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ORIGINAL PAPER

Spruce dieback as chance for biodiversity: standing deadwood promotes beetle diversity in post-disturbance stands in western Germany

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Abstract
Anthropogenic climate change poses a major threat to ecosystems and their biodiversity. Forests, for example, are suffering from climate-amplified disturbances like droughts or pest outbreaks. Throughout Europe, such disturbances resulted in large-scale diebacks of managed spruce stands in recent years. While such stands are often salvage-logged to reduce economic losses, it is still rather unclear how post-disturbance management affects forest biodiversity in anthropogenic spruce stands. By comparing epigeal beetle communities among salvage-logged sites, standing deadwood patches, and succession areas, we show that spruce dieback can be a chance for biodiversity conservation. Even though individual beetle families responded partly differently to post-disturbance management, standing deadwood enhanced the overall diversity of ground-dwelling beetles compared to salvage logging, while succession sites were intermediate. We also show that community composition and functional guilds vary strongly between management categories.

Implications for insect conservation: We suggest to set-aside areas of standing deadwood for natural succession to enhance beetle taxonomic and functional diversity, especially of deadwood-dependent species. As different types of management support different species assemblages, well-planned post-disturbance management, including a partial abandonment of salvage logging and a consideration of natural succession, may counter biodiversity losses in forests.

Keywords Forest dieback · Norway spruce · Post-disturbance management · Biodiversity conservation · Coleoptera · Beetle communities

Introduction

Anthropogenic climate change is one of the biggest challenges of our time. Recently, scientists projected that the 1.5-degree target, agreed upon at the UN climate change conference 2015 in Paris (United Nations 2015), will most likely be exceeded even earlier than expected (IPCC 2022). This will have considerable impacts on human societies, but also on ecosystems and the services they provide for humanity (IPCC, 2018). For example, the frequency of climate-induced disturbances is constantly increasing, including for instance wildfires, droughts, and the outbreak of pest species as temperatures are rising (Seidl et al. 2017). However, the consequences of such disturbances can be quite distinct in different ecosystems. Due to their comparatively long live spans, trees for example can only adapt slowly to environmental changes and are therefore particularly affected by climate change (Brodribb et al. 2020). Accordingly, Seidl et al. (2014) forecasted that 60 million m^3 of timber will be annually damaged in Europe by storms and bark beetle outbreaks between 2021 and 2030. Since forests cover 30% of our planet's land mass (FAO 2020) and provide important resources along with many ecosystem services (Seidl et al. 2014; Morris et al. 2016; Muys et al. 2022), the predicted forest dieback will have serious consequences (IPCC 2022).

Forests harbor a substantial share of the global terrestrial biodiversity (Brodribb et al. 2020). This is true especially for tropical rainforests (Erwin 1982; Pillay et al. 2022), while intensively managed European forests are considered to be

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relatively species-poor (Paillet et al. 2010; Schulze 2018). Natural disturbances may contribute to ecosystem renewal and to creating heterogeneity, and thus tend to promote biodiversity (White and Pickett 1985; Müller et al. 2008; Swanson et al. 2011; Senf et al. 2020). Accordingly, studies investigating the effects of natural disturbances in European forests found beneficial effects for most taxa under investigation (Moretti et al. 2004; Winter et al. 2015; Beudert et al. 2015; Kortmann et al. 2021, 2022). However, for economic (Sessions et al. 2004; Prestemon et al. 2006; Kausrud et al. 2012) and aesthetic reasons (Morris et al. 2016; Hlásny et al. 2021), forests are rarely left untreated after disturbance, but are typically salvage-logged (Müller et al. 2019). Logging though may alter forest communities and even ecosystem stability (Thorn et al. 2016a; Doerfler et al. 2020). Beetles are a particularly important taxon in forest ecosystems, and may act as predators, seed dispersers, decomposers, prey for higher trophic levels or even as ecosystem engineers (Müller et al. 2008; Zumr et al. 2021; López-Bedoya et al. 2021). Due to such diverse roles, beetles are important for ecosystem functioning and resilience (Lange et al. 2014; Homburg et al. 2019). However, different beetle families or ecological guilds may respond differently to forest management. While some groups seem little affected by post-disturbance management (Thorn et al. 2016a), others, such as saproxylic beetles, strongly decline due to the associated deadwood removal (Thorn et al. 2014; Seibold 2015; Zumr et al. 2021; Uhl et al. 2022). This complicates the assessment of different management approaches, but also allows for a more holistic evaluation if beetles of different taxa or functional groups are taken into consideration (e.g. Desender et al. 2010).

Salvage logging after disturbance is still widespread in managed forests throughout Europe (Muys et al. 2022), where Norway spruce (*Picea abies*) is the economically most important tree species (Brus et al. 2012). In Germany, spruce stands have increased strongly since World War II. They now occupy one quarter of the national forest area (BMEL 2021), exceeding the natural range of spruce by far. However, spruce is highly susceptible to natural disturbances like storm, drought, and bark beetle outbreaks (Overbeck and Schmidt 2012). For example, in the German federal state of Rhineland-Palatinate, 70% of all spruce trees were killed by the bark beetle *Ips typographus* during the unusually dry years 2018–2020 (MUEEF 2020). The consequences of spruce dieback and the subsequent management for biodiversity conservation are largely unclear, at least in managed spruce forests (Hlásny et al. 2017; Thorn et al. 2018). Previous studies have often focused on nature reserves or stands within the natural range of *Picea abies* (e.g. Müller et al. 2008; Thorn et al. 2016b), other disturbance types (e.g. fire: Cobb et al. 2011; windthrow: Georgiev et al. 2022) and / or single response groups (Lange et al. 2014). Though managed spruce forests are considered to have a comparatively low biodiversity (Magura et al. 2000; Morris et al. 2016; Hlásny et al. 2017; Zumr et al. 2021), their dieback and subsequent management will significantly alter local species communities and thereby forest biodiversity (Muys et al. 2022).

