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Historical Disturbances Determine Current Taxonomic, Functional and Phylogenetic Diversity of Saproxylic Beetle Communities in Temperate Primary Forests

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ABSTRACT

The expected future intensification of forest disturbance as a consequence of ongoing anthropogenic climate change highlights the urgent need to more robustly quantify associated biotic responses. Saproxylic beetles are a diverse group of forest invertebrates representing a major component of biodiversity that is associated with the decomposition and cycling of wood nutrients and carbon in forest ecosystems. Disturbance-induced declines or shifts in their diversity indicate the loss of key ecological and/or morphological species traits that could change ecosystem functioning. Functional and phylogenetic diversity of biological communities is commonly used to link species communities to ecosystem functions. However, our knowledge on how disturbance intensity alters functional and phylogenetic diversity of saproxylic beetles is incomplete. Here, we analyzed the main drivers of saproxylic beetle abundance and diversity using a comprehensive dataset from montane primary forests in Europe. We investigated cascading relationships between 250 years of historical

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disturbance mechanisms, forest structural attributes and the taxonomic, phylogenetic and functional diversity of present-day beetle communities. Our analyses revealed that historical disturbances have significant effects on current beetle communities. Contrary to our expectations, different aspects of beetle communities, that is, abundance, taxonomic, phylogenetic and functional diversity, responded to different disturbance regime components. Past disturbance frequency was the most important component influencing saproxylic beetle communities and habitat via multiple temporal and spatial pathways. The quantity of deadwood and its diameter positively influenced saproxylic beetle abundance and functional diversity, whereas phylogenetic diversity was positively influenced by canopy openness. Analyzing historical disturbances, we observed that current beetle diversity is far from static, such that the importance of various drivers might change during further successional development. Only forest landscapes that are large enough to allow for the full range of temporal and spatial patterns of disturbances and post-disturbance development will enable long-term species coexistence and their associated ecosystem functions.

Key words: Disturbance processes; Climate change; Ecological traits; Phylogenetic diversity; Primary forest; Carpathians; Coleoptera.

HIGHLIGHTS

- Disturbance history determines current beetle diversity
- Deadwood amount and canopy openness play key roles
- Diversity measures respond to different disturbance characteristics
- Disturbance effects are diverse across temporal scales

INTRODUCTION

Anthropogenic climate change is expected to have substantial effects on future disturbance frequency and severity in Europe (Seidl and others 2011). The frequency, size and severity of disturbances are expected to increase with climate warming. Changes in disturbance regimes have the potential for both positive and negative effects on forest biodiversity and associated ecosystem function varying by species and their habitat preferences (Thom and others 2017). Scenarios may arise in which forest stands are impacted by multiple contemporaneous or synchronous events such as windthrows and subsequent insect outbreaks (Kulakowski and others 2011). The intensification and potential interaction of future disturbance processes highlights a critical need to better understand associated biotic responses, particularly relationships between species diversity and ecosystem functions (Loreau and others 2001; Thom and Seidl 2016).

Mixed-severity disturbances, characterized by substantial heterogeneity in frequency, size and severity, are predominant in temperate forest ecosystems of Europe (Nagel and others 2014). These processes strongly influence the physical attributes, light environment and associated species composition of forest ecosystems (Hanson and Lorimer 2007). Disturbances create key elements of forest structural complexity, such as canopy gaps, snags, habitat trees and forest-floor deadwood, which in turn provide a range of habitat substrates for specialized organisms including saproxylic insects (Lachat and others 2016). However, the abundance, distribution and persistence of these habitat features, often referred to as legacies of disturbance, are not static but continuously shaped by ongoing successional processes. A complex interplay of disturbance and succession generates an array of habitat conditions that may potentially support a diverse assemblage of invertebrate fauna ranging from early successional species adapted to high-light conditions (Franklin and others 2000) to late-successional, shade-tolerant taxa (Spies and others 2006).

Saproxylic beetle species are a functionally vital constituent of forest invertebrate communities. Many indicator species, due to their obligate and highly specified associations with particular substrate types (Grove 2002), and endangered taxa are only found in primary, unmanaged forests (Lachat and Müller 2018) suggesting a dependence on structural legacies created by intermittent disturbance events. Saproxylic species are, by definition, associated with decay processes and are thus dependent on the availability of deadwood (Alexander 2008). However, the assemblage of saproxylic beetle species at a given site varies according to the physical characteristics of available wood substrates, including size, density, volume and their spatial distribution (Lassauce and others 2011; Stokland and others 2012; Lachat and others 2016). Further, beetle species are differentially adapted to utilize deadwood in varying stages of decomposition (Ulyshen and Hanula 2009; Stokland and others 2012). They are additionally segregated by variation in understory light availability (Lindhe and others 2005). This divergence in habitat preferences indicates that beetle communities are dynamic, changing with stand age and the length of disturbance intervals.

Saproxylic beetle populations make up an important component of trophic food webs and provide an array of essential ecosystem functions including organic matter decomposition and nutrient cycling (Stokland and others 2012). As a consequence of trophic interactions, these functions may ultimately affect site productivity and regional-scale carbon budgets. The specific scope of functions provided by saproxylic beetles depends on the species composition of the respective communities (Pielou 1966). A single species can have strong effects on ecosystem processes by directly mediating energy and nutrient fluxes or by altering abiotic conditions that regulate the rate of these processes (Chapin and others 2000). Evidence suggests that a diverse assemblage of species is required to maintain ecosystem functions (Tilman 2001; Cadotte and others 2009) through either an aggregation of complementary traits associated with multiple taxa, or by functions provided by the presence of a few key species recruited from a regional species pool (Loreau and others 2001). In either case, the provision of ecosystem functions is related to phenotypical trait characters (Tilman 2001; Cadotte and others 2013). Phenotypes are determined, in part, by an individual's environment, but are also an expression of evolutionary ancestry. Thus, in studies exploring relationships between species richness and ecosystem processes, phylogenetic diversity is often used as an indicator and surrogate for the breadth of ecosystem functions provided by a taxonomic group (Ding and others 2012).

Relationships between species diversity, ecosystem functions, and abiotic factors constitute a major research challenge due in part to extensive data requirements (Seibold and others 2016a, b). Significant associations between the extant structural heterogeneity of forests and saproxylic beetle diversity have been previously established (for example, Gossner and others 2013; Seibold and others 2016a, b; Thorn and others 2018a). However, the more complex, long-term and dynamic effects of fluctuating resource availability driven by disturbance interactions with forest structure are less clear. A limited number of studies have documented short-term, decadal-scale effects of disturbance on beetle communities (Müller and others 2008; Winter and others 2015; Beudert and others 2015), but their limited temporal depth constrains the generality of those results.

