ORIGINAL ARTICLE

Bark-beetle disturbance severity only moderately alters forest affinity of arthropod communities

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Abstract

1. Forest ecosystems are facing increasing challenges like natural disturbances. Despite positive disturbance impacts on the diversity of several taxonomic groups, there are still concerns, whether the drastic canopy opening can lead to a turnover from forest to open habitat species.

2. We sampled arthropods along a disturbance gradient in Norway spruce (*Picea abies*)-dominated protected areas across Central Europe using Malaise traps and metabarcoding.

3. To analyse changes in arthropod communities in terms of forest affinities along the disturbance gradient, we explored the potential of a list of forest affinities (LFA) that provides information about species affinities from closed forest to open habitats.

4. Our results show that the mean forest affinity decreased with increasing disturbance severity. This trend was accompanied by a decrease in forest-associated species as well as community shifts for open and mixed habitat species. Responses varied between taxa and were most apparent in Coleoptera.

5. Overall, the changes did not come with a complete replacement of forest specialists by species with higher affinities for mixed and open landscapes nor a drastic loss of forest species. Furthermore, we observed severely disturbed plots with a high mean forest affinity and vice versa, which calls for further studies using these kinds of species classifications.

6. The LFA can provide additional information how species associated with forests habitats can react to environmental changes beyond increasing amounts of deadwood resources. Using additional trapping methods and determination techniques might increase the explanatory power of such analyses along ecological gradients.

KEYWORDS
arthropod diversity, forest conservation, list of forest affinities, metabarcoding, national park, natural disturbance

INTRODUCTION

Natural disturbances have increasing impacts on forest dynamics (Jakoby et al., 2019; Seidl et al., 2011). Although disturbance activity is highly variable, climate change is likely to amplify future disturbance regimes (Sommerfeld et al., 2018). The major drivers of biotic disturbances include *Ips typographus* (L.) in European forests and *Dendroctonus ponderosae* (Hopkins) in western North American forests (Bentz et al., 2019). Infestations by these bark beetles largely alter forest structures in affected landscapes. The most conspicuous change subsequent to infestations is the dieback of forest canopy, which leads to a decreasing canopy cover and increasing deadwood amounts (Swanson et al., 2011). Such alterations can also affect forest structures and plant communities beyond the forest canopy. For example, disturbed forests show more natural regeneration (Pappas et al., 2020) and increasing vascular plant diversity (Kortmann, Müller, et al., 2021).

Several studies analysed the response of different taxonomic groups of arthropods to bark-beetle infestations (see, e.g., Beudert et al., 2015; Lehnert et al., 2013; Winter et al., 2015). Previous studies focused mainly on Coleoptera with an emphasis on Carabidae, as well as Arachnida, Heteroptera and Hymenoptera with an emphasis on Aculeata, showing overall positive effects on species densities and diversity (Viljur et al., 2022). Still, Lehnert et al. (2013) analysed indicator species for open, closed and transition forests and showed that the abundance of open forest indicator species increases in disturbed forests with a reduced canopy cover, whereas closed forest indicator species decreased in abundance.

The extent and specific form of all these community changes are, among other factors, dependent on the disturbance severity (i.e., amount of dieback of canopy trees) (Saab et al., 2014). In turn, it is also likely that the changes in species communities are more distinct with increasing disturbance severity, which can create large canopy gaps. In a previous study, we showed that the more severely a forest is disturbed, the more different are the arthropod communities compared with undisturbed forests (Kortmann, Roth, et al., 2021). In the present study, we define disturbance severity as the share of trees killed by spruce bark beetles (Brůna et al., 2013; Frelich & Reich, 1998). Other definitions include also basal area of killed trees (for human-induced disturbance) (Thom et al., 2020) or share of removed canopy cover (Sabo et al., 2009). Nevertheless, since spruce stands in our study areas were very homogeneous, these measures were highly correlated (Kortmann, Roth, et al., 2021).