Here, we investigate the effects of different post-disturbance management approaches on epigeal beetle diversity in managed spruce stands. Specifically, we compare former spruce stands that were (1) salvage-logged and cleared after a bark beetle outbreak in 2020, (2) left untreated following the same disturbance event, or (3) left untreated after a windthrow in 2008 to allow for secondary succession. The latter category was included to determine potential beneficial effects of set-aside stands over time, although type of and time since disturbance differs from the first two categories. We thus investigate to what extent the post-disturbance management of spruce stands affects epigeal beetle diversity and thus biodiversity conservation. As different families or ecological groups of beetles may respond differently, we analyze effects on overall epigeal beetle diversity as well as on Carabidae, Staphylinidae, Curculionoidea (Curculionidae and Scolytidae), and on saproxylic beetles. We focus on the following research questions: (i) How does beetle taxonomic diversity respond to post-disturbance management? (ii) How do community composition and guilds differing in moisture, food, and habitat preferences respond to post-disturbance management? (iii) Which post-disturbance management is best suited to enhance beetle diversity?

Materials and methods

Study area

We investigated former spruce forests within the district of the forestry office Neuhäusel (50°38’N, 7°1’E), located within the Westerwald mountain range in western Germany (Fig. 1; Table 4, Supplementary material). All sites were located between 510 and 545 m above sea level in the vicinity of the mountain ‘Alarmstange’, which is the highest elevation of the ‘Montabaurer Höhe’ in turn representing a subunit of the Westerwald mountain range. The ‘Montabaurer Höhe’ is characterized by a high proportion of forests (61%), mainly anthropogenically planted spruce stands, while the natural vegetation would consist mainly of mixed beech forests. Agriculture (16%), settlements, and infrastructure (in total 21%) make up comparatively small shares and are mainly located at the foot of the ridge (MKUEM RLP 2022; Statistisches Landesamt Rheinland-Pfalz 2020). Our

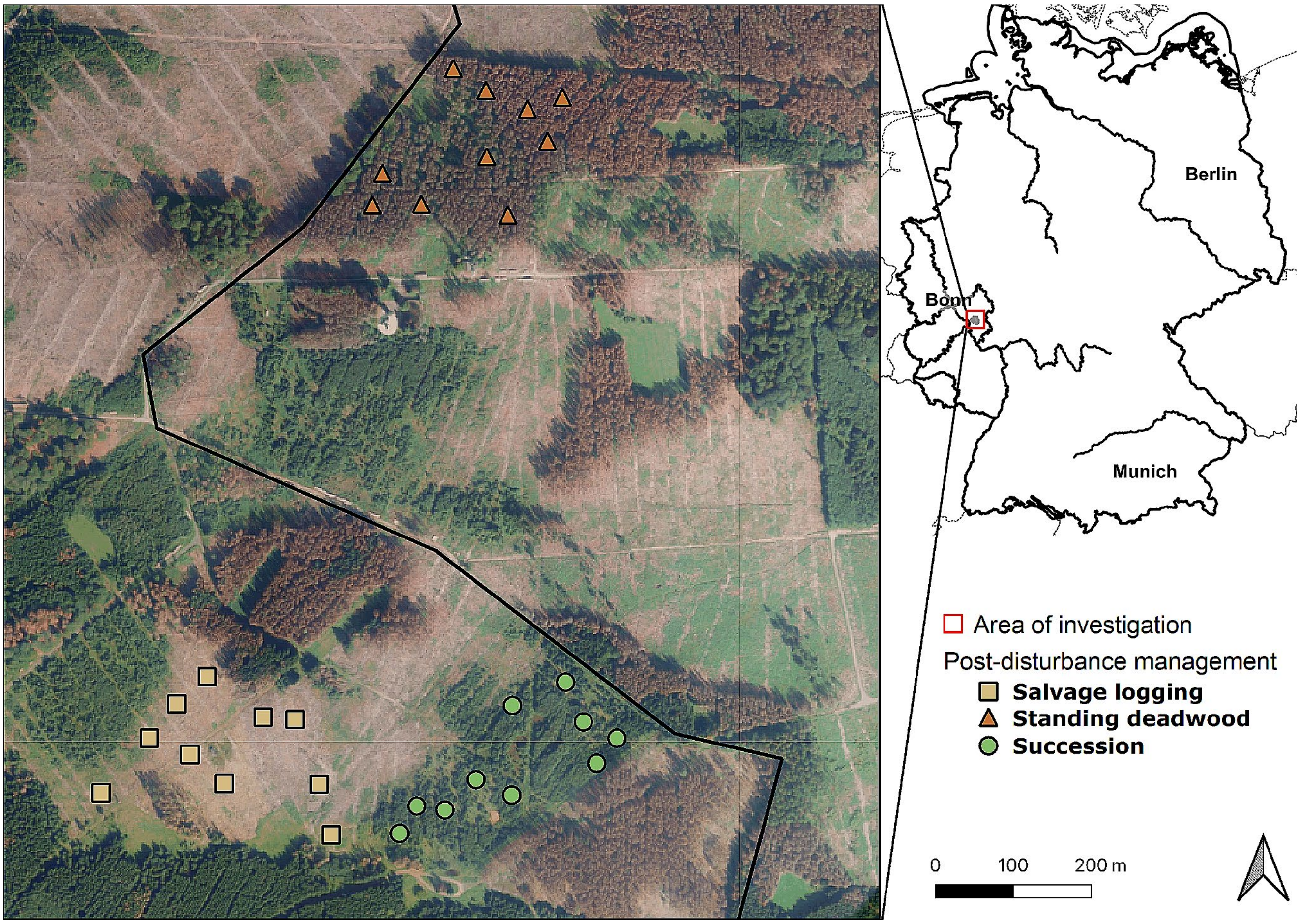

Fig. 1 Location of our study area in Rhineland-Palatinate, Germany, and of the study sites within different post-disturbance management categories ((LVermGeo RLP 2021); modified with QGIS 3.4 (QGIS Development Team))

study area is dominated by Devonian quartzites, on which mainly loose brown soils and pseudogleys have developed (Landesamt für Geologie und Bergbau Rheinland-Pfalz 2013 a, b). The climate is oceanic with a long-term average precipitation of 890 mm and an annual mean temperature of 9.0 °C (years 2014–2021; Agrarmeteorologie Rheinland-Pfalz 2022). In 2020, though, the average temperature was 9.8 °C and the precipitation 740 mm. This not only accelerated the spruce forest dieback on the Montabaurer Höhe, but has also sparked an ongoing discussion about appropriate management strategies between foresters, conservationists and citizens, as also experienced in other regions (Thorn et al. 2018).