The overall objective of this study was to determine the long-term, potentially interactive effects of forest disturbance and variation in stand structure on the taxonomic, functional and phylogenetic diversity of associated current saproxylic beetle communities. As disturbance processes potentially exert multiple direct and indirect effects on beetle populations, we collected a comprehensive, large-scale dataset quantitatively describing beetle community demography, structural characteristics of forest stands and the associated, centuries-long disturbance history of the surveyed primary forest locations. Tree core samples and dendrochronological analyses were used to quantify various aspects of past disturbance spanning an approximate 250-year period. We sampled current beetle communities using insect traps and identified the taxonomic composition of samples. We compiled data describing corresponding ecological traits and generated a phylogeny for the sampled communities and calculated functional and phylogenetic diversity indices. We restricted data collection to primary forests in montane regions of central Europe. As natural disturbance regimes are still prevalent in these systems (Svoboda and others 2012), we assume that statistical analyses are not confounded by management effects. Further, inferences gained from primary forests may serve as baseline data with which to assess biotic responses in other systems (Kuuluvainen and Aakala 2011; Kulakowski and others 2017).

We investigated evidence for three specific hypotheses: (1) Attributes of the long-term disturbance regime modulate the taxonomic, functional and phylogenetic composition of current beetle communities. (2) Fluctuating, nonsynchronous disturbance processes modulate current beetle populations by generating a spatial mosaic of forest conditions characterized by variable light environments and heterogeneous reservoirs of deadwood. Specifically, forest structure as the result of disturbance timing, severity and frequency in the past determine beetle taxonomic diversity. (3) Variability in the abundance, size and characteristics of deadwood along with heterogeneous light environments—both of which are legacies of the most recent disturbance event—determine the composition and diversity of current beetle communities due to niche specialization among divergent taxa irrespective of the historical disturbance regime.

MATERIALS AND METHODS

Study Area

The study region was restricted to primary forests in the Slovakian portion of the Western Carpathian Mountains (Fig. 1; 48° 63′–9° 52′ N latitude, 19° 30′–20° 12′ E longitude). The Carpathian region supports a substantial component of all remnant primary forest area in Europe (Sabatini and others 2018; Mikoláš and others 2019). The climate is continental with four distinct seasons and a notably absent dry period. Annual precipitation ranges from 1205 to 1365 mm yr^{-1}, which is approximately evenly distributed across seasons. Mean annual temperatures range from 1.6 to 3.4°C. Field surveys were limited to high-elevation areas (1244 to 1534 m) that are occupied by broadly monodominant *Picea abies* (L.) Karst. (Norway spruce) forest. Minor tree species, in terms of abundance, include *Sorbus aucuparia* L.(rowan), *Abies alba* Mill. (silver fir), *Fagus sylvatica* L. (European beech) and *Acer pseudoplatanus* L. (sycamore maple).

Disturbance regimes are highly variable in terms of standard metrics of severity, size and return intervals (Janda and others 2017). Low- and

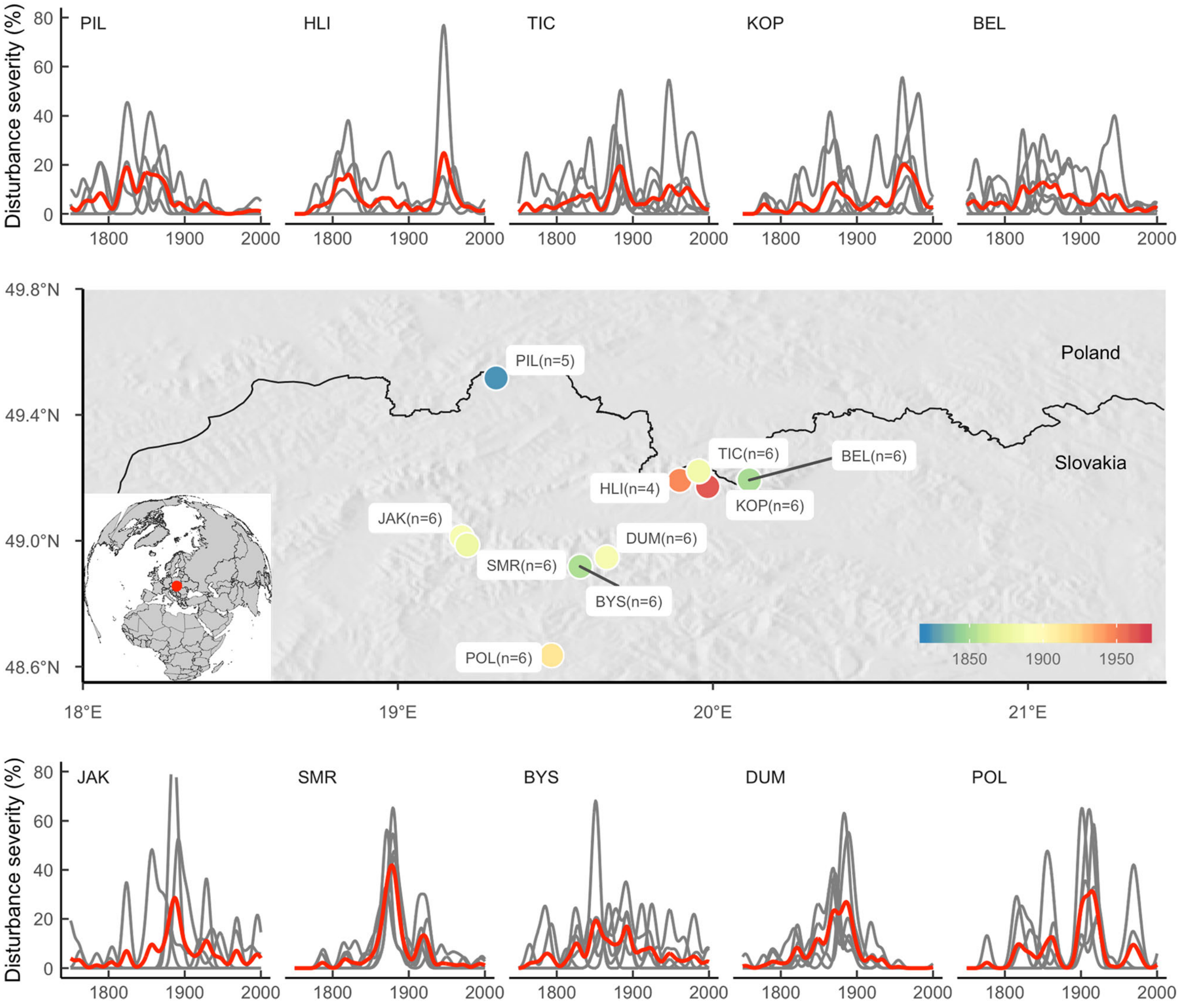

Fig. 1. Study area and plot locations. Data collection was based on a hierarchical stratified random sampling design. Forest stands (circles) were randomly distributed within remnant primary forest and across broad environmental gradients. Individual survey plots were located within stands (circles). Sample sizes (n) in terms of plot numbers within individual stands ranged from four to six. The color gradient indicates the maximum severity disturbance (color gradient) of the ten stands. The reconstructed disturbance history for all studied stands is based on the growth pattern of 15–25 trees per plot. Red line represents mean disturbance severity of given stands smoothed with kernel density function

moderate-severity gap-forming processes prevail in terms of frequency. At a landscape scale, disturbance processes require between 200 and 300 years (Janda and others 2017) to cause complete canopy replacement within a particular area of forest: a frequency metric termed disturbance rotation. At a plot scale, disturbance events re-occur with an average frequency of ~ 40 years (Fig. 1). Windstorms and population outbreaks of insects, particularly of the native saproxylic bark beetle, *Ips typographus* L., predominate as disturbance agents (Emborg and others 2000). Fire occurrence is notably rare in the historical record (Meigs and others 2017). Modern disturbance regimes appear to be essentially unaltered by modern management effects, and disturbance process variability remains within historical bounds (Janda and others 2017).

