently disturbed plots and another peak 140 and 200 years ago, respectively. The different fungal groups also differed in their response to disturbance severity, with ephemeral fungal fruiting bodies occurring most often at low severities, whilst perennial fungal fruiting bodies were more frequent at moderate severities. Nests

Table 3. Summary of GAMMs Testing for the Effect of Time Since Max. Disturbance and Severity of that Event on TreM Groups Diversity and on Occurrence Frequency of TreM Groups in Forest Plots

	Time since maximum disturbance			Maximum disturbance severity			Stand		
Variable	edf	x^2/F	p	edf	x^2/F	p	edf	x^2/F	p
TreM diversity									
Total	1.00	1.693	0.194	1.00	2.361	0.126	**19.51**	**3.020**	**< 0.001**
Alive	**7.79**	**2.877**	**0.003**	**1.28**	**12.247**	**< 0.001**	**18.72**	**2.487**	**< 0.001**
Dead	**2.45**	**5.73**	**< 0.001**	2.03	0.78	0.401	**19.63**	**3.40**	**< 0.001**
Occurrence frequencies									
Woodpecker breeding cavities	1.00	0.416	0.5196	**1.00**	**4.014**	**0.0461**	**20.66**	**7.117**	**< 0.001**
Rot-holes	1.00	2.515	0.114	1.86	2.192	0.140	**19.86**	**5.174**	**< 0.001**
Insect galleries	**4.50**	**8.718**	**< 0.001**	**1.00**	**29.336**	**< 0.001**	**19.90**	**4.108**	**< 0.001**
Concavities	**2.32**	**3.530**	**0.021**	1.00	1.457	0.228	**12.04**	**1.112**	**< 0.001**
Exposed sapwood only	1.00	1.696	0.194	**1.00**	**7.609**	**0.006**	**18.44**	**3.017**	**< 0.001**
Exposed sapwood and heartwood	1.00	0.719	0.397	1.56	1.069	0.337	**15.30**	**1.883**	**< 0.001**
Remaining broken limb	1.00	2.025	0.156	1.00	0.600	0.439	**19.48**	**1.815**	**< 0.001**
Twig tangles	1.00	3.737	0.054	1.00	1.620	0.204	16.73	0.942	0.107
Burrs and canker	1.00	0.727	0.394	**1.00**	**14.260**	**< 0.001**	**15.66**	**49.293**	**< 0.001**
Perennial fungal fruiting bodies	**4.90**	**34.20**	**< 0.001**	**2.49**	**10.87**	**0.014**	**20.72**	**127.19**	**< 0.001**
Ephemeral fungal fruiting bodies	**3.81**	**2.501**	**0.038**	**1.00**	**4.814**	**0.029**	**18.43**	**5.217**	**< 0.001**
Epiphytic and parasitic crypto- and phanerogams	**3.09**	**4.569**	**0.001**	1.00	3.745	0.054	**20.69**	**5.582**	**< 0.001**
Nests	**4.75**	**18.833**	**0.003**	**1.00**	**4.645**	**0.031**	**14.54**	**50.723**	**< 0.001**
Microsoils	2.05	2.678	0.092	1.00	0.091	0.764	**20.33**	**4.903**	**< 0.001**
Exudates	**5.45**	**3.698**	**0.001**	**1.00**	**14.286**	**< 0.001**	**19.49**	**4.391**	**< 0.001**

The effective degrees of freedom (edf), test statistics (F/χ^2) and probabilities (p) are displayed. Results significant at $\alpha = 5\%$ are highlighted in bold. Note that the stand identity ($n = 26$) was treated as a random effect in the models.

were typical for recent, low-severity disturbances with another peak about 170–200 years ago. Exudates also had the highest occurrence frequencies with low severities and had two peaks representing disturbances that occurred 50–60 years ago and 250–260 years ago. Concavities and epiphytic and parasitic crypto- and phanerogams reached the highest frequencies on plots disturbed about 100–150 years ago. Finally, woodpecker breeding cavities and burrs and cankers occurred most frequently on plots disturbed by low severities.

Discussion

We conducted the first empirical study on the relationship between present-day TreM profile (frequencies and diversity) and natural disturbance history of European spruce primary forests. Our results show that natural forest dynamics characterised by variable disturbance severities, their timing and multiple successional pathways maintained forest landscapes rich and diverse in tree-related microhabitats. Whilst total TreM groups diversity was not significantly affected by disturbance history in the primary forests, the effect of disturbance severity and timing differed significantly amongst live and dead trees and particular TreM groups.