Field methods

We examined former spruce stands in which all spruce trees had died, according to three post-disturbance management categories for our sampling: (1) salvage-logged sites, where spruce trees had been cut and cleared after bark beetle infestation in 2020 (hereafter 'salvage logging'); (2) stands with standing dead spruce which had also died in 2020 (hereafter 'standing deadwood'); (3) successional areas, which were left to secondary succession after a storm had uprooted all trees in 2008 (hereafter 'succession'). Even though the disturbance type (windthrow, no subsequent bark beetle infestation) and time since disturbance differs from the other two categories, the succession sites were included in this study to assess the longer-term effects of secondary succession on the epigeal beetle diversity of disturbed stands. Thus, while uprooted trees may provide a different habitat and cause different changes in microclimate than dead trees following a bark beetle infestation (Swanson et al. 2011), we assume that subsequent succession may follow similar patterns, when dead trees fall down in the course of the decay process. Moreover, we were interested in the beetle community of the former as storms are among the most common disturbance events in Central European forests, and their frequency is predicted to increase in the future (Seidl et al. 2014, 2017). All categories were thus chosen to represent different management strategies after spruce forest disturbance, either salvage-logging, leaving the standing deadwood untreated, and long-term succession. For each category, we selected ten sites based on accessibility as granted by the forestry office (Fig. 1; Table 4, Supplementary material). Per site, two pitfall traps were buried ten meters apart with their rims at ground level. 125 ml PET cups, filled with 60 ml of a mixture of water and monopropylene glycol (70:30%), were used as traps and protected against rain with a plastic roof. All 60 traps were emptied every two weeks (six times) between the 27th of April and 21st of July 2021 (85 trapping days in total for each trap, see Niemelä et al. 1990), corresponding to the period with highest beetle activity in Germany (e.g. Renner 1980; Benisch 2023). After sorting, the collected beetles were stored in 70% ethanol until identification using taxonomic keys (Freude et al. 1965–1983; Lompe 2002).

Data collection

For each site, we calculated the numbers of individuals and species. Alpha diversity, considering the number of species and their abundance, was determined using the effective number of species, which is a derivate of the Shannon-Wiener index (Jost 2006). We are aware that, rather than recording abundances, pitfall traps record activity densities (Sunderland et al. 1995), which can be influenced by various factors (Saska et al. 2013). Therefore, the rarefied species richness of each site was estimated for a sample coverage of 90% (iNEXT-Package in R; Hsieh et al. 2016) to account for differences in the detection probabilities among management categories. Furthermore, we assigned a point score to every species according to its status on the red list of Germany (Geiser 1998). The score values correspond to an exponential distribution, so that endangered species have a greater weight according to their status (least concern = 1 point, near-threatened = 4, vulnerable = 16; no other categories were found). All point scores per site were then added up as 'conservation value' (Görn and Fischer 2011) to identify management categories that harbor species of relevance for conservation. The five parameters described above were calculated for all beetles as well as separately for Carabidae, Staphylinidae, Curculionoidea (Curculionidae and Scolytidae), and saproxylic beetles (beetles with an ecological preference for deadwood, according to Koch 1989–1996). Additionally, we determined indicator species for each management category (Dufrêne and Legendre 1997; indval-function, labdsv-package in R; Roberts 2023).

If known, species were allocated to different categories regarding their ecological preferences for moisture (hygrophilic; hemihygrophilic; mesophilic; xerophilic; unknown for 9 out of 231 species), food (xylophagous; phytophagous; mycetophagous; zoophagous; omnivorous; unknown for 14 out of 231 species), habitat type (forest stenotopic; forest eurytopic; ubiquitous; open landscape; unknown for 10 out of 231 species), and habitat niche (deadwood; tree-layer; herb-layer; litter-layer; ground-dwelling; unknown for 7 out of 231 species) according to Koch (1989–1996). We then calculated the relative abundance (percentage of all individuals of an ecological type relative to the total number of individuals; species with unknown preferences were excluded from these analyses) among management types for each ecological preference. Also, the relative abundances of the five most common families and species were compared among management categories.

Statistical analyses

We used ANOVAs to test for significant variation in the numbers of individuals and species, the effective number of species, rarefied species richness, and conservation value across management categories. Afterwards, Tukey HSD tests were performed to identify significant differences between categories. The following parameters had to be Ln-transformed prior to analyses to meet ANOVA requirements: individual numbers of all beetles, Carabidae, Staphylinidae, and Curculionoidea; the number of species of Carabidae; the effective species numbers of all beetles, Carabidae, and Staphylinidae; the rarefied species richness of all beetles, Carabidae, Staphylinidae, and saproxylic beetles; and the conservation value of Carabidae and Curculionoidea. The number of species of the Curculionoidea was square-root-transformed prior to analysis. To account for the spatial aggregation of sampling locations, we tested for spatial autocorrelation using the Moran's I test (ape-package in R; Dormann et al. 2007; Paradis and Schliep 2019). As the results were non-significant throughout (results not shown), an influence of spatial autocorrelation on any dependent variable could be excluded. Variation in the relative abundance of species with different ecological preferences across management types were identified using PERMANOVAs (permutations = 999). Subsequently, pairwise PERMANOVAs were carried out to locate significant differences between categories. PERMANOVA was also used to test for significant differences in community composition. To this end, we used the Bray-Curtis dissimilarity index based on our abundance data, and we visualized the results with the help of a non-metric multidimensional scaling (NMDS) analysis. If not mentioned otherwise, statistical analyses were performed using the vegan-package (Oksanen et al. 2020) in R (R Core Team 2020).