Since the preservation of forest specialists (i.e., species with high affinity to forest habitats) is one of the major goals in forest conservation (Gustafsson et al., 2012), a concern about natural disturbances and the associated change of communities is the possible loss of forest specialists. In this context, it is assumed that the creation of large forest gaps can lead to species-rich forests, by promoting open-habitat species, but put forest specialists at a disadvantage, similarly to clear-cuts (Fedrowitz et al., 2014). Still, a major difference between natural disturbances without intervention (as practiced in most protected areas) and clear-cuts is the continuous presence of disturbance legacies such as standing and lying deadwood. Furthermore, disturbance events can

occur at different scales from the creation of small gaps to stand replacing events. Hence, a consensus exists, that especially heterogeneous natural disturbances increase forest structures and deadwood resources (Swanson et al., 2011), and consequently can promote arthropod species, which are linked to natural forests (Müller et al., 2010). For example, Cours et al. (2022) show that forest dieback due to natural disturbances increases the diversity of saproxylic beetles. Another study from the French Pyrenees shows that forest dieback can lead to compositional changes in insect communities, while species numbers remain stable (Sire et al., 2022). Still, there is a lack of knowledge, if forest specialists within arthropod communities disappear after bark-beetle disturbance events or get replaced by open habitat species.

To classify the different affinities of species to forest ecosystems, we used the list of forest affinities (LFA) by Dorow et al. (2019). The list was designed as a tool for forest conservation research and contains information on Coleoptera, Arachnida, Heteroptera and Aculeata, among others. The affinities to forest habitat are separated into three broad categories: strong affinity to forest habitat, occurring in both open and forest habitats and occurring only in habitat without forest cover. A detailed overview of the LFA is given in Schneider et al. (2021). To collect species from all the above-mentioned taxa in a sufficient way, we used Malaise traps, which are known to have a high sampling success (Uhler et al., 2022). Malaise traps catch predominantly flying insects but also ground dwelling insects that climb up the nets touching the forest floor (Skvarla et al., 2021). In contrast to other trap types like flight interception traps and barber traps, which are more specific regarding their target taxa, Malaise traps can cover a very broad spectrum of taxa. Nevertheless, one should be aware that a combination of different trap types generally results in more comprehensive assessments of arthropod communities (Knuff et al., 2019).

The aim of this study was to test the applicability of the LFA along an ecological gradient created by bark-beetle infestations that represents a changing habitat from closed forest to more open habitat. Since metabarcoding is increasingly used in ecological and monitoring studies and is a useful tool to determine a broad range of taxa relatively expeditiously, we tested the compatibility of the LFA with a modern method like metabarcoding. We analysed different arthropod taxa and their forest affinities in Norway spruce forests covering a gradient of different disturbance severities in five European protected forests. Furthermore, we used the LFA to analyse changes in arthropod communities regarding their affinity to forest habitat. We hypothesised that instead of species with an affinity to forest habitat being replaced by open-habitat species, species with an affinity to forest habitat will be promoted by more natural forest structures and increasing deadwood resources; hence, forest affinities would remain stable or change only moderately.

METHODS

Study areas and experimental design

The study was conducted in 2018 in five protected areas: Black Forest National Park (Germany), Berchtesgaden National Park (Germany),

Bavarian Forest National Park (Germany), Kalkalpen National Park (Austria) and Białowieża Forest (Poland). In each area, except for Black Forest National Park, we selected 15 circular study plots covering a gradient of disturbance severities from 0% to 100%. Disturbance severity was measured as the percentage of spruce trees killed by bark beetles. The respective disturbance severities were calculated within a 100 m radius surrounding each plot in order to robustly describe the habitat conditions for arthropods. Since the Black Forest National Park was only established recently and had rather low levels of bark-beetle infestation, we only studied nine plots in this particular study area. We considered only forest stands with bark-beetle infestations older than 2 years and younger than 20 years. Time since bark-beetle outbreaks was approximately the same across study areas. For additional information and a map of the study areas, see Kortmann, Müller, et al. (2021).

Arthropod sampling and identification

In the centre of each plot, a Malaise trap was exposed from April until September 2018. Traps were equipped with collecting bottles filled with 70% ethanol, which were emptied once a month to ensure high DNA quality for sequencing (see below). The sampled arthropods were separated into two size classes using a sieve (7 mm mesh size) to improve sequencing results by reducing the risk that smaller specimens with underrepresented DNA remain undetected during sequencing (Hardulak et al., 2020). Binning also reduces the differences in the number of hits caused by differences in the size of individuals. Species identification of arthropods was performed using DNA metabarcoding following the laboratory and bioinformatic pipelines, as reported by Hausmann et al. (2020). The full protocols for molecular laboratory work as well as for the performed bioinformatic workflow are described by Kortmann, Roth, et al. (2021). For further analyses, we only used species with a hit percentage >97% and a species name to allow an alignment with the forest affinities. Since metabarcoding provides no reliable abundance data, we used presence–absence data and species numbers for the statistical analyses.

