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Policy analysis

Ecology versus society: Impacts of bark beetle infestations on biodiversity and restorativeness in protected areas of Central Europe

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A R T I C L E I N F O

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A B S T R A C T

Protected areas worldwide are important to maintaining biodiversity and providing recreational opportunities to society. However, many protected areas are affected by unprecedented, large and severe natural disturbances, like bark beetle outbreaks. Due to the contrasting responses of different taxonomic groups to disturbance events and largely negative human perceptions of disturbed landscapes, there are conflicting opinions about the appropriate way of managing affected stands. Aligning these different objectives and understanding the responses of biodiversity and visitors' perceptions to different disturbance severities is a prerequisite for disturbance management in protected areas. We conducted multi-taxon biodiversity surveys – including meta-

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barcoding hyperdiverse groups such as insects and fungi – and analysed the restorativeness (i.e. the landscape's ability to renew personal cognitive capacities for forest visitors) using visitor surveys in five national parks throughout Europe. Response curves of biodiversity and restorativeness were analysed along a continuous gradient of bark beetle infestation severities in Norway spruce forests on the same study plots. Arthropod biomass and the diversity of primary producers and pollinators increased linearly with increasing disturbance severity, while overall multi-diversity (an index of the average scaled species richness per taxonomic group) did not change. Restorativeness decreased linearly with increasing disturbance severity; however, even heavily disturbed forests still had high restorativeness. In spite of the ongoing debates about disturbance management, the high biodiversity and restorativeness that accompany disturbance suggest that major goals of protected areas are not threatened by bark beetle disturbances.

1. Introduction

Protected areas are social-ecological systems (Matthews and Selman, 2006) fulfilling different objectives, like supporting biodiversity (Di Marco et al., 2019) and providing recreational space in otherwise densely populated areas. Furthermore, protected areas are subject to natural ecosystem dynamics as well as to climatic changes. Yet the ways in which these dynamics influence the protection of biodiversity and the provision of space for recreation remains an unresolved question. Since the second half of the 20th century, climate change has led to more frequent forest disturbances (Senf and Seidl, 2020), and the amount of damaged wood will likely increase further in future (Schlyter et al., 2006; Kurz et al., 2008; Seidl et al., 2011, 2014; Temperli et al., 2013; Sommerfeld et al., 2018). In Central Europe, the European spruce bark beetle (*Ips typographus* (L.)) is a key driver of forest disturbance regimes and causes severe mortality in Norway spruce (*Picea abies* (L.) H. Karst) forests. Over 39% of the protected areas in Europe are in conifer-dominated forests that are naturally susceptible to such disturbance events (Hagge et al., 2019).

The ongoing biodiversity crisis results in severe species loss and accelerated extinctions (Pimm and Raven, 2000; Koh et al., 2004; Johnson et al., 2017). Consequently, conservation of nature has become increasingly important. Current research indicates that increased habitat heterogeneity resulting from disturbances may reduce biodiversity loss in forests (Thom et al., 2017; Seibold et al., 2019) and letting disturbances take their course without intervention has thus been suggested as a promising "conservation tool" (Müller et al., 2010; Lindenmayer et al., 2017). In this context, for most taxonomic groups species richness increases after bark beetle infestations (Beudert et al., 2015). Open forests in early successional stages are dynamic systems with high structural and biological diversity (Swanson et al., 2011). For example, herbaceous plants and pollinators benefit from early seral stages after disturbances (Winter et al., 2015), and rare or endangered species can benefit from structures, such as dead wood, that are missing or rare in even-aged monocultures (Bässler and Müller, 2010; Kortmann et al., 2017). However, individual species as well as taxonomic and functional groups respond differently to the changes induced by disturbances (Lehnert et al., 2013). For example, populations of Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis* (J. A. Allen, 1894)) in Northern America declined after bark beetle infestations due to a loss of food sources (Koprowski et al., 2005).

Impacts of bark beetle infestations on the visual quality of a landscape for visitors are often perceived as negative, especially during the first years after tree death (Sheppard and Picard, 2006). This is of growing importance since the ability of natural environments to improve mental and physical health in humans has gained increasing attention in recent decades (Ulrich et al., 1991; Barton and Pretty, 2010; McMahan and Estes, 2015; Rathmann et al., 2020a). Restorative environments allow a shift towards more positive emotional states, positive changes in physiological activity levels and in behaviour and cognitive functioning (Korpela and Hartig, 1996). According to Kaplan's Attention Restoration Theory, ART (Kaplan, 1995), environments with particular characteristics (i.e. *being away*, *fascination*, *coherence*, *compatibility* and *scope,* detailed descriptions of the characteristics are in Box 1) should help people recover from mental fatigue, i.e. exhausted directed attentional capacities (Tenngart Ivarsson and Hagerhall, 2008). Hence, restorativeness is an important factor of natural environments for mental and physical health (Berto, 2014). Previous studies on how bark beetles affect humans have focused on the perceived risk to recreational opportunities and scenic quality (Flint et al., 2012), risk to ecosystems (McFarlane and Witson, 2008) or visitors` attitudes towards the bark beetle (Müller and Job, 2009; Sacher et al., 2017). Until now, there has been a lack of evidence on how bark beetle infestations affect the restorativeness of a landscape.

Box 1
Descriptions of restorativeness factors.

Restorativeness can be defined as the landscape's ability to renew personal cognitive capacities or adaptive resources to cope with environmental stressors. (Kaplan, 1995).