Field data were collected to describe disturbance history, forest structure, associated habitat characteristics, and beetle community demography. Survey locations were based on an existing international network of permanent inventory plots (REMOTE; https://www.remoteforests.org) that span primary forests in Central and Eastern Europe and that are randomly distributed across various environmental and climatic gradients (Meigs and others 2017). Disturbance history was reconstructed using increment cores collected from that plot network. Associated results have been previously published (Janda and others 2017) and are used in this study. Data describing beetle habitat and population demographics were collected within a selected subset (N = 57) of available REMOTE plots located within our target study region and distributed across gradients of disturbance severity and frequency as determined by Janda and others (2017). All data were collected within 0.1 ha circular plots, corresponding to the extent of the original REMOTE plots. Minimum distance between selected plots was 300 m.

Disturbance History

As described previously, we used data from a published, approximately 250-year long, record of disturbance history encompassing our study plots to infer relationships between the variability of past disturbance processes and current patterns of beetle community diversity. Specifically, we acquired disturbance chronologies from Janda and others (2017) that, both, delineate plot-scale past disturbance occurrences with high temporal resolution, and also estimate the magnitude of associated events. These chronologies were derived from analyses of temporal patterns in interannual 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. Disturbance events were reconstructed based on an assumption that disturbance processes affect levels of neighborhood competition and resource supply, and hence, growth responses in extant individuals (Svoboda and others 2014). In brief, 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). Corresponding event severity was defined in terms of the proportional area of tree canopy removed by the process, which was estimated 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). We used the resulting reconstructed time series of event occurrences and associated severity estimates (Table 1) to derive a total of six disturbance-based metrics that we hypothesized may influence current forest structure and the corresponding composition of saproxylic beetle species assemblages.

Forest Structure

We collected comprehensive inventory data to quantify and classify the variation and abundance of saproxylic beetle habitat comprising all study plots. Field measurements were used to parametrize a total of 15 explanatory variables, in addition to the disturbance-derived variables described previously, for use in statistical analyses (Table 1).

Firstly, we described the coarse structure of stands by precisely mapping all standing trees using laser rangefinders and customized software (Field-Map; Monitoring and Mapping Solutions, Jílové u Prahy, Czech Republic). As tree ontogeny has been associated with the character and availability of substrates (for example, cavities, cracks, bark decay) that potentially support invertebrate occurrence (Vuidot and others 2011), we measured the size (diameter at breast height; DBH) of all adult (> 6 cm DBH) trees and determined ages for a subset of canopy trees (N = 15–25) based on increment core samples. We identified occurrences of distinct substrate or tree-related microhabitat (TreM) types on all live and dead standing trees based on a previously defined typology created to

Table 1. Explanatory Variables Derived From Reconstructed Chronologies of Disturbance Events and Measurements of Structural Habitat

Category	Explanatory variable	Description	Units
Disturbance	Time since max dist	Time since the occurrence of the most severe disturbance event	Years
	Max dist severity	Maximum severity of any disturbance event in a chronology in terms of CA*	Percent
	Dist freq	Mean frequency of disturbance events	No. events
	Time since last dist	Time since most recent disturbance event	Years
	Last dist severity	Severity of most recent disturbance event in terms of CA	Percent
	Dist index	Shannon index based on the cumulative sum of CA per decade from 1800 to 1980	NA
Stand structure	Mean tree age	Mean age of all adult trees	Years
	DW RMS DBH	Root mean square of DBH for standing DW±	mm
	Standing DW BA	Basal area standing DW	m^2/ha
	Standing DW volume	Total volume standing DW	m^3/ha
	TreM Diversity	Shannon's diversity index for 11 microhabitat (TreM) types	NA
	TreM Density	Spatial density of TreM bearing trees	trees/ha
	Canopy openness mean	Mean canopy openness (see Methods)	Percent
	Canopy openness gini	Gini coefficient of openness (0–1)	NA
	Logs volume decay 1–5	Volume of lying DW calculated for 5 discrete decay classes (5 variables)	m^3/ha
	Logs volume	Total volume lying DW	m^3/ha
	total DW volume	Standing DW volume + lying DW volume	m^3/ha

Disturbance-based variables were computed for disturbance events with severities that exceeded a 15 percent threshold level in terms of percent canopy removed. Stand structural variables were derived from data for adult trees with a minimum DBH of 60 mm and minimum height of 1.3 m

** CA Canopy area removed by disturbance as a percent of the total canopy area of the stand*

± DW Standing dead trees (snags) or forest floor deadwood

standardize field inventories (Larrieu and others 2018). We subsequently aggregated observations of individual TreM types ($N = 29$) into broader categories (Table S1; $N = 11$; Paillet and others 2017) and then calculated two plot-scale indices (Table 1) of microhabitat diversity based on the relative abundance of aggregated TreM classes. Specifically, we calculated Shannon's diversity index, as well as a density metric based on the sample size (per ha) of all TreM-bearing trees on a plot (for example, Paillet and others 2017; Kozák and others 2018).

Forest canopy architecture and the associated understory light environment were quantified with 180°-field-of-view hemispherical photographs collected at six predetermined locations within each plot. The collected digital photographs were processed and analyzed using image processing software (WinSCANOPY; Regent Instruments, Ste-Foy, Quebec, Canada). Individual image pixels were classified into sky- or leaf-dominated classes based on their spectral properties. Pixel classification results were aggregated to determine the overall mean sky fraction of a plot canopy and the spatial continuity or evenness of canopy openness.

Finally, we described the diversity, quantity and quality of habitat substrates available on the forest floor. All lying deadwood material was mapped and measured to determine size and volume. We categorized the associated structural integrity and state of decomposition of this material based on a hypothesis that variation in size and decay class segregates beetle taxa (Thorn and others 2018a). We used a five-category decay classification system (Stokland 2001) to categorize wood condition and computed the volume of wood in each class (Table 1).