Forest affinities

We used the forest affinity classifications of Dorow et al. (2019), which specifies seven categories ranging from open landscapes to closed forests. Since we had only one species affiliated with closed forest habitats, we dropped this category, resulting in six categories, which are shown in Table 1. The six categories were subsumed in three broader categories (forest, mixed and open) to guarantee a sufficient number of species per category (Table 1). A more detailed description of the categories can be found from the work by Schneider et al. (2021).

Statistical analyses

All statistical analyses were conducted with R 4.2.1 (R Core Team, 2023). To achieve an overview of the distribution of each forest affinity class along the disturbance gradient, we calculated portions of each group for each disturbance severity.

To analyse how the overall forest affinity of the arthropod communities changes over the disturbance severity gradient, we transformed the forest affinities into a Likert scale where open habitat affinity equalled 1, mainly open habitat affinity equalled 2 and so forth (Table 1). The mean forest affinity per study plot was then modelled with a linear mixed-effects models (LMMs) from the lme4 package as a function of disturbance severity with the study areas as random intercept. The LMMs were also computed for each arthropod group (Coleoptera, Arachnida, Heteroptera and Aculeata) separately. To have a meaningful sample size of each forest affinity category, we used the broad affinity classes (open, mixed and forest) for further calculations. We calculated species richness per broad category and arthropod group using generalised additive mixed models (GAMMs) as a function of the disturbance severity the broad category itself and the study areas as random factor and used a quasi-Poisson conditional distribution of the response using the mgcv package (Wood, 2017).

To analyse changes in species compositions, we calculated a partial correspondence analysis using the cca function from the vegan

TABLE 1 Description of the forest affinity categories, the attribution to broader categories (F—forest, M—mixed, O—open, Likert scale value and corresponding species number).

Forest affinity	Broad category	Likert scale	Number of species
f—in forests, without preference for light or closed forests	F—forest	6	108
fl—in forests, with strong affinity to light forests, forest edges, or glades	F—forest	5	50
m—in both open landscapes and forest habitats, but without a preference for forest habitats or where a distinction between mm or mo was not possible	M—mixed	4	16
mm—equally in open landscapes and forest habitats	M—mixed	3	78
mo—mainly in open landscapes, but also regularly occurring in forests, at forest edges, or in glades	O—open	2	28
o—only in open landscapes or other habitats without forest cover like caves or buildings	O—open	1	20

package with the study area as condition to control for area specific differences in community composition. Hence, the study area is partialled out before analysis. Note that apart from the study area as a condition, the ordination is unconstrained. To enhance clarity, we will therefore refer to it as correspondence analysis (CA) in the following. To test if the differences in species composition were correlated with disturbance severity or forest affinity, we fitted the mean forest affinity and the disturbance severity per plot on the CA ordination using the *envfit* function within the *vegan* package (Oksanen et al., 2022). We used only presence–absence matrices as abundances cannot reliably be derived from metabarcoding data.

To further analyse the differences in species composition, we calculated the Sørensen dissimilarity between each study plot and the difference in disturbance severity with the *vegdist* function from the *vegan* package. We calculated the median Sørensen dissimilarity per study area, forest affinity group and difference in disturbance severity. To test how the beta diversity changes along the disturbance gradient, we calculated GAMMs with the median Sørensen dissimilarity as dependent variable and difference in disturbance severity by forest affinity category as independent variables. We also included the study area as random term to control for area-specific effects and used a quasi-binomial conditional distribution of the response as the Sørensen dissimilarity values featured also values between 0 and 1. We omitted this analysis for the Heteroptera because of very small sample sizes in each forest affinity group.

To ensure that our results were not skewed by species that only appeared on a single study plot, we reanalysed the dataset by excluding single-occurrence species. The results of these analyses were very similar to the one including all species, which led us to conclude that no single species had a disproportionate impact on our findings. The detailed results of these analyses, including tables and figures, are provided in Supporting Information S3 for further reference.

RESULTS

Overview

Distributions of the overall mean forest affinity along the disturbance severity gradient showed that the share of species with an affinity for forest habitats was slightly decreasing and species with mixed preferences were slightly increasing (Figure 1). Since some of the forest affinity categories contained only small species numbers, we reclassified them into broader categories for further analyses (Table 2).