Being-away refers to the extent to which a place enables people to distance themselves from problems and daily concerns. This includes distance from demands ranging from annoying trifles to matters of great personal significance. The distance does not need to be geographical but can be purely psychological or a mix of both (Hartig et al., 1997).

Fascination is the capacity of the environment to effortlessly capture people's attention. Such involuntary attention does not demand mental effort and is attracted by stimuli having directly fascinating qualities (Hartig et al., 1997, Tenngart Ivarsson and Hagerhall, 2008).

Coherence represents the belonging of different parts of a place to a whole. It is perceived as ease with which one can organise and structure a scene as well as a level of connectedness (Negrín et al., 2017).

Compatibility represents the extent to which a place fits a person's inclinations and interests. It is the match between the person's goals and inclinations, the demands made on the person by environmental conditions and the patterns of information available in the environment for support of purposive and required activities (Hartig et al., 1997).

Scope refers to the scale of a landscape, where the landscape is a place in which the person enters and remains (Hartig et al., 1997).

Responses of biodiversity and ecosystem services to natural disturbances have traditionally been analysed separately (reviewed in e.g. Sheppard and Picard, 2006, Kulakowski et al., 2017, Thom and Seidl, 2016; but see Beudert et al., 2015). Nevertheless, a simultaneous consideration of ecological and social aspects is indispensable for decision makers in protected areas who have to balance different objectives in their day-to-day decision-making.

A key element for assessing the impacts of bark beetle infestations on biodiversity and restorativeness is disturbance severity. Disturbance severity can explain different responses of taxonomic groups to disturbance events, yet disturbance severity is rarely documented (Saab et al., 2014). Moreover, definitions of disturbance severity are inconsistent. Some definitions include only the amount of forest overstorey removed in a disturbance (Frelich and Reich, 1999) while others also consider effects on understorey vegetation, forest floor and soil (Roberts and Gilliam, 2003). Furthermore, previous analyses often considered multiple disturbance agents, from selection cutting or thinning to severe wildfires (Frelich and Reich, 1998; Sabo et al., 2009) or considered different categories of disturbances such as the removal of vegetation, litter or soil (Rydgren et al., 2004). In order to exclude possible confounding effects of different disturbances, we here focus exclusively on bark beetle infestations along a continuous gradient of severity. Specifically, we define disturbance severity as the proportion of overstorey spruce trees killed by *I. typographus*.

To study ecological and social responses to a gradient of bark beetle disturbance severities (0–100%) we simultaneously assessed changes in biodiversity and restorativeness in five protected areas across Central Europe. Our specific questions were (i) how vascular plants, bryophytes, lichens, fungi, arthropods and birds are affected by different disturbance severities, (ii) how perceived restorativeness is affected by different disturbance severities, (iii) and in which shape different indicators respond (linear, hump-shaped, etc.).

2. Materials and methods

2.1. Study areas and experimental design

The study was conducted in 2018 in the following protected areas: Black Forest National Park (Germany), Berchtesgaden National Park (Germany), Bavarian Forest National Park (Germany), Kalkalpen National Park (Austria), and Białowieża Forest (Poland) (Table A.1). In order to exclude impacts of post-disturbance forest management, we only selected forest stands where intervention in the form of salvage logging was not conducted after bark-beetle disturbance. Sites in Białowieża Forest were located outside the national park but were still not salvage logged. All areas comprised at least 70% Norway spruce trees (*Picea abies* (L.) H. Karst) and were affected by *I. typographus*. In each area we selected 15 circular study plots ($r = 50$ m) covering a gradient of disturbance severities from 0 to 100%. Since Black Forest National Park was only recently established and had rather low levels of bark beetle infestation, we only selected 9 plots in that area. Disturbance severity was calculated as the percentage of beetle-killed spruce trees out of the total number of spruce trees at each plot. The respective disturbance severities were calculated within a 100 m-buffer surrounding each plot to assure homogeneity of the sampled plots.

Processes of decomposition and regeneration after outbreaks of *I. typographus* occur gradually over the course of years and even decades. In this study, only forest stands with bark beetle infestations older than two years and younger than 20 years were considered, such that all affected spruces had lost their needles, but the collapse of snags and decomposition of dead wood was not yet far advanced. Time since bark beetle outbreaks was approximately the same across study areas (Table A.1.).

For the biodiversity surveys on lichens and epiphytic bryophytes we created ten disturbance severity classes (0%; 1–10%; 11–20%, 21–30%, etc.) and selected 10 trees per plot proportional to the respective severity class. Specifically, we selected 10 life trees on plots with 0% disturbance severity, 9 life trees and 1 dead tree on plots with 1–10% disturbance severity, 8 life trees and 2 dead trees on plots with 11–20% disturbance severity, etc.

2.2. Dead-wood inventory

We measured all dead Norway spruce trees within a 17.84-m radius (0.1 ha) of the centre of each study plot. The heights of standing dead trees were measured with a Vertex IV (Haglöf Sweden AB). Diameter was measured using a caliper at breast height (1.3 m) for standing trees and at the middle of the stem for downed trees. The length of downed dead wood was measured with a measuring tape. The volume of standing dead trees was calculated as: $DBH^2 \times \pi \times \frac{length}{4} \times 0.43$, with 0.43 being the form factor for Norway spruce (Kramer and Akca, 2008). The volume of downed dead wood was calculated as: $DBH^2 \times \pi \times \frac{length}{4}$. The volume of standing broken trees was calculated as: $D2^2 \times \pi \times \frac{length}{4}$. With the calculation for $D2$ as: $DBH - \left(DBH^2 \times 0.04 \times \frac{length}{2}\right)$ given that the diameter decreases by 4% per meter (Kramer and Akca, 2008). The amount of dead wood was calculated as cubic meters of dead spruce per hectare. Live spruce trees were not included in the analysis. To control for variation in the amount of deciduous trees and for different climate conditions between plots, we calculated the percentage of deciduous trees for each plot and included elevation as an explanatory variable.