Beetle Surveys

We sampled current saproxylic beetle populations in each survey plot using insect traps to characterize the taxonomic composition and species richness of local communities. We used flight intercept (window) traps to collect beetle specimens due to their efficacy in previous quantitative studies (Hyvärinen and others 2006; Gossner and others 2013; Økland 1996). Comparative analyses of trap performance have shown that window traps facilitate the collection of large sample sizes and a wide range of taxa compared with other methods (Alinvi and others 2006). A single trap was mounted on two metal rods approximately 1 m above the ground at the center of each plot. We avoided the use of insect bait to minimize the collection of random, long-distance dispersers that would bias estimates of local species diversity. Traps were installed continuously from May to September 2017 and emptied monthly. The taxonomic identity of all beetle specimens was determined to species level, excluding specimens in the family Staphylinidae, which were omitted from further analysis following previous studies (Parmain and others 2015). After taxonomic classification of the remaining specimens, individual species were aggregated into four separate, nonmutually exclusive subgroups comprised of: (1) all taxa; (2) species only associated with coniferous trees; (3) endangered or red-listed species as classified by the International Union for Conservation of Nature (IUCN 2019); and (4) species that are both red-listed and conifer-tree specialists (Schmidl and Büche 2016; Seibold and others 2015).

Diversity Metrics

Our goal in this study was to understand the nature of disturbance and habitat effects on not only the composition of current saproxylic beetle communities, but also on the breadth of ecosystem functions provided by associated communities. Thus, we selected various standard diversity indices from the ecological literature to quantify a range of compositional (taxonomic) as well as functional and phylogenetic metrics that were subsequently used as response variables in regression models.

Compositional attributes of beetle communities were quantified using three diversity metrics: (1) overall abundance for all taxa combined; (2) species richness; and (3) Shannon diversity (Jost 2006). We used trap data to compute each of the selected diversity indices at a plot scale for each of the previously described species subgroups. However, since sample sizes for beetle trap collections varied substantially among plots ($N = 5–705$ individuals/plot), we standardized all trap data before calculating diversity indices following protocols associated with a unified framework for extrapolation and rarefaction based on an effective number of species (Hill numbers; Chao and others 2014). Trap data in a particular plot were standardized on the basis of the overall mean per plot sample size.

We calculated functional and phylogenetic diversity, both based on proxy information, using the following approaches: (1) We acquired selected key ecological traits data to estimate the relative distribution of species in a composite traits or niche space and used species-specific mean niche positions within this construct to quantify an associated trait or functional diversity index; and (2) we compiled data describing phylogenetic relationships between surveyed beetle taxa and computed a diversity index based on the overall complexity and depth of the derived evolutionary tree.

The functional diversity was derived from previously assembled and published comprehensive species-specific datasets representing life history and reproductive qualities for saproxylic beetles (Möller 2009; Gossner and others 2013; Seibold and others 2015). Specifically, we selected and acquired data for fundamental trait characteristics: mean body size, diameter of deadwood in which a species is known to occur, decay stage of deadwood, canopy cover and elevational distribution of forests in which the species is known to occur. Relative distributions of species across the five selected multivariate trait axes were computed using Gower distance (Gower 1971), which accounts for both categorical and continuous variable types.

The phylogenetic richness index was similarly generated using previously published data. We extracted phylogenetic relationships for sampled beetle species based on a comprehensive genetic phylogeny for all taxa within the order Coleoptera originally developed by Hunt and others (2007) and extended by Gossner and others (2013) and Seibold and others (2015). Observed, local phylogenetic richness was subsequently determined by summing total phylogenetic branch lengths (that is, Faith's D; Faith 1992).

Both the functional trait and phylogenetic richness metrics are correlated with species numbers (Winter and others 2013). Thus, we used null models that compare observed levels of diversity across multiple sampling locations to levels expected when species are randomly selected from a regional species pool (Gotelli 2000). Null models provide a standardized effect size which represents the difference between observed mean similarities and expected similarities for 999 artificial assemblages. The regional species pool of the present study was defined as all species recorded in our study. Resulting null model effect size values above 0 indicate higher diversity per number of species than expected by chance; effect size values below 0 indicate lower diversity per number of species than expected by chance (Pausas and Verdú 2010). Consequently, null model effects were used in subsequent modeling analyses to represent standardized species-specific functional and phylogenetic diversity metrics (Thorn and others 2018a).

Data Analysis

Our main hypothesis is that past disturbance frequency and magnitude indirectly modulate current beetle communities by shaping the physical structure of forests and availability of deadwood substrates for beetle colonization. We explored the strength of evidence supporting our hypotheses using linear mixed-effect models (LMMs). A suite of models was formulated to quantify community responses in terms of the range of previously described indices of diversity, including the three taxonomic-based measures (abundance, species richness and Shannon diversity), functional and phylogenetic diversity. Disturbance parameters (Table 1) were used as explanatory variables to estimate their direct effects on both forest structure (habitat) and, in alternate models, beetle diversity. Additional models were formulated to estimate the effects of habitat on beetle diversity. Forest stands were treated as random effects in all models to account for the hierarchical nature of the sampling design (see Fig. 1). Because a high degree of redundancy was observed among the 15 structural explanatory variables (Table S2), correlated terms were excluded from the analyses and a subset of seven parameters were used to formulate models (Table S1) to prevent multicollinearity problems. We evaluated variance inflation factors (VIFs, Quinn and Keough 2002) of each model and did not find any serious multicollinearity pattern (all VIFs < 3.5). Residuals of all models were checked for normality and homoscedasticity. Abundances were log-transformed to reduce skewness. Full models were simplified in a backward elimination procedure based on F tests with Satterthwaite approximation to degrees of freedom (Kuznetsova and others 2017). To compare the relative importance of significant variables retained in the final LMMs, we calculated standardized regression coefficients and their 95% parametric bootstrap confidence intervals. Marginal (R^2_{m}) and conditional (R^2_{c}) determination coefficients were calculated for the final LMMs to quantify the proportion of the total variance explained by the fixed effects and by both fixed and random effects, respectively (Nakagawa and others 2017). To further explore evidence for potential synergies or interactions between processes that shape current beetle communities, associations between disturbance effects and habitat condition, and relationships between habitat effects and beetle diversity, were integrated in a network of confirmatory path analysis (Shipley 2009).

All data management and analyses were conducted in R (R Core Team 2019). We used the function daisy from the cluster package to compute Gower distances. The function ses.mpd from the picante package (Webb and others 2002) was used to develop null models. Modeling analyses were performed using the R-dependent packages car (Fox and Weisberg 2011), iNEXT (Hsieh and others 2019), nlme (Pinheiro and others 2019).