Mean forest affinity along the disturbance gradient

Linear models showed that, overall, the mean forest affinity decreased significantly with increasing disturbance severity ($p = 0.001$, $R^2 = 0.306$). Analyses of the mean forest affinity per taxonomic group showed that the mean forest affinity of Coleoptera and Arachnida decreased significantly with increasing disturbance severity ($p = 0.01$, $R^2 = 0.462$ and $p = 0.004$, $R^2 = 0.209$,
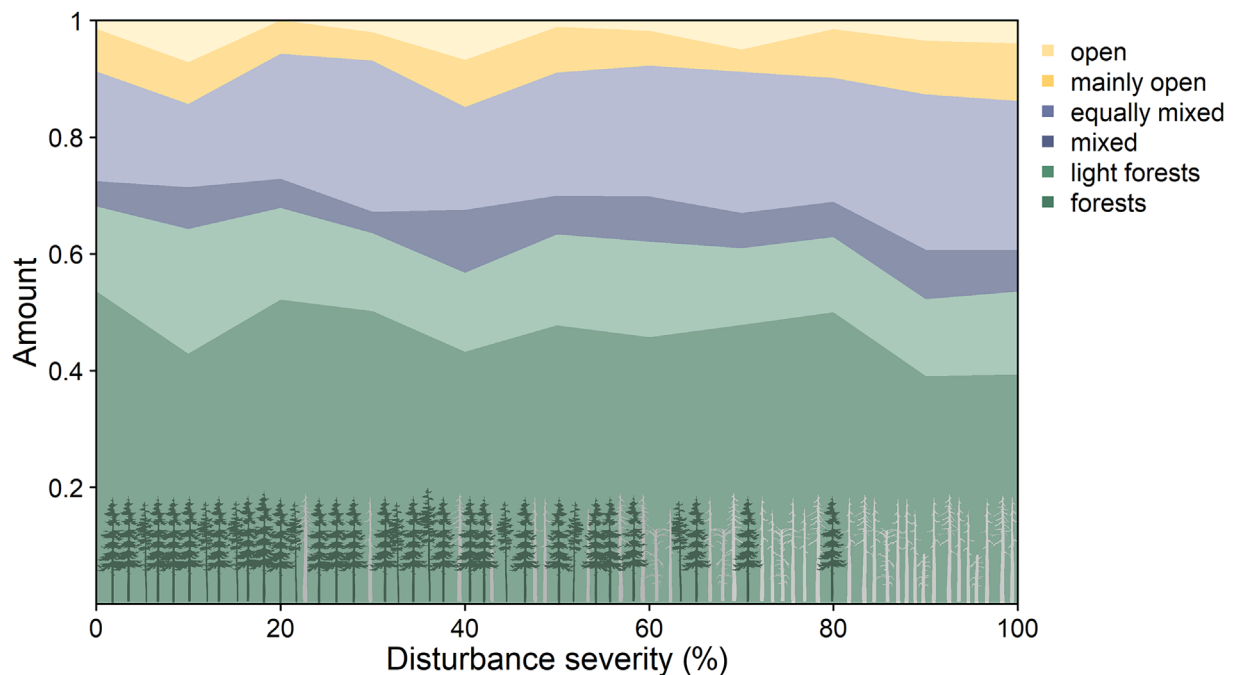

FIGURE 1 Amounts of species associated to the different habitat types along a gradient of different bark-beetle disturbance severities.

respectively). Heteroptera and Aculeata showed no significant shifts in mean forest affinity along the disturbance gradient (Figure 2 and Table S1.1).

Analyses of the species numbers per forest affinity category and taxa showed that species numbers of forest species decreased significantly with an increasing disturbance severity ($p = 0.025$, $F = 5.069$, Figure S1.1). In addition, species numbers of forest-associated Coleoptera decreased significantly ($p = 0.009$, $F = 7.02$, Figure S1.1), whereas open habitat-associated Coleoptera and mixed habitat-associated Aculeata increased significantly with increasing disturbance severity ($p = 0.04$, $F = 4.1$ and $p = 0.026$, $F = 2.33$, respectively) (Figure S1.1 and Table S1.2).

TABLE 2 Species numbers per taxon and forest affinity category.

Forest affinity	Arachnida	Coleoptera	Heteroptera	Aculeata
f	24	75	3	6
fl	4	27	4	15
F	**28**	**102**	**7**	**21**
m	1	15	0	0
mm	6	30	12	30
M	**7**	**45**	**12**	**30**
mo	1	16	5	6
o	2	16	0	2
O	**3**	**32**	**5**	**8**
Overall	**38**	**179**	**24**	**59**

Note: Broader forest affinity categories were summarised based on the smaller categories and are in bold.