2.3. Biodiversity surveys

An overview of all sampling methods and the number of detected species is given in Table 1. At the centre of each plot, a subplot of 200 m^2 was installed to survey vegetation. Epigeic bryophytes and vascular plants were recorded once between June and August 2018, and the estimation of vascular plant and bryophyte species cover was determined according to Londo's (1976) ten-step scale. We selected 10 dead and/or life trees closest to the centre of each plot in proportion to the respective disturbance severity class and recorded lichens and epiphytic bryophytes present on these trees (see above the description of disturbance classes) up to a height of 2 m.

Birds were recorded in a 50 m-radius by fixed-radius point-stop counts (Hutto et al., 1986) five times between March and June 2018 for five minutes from the centre of each plot. All birds that could be identified visually or acoustically were recorded. Overflying birds were excluded. Bird surveys were performed during morning hours and only on days without rain or strong wind (Bibby et al., 1998).

In the middle of every plot, a Malaise trap was installed from April until September 2018. Traps were filled with 70% ethanol and were emptied once a month to ensure high DNA quality for sequencing (see below). Each sample was drained in a sterile gauze and weighed to

Table 1
Methods used for biodiversity surveys and total number of species across all plots. For arthropods and fungi, operational taxonomic units (OTU) were used for the analyses.

Species group	Method	Study plot	Species
Vascular plants	Survey	200 m^2 subplot	323
Epigeic bryophytes	Survey	200 m^2 subplot	91
Epiphytic lichens	Survey	10 life and dead trees	96
Epiphytic bryophytes	Survey	10 life and dead trees	90
Birds	Point-stop counts	50 m radius	65
Arthropods	Malaise-traps and meta-barcoding	Plot centre	3575 OTUs
Fungi	Wood samples and meta-barcoding	5 dead trees	1493 OTUs

calculate arthropod biomass. After weighing, the sampled arthropods were separated into two size classes using a sieve (7 mm mesh size) to improve sequencing results by decreasing the risk that smaller specimens with underrepresented DNA would not be detected during sequencing (Hardulak et al., 2020). We classified arthropods in functional groups (destruents, pollinators, parasites, parasitoids, primary consumers, and predators) at the family level based on literature information. In families with genera from different functional groups we classified the different genera. If genera were inconsistent, we classified different species or excluded them from classification (Appendix B).

To sample fungi DNA, starting from the middle of every plot five pieces of dead wood were selected to represent the overall dead-wood inventory of the respective plot. From each piece of dead wood we took a sample of wood using a 0.8 cm × 30 cm long auger bit. We drilled through the whole radius of each trunk to get a comprehensive sample of fungi communities, which vary between different layers of a trunk (Leonhardt et al., 2019). To minimize the effect of microorganisms occurring on the surface of the tree, and to exclude bark layers, we debarked the point of drilling and cleaned it with ethanol. To avoid cross-contamination between different plots, the auger bit was cleaned with ethanol and flamed after each plot. Sawdust samples were stored in clean plastic bags at −40 °C to prevent further development of fungi in the samples.

We pooled saw dust from each plot in further analyses. Samples were homogenized and ground to a fine powder using solid carbon dioxide and a swing mill (Retsch, Haan, Germany). Total fungal community DNA was isolated from 0.25 g of each sample using the Quick-DNA Fecal/Soil Microbe Miniprep kit (D6010) (Zymo Research, Irvine, CA, USA) (Purahong et al., 2018). Amplification, sequencing and processing of the data were performed as described below for arthropod samples.

2.4. Meta-barcoding and bioinformatics

Species identification of arthropods was performed using DNA metabarcoding following the laboratory and bioinformatic pipelines as reported in Hausmann et al. (2020). The full protocols for molecular laboratory work as well as for the performed bioinformatic workflow are described in Appendix C.

2.5. Visitor surveys

We conducted on-site visitor surveys using standardized photographs of each study plot. Photographs were taken at eye level with a tripod to ensure consistent perspectives with a fixed height and angle in each photograph. We defined the restorativeness of a landscape as the ability to renew personal adaptive resources and cognitive capacities to meet the demands of everyday life (Berto, 2014). Such restorative environments should have the following characteristics, which are represented by Berto (2005) as five factors of the Perceived Restoration Scale (PRS): *being away*, *fascination*, *coherence*, *compatibility* and *scope*. We applied a short version of the PRS that uses a single item to measure each of the five restorativeness factors. Definitions of the five factors are given in Box 1. Each factor was presented in the form of a short statement (see Table A.2) and rated on a 5-point Likert scale (1 = strongly disagree, 3 = unsure, 5 = strongly agree). We translated the PRS into German and Polish and verified our translation with a back translation into English (for English, Polish and German versions see Table A.2). All interviews were conducted in the five study areas in public spaces like information centres, parking lots and snack bars to ensure access to sufficient numbers of respondents. Participants were asked to look at five photographs (Appendix D), each depicting a study plot in the respective study area, and to rate the restorativeness factors for each of them. We also included a question about the perceived biodiversity on each plot, which was also rated on a 5-point Likert scale (1 = very low, 3 = medium, 5 = very high). The questionnaire further included the option to provide socio-demographic parameters – age, gender, and education level – with the option to give no answer.