Figure 3. Predicted occurrence frequencies (isolines) of ten TreM groups along the gradients of maximum disturbance severity and time since that event. Occurrence frequencies are predicted by significant GAMMs. For model details see Table 3 (miniatures of TreMs are courtesy of Kraus and others 2016).

Effect of Natural Disturbance on Total Trem Diversity

Despite the contrasting trends of TreM diversity between living trees, which followed similar trends as found in previous studies from primary forests (Martin and others 2021), and dead trees, the total diversity of TreMs did not significantly change in time, which is in accordance with results by Larrieu and others (2014). As we analysed the total TreM diversity at the plot level, the sharp increase in diversity in the initial phase after a disturbance amongst dead trees can be explained by an increase in the number of dead trees, and conversely, the decline of TreMs amongst live trees was caused by the decline in the number of living trees. This interesting pattern maintains balanced TreMs diversity across different developmental phases in the primary forests and shows that high biodiversity potential and complexity may persist through

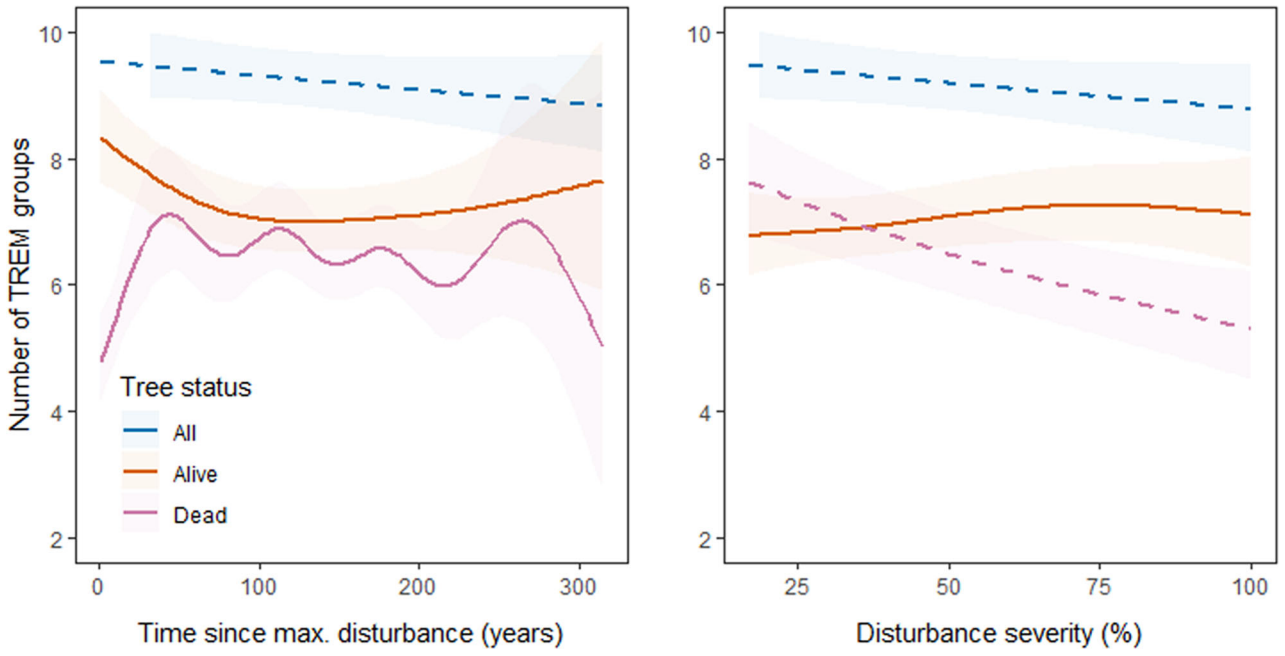
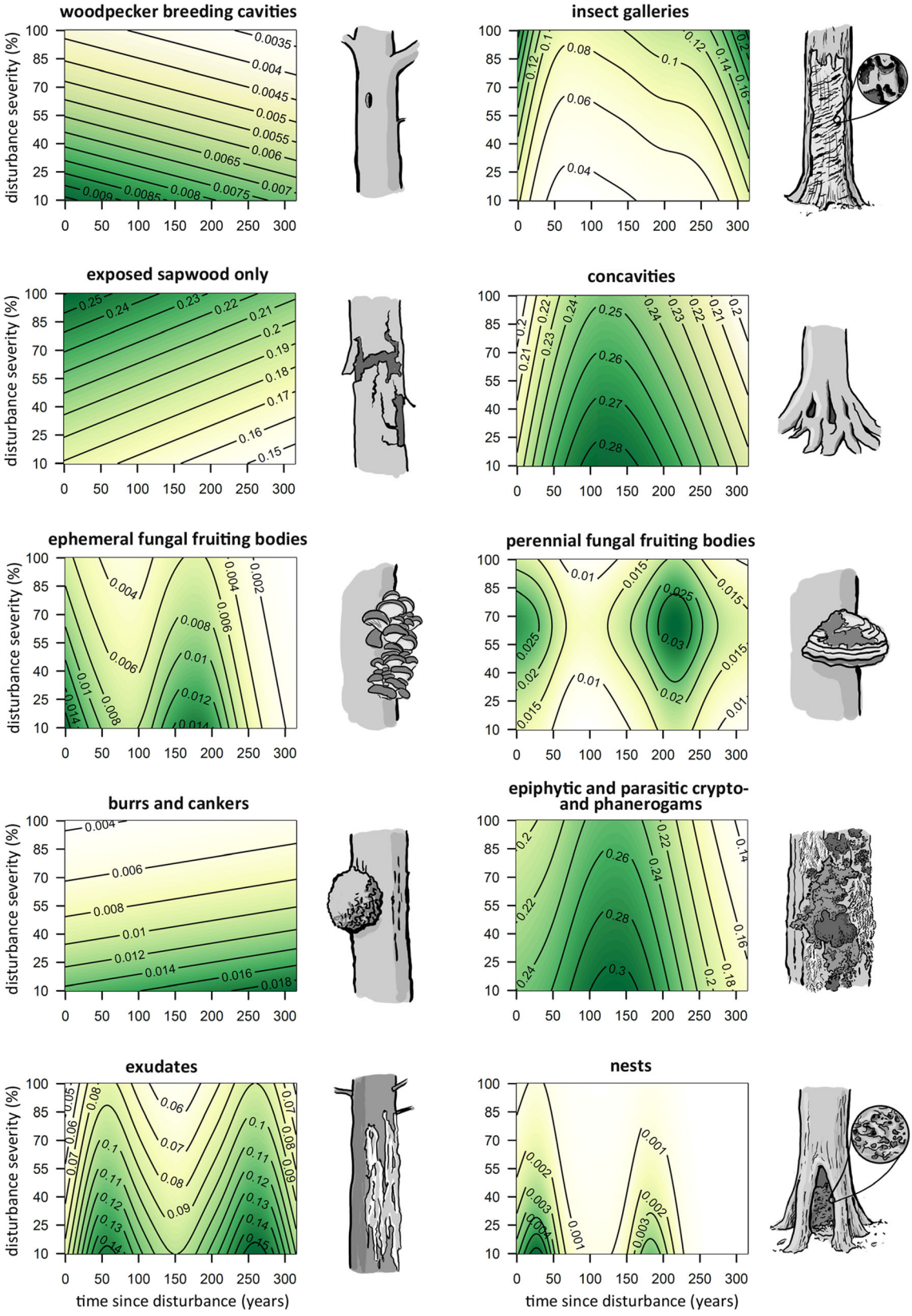