Species composition

Partial CA had a total inertia of 10.48. The conditioned component accounted for 12.7% of the total inertia. Plot coordinates along axes CA1 (eigenvalue: 0.34, proportion explained: 0.04) and CA2 (0.31, 0.03) indicated patterns following mean forest affinity and disturbance severity on the plots (CA plot, Figure 3). Fitting of these two variables onto the CA showed a significant correlation between the ordination and the forest affinity (PERMANOVA (Permutational Multivariate Analysis of Variance) $p < 0.001$, $F = 4.07$) and the disturbance severity ($p < 0.001$, $F = 2.53$, Figure 3).

Beta diversity

Analyses of the beta diversity for all species indicated that overall Sørensen dissimilarities of species associated with open and mixed habitats increased significantly with increasing dissimilarity in disturbance severity ($p = 0.032$, $F = 4.53$ and $p = 0.008$, $F = 7.03$, respectively). Communities of species with preference for forests did not change significantly.

Analyses of the beta diversity per taxa showed that with increasing difference in disturbance severity, the Sørensen dissimilarity of open habitat-associated Arachnida increased significantly ($p = 0.002$, $F = 10.76$). We observed that Sørensen dissimilarity of mixed habitat-associated Coleoptera increased significantly ($p = 0.012$, $F = 4.41$), whereas dissimilarity of open habitat-associated Aculeata decreased significantly with increasing difference in disturbance severity ($p = 0.036$, $F = 2.52$) (Figure 4 and Table S1.4).
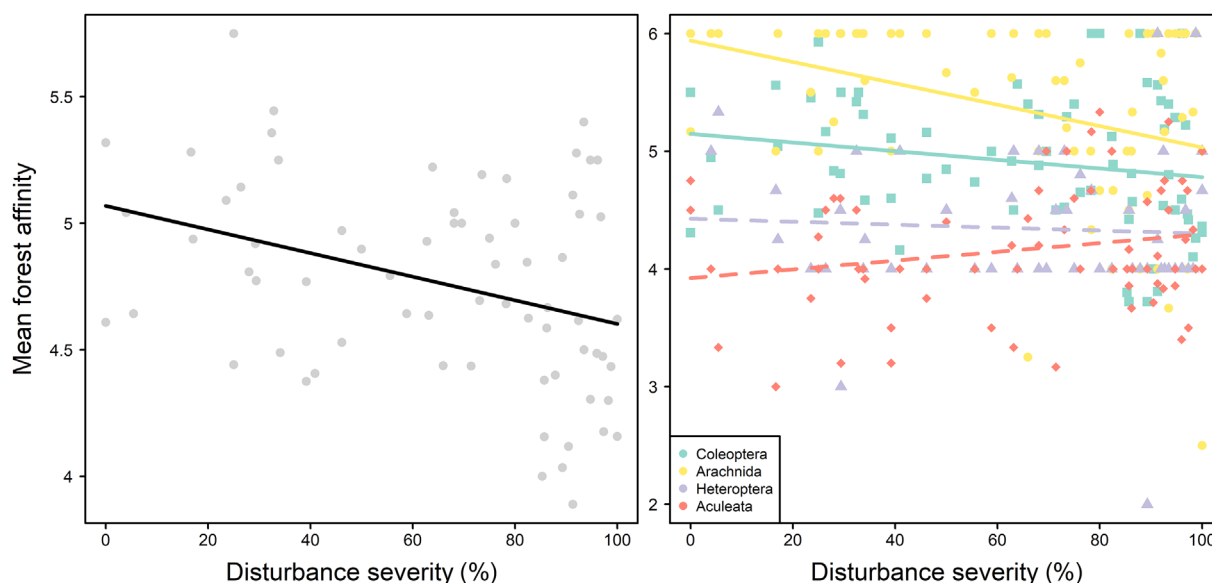