RESULTS

Disturbance and Current Beetle Communities

Modeling analyses reveal that historical disturbance processes had significant and strong effects on current beetle communities in addition to the interactions with habitat described previously. Associated LMMs explained between about 7 and 22 percent of variance according to marginal determination coefficients (Table 2). Time since disturbance was arguably the most important determinant of beetle community attributes having strong, inverse effects on the species richness of beetles in every species subgroup, except the red-listed conifer specialist assemblage. Although the severity of maximum disturbance event in the last 250 years negatively affected species richness of the current beetle community, the severity of the last disturbance event had a positive effect (Fig. 2).

Disturbance frequency also had similar unexpectedly negative direct effects on taxonomic diversity; more frequent disturbance occurrences were associated with fewer observed beetle taxa (Table 2). However, this pattern was only observed for conifer specialist species.

Functional and phylogenetic diversity was mostly not significantly affected by the range of disturbance processes that were modeled. A single significant effect was identified; functional diversity was found to decline with the magnitude of the last severe disturbance in the historical record. The corresponding effect size was among the lowest of any disturbance variable tested (0.27; Table 2) and significant only for conifer specialist beetles.

Table 2. Summary Statistics for Final LMMs that Estimated the Direct Effects From 5 Alternate Disturbance Metrics on Beetle Community Diversity

Species subgroup	**Model response (Beetle diversity index) diversity index**	**Time since max. disturbance**			**Max. disturbance severity**			**Disturbance frequency**		
		β (95%CL)	***F***	***p***	**β (95%CL)**	***F***	***p***	**β (95%CL)**	***F***	***p***
All species	Richness	0.40 (0.05, 0.75)	5	0.03	− 0.40 (− 0.79, − 0.02)	4.1	0.049			
	Shannon diversity									
	Functional trait diversity									
	Phylogenetic diversity									
	Abundance									
Conifer specialists	Richness	0.35 (0.01, 0.64)	4.2	0.046				− 0.39 (− 0.69, − 0.09)	6.7	0.012
	Shannon diversity	0.33 (0.01, 0.66)	4.2	0.047				− 0.55 (− 0.87, − 0.27)	14.1	< 0.001
	Functional diversity									
	Phylogenetic diversity									
	Abundance									
All red-listed species	Richness									
	Shannon diversity									
	Abundance									
Conifer red-listed specialists	Richness									
	Shannon diversity							− 0.27 (− 0.55, − 0.01)	4.07	0.049
	Abundance									

Species subgroup	Model response (Beetle diversity index) diversity index	Time since last disturbance			Last disturbance severity			Stand		R_m^2/R_c^2
		β (95%CL)	*F*	*p*	β (95%CL)	*F*	*p*	χ^2	*p*	
All species	Richness	− 0.54 (− 0.87, − 0.21)	10.5	0.002	0.49 (0.07, 0.91)	5	0.03	2.1	0.147	18.2/31.5
	Shannon diversity	− 0.31 (− 0.58, − 0.04)	5.58	0.022				0.2	0.693	9.2/12.8
	Functional trait diversity							1.1	0.304	–/9.6
	Phylogenetic diversity							0.6	0.448	–/11.2
	Abundance							0.7	0.393	–/7.9

Table 2. continued

Species subgroup	Model response (Beetle diversity index) diversity index	Time since last disturbance			Last disturbance severity			Stand		R^2_m/R^2_c
		β (95%CL)	F	p	β (95%CL)	F	p	χ^2	p	
Conifer specialists	Richness	− 0.45 (− 0.80, − 0.05)	5.9	0.019				1	0.33	13.9/24.8
	Shannon diversity	− 0.57 (− 0.94, − 0.18)	10.1	0.003				2.9	0.087	22.3/43.0
	Functional diversity				− 0.27 (− 0.54, − 0.02)	4.41	0.04	1.8	0.182	7.1/20.6
	Phylogenetic diversity							0.2	0.646	–/4.3
	Abundance							1.3	0.248	–/13.5
All red-listed species	Richness							0.3	0.514	–/6.3
	Shannon diversity	− 0.29 (− 0.55, − 0.01)	5	0.03				< 0.1	0.975	8.3/8.5
	Abundance							0.8	0.38	–/9.9
Conifer red-listed specialists	Richness							< 0.1	1	–/< 0.1
	Shannon diversity							< 0.1	0.985	6.9/7.1
	Abundance							1.2	0.277	–/12.8

Alternate models were fit to quantify disturbance effects on both taxonomic and functional (traits and phylogenetic) based measures of diversity. Independent models were fit for 4 species subgroups. Forest stand was used as a random effect. Shown are standardized regression coefficients (β) along with their 95% parametric bootstrap confidence limits (95% CL), test statistics (F, χ^2), and significance values (p) for all significant effect terms. Marginal (R^2_m) and conditional (R^2_c) determination coefficients were computed for each model. Note that the disturbance index (dist index in Table 1) was not a significant predictor for any subgroup and is not shown

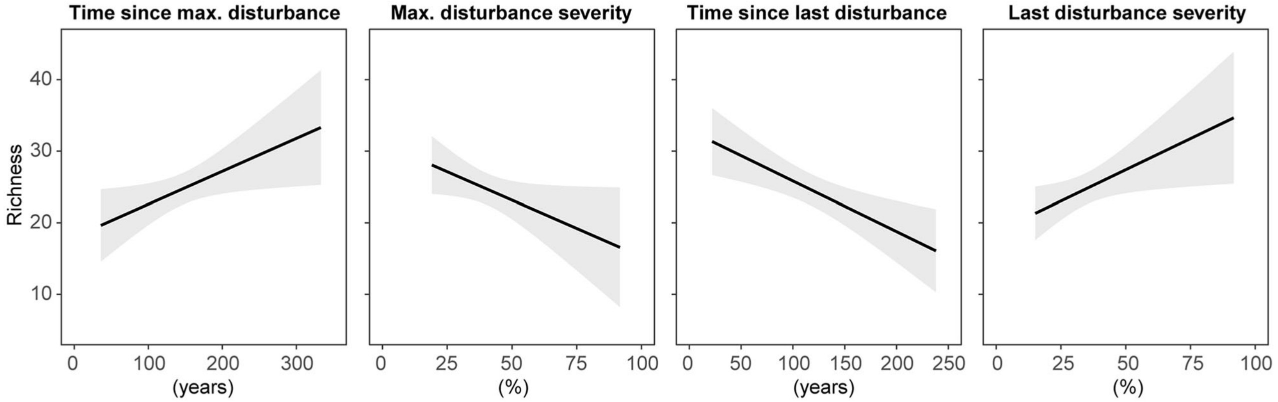

Fig. 2. Magnitude of disturbance effects on the taxonomic richness of current beetle communities based on linear mixed effects models. Each effect plot shows expected response to a particular variable keeping other variables constant at their mean value. Gray shading delineates 95% confidence limits

Disturbance and Forest Structure

Results from regression analyses reveal a range of important disturbance effects on various structural attributes of sampled forest stands, specifically deadwood amounts and canopy openness. Fixed effects in associated models explained between about 10 and 22 percent of relative variance in the observational data, excluding the forest age model which was much stronger (Fig. 3). Frequency was arguably the most important attribute of the disturbance regime, influencing the temporal and spatial heterogeneity of beetle habitat in several ways. For example, increases in disturbance event frequency were positively related to both the volume of logs on the forest floor and total volume of all (standing and lying) deadwood with relatively large positive standardized regression coefficients of 0.33 and 0.56, respectively (Table S4). Canopy openness declined with disturbance frequency, though this was perhaps a minor effect ($\beta = -0.26$).