Results

Sampling results

In total, we collected 7878 beetle individuals from 231 species and 32 families. We found five species listed in the red list of Germany (Geiser 1998) as near-threatened (salvage-logged: *Astenus longelytratus* (1 individual), *Hypoganus inunctus* (1); standing deadwood: *Pterostichus cristatus* (14); succession: *Acupalpus dubius* (6), *Amara nitida* (4) and two listed as vulnerable (standing deadwood: *Rutidosoma graminosus* (3); succession: *Agonum gracile* (2); Table 5, Supplementary material). Eleven species had a preference for salvage-logged sites, 32 for standing deadwood, and 15 for succession areas (Table 6, Supplementary material). The five most common families were Staphylinidae (36.3% of all individuals), Curculionidae (23.8%), Carabidae (15.9%), Scolytidae (11.0%), and Geotrupidae (2.7%). The distribution of families in standing deadwood differed significantly from that of both other categories (Table 2; Fig. 2a). Standing deadwood was characterized by a low proportion of Curculionidae but a high one of Scolytidae (bark beetles). At the species level, all three management categories differed significantly (Table 2; Fig. 2b). The most frequent species, *Exomias araneiformis* (16.3% of all individuals), reached the highest proportion on salvage-logged followed by succession and finally standing deadwood sites. *Atheta negligens* (9.3%) was particularly abundant in succession areas. As expected, the bark beetle *Ips typographus* (8.8%) was largely restricted to standing deadwood. Throughout, more than 50% of the individuals were other species than the five most numerous ones, documenting high proportions of species with low abundance.

Taxonomic diversity

For all beetles, post-disturbance management significantly affected the numbers of individuals and species as well as the conservation value (Table 1).

For all beetles, standing deadwood showed the highest numbers of individuals and species as well as the highest conservation value, while differences between salvage-logged and succession sites were non-significant throughout (Fig. 3; Table 7, Supplementary material). Significant differences were also found within the separately analyzed groups except from Carabidae, which showed no significant responses throughout. In the Staphylinidae, all five parameters differed significantly among management types. The number of individuals was significantly higher at standing deadwood than at succession sites (Fig. 3). The number of species and the effective number of species were significantly lower at salvage-logged as compared with standing deadwood or succession sites. Similarly, the rarefied species richness and conservation value were significantly lower at salvage-logged than at succession sites.

Weevils (Curculionoidea) and saproxylic beetles showed significantly higher values at standing deadwood than at succession sites throughout, except from rarefied species richness in saproxylic species. In Curculionoidea, salvage-logged sites also showed significantly higher values than succession sites for the effective number of species and rarefied species richness, while the conservation value of salvage-logged sites was equal to that of succession sites, and thus significantly lower than the value of standing deadwood. In terms of individual and species numbers, the values for salvage-logged sites were in between those for standing deadwood and succession sites. In saproxylic beetles, individual and species numbers of salvage-logged sites were significantly lower compared with deadwood sites, while effective species number and conservation value of salvage-logged sites ranged between the figures for standing deadwood and succession sites.

Community and guild composition

The relative abundance of individuals differed significantly across management regimes for all ecological parameters (Table 2). The distributions of moisture and habitat type

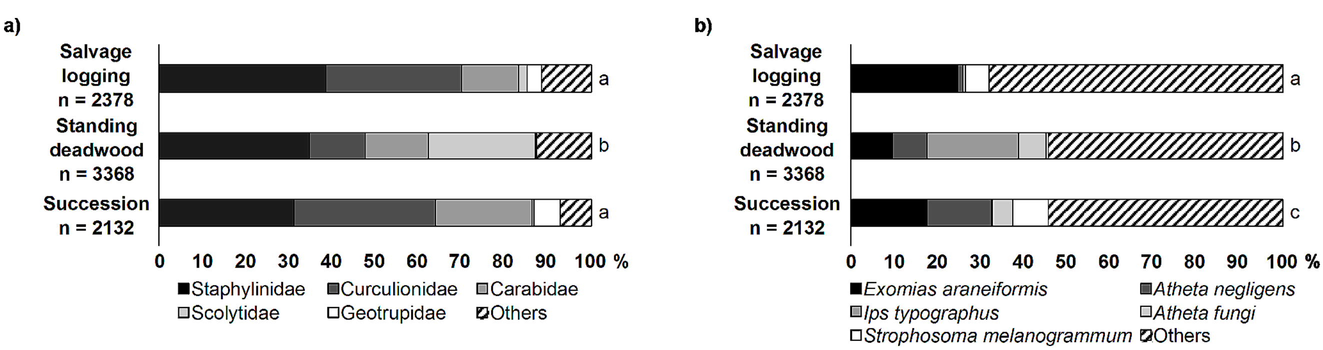

Fig. 2 Relative abundance of the five most common families **(a)** and species **(b)** across post-disturbance management categories. Percentages were calculated based on the number of individuals per management type (n). Different letters behind bars indicate significant differences among categories (PERMANOVA pairwise comparisons)

Table 1 Results of ANOVAs for the effects of management type on the number of individuals, number of species, effective number of species, rarefied species richness, and conservation value for all beetles as well as separately for Carabidae, Staphylinidae, Curculionoidea, and saproxylic beetles. Significant *p*-values are given in bold