2.6. Statistical analyses

All statistical analyses were conducted with R 3.6.1 (R Core Team, 2019). We fitted generalized linear mixed models (GLMMs) with the glmer function and linear mixed-effects models (LMMs) with the lmer function from the lme4 package (Bates et al., 2015). We used LMMs to analyse the impact of disturbance severity on dead-wood amount, total arthropod biomass and restorativeness. In all models we controlled for elevation and the percentage of deciduous trees; and, we included the study area as a random factor to control for general differences between study areas. For comparability to biodiversity indicators we used the mean perceived restorativeness (calculated as mean across the 5 items of the scale) for each plot across all respondents. We fitted GLMMs with Poisson distribution to analyse the impact of disturbance on species numbers and numbers of operational taxonomic units (OTUs) of arthropods, fungi, birds, vascular plants, epigeic and epiphytic bryophytes and lichens, controlling for elevation and the percentage of deciduous trees. In addition to these control variables, all GLMMs included an observation-specific random factor to control for Poisson overdispersion (Elston et al., 2001). GLMMs with Poisson distribution were also fitted to analyse the impact of disturbance on the number of OTUs of different functional groups (destruents, pollinators, parasites, parasitoids, primary consumers, and predators). Furthermore, we created LMMs with the perceived restorativeness and all five factors in the PRS as well as perceived biodiversity as response variables using disturbance severity, age, gender and education as predictors. We calculated Cronbach's alpha to check the reliability of the scale (Cronbach, 1951), which resulted in an alpha of 0.77. We controlled for percentage of deciduous trees and elevation and included respondent ID and picture as random factors. To calculate a multi-diversity index, we rescaled data for all species groups, including functional groups of arthropods, to values between 0 and 1 as described by Allan et al. (2014). We used an LMM to analyse the impact of disturbance severity on multi-diversity. To test for possible non-linear effects, we additionally created generalized additive models using the gamm function from the mgcv package (Wood, 2011), which included the same variables as the GLMMs and LMMs.

3. Results

We inventoried 3449 dead-wood objects and sequenced samples of 345 objects for fungi diversity. Sequencing resulted in 1493 fungi OTUs. We recorded 65 bird species and 1871 bird individuals, 91 epigeic and 90 epiphytic bryophyte species, 96 lichen species and 323 vascular plant species. Sequencing of arthropod samples resulted in 3575 arthropod OTUs. We interviewed 191 respondents in the Bavarian Forest, 202 in Berchtesgaden, 276 in Białowieża Forest, 229 in Kalkalpen and 203 in the Black Forest (1101 respondents in total across all protected areas). Out of the respondents, 544 of the respondents declared themselves to be female and 557 male. The respondents' ages ranged from 14 to 83 with a mean age of 42.1 ± 16.2. In total, 48 respondents had not yet graduated, 146 graduated from middle school, 179 graduated from secondary school, 640 achieved a higher education entrance qualification, 5 indicated that they had no education and 83 preferred not to say.

Model results of the generalized additive models showed only linear effects, and so we proceeded with the linear models. In general, the amount of dead wood increased with increasing disturbance severity. Highest amounts of dead wood occurred in the Bavarian Forest National Park and Białowieża Forest, but differences between the study areas were not significant (Fig. A.1). Multi-diversity was not significantly influenced by disturbance severity (Fig.1 and Table 2). Mean perceived restorativeness ranged from 2.6 to 4.0 (Fig.1). Mean perceived restorativeness significantly decreased with increasing disturbance severity ($z = -2.03$) and with the increasing age of the respondents (Table 2). In