In addition to disturbance occurrence frequency, the length of disturbance-free intervals significantly influenced forest structure. Canopy openness decreased with time since the last disturbance ($\beta = -0.28$) due to promoted growth of the trees and associated canopy gaps filling. Also, the mean size of standing deadwood varied as, over time, standing dead trees deteriorated and fell to the forest floor. Positive relationships ($\beta = 0.31$) indicate that larger diameter dead trees persisted for longer periods as compared with smaller snags. The total reservoir of deadwood increased with time in the absence of disturbance.

Disturbance severity had strong effects on the amount of deadwood supplies. The overall volume of deadwood strongly covaried with event severity ($\beta = 0.59$); in other words, stronger disturbances (last disturbance severity; Table S4) caused greater tree mortality and produced more deadwood. Negative relationships ($\beta = -0.27$) between the most severe events (maximum disturbance severity; Table S4) at our study plots and the mean size of the standing reservoir of deadwood suggest that a majority of these events happened several decades ago (mean time since maximum severity disturbance was 147 years; Table S5) and due to post-disturbance development, the snags most likely decayed and forest patches affected with historical high severity events became relatively homogenous with a poor deadwood pool. This effect was, however, only marginally significant ($p = 0.049$; Table S4).

We did not detect evidence for a corresponding increase in microhabitat (TreM) diversity associated with the frequency or severity of disturbances.

Habitat and Current Beetle Communities

Modeling results reveal that a range of forest stand structural attributes significantly influenced the current saproxylic beetle communities in this study, consistent with our hypotheses. Depending on the species subgroup and response variable, alternate models having significant fixed effects explained between about 8 and 16 percent of the variance in the observational data according to marginal determination coefficients. Our model selection process resulted in single-factor models for all diversity-based response variables (Table S3). A total of four different explanatory variables were important in the final most parsimonious models. All selected variables had positive effects on corre-

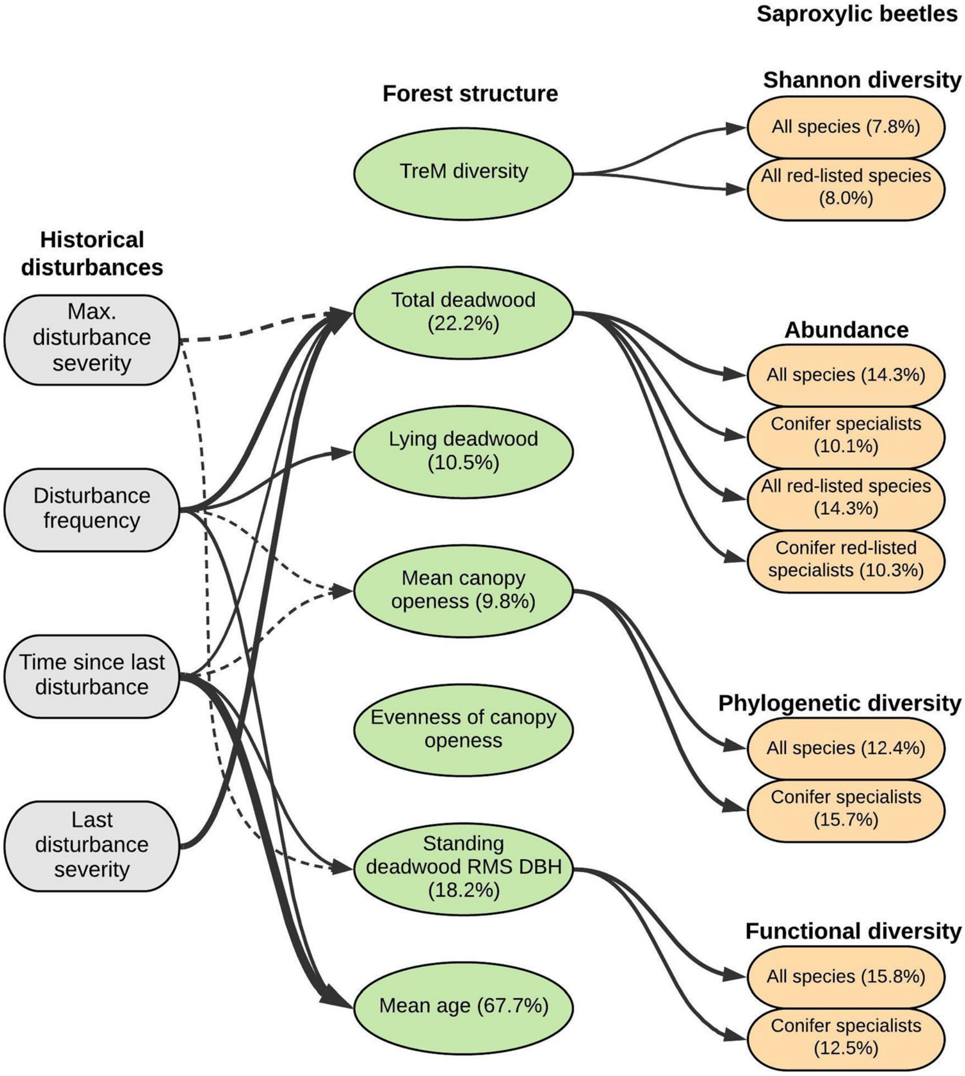

Fig. 3. Directed acyclic graph of confirmatory path analysis linking historical disturbances and forest structure with abundance and diversity of current saproxylic beetle communities. Models were fit with data from four subgroups. Arrows represent significant ($p < 0.05$) positive (solid line) and negative (dashed line) relationships between predictors and responses. Width of the arrows is proportional to standardized regression coefficients. Relative proportion of variance explained by fixed effects (R^2_{m}) is given in parentheses. Note that variables without any significant link are omitted for brevity. Further details can be found in Tables S1 and S2

sponding diversity measures (Fig. 3). Different aspects of beetle community diversity, that is, total abundance, taxonomic richness, phylogenetic and functional diversity, responded to different, unique features of the environment. For example, the volume of deadwood on the plot and the length of disturbance-free intervals (Table S4) were the consistent predictors of beetle abundance, influencing abundance in each subgroup ($\beta = 0.34$–0.41). Models indicate that species diversity was associated only with the range of microhabitats available at a site. This TreM relationship was valid for the all-inclusive species subgroup and not for conifer specialist species (Table S3). The diversity of TreM types was not significantly determined by any disturbance process (Fig. 3), thus indicating that, at least for the variables tested, we did not detect a common indirect disturbance effect that could result in covariation between abundance and species diversity.