FIGURE 2 Results of the linear model of mean forest affinity along the disturbance gradient for all species (left) and separated into taxonomic groups (right). Mean forest affinity is based on a Likert scale ranging from 1 (=open) to 6 (=closed canopy specialists). Plain lines indicate significant and dashed lines non-significant trends.
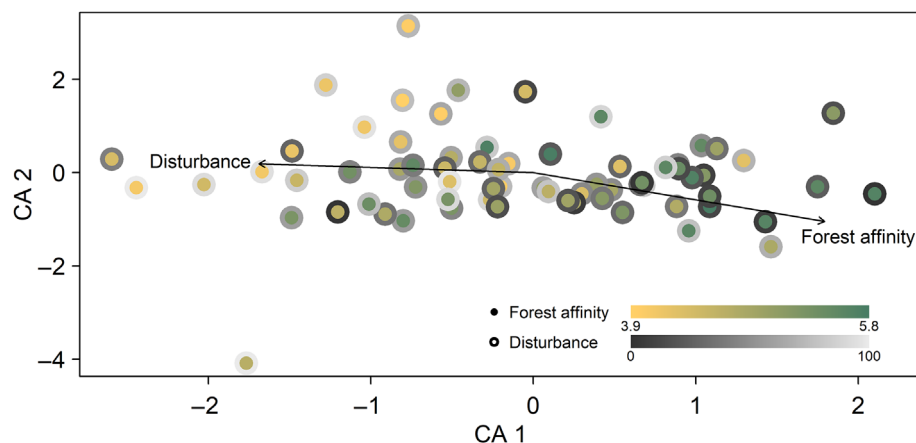
FIGURE 3 Partial correspondence analysis (CA) with the study area as condition to control for area-specific differences in community composition. Mean forest affinity is indicated on a colour gradient from yellow to green, disturbance severity on a gradient from grey to black. Arrows are fitted with a PERMANOVA (Table S1.3).
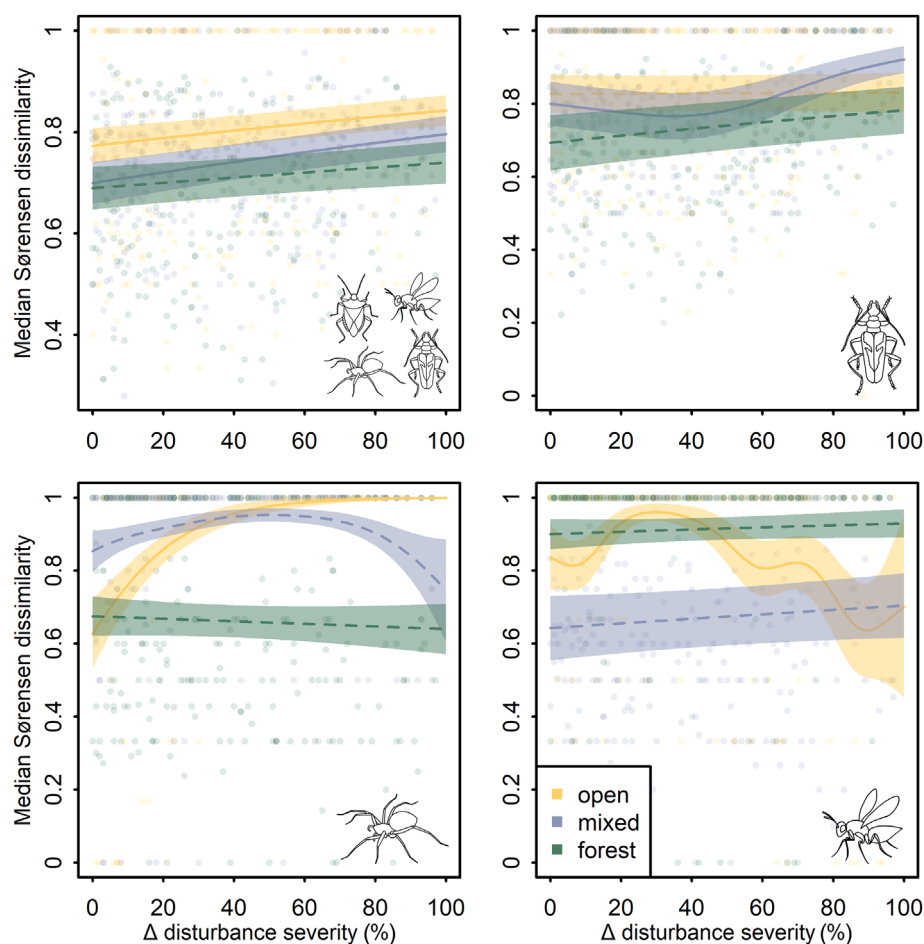

FIGURE 4 Predictions of the median Sørensen dissimilarity with increasing difference in disturbance severity per forest affinity category for all species (upper left) and separated into taxonomic groups (except Heteroptera). Predictions are based on generalised additive models (Table S1.4). Plain lines indicate significant and dashed lines non-significant trends.

DISCUSSION

Our results show that the mean forest affinity of arthropod communities decreased significantly with increasing disturbance severity, but without a complete replacement of forest specialists by species with higher affinities for mixed and open habitats. Analysing these changes in more depth, we observed that the changes in mean forest affinity differed between taxa and forest affinity categories.