Figure 2. Result of GAMM showing relationships between the diversity of TreM groups, time since the most severe disturbance and disturbance severity (% canopy area removed). Predicted diversity (line) is displayed along with 95% confidence intervals (band). Significant relationships ($p < 0.05$) are represented by *solid lines* and non-significant relationships by *dashed lines*.


woodpecker breeding cavities
insect galleries
exposed sapwood only
concavities
ephemeral fungal fruiting bodies
perennial fungal fruiting bodies
burrs and cankers
epiphytic and parasitic crypto- and phanerogams
exudates
nests
disturbance severity (%)
time since disturbance (years)

natural forest development after disturbances (Donato and others 2012; Meigs and others 2017).

Disturbance severity had a significant effect on TreM diversity for live trees, whilst there was no significant pattern found for total and dead trees. This observed pattern might be explained by the natural disturbance regime of the studied primary forests. The studied area (the Carpathian Mountains) is characterised by a mixed-severity disturbance regime with predominant low and moderate disturbance severities (Janda and others 2017). The mean disturbance severity in our dataset varies from 34.9 to 68.4% between stands and moderate severity disturbance are the most frequent disturbance types. Moderate severity disturbances leave behind complex forest structures, including a significant number of standing mature live and dead trees (Čada and others 2020) bearing high TreMs diversity. They also cause injuries on remaining trees that could further develop into TreMs. The highest TreM abundance and diversity on the tree level are typically found on snags and large trees (Paillet and others 2017; Kozák and others 2018; Paillet and others 2019). Due to prevalence of moderate severity disturbances in the studied areas and the lack of stand-replacing disturbance events that cause mortality of almost all trees, the diversity of TreMs did not significantly change with disturbance severity. However, the effect of natural disturbances on occurrence frequencies differs between individual TreM groups.