Group	Parameter	DF	MS	F	*p*-value
All beetles	Number of individuals	2	0.8	5.82	**0.008**
	Number of species	2	410.6	5.80	**0.008**
	Effective species number	2	0.2	1.74	0.195
	Rarefied richness	2	0.2	1.35	0.276
	Conservation value	2	568.4	4.67	**0.018**
Carabidae	Number of individuals	2	1142.4	1.35	0.276
	Number of species	2	0.4	0.04	0.961
	Effective species number	2	0.2	1.22	0.310
	Rarefied richness	2	0.4	1.50	0.241
	Conservation value	2	0.1	0.27	0.766
Staphylinidae	Number of individuals	2	1.1	3.54	**0.043**
	Number of species	2	139.3	4.87	**0.016**
	Effective species number	2	1.2	13.55	**< 0.001**
	Rarefied richness	2	2.2	7.44	**0.003**
	Conservation value	2	122.6	3.83	**0.034**
Curculionoidea	Number of individuals	2	1.7	5.00	**0.014**
	Number of species	2	2.3	20.13	**< 0.001**
	Effective species number	2	7.1	8.31	**0.002**
	Rarefied richness	2	21.7	8.68	**0.001**
	Conservation value	2	2.3	15.42	**< 0.001**
Saproxylic beetles	Number of individuals	2	4.3	19.02	**< 0.001**
	Number of species	2	37.7	10.24	**< 0.001**
	Effective species number	2	15.6	6.36	**0.005**
	Rarefied richness	2	1.4	2.42	0.108
	Conservation value	2	36.4	7.24	**0.003**

preferences differed between all three management regimes. Regarding moisture, hygrophilic species were most abundant in succession areas, hemihygrophilic species at salvage-logged, and xerophilic species in standing deadwood sites (Fig. 4a).

Regarding habitat type preferences, the largest proportion were eurytopic forest species throughout. The highest proportion of stenotopic forest species was found in standing deadwood stands, while the highest proportion of open land species was found on succession areas (Fig. 4c). For food and habitat niche preferences, standing deadwood differed significantly from both other management regimes, which were statistically indistinguishable from one another. Standing deadwood was characterized by the highest proportions of xylophagous (Fig. 4b), dead wood and tree layer species (Fig. 4d) compared to salvage-logged and succession sites. The NMDS analysis shows that the beetle assemblages of the three management categories differed strongly, with all three categories being significantly differentiated from each other (Fig. 5; Table 3).

Discussion

Our results indicate a strong impact of post-disturbance management on the diversity and composition of epigeal beetle communities in the investigated former spruce stands. However, this study is facing some limitations that need to be acknowledged when interpreting our results. Our area of investigation is relatively small and therefore the trapping sites are rather close to each other. We addressed this problem by testing for spatial autocorrelation, which did not reveal any significant effect. However, this study only compares clustered sites within neighboring patches and is thus limited in its transferability to other stands or larger spatial scales. We further used post-disturbance management categories covering different time periods since disturbance as well as two different disturbance types. This complicates the interpretation of our results, as it remains unclear whether different patterns found for a given category are affected by the time period since disturbance or the disturbance type. Nonetheless, we believe that our study provides valuable insights into the effects of post-disturbance management on epigeal beetles in former spruce plantations, as the observed responses of various beetle groups can be largely attributed to their ecological demands, which are related to the different on-site conditions. As storms are also among the most common disturbance events in Central European forests, windthrow areas are often part of forest landscapes, especially in spruce-dominated ones (Seidl et al. 2014, 2017). Our study thus additionally addresses the question of how secondary succession on such sites contributes to beetle diversity, which may also be helpful for the management of beetle-infested sites, possibly undergoing similar succession dynamics despite potential initial differences caused by different disturbance regimes (Swanson et al. 2011; Winter et al. 2015).

(i) Responses of beetle taxonomic diversity to post-disturbance management

Previous studies (e.g. Lange et al. 2014; Thorn et al. 2018) identified inconsistent responses among and within species