Decrease in forest-associated Coleoptera and Arachnida

While the mean forest affinity of Coleoptera and Arachnida decreased significantly with increasing disturbance severity, Aculeata and Heteroptera showed no significant change (Figure 2 and Table S1.1). Mean forest affinity of Coleoptera and Arachnida was also generally higher than the other two taxa (Figure 2). Furthermore, we have high shares of forest species for Coleoptera in our data (more than 50% of the analysed community). This is in line with the LFA that includes generally more species that are closely associated with forest habitats within Coleoptera and Arachnida than Heteroptera and Aculeata (Dorow et al., 2019). Another study from different forest regions in Germany also showed high shares of forest species for Coleoptera (Lange et al., 2014). Despite the significant decrease in mean forest affinity, we still observed high mean forest affinity values in severely disturbed forest patches for all studied taxa (Figure 2). The high impact of the area-specific random factor in our linear model for Arachnida is based on large differences in the variance in forest affinity between the plots of different regions. In Białowieża Forest and the Bavarian Forest, the variance in forest affinity between the plots was considerably larger than that in the other areas.

Analysing the species numbers for each forest affinity category along the disturbance gradient, we observed that forest habitat species decreased significantly in species numbers. This trend seems to be mainly driven by forest-associated Coleoptera (Figure S1.1). Our results are in line with those from boreal forests in Finland, where more open habitat species were observed in forest gaps and more forest species in closed forests (Heliölä et al., 2001). Our results are also similar to Lehnert et al. (2013) who showed an increase in open habitat indicators and a decrease in closed habitat indicators with increasing habitat opening.

Compared with other studies that find beneficial effects of bark-beetle disturbance on arthropod diversity (Beudert et al., 2015; Thom et al., 2017), our results did not show such a general pattern, but more diverse responses (similar to Kortmann, Müller, et al., 2021; Kortmann, Roth, et al., 2021). These differences in the observed diversity responses might result from different sampling methods and the diversity parameters observed. For example, studies focusing mainly on species richness are not able to detect changes in habitat preferences or specific functional groups within communities. Our results suggest that especially forest-associated Coleoptera can decrease in species numbers with increasing bark-beetle disturbance severity, whereas other taxa show mixed responses. Still, we like to emphasise that species pools vary largely across regions. Hence, the different communities can respond differently to bark-beetle disturbance and the concomitant changes in forest structures. Although we accounted for such differences in the statistical methods, we cannot rule out that local characteristics could lead to deviations from our results regarding the community response.

Changes in beta-diversity occur mostly in open and mixed habitat species

Our results show that, overall, the changes in beta diversity occur mainly in open and mixed habitat communities. Similar to the results on species numbers and mean forest affinity in our study, community changes differed between the observed taxa. Coleoptera showed only significant changes for the mixed habitat species, whereas Arachnida showed changes in open habitat species over the disturbance severity gradient. Our results on Arachnida communities are in line with a study in beech forests that shows that spider communities differ significantly between forests with open and closed canopies (Černecká et al., 2020).

Other studies on Coleoptera show that communities of open and closed forests differ, but without analysing the preferences for open or closed habitats of the observed species (see, e.g., Sire et al., 2022). Results of the CA show that, in general, open patches are characterised by a community slightly more associated with open landscapes. Still, there are also disturbed plots with communities showing a high forest affinity as well as undisturbed plots with a lower forest affinity (mismatch between mean forest affinity and disturbance severity). Our results suggest that forest arthropod communities are affected by bark-beetle disturbance but remain dominated by species associated with forests.

Applying the list of forest affinities on an environmental gradient

All species within the analysed taxa in our data could be attributed to a forest affinity category. Still, we were limited by the represented taxa in the LFA, where some taxonomic groups are not included (e.g., non-apocritan Hymenoptera and non-heteropteran Hemiptera). Because of these limitations, we have small sample sizes for the subsets with separated taxonomic groups and forest affinity category. In addition to that, our species data are based on Malaise trap sampling that predominantly capture flying insects. Hence, Hymenoptera and Diptera are generally well represented, whereas Coleoptera and Arachnida can be underrepresented (Lamarre et al., 2012; Skvarla et al., 2021; Uhler et al., 2022). Since Diptera are not represented in the LFA, a huge share of species data could not be used for our analysis.

The LFA allows us to analyse changes in community structures regarding the habitat preferences of the included species with data independent of the sampled species. In comparison, Lehnert et al. (2013) evaluated species richness trends of indicator species calculated based on the same data set, which can reduce the transferability of the results, since this approach produces only area- or study-specific indicator species. Furthermore, the LFA provides information on habitat preferences beyond trophic guilds or dependencies on specific resources. For example, other studies on arthropods in naturally disturbed landscapes show an increase in saproxylic beetles after natural disturbances (Cours et al., 2022; Kozák et al., 2020). Our study shows that analysing non-saproxylic taxa can enlighten how species associated with forest habitats may react to environmental changes beyond increasing amounts of deadwood resources. For example, Seibold et al. (2016) observed the effect of deadwood and canopy opening on saproxylic and non-saproxylic arthropods and found that the beneficial effects of increasing amounts of deadwood are mediated by an open canopy.