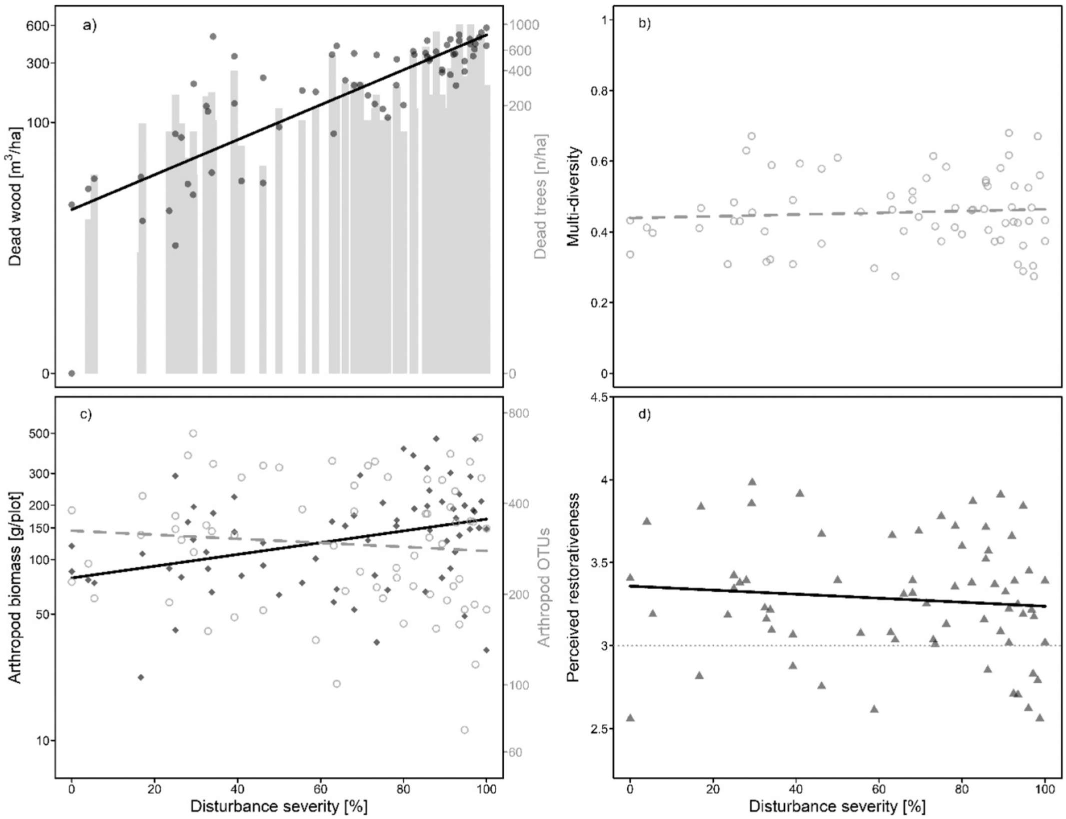

Fig. 1. Measured (dots) and predicted (lines) a) amount of spruce dead wood [m^3/ha] and number of dead trees for each study plot (grey bars) b) multi-diversity index (following Allan et al. (2014)), c) predicted arthropod biomass [g/plot] (black line) and number of arthropod operational taxonomic units (OTUs) (grey circles), and d) perceived restorativeness, all plotted over disturbance severity (0–100% beetle-killed trees). Grey dotted line in plot d) at y = 3 indicates the threshold for environments that are high in restorativeness (following Berto (2005)). Scatter plots depict raw data. Solid black lines depict significant predictions, dashed grey lines depict not significant predictions.

Fig.1, only the mean restorativeness values for all respondents were considered in the scatter plot and prediction. For predictions with data for all respondents, see Fig. 3.

Number of arthropod OTUs was not influenced by disturbance severity (Fig. 1). However, arthropod biomass increased significantly with increasing disturbance severity (Fig. 1 and Table 2). The number of destruent OTUs decreased significantly with increasing disturbance severity. Species numbers of vascular plants, lichens and pollinators increased significantly with increasing disturbance severity (Fig. 2 and Table A.5).

Different factors of the perceived restorativeness scale were influenced by different predictors in our models (Fig. 3). *Being away* and *fascination* had the highest mean values with 3.6 ± 1.2 and 3.6 ± 1.1, respectively. *Being away* decreased with the increasing age of the respondents but was not related to disturbance severity. *Fascination* decreased with increasing disturbance severity and increasing respondent's age. *Coherence* and *scope* had lower mean values compared to the other factors with 2.7 ± 1.2 (*coherence*), and 3.0 ± 1.1 (*scope*). *Coherence* was not related to disturbance severity. *Scope* decreased with increasing disturbance severity and increasing respondent's age and increased with increasing amount of deciduous trees. Male respondents had higher values for *scope* than female respondents. *Compatibility* (mean = 3.4 ± 1.1) decreased with the increasing age of the respondents. Perceived biodiversity was not related to disturbance severity but decreased with the increasing age of the respondents (Table A.3). Forests with more than 90% disturbance severity still had a mean restorativeness of 3.4 ± 1.1.

4. Discussion

Our results show that multi-diversity and overall number of arthropod OTUs were not affected by disturbance severity. By contrast, arthropod biomass and species numbers of primary producers and pollinators increased linearly while OTU numbers of destruents and the perceived restorativeness of forest stands decreased linearly with disturbance severity. However, severely disturbed forests were still perceived as restorative.

4.1. Impacts on biodiversity

Depending on habitat requirements, taxonomic groups showed different responses to bark beetle infestations (see also Lehnert et al., 2013). Therefore, negative and positive diversity responses can cancel each other out. Such different responses might explain the absence of an effect of disturbance severity on multi-diversity. While species and OTU numbers of vascular plants, lichens and pollinators increased, numbers of destruent OTUs decreased and the remaining groups showed no response to increasing disturbance severity. Habitat openness and increased availability of light after a disturbance event can promote lichen diversity (Moning et al., 2009; Bässler et al., 2016) if moisture is not a limiting factor, which applies to our study areas. Bryophytes are bound more closely to moist and shady conditions and can therefore decline with high light intensities and increasing temperatures (Raabe et al., 2010). Nevertheless, different bryophyte species have different sensitivities to temperature (Raabe et al., 2010) and should therefore react differently to increased canopy openness. These varying habitat requirements could explain the overall lack of response of bryophyte species numbers to disturbance severity. The increased availability of

Table 2
Results of linear mixed effects models testing the influence of disturbance severity on multi-diversity, perceived restorativeness, arthropod biomass and number of arthropod OTUs. Boldface indicates significance.