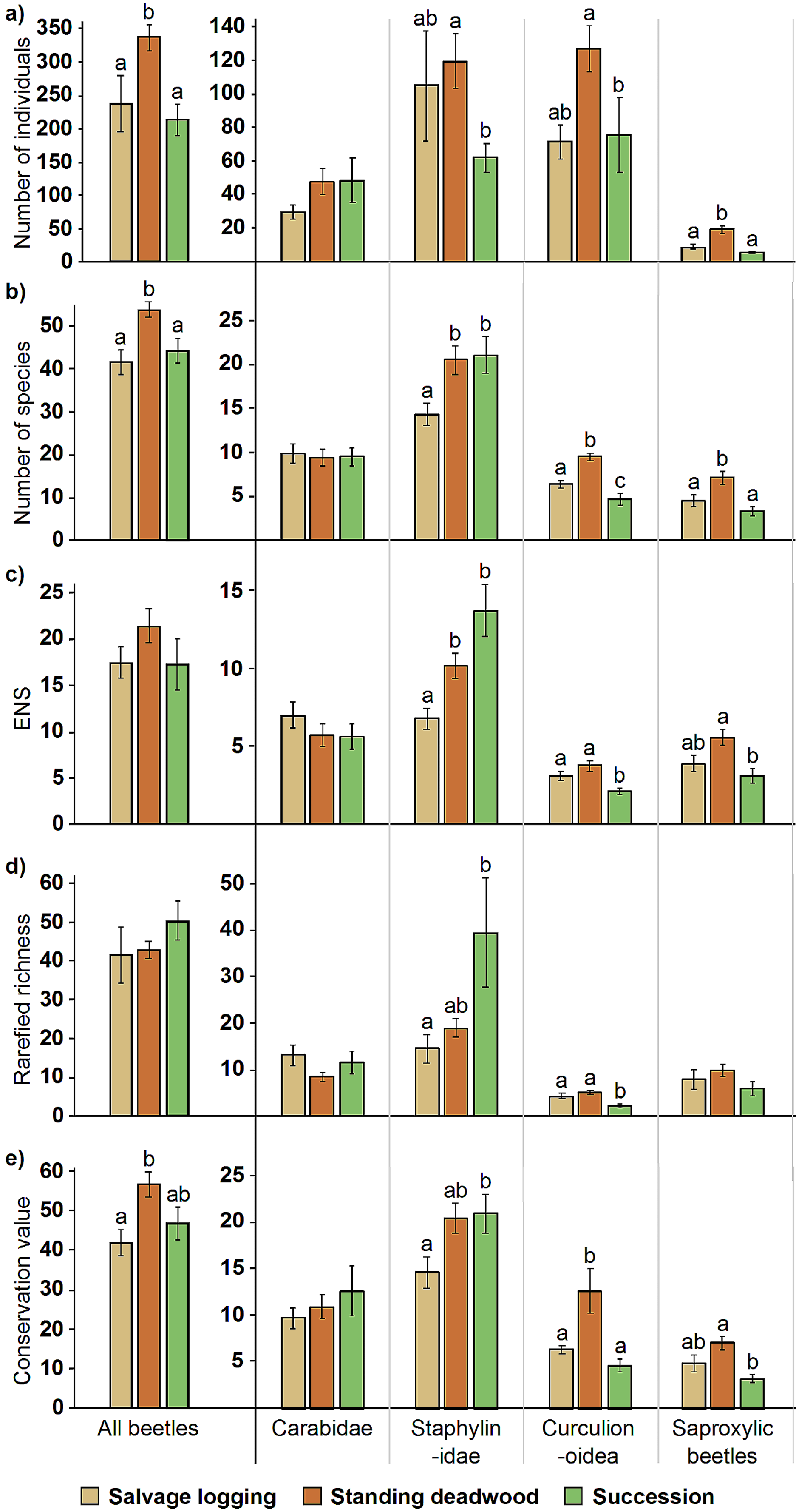

Fig. 3 Means and SE for the number of individuals **(a)**, number of species **(b)**, effective number of species (ENS; **c**), rarefied species richness **(d)**, and conservation value **(e)** across post-disturbance management categories for all beetles and for four different beetle groups. Different letters above bars indicate significant differences among management types (Tukey HSD after ANOVA). The results for Carabidae were non-significant throughout

Table 2 Results of PERMANOVAs (permutations = 999) for the relative abundance of the five most common beetle families, species, and groups with different preferences for moisture, food, habitat type, and habitat niche (according to Koch, 1989–1996) across post-disturbance management categories. Additionally, the PERMANOVA results for the Bray-Curtis dissimilarity of beetle assemblages across post-disturbance management categories are shown. Significant *p*-values are given in bold

Parameter	DF	MS	R^2	F	*p*
Families	2	0.35	0.37	7.81	**< 0.001**
Species	2	0.35	0.42	9.79	**< 0.001**
Moisture	2	0.23	0.43	10.22	**< 0.001**
Food	2	0.32	0.41	9.24	**< 0.001**
Habitat type	2	0.10	0.31	6.03	**< 0.001**
Habitat niche	2	0.20	0.30	5.68	**< 0.001**
Bray-Curtis	2	1.30	0.37	7.94	**< 0.001**

groups to post-disturbance management, which might blur its overall effect on biodiversity. In our study, we also found that post-disturbance management had partly different influences on beetle groups (Fig. 3). Carabids showed no clear response to different management approaches, while all other groups considered here showed reduced values at salvage-logged compared to standing deadwood sites. Similarly, studies focusing on carabid versus saproxylic beetles revealed contrasting responses to logging (Koivula and Spence 2006; Thorn et al. 2014, 2018). In general, intense management and according harvesting activities may reduce the population sizes of forest-dwelling arthropods (Lange et al. 2014). In particular, salvage-logging reduces habitat heterogeneity, deadwood volumes and quality (Thorn et al. 2014, 2018), which is especially detrimental to saproxylic beetles (Grove 2002; Thorn et al. 2016a). Consequently, previous studies also found negative impacts of logging on beetle communities (Cobb et al. 2011; Thorn et al. 2018). Concomitantly, Curculionoidea and saproxylic beetles showed the highest abundance and species richness in standing deadwood stands in our study (Fig. 3). This was expected since both families are often associated with the occurrence of dead or at least sick trees (Cours et al. 2021). Note, however, that many Curculionoidea and saproxylic beetles are flight-active and therefore probably under-represented in pitfall traps. Thus, our results likely only relate to the ground-dwelling minority of these groups and may not be representative. Some Curculionoidea species found in or study though are known as pest species (e.g. *Ips typographus, Pityogenes chalcographus, Hylobius abietis*), and many saproxylic beetles benefit from the damage legacies they cause. In contrast to deadwood-dependent species, ground-active beetles such as Carabidae are often adapted to open habitats, and hence seem to be less affected by logging activities and may even show positive responses (Pearce and Venier 2006; Koivula and Spence 2006; Thorn et al. 2018; Georgiev et al. 2022; Plath et al. 2024). Interestingly, the response of rove beetles, mainly comprising generalist ground-dwelling predators (Lange et al. 2014), to post-disturbance management differed substantially from all other beetle groups. Rove beetles performed best on succession followed by standing deadwood and finally salvage-logged sites. This underlines the importance of early successional stages for the conservation of specific beetle families, which has also been shown for other taxonomic groups (Swanson et al. 2011; Lehnert et al. 2013; Hilmers et al. 2018).