Similarly, model results show that phylogenetic diversity was significantly influenced only by canopy openness. Lastly, the functional diversity was associated only with the mean size of standing dead trees. In this case, attributes of the disturbance regime, specifically disturbance-free interval length and maximum event severity, may similarly influence both functional trait diversity and total species abundance through congruent indirect effects on forest structure (Fig. 3).

DISCUSSION

Elucidating mechanisms of how disturbance influences structure of ecological communities and facilitates species coexistence and associated ecosystem functions is central to ecological theory (Shea and others 2004). Our comprehensive dataset covering 250 years of disturbance history and associated changes in forest structure expanded the current knowledge about the effect of disturbance regimes on current beetle communities. Disturbances played an important role in determining the diversity of saproxylic beetle communities, with the frequency and time since disturbance as the most important factors. Our results further demonstrate that the dynamics of natural disturbance determine heterogeneity in resources, most importantly deadwood supplies and canopy openness, which positively contributed to the maintenance of diverse beetle assemblages.

Effect of Natural Disturbances on Saproxylic Beetle Communities

We demonstrated that the more recently the disturbance occurred, the more species-rich the current communities of saproxylic beetles were. This effect was observed for the diversity of all beetles and for conifer specialists separately. The observed pattern might be an effect of higher canopy openness immediately following a disturbance event as saproxylic beetle communities are often more species-rich in gaps than under a closed canopy (Seibold and others 2016a, b). Another possibility is that this observation is a transient effect and caused by the higher proportion of fast-developing freshwood dwellers present in post-disturbance beetle communities, such as bark beetles and species associated with them (Saint-Germain and others 2007). Decreasing amounts of nutrients in decaying woody debris decreases the attractiveness of deadwood over time (especially coniferous wood; Saint-Germain and others 2007) for saproxylic beetles (Kopf and Funke 1998). Similar findings were observed by Winter and others (2015) with the highest numbers of saproxylic beetles preferring wood of early decay stages in the initial early-seral stage following the availability of fresh deadwood. As observed by Gossner and others (2016), for *Picea abies*, species richness of saproxylic beetles was highest in the first year of decay followed by a decrease in species richness. Moreover, species richness increased with the severity of the last disturbance, probably as a result of deadwood pool enrichment across disturbed plots (Table S4).

The severity of the last historical disturbance (events occurred on average 120 years ago; Table S5) negatively affected functional diversity of conifer specialists. This finding might be explained by the post-disturbance development and highlights the need to understand long-term disturbance effects on biological communities. Gaps or patches after high-severity disturbance close between 50 and 100 years following a disturbance (Svoboda and others 2014), and as a result, forest stands become more homogenous and the structural elements, for example deadwood, decline. Thus, altered environmental conditions may exclude functionally diverse early and mid-successional species and lead to the co-occurrence of functionally similar species that are adapted to changing habitat conditions (Winter and others 2017; Thorn and others 2018a). Our findings agree with the results of Hilmers and others (2018) which showed a U-shaped response of beetle communities to forest succession.

Predicting the effect of future disturbance regimes on forest diversity, Thom and others (2017) observed that an increase in disturbance frequency and severity had consistently positive effects on biodiversity. High disturbance severity and increasing disturbance frequency create a complex pattern of open areas, forest edges and remaining closed canopy forests, increasing the variation in environmental conditions (Perry and others 2011; Lehnert and others 2013). However, these findings only partially match ours, which could be because Thom and others (2017) did not specifically focus on spruce-dominated forests. Although the severity of the last disturbance was associated with an increase in species richness for all species, the increases in the maximum detected disturbance severity were related to declines in species richness. The high-severity disturbances cause higher tree mortality which might lead to more homogenous forest structure with limited amounts of forest edges and old-growth structures (Svoboda and others 2014), making such a forest unfavorable for certain beetle species.

We observed a negative impact of disturbance frequency on conifer specialist species richness and diversity. Higher disturbance frequencies generate more gaps that support more diverse tree species, including broad-leaved species, which might cause a decline of conifer specialists as the deadwood pool contains more diverse tree species composition. Environmental changes such as the removal of the overstory forest canopy and the subsequent effect on the light regime may favor some species, while creating suboptimal or intolerable conditions for other species (Swanson and others 2011): for example, species that prefer shaded deadwood (Lachat and others 2016). Devictor and Robert (2009) showed that generalist species might benefit strongly from disturbance events while specialists and late-seral species could be affected negatively. Possibly, other drivers not included in our data, such as microclimate, shrub and herb layer vegetation, and fungal occurrence may explain diversity patterns of beetle communities present at the studied plots.

Effect of Disturbance-Related Structural Characteristics on Saproxylic Beetles

Saproxylic beetle communities are largely reliant on structural characteristics created by natural disturbance. Our results support previous findings that beetle abundance and diversity are associated with heterogeneous and dynamic forests with high amounts of deadwood and canopy gaps (for example, Wermelinger and others 2002; Müller and others 2010).

Deadwood is an important component of forest ecosystems, biogeochemical cycles, trophic chains and provides key niches for many species (Vandekerkhove and others 2009). The total amount of deadwood was the most important structural characteristic, positively influencing the abundance of all studied subgroups. Similarly, Müller and others (2010) observed a positive response of beetle populations to deadwood amount which was also true for the specialized and red-listed species.

Mean canopy openness positively influenced the phylogenetic diversity of all beetles and conifer specialists. Mountain spruce forests of the Carpathians are characterized by mixed-severity disturbance dynamics (Svoboda and others 2011, 2014) of wind and bark-beetle origin, which provide periodically a large amount of freshly killed trees with lots of canopy openings and thus might have favored the evolution of species adapted to utilize sun-exposed deadwood (Gossner and others 2016). Another possibility is that changed light conditions in canopy gaps attract more flower-visiting beetles and higher temperatures of sun-exposed deadwood allow emergence of beetles from different phylogenetic lineages.

Amount of deadwood, particularly of large diameter and in a late decay stage, influences the functional composition of saproxylic beetles (Gossner and others 2013). We observed that functional diversity of all saproxylics and conifer specialists was positively influenced by the diameter of standing deadwood. These findings confirm the importance of the high-diameter standing deadwood for saproxylic beetles as they can provide diverse habitats for functionally diverse assemblages (Stokland and others 2012; Larrieu and others 2012; Martikainen and others 2000). Moreover, our results support earlier findings which emphasize the positive effect of bark-beetle infestations on saproxylic beetle communities (Müller and others 2010). Finally, we observed the significant positive influence of tree-related microhabitat diversity on overall and red-listed beetle diversity. This finding is consistent with studies emphasizing the role of tree-related microhabitats as important habitat for saproxylic beetles (Parisi and others 2019).