Response	Predictors	Estimate	Std. Error	Z value	*P* value
Multi-diversity	**Intercept**	**$3.02\ e^{-1}$**	**$7.32\ e^{-2}$**	**4.13**	**< 0.001**
	Disturbance severity	$3.05\ e^{-4}$	$2.89\ e^{-4}$	1.06	$2.91\ e^{-1}$
	Elevation	**$1.68\ e^{-2}$**	**$7.12\ e^{-3}$**	**2.36**	**$1.81\ e^{-2}$**
	Deciduous trees	$7.33\ e^{-4}$	$6.77\ e^{-4}$	1.08	$2.79\ e^{-1}$
Arthropod biomass	**Intercept**	**5.27**	**$2.69\ e^{-1}$**	**$1.96\ e^{1}$**	**< 0.001**
	Disturbance severity	**$6.59\ e^{-3}$**	**$2.21\ e^{-3}$**	**2.98**	**$2.87\ e^{-3}$**
	Elevation	**$-8.91\ e^{-2}$**	**$2.24\ e^{-2}$**	**−3.98**	**$6.75\ e^{-5}$**
	Deciduous trees	**$-1.15\ e^{-2}$**	**$5.03\ e^{-3}$**	**−2.29**	**$2.22\ e^{-2}$**
Arthropod OTUs	**Intercept**	**5.40**	**$2.94\ e^{-1}$**	**$1.83\ e^{1}$**	**< 0.001**
	Disturbance severity	$-1.11\ e^{-3}$	$1.72\ e^{-3}$	$-6.43\ e^{-1}$	$5.20\ e^{-1}$
	Elevation	$4.60\ e^{-2}$	$2.82\ e^{-2}$	1.63	$1.04\ e^{-1}$
	Deciduous trees	$-1.98\ e^{-3}$	$4.01\ e^{-3}$	$-4.95\ e^{-1}$	$6.21\ e^{-1}$
Restorativeness	**Intercept**	**3.80**	**$1.75\ e^{-1}$**	**$2.17\ e^{1}$**	**< 0.001**
	Disturbance severity	**$-2.76\ e^{-3}$**	**$1.29\ e^{-3}$**	**−2.14**	**$3.25\ e^{-2}$**
	Elevation	$-1.51\ e^{-2}$	$1.22\ e^{-2}$	−1.24	$2.16\ e^{-1}$
	Deciduous trees	$3.64\ e^{-3}$	$2.94\ e^{-3}$	1.24	$2.15\ e^{-1}$
	Age	**$-2.51\ e^{-3}$**	**$1.02\ e^{-3}$**	**−2.46**	**$1.38\ e^{-2}$**
	Gender	$1.55\ e^{-2}$	$3.35\ e^{-2}$	$4.63\ e^{-1}$	$6.44\ e^{-1}$
	Education level 2	$7.72\ e^{-2}$	$8.53\ e^{-2}$	$9.05\ e^{-1}$	$3.80\ e^{-1}$
	Education level 3	$-3.02\ e^{-1}$	$1.50\ e^{-1}$	−2.02	$4.30\ e^{-2}$
	Education level 4	$-2.21\ e^{-1}$	$1.50\ e^{-1}$	−1.51	$1.30\ e^{-1}$
	Education level 5	$1.05\ e^{-1}$	$3.21\ e^{-1}$	$3.29\ e^{-1}$	$7.43\ e^{-1}$
	Education level 6	$-2.35\ e^{-1}$	$1.12\ e^{-1}$	−2.08	$3.72\ e^{-2}$

light and nutrients after a disturbance event is also beneficial for the development of a diverse herb and shrub layer (Swanson et al., 2011; Winter et al., 2015). The increasing light availability (Proctor et al., 2012; Hanula et al., 2015) and diversity in vascular plants might also explain the increase in pollinator OTUs (Campbell et al., 2007; Winter et al., 2015). Contrary to expectations, the number of primary consumers did not change over the disturbance gradient. Primary consumers are predominantly more specialized than pollinators regarding their plant resources (Jones and Agrawal, 2017) and should benefit from an increased species number of vascular plants. Nevertheless, looking at single families separately, we observed that families classed as primary consumers in this study reacted differently to increasing disturbance severity. Whereas species numbers of most families classified as primary consumers showed no or increasing effects, some of the Diptera families decreased in species numbers with increasing disturbance severity. The dieback of canopy trees and the associated reduction of leaf-litter fall might also explain the decline of OTUs of arthropodal destruents with increasing disturbance severity in our study. Our results are contrary to expectations on destruents depending on dead wood, which should increase with increasing amounts of dead wood after a disturbance event. Still, arthropodal destruents feeding on leaf litter, which are also represented in our data, are known to be influenced by the amount and composition of litter as well as its humidity (Cornelissen et al., 1999; Cornwell et al., 2008). Both decreasing amount of litter and humidity and the change in litter composition might cause a decline of OTU numbers for arthropodal destruents exceeding the effects on dead-wood-dependent arthropods.

In our study, the number of arthropod OTUs and arthropod biomass responded differently to increasing disturbance severity (see Fig. 1). Whereas the overall number of arthropod OTUs did not change with disturbance severity, arthropod biomass increased. This suggests that changes in arthropod biomass in our study depend on habitat features in a different way than OTU numbers. Furthermore, increasing arthropod biomass indicates an increase in productivity (Borer et al., 2012). Considering the dieback of canopy trees that leads to decreased productivity of the overstorey after a disturbance event, increasing productivity should be linked to changes in microclimate and/or the herbaceous layer. An increase in resources for herbivores could have effects on biomass traveling up the food chain. Still, due to the lack of abundance data it is not possible to separate different effects on species numbers and biomass.