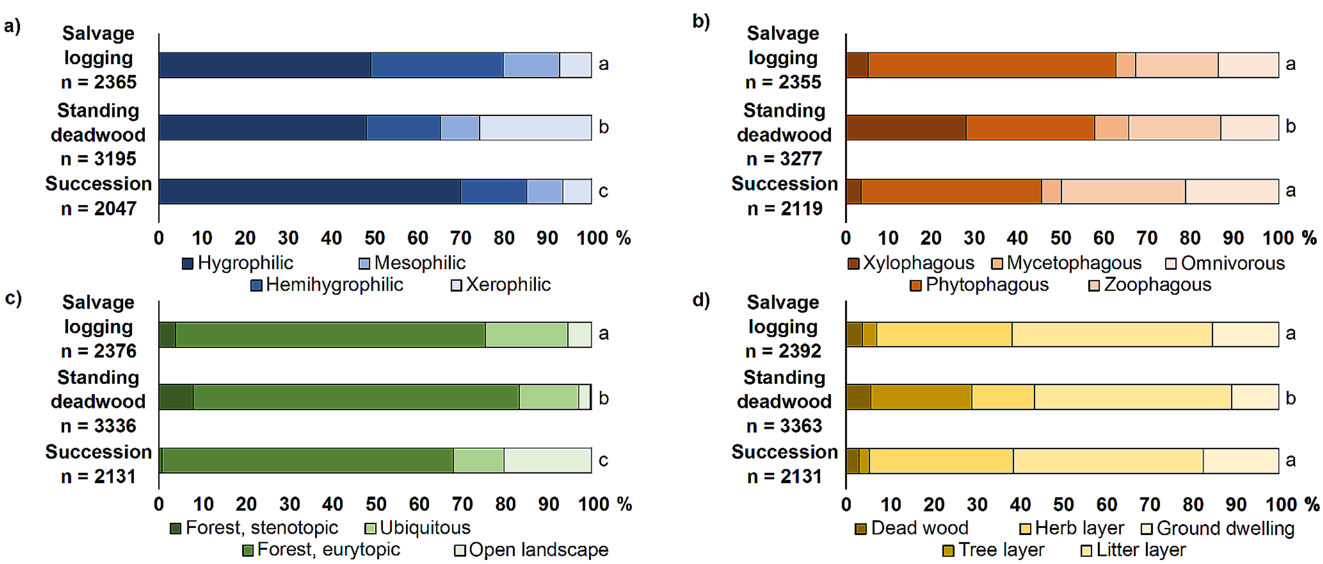

Fig. 4 Relative abundance of species with different preferences for moisture (**a**; 222 species), food (**b**; 217 species), habitat type (**c**; 221 species), and habitat niche (**d**; 224 species) (according to Koch 1989–1996) across post-disturbance management categories. Percentages were each calculated based on the number of individuals per management type (n). Different letters behind bars indicate significant differences among categories (PERMANOVA pairwise comparison)

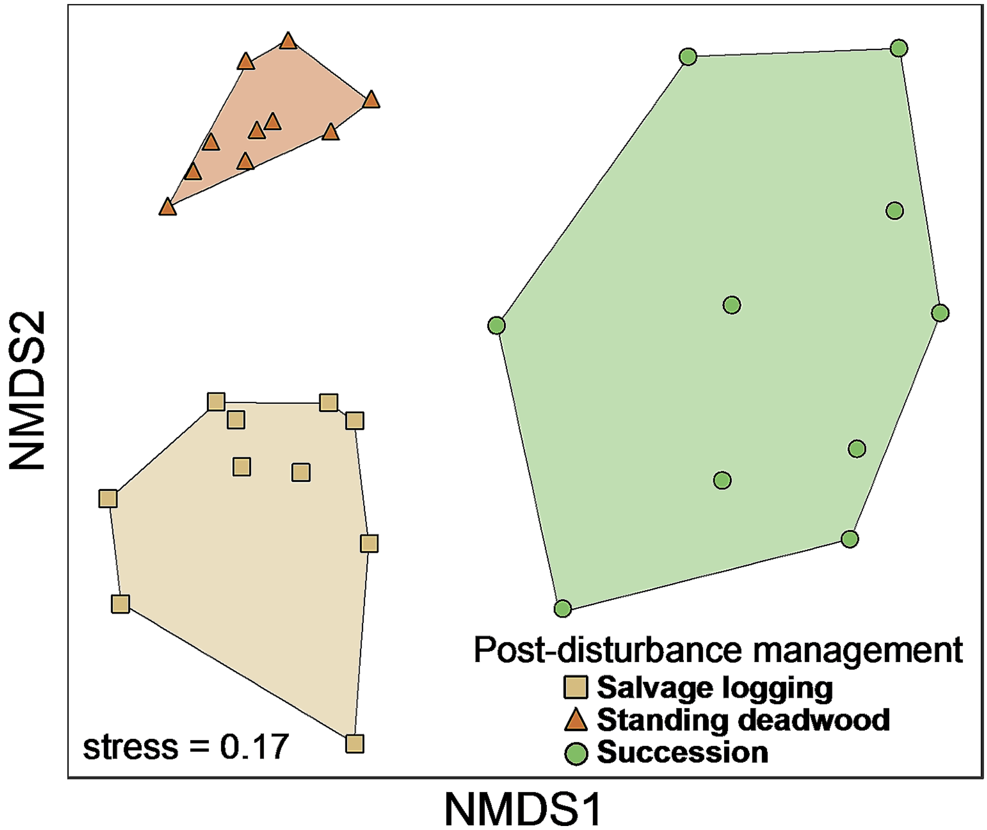

Fig. 5 Non-metric multidimensional scaling (NMDS) analysis of beetle assemblages for the three post-disturbance management categories salvage logging, standing deadwood, and succession ($n=10$ plots each, 2 dimensions, Bray Curtis distance, tries = 20). The ordination is based on 7878 individuals of 231 species

Table 3 Bray-Curtis indices for the dissimilarity of beetle assemblages among different post-disturbance management categories. Bottom left: Bray-Curtis dissimilarity. Higher values indicate a higher dissimilarity (permutations = 999). Top right: *p*-values. Significant values are given in bold

	Salvage logging	Standing deadwood	Succession
Salvage logging		**< 0.001**	**< 0.001**
Standing deadwood	54.99		**< 0.001**
Succession	54.63	70.83	

Our results underline the benefit of investigating different taxa and response groups to properly assess forest biodiversity, as individual groups may show divergent patterns. Thus, for effective conservation-planning, especially in times of changing disturbance regimes, different ecological groups and / or taxa should be considered. Considering ground-living beetle groups, we overall found significantly higher values for individual number, species number, and conservation value at standing deadwood compared with salvage-logged sites. In contrast to the number of species, solely representing the actual species count, the effective number of species was non-significant. As the effective number represents the alpha-diversity and thus also takes into account the balance of taxa within a community (Jost 2006), this could be influenced by the high proportion of species with low abundance and the dominance of a few species only (e.g. *I. typographus* in standing deadwood, *E. araneiformis* on salvage-logged and succession sites; Fig. 2), leading to similar diversity values in all categories. Moreover, the rarefied richness showed no significant differences, indicating that some differences among categories found for the numbers of individuals and species might be due to differences in detection probability among sites (Hsieh et al. 2016). Nevertheless, standing deadwood was overall most beneficial for the taxonomic diversity of epigeal beetles. Similarly, positive effects of bark beetle outbreaks and the resulting deadwood stands were reported for plants, lichens, spiders, cicadas, hoverflies, bees, and wasps (Beudert et al. 2015). Also, springtails were found to peak in sites with standing deadwood one to five years after bark beetle induced spruce dieback (Winter et al. 2015). Later successional stages, which were about the same age as our succession sites, on the other hand, promoted herbs, shrubs, Heteroptera, and Aculeata, while fungi, molluscs, and spiders showed no clear response. The latter two groups, though, were reported to react positively to salvage logging, along with carabid beetles, indicating that organisms associated with open habitats might benefit from clear cuts, while mosses, lichens, wood-inhabiting fungi, saproxylic beetles, springtails and birds were negatively affected (Thorn et al. 2018). These divergent responses demonstrate the need to apply different management approaches in order to provide as many different habitats as possible for various organisms and enhance overall biodiversity.