In addition, metabarcoding allows the determination of a broad range of species but has still some flaws when it comes to the determination of certain arthropod taxa on species level (Gossner et al., 2014). So far, it is also not possible to gain reliable abundance values for metabarcoding data. Bioinformatics of metabarcoding data is still in the development of methods to calculate abundance data (Krehenwinkel et al., 2017). There are new techniques that are quite promising, but include a lot of additional sorting of the specimens before the sequencing (Leroy et al., 2022). Still, metabarcoding leaves us with some uncertainties and restrictions regarding further analysis, so far. Abundance data would allow us to also consider the evenness of species within arthropod communities (Konopiński, 2020) as well as changes in occurrence beyond the presence or absence of a species along the environmental gradient.

Conclusions

Our results suggest that Coleoptera and Arachnida communities, which are more dominated by forest specialists, can react stronger to changes in forest structure and drastic canopy opening as we can observe after severe bark-beetle disturbance than Aculeata and Heteroptera. Overall, the decrease in forest affinity is not based on a drastic loss of forest species, but rather amplified by an increase in open habitat species. It is worth to note that our results were observed in natural forest ecosystems, where heavily disturbed forest patches are still surrounded by a forest matrix. Such landscapes may be able to buffer canopy loss to a certain extent. To be able to observe changes in species abundances along environmental gradients, future research should consider using species data, where abundances can be reliably calculated. In general, it might also be advisable to use traditional determination methods when working with species-based data like the LFA for a higher reliability of the species information.

AUTHOR CONTRIBUTIONS

Mareike Kortmann: Conceptualization; methodology; data curation; investigation; validation; formal analysis; funding acquisition; writing – original draft; writing – review and editing; visualization. **Jörn Buse:** Writing – review and editing; investigation; resources. **Jacek Hilszczański:** Writing – review and editing; investigation; resources. **Tomasz Jaworski:** Writing – review and editing; investigation. **Jörg Müller:** Resources; writing – review and editing; funding acquisition. **Simon Thorn:** Writing – review and editing; project administration; funding acquisition. **Nicolas Roth:** Writing – review and editing; visualization; supervision; conceptualization; methodology; software; validation; formal analysis.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1.1. Model outputs of linear mixed models of the mean forest affinity as model disturbance severity and region as random factor.

Table S1.2. Model outputs of generalised additive mixed models of species numbers as model of disturbance severity per forest affinity category for all species and separated into taxonomic groups.

Table S1.3. Permanova Results.

Table S1.4. Model outputs of generalised additive mixed models of the median Sørensen dissimilarity as model of disturbance dissimilarity per forest affinity category for all species and separated into taxonomic groups.

Figure S1.1. Predictions of the species numbers along the disturbance gradient per forest affinity category for all species (upper left) and separated into taxonomic groups. Predictions are based on generalised additive models (Table A2).

Figure S1.2. Distribution of forest affinity categories within saproxylic and non-saproxylic Coleoptera.

Data S2. Species list with forest affinities based on Dorow, Wolfgang HO, et al. "Waldbindung ausgewählter Tiergruppen Deutschlands." BfN-Skripten 544 (2019): 388.

Figure S3.1. Results of the linear model of mean forest affinity along the disturbance gradient for all species (left) and separated into taxonomic groups (right), after exclusion of unique species. Mean forest affinity is based on a Likert scale ranging from 1 (= open) to 6 (=closed canopy specialists). Plain lines indicate significant and dashed lines non-significant trends.

Figure S3.2. Predictions of the median Sørensen dissimilarity with increasing difference in disturbance severity per forest affinity category for all species (upper left) and separated into taxonomic groups (except Heteroptera), after exclusion of unique species. Predictions are based on generalised additive models (Table S3.2). Plain lines indicate significant and dashed lines non-significant trends.

Table S3.1. Model outputs of linear mixed models of the mean forest affinity as model disturbance severity and region as random factor, after exclusion of unique species.

Table S3.2. Model outputs of generalised additive mixed models of the median Sørensen dissimilarity as model of disturbance dissimilarity per forest affinity category for all species and separated into taxonomic groups after exclusion of uniques.