4.2. Impacts on perceived restorativeness

The perceived restorativeness of affected forests decreased with increasing disturbance severity. Nevertheless, the absolute decline in restorativeness was low, and forests with more than 90% disturbance severity still had a mean restorativeness of 3.2 (±0.8). By comparison, forest stands with less than 30% disturbance severity had a mean restorativeness of 3.4 (±0.8). This indicates that even severely disturbed forests are still perceived as restorative environments according to the threshold of 3 given by Berto (2005) (adapted to a 5-point-scale). This finding is in line with recent results from a visitor-employed photography study by Rathmann et al. (2020b), which showed that although dead wood is among the least liked forest elements it is nevertheless an appreciated landscape element and positively correlated to recreational experiences. Still, one should keep in mind that national park visitors could have different perceptions than the general public. Nevertheless, national park visitors are in the end the target group of national park management.

Perceived biodiversity was not influenced by disturbance severity (Fig. 3). This is in contrast to McFarlane et al. (2006) where the majority of respondents perceived bark beetle infestations as a threat to biodiversity. Nevertheless, people can have contradictory attitudes towards biodiversity and dead wood. Pelyukh et al. (2019) have shown that even if people consider dead wood to be important for biodiversity, those same individuals might still prefer intensively managed forests without dead wood. Preferences for certain landscapes and the perceived biodiversity of those landscapes are not necessarily correlated. In our study, especially *fascination, scope* and *compatibility* in the relevant landscapes were diminished by bark beetle infestations (Fig. 3). Making these landscapes more accessible with boardwalks and small trails or guided tours through the affected areas might counteract such perceived limitations. Our results suggest that the impacts of bark beetle infestations on the perceived restorativeness of an affected landscape might be slightly overestimated. This overestimation might be caused in part by visitors' predisposition to perceive bark beetle infestations as a negative (Müller and Job, 2009) and perceived threats by bark beetle infestations (McFarlane and Witson, 2008; Flint et al., 2012). Hence, expectations before and perceptions after a disturbance event might diverge. In our study, both perceived and collected biodiversity did not decrease with increasing disturbance severity. In addition, the perceived restorativeness decreased only to a small extent. These results stand in

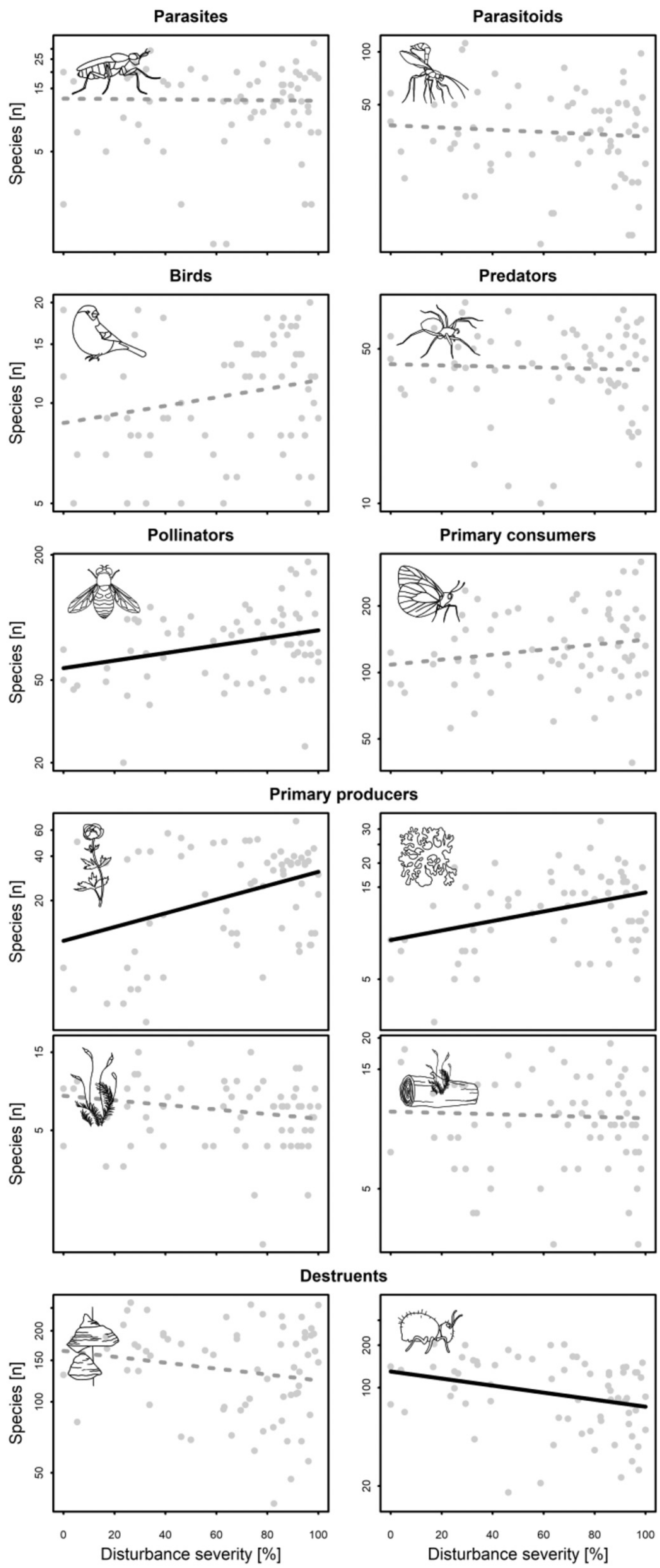

Fig. 2. Predictions of generalized linear mixed models for arthropodal parasites and parasitoids; birds; arthropodal predators, pollinators and primary consumers; primary producers (including vascular plants, lichens, epigeic bryophytes and epiphytic bryophytes); fungi and arthropodal destruents over the disturbance gradient (0–100%). Only significant correlations are shown by black lines. Scatter plots depict raw data.