(ii) Responses of beetle community and guild composition to post-disturbance management

Post-disturbance management significantly influenced community and guild composition (Figs. 2 and 4), which is in line with other studies showing that community composition differs among forest management practices either at the species (Work et al. 2013) or ecological level (Koivula and Spence 2006; Lange et al. 2014; Thorn et al. 2018; Plath et al. 2024). The latter three studies reported that salvage logging caused a shift from forest specialists to open-land generalists. In our study, standing deadwood harbored the highest abundance of (stenotopic) forest species, while that of open-land species was surprisingly highest on succession rather than salvage-logged sites. This may have been caused by a longer time period post disturbance for succession sites. Presumably owing to the relatively young tree age in combination with a high tree density and dense vegetation structure of succession sites, these also showed the highest relative abundance of hygrophilic species. As expected, standing deadwood was characterized by a high proportion of xylo- at the expense of phytophagous species, and higher proportions of deadwood and tree-inhabiting species compared to both other management types. In turn, the higher solar radiation on salvage-logged and succession sites may promote herbaceous ground vegetation (Thorn et al. 2014) favoring phytophagous herb layer species. In summary, guild composition differed clearly among management types, with standing deadwood showing overall the strongest divergence from other types.

(iii) Management strategies and insect conservation

Managed forests are often characterized by low tree diversity, reduced deadwood availability, closed canopies, and even age structures (Lange et al. 2014). This typically results in reduced forest biodiversity across Europe (Paillet et al. 2010). Natural disturbances create habitat heterogeneity by disrupting uniform structures and leaving so called disturbance legacies (Müller et al. 2008; Swanson et al. 2011; Thorn et al. 2016b). Thus, disturbances, including bark-beetle outbreaks, tend to enhance forest biodiversity (Swanson et al. 2011; Beudert et al. 2015). By killing mature spruce trees, such infestations produce high amounts of deadwood, which is a rare resource in most managed forests. Müller et al. (2008) even identified *Ips typographus* as a possible keystone species creating forest gaps on which many forest insects rely, due to higher solar-radiation and elevated ground temperatures. The resulting sun-exposed deadwood habitats are especially preferred by saproxylic beetles, and their diversity is further increased by habitat heterogeneity (Seibold et al. 2016; Uhl et al. 2022). Preserving different types of deadwood under various microclimatic conditions seems to be especially suitable to enhance saproxylic beetle diversity (Grove 2002). A high structural diversity consisting of snags, logs, and branches as well as a wide range of microclimatic conditions were also present at our standing deadwood sites, which also promoted overall beetle diversity (Fig. 3). However, the within-management variation of beetle assemblages was rather small among standing deadwood compared with salvage-logged or succession sites (Fig. 5), and the alternative management types may favor different groups such as staphylinids in our study. This, in combination with the occurrence of unique assemblages (Fig. 5), suggests that open habitats generated by salvage logging as well as succession sites may also significantly contribute to β-diversity. We therefore suggest a post-disturbance management that includes set-aside stands of standing deadwood followed by secondary succession for formerly spruce-dominated forests. Although bark beetle outbreaks reduce the quality and quantity of timber in managed stands, subsequent succession may be an effective means to resilient forest restoration (Seidl 2014; Seidl et al. 2016; Sommerfeld et al. 2021). For example, the succession areas in our study were dominated by birch (*Betula* pendula) in addition to spruce, but some oak (*Quercus petraea)* trees could also be found amongst them. Also stands included rather open patches with grassy vegetation. Accordingly, Georgiev et al. (2022) proposed a balanced proportion between set-aside and salvage-logged stands. Thus, to enhance biodiversity, forest landscapes should consist of a mosaic of different forest types (in terms of age structure, tree composition, managed/unmanaged etc.) and should avoid large-scale forest plantations as well as fragmentation by large clear cuts (Desender et al. 2010; Plath et al. 2024).

Conclusions / management implications

We here compared three former spruce stands with different post-disturbance management approaches after natural disturbances in western Germany. Our results show that standing deadwood, i.e. abandoning salvage-logging, provided highest returns for preserving diversity of ground-dwelling beetles, especially for forest specialists. However, Staphylindae benefitted most from secondary succession, stressing the need for considering variation among taxa or guilds. Additionally, community and guild composition varied greatly among management categories, stressing the need for a combination of different management regimes to enhance overall diversity. We therefore suggest a post-disturbance management that includes set-aside stands with standing deadwood, followed by secondary succession and also clearings within spruce-dominated forests in order to enhance beetle biodiversity. Thus, management should promote heterogenous forest landscapes. In addition, secondary long-term succession may comprise an effective means to resilient forest restoration, which gains in importance in times with amplifying disturbance regimes.

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Author contributions Both authors designed the study, edited, and revised the manuscript. K.F. was responsible for project administration and funding acquisition and supervised the project. E.P. carried out the field work, beetle identification, and formal analysis, and prepared the original manuscript draft.

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Declarations

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

Research involving human and animal participants To obtain the data presented in the manuscript it has been necessary to involve animals. Therefore, individuals had to be killed and removed from the field. However, all applicable international, national, and institutional guidelines for the care and use of animals were followed. No human participants were involved in the work.

Informed consent All authors consent to submission of this manuscript.

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