Effect of Natural Disturbance on TreM Groups Occurrence Frequencies

To fully understand the effect of natural disturbance on TreM diversity and occurrence, it was essential to show the individual responses of particular TreM groups, as each of them represents essential habitats for different forest-dwelling organisms. Here, not only the effect of disturbance timing but also the effect of disturbance severity played an important role.

Low Severity

(1) Burrs and cankers occurred on plots disturbed with low severities. For the creation of these structures, the tree has to survive the disturbance, and the occurrence rate increases with DBH (Courbaud and others 2021). Comparably we observed the highest occurrence frequencies on plots disturbed with low severities for (2) woodpecker breeding cavities. They are often present on snags or large living trees. The key significance of tree suitability for woodpeckers depends on DBH, tree age and fungal decay that soften the wood (Newton 1994; Jackson and Jackson 2004; Bütler and others 2004; Basile and others 2020). Similarly, we observed co-occurrence pattern with conks of fungi, which was observed also by Larrieu and others (2022).

Low Severity and Two Peaks in Time

(3) Nests, which consist of vertebrate and invertebrate nests, occur in the highest frequencies in recently disturbed plots with low severities, as they can be destroyed by high severity events. The second peak occurred about 170–200 years after the disturbance event, which can be linked with the presence of senescent, large trees. Similarly (4) exudates occur in plots disturbed with low severities and can be formed by subsequent disturbances with even lower severities, such as a single tree fall that injures other trees that remain alive. (5) Ephemeral fungal fruiting bodies and (4) perennial fungal fruiting bodies were significantly related to time and severity of disturbances. They follow a similar pattern with time and are most frequent right after a disturbance event, when trees can be infected after bark injury caused by a disturbance; thus, both groups profit from new substrate availability. The other peaks occur 140 and 200 years, respectively, after the disturbance event, which may be explained by mortality of senescent trees that survived the disturbance. However, the groups differ in relationship with severity. As a group of ephemeral fungal fruiting bodies covers a wide range of fungi groups with different ecological demands (Pouska and others 2010; Holec and others 2020), the higher occurrence can therefore indicate the higher heterogeneity of conditions caused by low severity disturbances. On the other hand, maximum occurrence of perennial fungal group represented only by perennial polypores after moderate severity disturbance (55–85%) can be a response to more homogenous conditions created by disturbance as the perennial polypores group is in spruce stands dominated by *Fomitopsis pinicola*, which is the common species in disturbed forests and occurrence of its fruiting bodies decreases with ongoing decay process (Pouska and others 2011, Bässler and others 2015; Holec and others 2020).

Time

(7) The group concavities consist mainly of root-buttress concavities in our dataset; they are formed on trees with roots large enough to bear such TreM (Chiatante and others 2002; Courbaud and others 2021). The highest occurrence frequency was found about 80–170 years after the most severe disturbance. That can be explained by the fact that

they are not formed directly by disturbance, but need the presence of large trees as they are more abundant on trees with higher DBH (Asbeck and others 2021b). (8) Epiphytic and parasitic crypto- and phanerogams represented mainly lichens and mosses whose frequencies were highest 100–170 years after disturbance. According to (Tanona and Czarnota 2022), the presence of natural forest disturbances increases lichen diversity in Carpathian spruce forests. After a short-term period of stabilisation following a disturbance event, the diversity of lichens increases. Due to the slow growth rate that is typical for lichens, they need enough time to gain significant size. Bryophyte diversity is mainly dependent on microclimatic conditions, with epixylic bryophyte abundance supported by a dense canopy closure (Raabe and others 2010) therefore, the abundance may be lower immediately after disturbance.