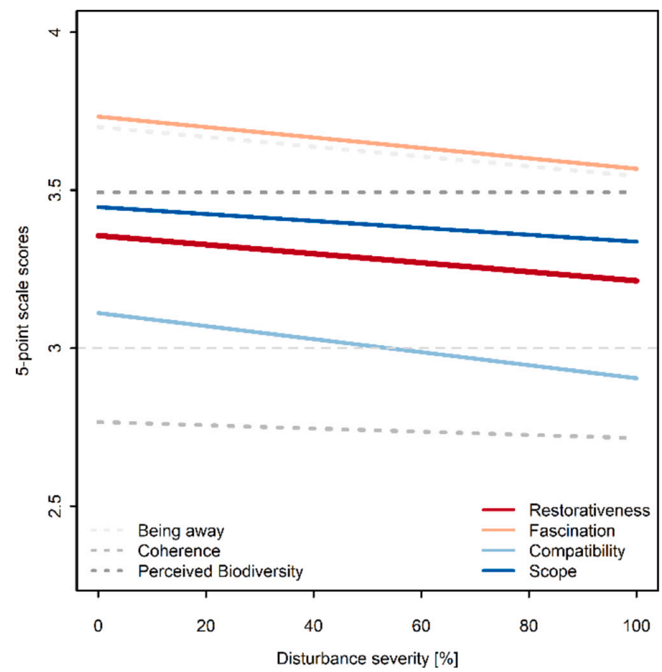

Fig. 3. Predictions of the different factors of the Perceived Restorativeness Scale and perceived biodiversity along the disturbance gradient. Not significant results of the predictions are shown with dotted lines, significant results with solid lines. Grey dashed line at 3 indicates the threshold for environments with high restorativeness (following Berto (2005)).

contrast to the widely discussed risks of natural disturbances for nature conservation and recreation. Beyond that, our results support the ambition to reconcile conservation and recreation in national park management.

Since the perceived restorativeness of severely disturbed forest stands is still high, we conclude that salvage logging to maintain the recreational value of bark-beetle affected landscapes might be obsolete (see also Sacher et al., 2017). Still, the impacts of salvage logging operations on perceived restorativeness have yet to be quantified. In times of climate change, future research should also focus on commercial forests to develop appropriate management options according to varying conditions and objectives.

5. Conclusions

By analysing the impacts of bark beetle infestations on biodiversity and restorativeness in a consistent way across protected areas in Europe, we provide scientific evidence for the contrasting effects on conservation and recreation. In addition, our results show that the restorativeness of forests is diminished by bark beetle infestations but remains high even in forests with high severity disturbances. Arthropod biomass is enhanced in disturbed forests, and several species groups, i.e. vascular plants, lichens and pollinating insects, show higher species numbers and can benefit from the changes caused by bark beetle infestations. Since different taxonomic and functional groups benefit from different disturbance severities, forests where nature conservation is an important objective can benefit from heterogeneous bark beetle infestations. Contrary to expectations, our results show that even severely disturbed forests have high biodiversity and restorativeness. Since biodiversity, conservation and recreation are not at risk in infested areas, management should consider strategies to reconcile both objectives by balancing the trade-offs between some taxonomic groups and restorativeness according to the overall objectives in a landscape.

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CRediT authorship contribution statement

Mareike Kortmann: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Jörg C. Müller:** Conceptualization, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Roland Baier:** Resources, Writing – review & editing. **Claus Bässler:** Writing – review & editing, Funding acquisition. **Jörn Buse:** Investigation, Resources, Writing – review & editing. **Olga Cholewińska:** Investigation, Writing – review & editing. **Marc I. Förschler:** Investigation, Writing – review & editing. **Kostadin B. Georgiev:** Investigation, Writing – review & editing. **Jacek Hilszczański:** Investigation, Resources, Writing – review & editing. **Bogdan Jaroszewicz:** Investigation, Resources, Writing – review & editing. **Tomasz Jaworski:** Investigation, Writing – review & editing. **Stefan Kaufmann:** Investigation, Writing – review & editing. **Dries Kuijper:** Writing – review & editing. **Janina Lorz:** Investigation, Writing – review & editing. **Annette Lotz:** Resources, Writing – review & editing. **Anna Łubek:** Investigation, Writing – review & editing. **Marius Mayer:** Writing – review & editing. **Simone Mayerhofer:** Resources, Writing – review & editing. **Stefan Meyer:** Investigation, Writing – review & editing. **Jérôme Morinière:** Investigation, Data curation, Writing – review & editing. **Flavius Popa:** Investigation, Writing – review & editing. **Hannah Reith:** Investigation, Writing – review & editing. **Nicolas Roth:** Investigation, Writing – review & editing. **Sebastian Seibold:** Writing – review & editing. **Rupert Seidl:** Writing – review & editing. **Elisa Stengel:** Investigation, Writing – review & editing. **Grzegorz J. Wolski:** Investigation, Writing – review & editing. **Simon Thorn:** Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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