Effect of Natural Disturbances on Forest Structure

We observed a significant influence of historical disturbance variables on structural characteristics in terms of deadwood volume and canopy openness. Such observation suggests that the effect of historical disturbance regimes on forest structure persists in the form of structural characteristics and may still be visible after several decades or even centuries from the disturbance event. These findings are consistent with the findings of Winter and others (2015) that structural changes such as reduced canopy cover and high volumes of deadwood after windthrow and bark-beetle outbreak remain high or even higher after multiple decades of succession, suggesting persistence of early-seral heterogeneity into succession.

We found a positive effect of the time since last disturbance on total deadwood volume and diameter of standing deadwood, suggesting that trees dying during a disturbance event are available habitat for several decades, as was observed by Spies and Franklin (1988), or even for a century. The observed increases in total deadwood volume during disturbance-free periods further suggest that decay processes in spruce wood are comparatively gradual, at least relative to decomposition rates in angiosperm-derived substrates (Weedon and others 2009) and that disturbance impacts on deadwood supply have substantial temporal persistence.

In primary forests, post-disturbance succession is frequently influenced by other disturbances of various severities which can continuously replenish the deadwood pool (Hansen and others 1991). Our results support those findings, since disturbance frequency positively influenced the total deadwood volume and lying deadwood volume. However, mean canopy openness decreased with increasing disturbance frequency and with longer times since disturbance, probably as part of the canopy trees survived frequent disturbance events and partly due to conditions favoring seedling recruitment and growth after disturbance events (Winter and others 2015).

Finally, natural disturbance characteristics did not significantly affect the tree-related microhabitat diversity. This supports the findings of Larrieu and others (2014) that tree-related microhabitat availability remained stable throughout the forest succession, both in terms of their quantity and diversity.

Varying Responses of Different Diversity Metrics to Disturbance History

Our studied diversity metrics of current saproxylic beetle communities responded to different disturbance and structural characteristics. Each historical disturbance characteristic influenced at least a part of the current beetle diversity, with frequency and time since the last disturbance event being the most important factors. With respect to saproxylic beetle richness, we observed contrasting effects between maximum disturbance severity (negative) and severity of the last disturbance (positive); a contrast was also observed between the effects of time since most recent disturbance (negative) and time since maximum disturbance (positive). Disturbances, habitat fluctuations and changes in environmental conditions cause variations in ecosystem properties and variable responses of different components of biodiversity (Cadotte 2007). Thus, the observed influence of disturbance on current beetle diversity may be caused by beetle species inhabiting temporary niches created by forest succession after disturbance. Saproxylic beetle communities show pronounced successional changes with ongoing decay of deadwood material (Jonsell 2008) due to changes in the physical structure and nutritional quality of deadwood (Wende and others 2017). For instance, the presence of late-successional species often depends upon earlier colonists creating suitable conditions by initiating deadwood decomposition (Jacobsen and others 2015).

Composition of a saproxylic beetle communities also depends on the ratio of different functional groups such as xylophages, fungivores and predators. For example, xylophages are highly abundant in early successional phases of deadwood colonization, whereas fungivores and predators are commonly present later in the successional food chain (Grove 2002). Thus, the heterogeneous arrangement and decomposition of deadwood resources, both spatially and temporally, might influence taxonomic and functional diversity of the current saproxylic beetle communities.

Implications for Forest Management

Our results demonstrate that natural disturbances are an indispensable part of forest ecosystems and provide a diverse range of habitat conditions for the beetle community. Saproxylic beetles provide important ecosystem functions that depend on the species composition of the beetle community (Pielou 1966). Evidence suggests that a diverse assemblage of species is required to maintain ecosystem functions (Tilman 2001; Cadotte and others 2009). Thus, our results further suggest that diverse natural disturbance components that act across different timescales are necessary to create heterogeneous habitats and maintain taxonomic, functional and phylogenetic diversity and consequently the ecosystem functioning. The disturbance regime influences the spatiotemporal variation of deadwood, on both the stand and landscape scale (Jonsson and others 2005), and this variation may influence the occurrence of saproxylic beetle species (Stokland and others 2012).

Various species have different habitat requirements and thus need to be able to disperse across the landscape when an area is no longer suitable (Jonsson and others 2005). Previous studies suggest that total amount of deadwood available within a given landscape is the main driver of the number of saproxylic beetle species and that the spatial arrangement of deadwood, that is, connectivity, plays no or only a minor role (Seibold and Thorn 2018). In our study, we focused on plot-scale effects of disturbance on alpha diversity of saproxylic beetles. However, when we consider the stand-scale or landscape perspective, shifting mosaics of forest structures developing after disturbance in space and time may lead to high species turnover (Gossner and Müller 2011). Some species require open areas with high amounts of deadwood and thus have a rapid increase in their population following a high-severity disturbance. Subsequently, a major decline follows in conjunction with succession in disturbed patches, but species should be able to persist when a nearby forest stand undergoes natural disturbance.

The adverse effect of homogenized forest structure on forest biodiversity and survival of specialized forest species has strong implications on active forest management. Large-scale homogenization and simplification of forest structure, and consequent biodiversity decline, is often a characteristic feature of intensive forestry practices (but see Schall and others 2018). This is particularly relevant following large-scale clearing of disturbance legacies due to salvage and sanitary logging after wind and insect disturbance (Thorn and others 2017, 2018b). In the Carpathian region, the situation is especially critical and controversial because such treatments regularly occur in protected areas, such as national parks (Mikoláš and others 2017a), which have presumably been established to protect native biodiversity and maintain natural processes.

CONCLUSIONS

Our study documented that disturbance-created structures promote species-rich communities of saproxylic beetles. Species-rich beetle communities were favored by the structure created by historical disturbances that increase the structural heterogeneity, whereas historical disturbances which homogenized the forest environment appear to have unfavorable present-day forest structure. Present-day forest structure such as the amount and diameter of deadwood and changed light conditions positively influenced the abundance and diversity of beetle communities. We should acknowledge that current beetle diversity is far from temporally static so that the importance of these aspects might be changed during further successional development. Ongoing climate change will likely increase disturbance frequency and severity in many parts of the world (Thom and others 2017). Our results suggest that climate-induced changes in natural disturbance regimes may temporarily impact saproxylic beetle communities, whereas these changes are highly dependent on post-disturbance successional pathways. The time-scale and long-term post-disturbance development trajectories may pose a challenge for local conservation planning. Therefore, we emphasize the importance of setting aside large areas (strictly protected forest landscapes) where wide range of timing and severity of disturbance can act and create a heterogeneous environment that can support a full array of biodiversity (Mikoláš and others 2017b; Nagel and others 2017; Watson and others 2018). When the area on which natural disturbances operate is too small, large-scale disturbances may change the habitat across small protected forests to conditions that are not appropriate for certain species.

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