High Severity

(9) Insect galleries reached an occurrence frequency maximum right after a disturbance event with high severity; the second peak occurred after 250 years. The second peak around 250 years after the most severe disturbance might be connected to another less severe disturbance event that may have affected the trees that survived the most severe one. Their formation is relatively rapid and require just several years to develop. Bark–beetle outbreaks are one of the most important disturbance agents in Carpathian spruce forests (Temperli and others 2013). As the development of insect galleries is very quick (Bütler and others 2020), these injuries can further develop in other TreMs. (10) Exposed sapwood followed a similar pattern; however, we found a significant relationship with disturbance severity only. The high abundance of TreM types such as bark pockets and bark shelters is associated with insect outbreaks and the presence of snags. The fall of trees caused by windthrows can also cause superficial tree injuries leading to exposed sapwood TreMs such as bark loss.

No significant effect was found for the rest of the groups, which may be due in part to a lack of data for TreM groups which are rare (twig tangles) or not very common (rot-holes, exposed sapwood and heartwood) in spruce forests, or there is no presumption of relationship with disturbances and post-disturbance development.

Study Limitations

While our statistical analyses relied on established approaches, our study has some limitations that require mentioning. Firstly, while calculating the disturbance history characteristics, we are not able to distinguish between the drivers of disturbances (wind or bark–beetle). Secondly, we are not able to infer the most recent (cca 20–30 years) disturbances from tree cores; therefore, we calculated them as a proportion of the current canopy openness of standing dead trees, not taking in account uprooted ones. Moreover, we only considered disturbance events of maximum severity and time since such an event; thus, if any disturbances of similar severity occurred before or after the maximum severity event, their influence on TreM profile was not taken into account. Lastly, the disturbance history in this dataset dates back approximately 250 years. The maximum time since the most severe disturbance is 315 years. The majority of data in this dataset is within the interval of 0–250 years. Therefore, the 250–300-year interval may be less reliable.

Implications for Conservation and Management

Although our study focused on TreMs, our findings are relevant for the conservation of many other species. Primary forests are essential for providing habitats for forest-dwelling species through high richness and diversity of TreMs (Paillet and others 2018); however, their profile is dynamic and follows the long-term disturbance patterns. Distribution of highest TreM occurrence frequencies in forest development phases changes between individual groups, and therefore, the habitat availability may change for different taxa. For example, TreMs developed right after a disturbance event such as insect galleries provide habitats for bats, birds (Kameniar and others 2021), beetles and other invertebrates (Bütler and others 2020). In the mid-seral development stage, the highest TreM density was observed for groups of concavities and epiphytes that support various birds, amphibians, rodents, mustelids or invertebrates. In the late-seral phases and in low-severity disturbed plots, woodpeckers and fungi—the TreM groups that occur most frequently—enhance biodiversity itself but also provide opportunities for secondary inhabitants of cavities such as smaller birds, bats or parasites (Kraus and Krumm 2013; Robles and Martin 2014). Forest development driven by long-term natural disturbances leads to the balanced distribution of habitat availability in time in all forest development phases across large scales (Thorn and others 2017; Hilmers and others 2018; Mikoláš and others 2021). The mosaic of these different phases

at the forest scale then ensures the persistence and diversity of species across forest landscapes, providing the primaeval remnants are large and numerous enough to exhibit the majority of developmental phases (Seidl and Turner 2022). Our results thus show that all natural disturbance severities (that is, high, moderate, and low) across different time scales are necessary to maintain full variation of TreMs and highlight the importance of spatial and temporal scales to achieve the presence and sufficient quality of biodiversity habitats.

Conclusions

Our results reaffirm the critical role of historical processes in shaping landscape patterns of habitat suitability for dependent and niche-specialised forest organisms (Mikoláš and others 2021). We found that the fluctuation of disturbance activity over long time frames is correlated with the development, abundance and variety of available microhabitats. Heterogeneous disturbance dynamics maintain a constant supply and diversity of TreMs at large spatial scales, leading to patchiness in habitat availability which fosters high biodiversity potential. We suggest that efforts to address biodiversity losses in forests should focus on the establishment and maintenance of complex, multilayered canopy structures, rather than solely on species composition. The effect of disturbance severity and timing on TreM groups differed significantly among live and dead trees and particular TreM groups, highlighting the importance of considering both the severity and timing of disturbances in assessing their impact on forest biodiversity and TreM distribution. Thus, management strategies, such as live-tree retention, designed to enhance habitat for non-commercial species (Kraus and Krumm 2013; Bütler and others 2013) will be unlikely to replicate levels of TreM diversity that evolve as a consequence of complex stand dynamics in natural systems, as demonstrated here. We suggest efforts to address biodiversity loss in forests should focus on the establishment of larger reserves or non-intervention zones where natural processes and successional pathways predominate.

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