



## Response of moth communities (Lepidoptera) to forest management strategies after disturbance

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**Abstract.** Spruce forests face many threats such as climate change and bark beetle outbreaks. Yet, bark beetle dynamics have a long co-evolutionary history strongly linked to spruce forest structural dynamics. Disturbed spruce forest sites resulting from bark beetle outbreaks therefore should not be regarded as degraded land, but as early successional stages following natural forest dynamics. Three post-bark-beetle disturbance sites and one closed-canopy site in the Bavarian Forest and Šumava National Parks were investigated with the focus on moth communities. The three disturbed sites had undergone different post-disturbance management regimes, with one being treated by salvage logging, while at the other two forest sites deadwood was kept in the forest. To avoid the spread of bark beetles, however, the bark of dead trees was either gouged or removed. The aim was to determine how many moths can be found at the undisturbed and disturbed forest sites and if differences in community composition can be explained by different management regimes. The results highlight that natural forest disturbance can increase moth diversity, especially by favouring species that are associated with open and shrub habitats. Many rare and endangered species benefit from bark beetle outbreaks, indicating that accepting natural forest dynamics is an important part of conservation management. Post-bark beetle management seems to have a minor effect on moth communities.

### INTRODUCTION

Central European forest habitats have undergone substantial changes in the last few decades. Many forests face increased drought stress due to climate change (Lindner et al., 2010). As a result, bark beetle infestations become more common, increasing the area of disturbed forests at a regional scale (Dobbertin et al., 2007; Seidl et al., 2015; Netherer et al., 2019; Hlásny et al., 2021). For forest managers, bark beetle outbreaks always result in big economic losses, which have to be treated with massive interventions, such as salvage logging, in order to prevent the spread of bark beetles (Hlásny et al., 2021). Even at protected forest sites such as the Bavarian Forest and Šumava National Parks, some parts have to be managed after bark beetle infestations, e.g. to protect neighbouring commercial forests from such natural disturbance agents. Yet, the open forest structures resulting from bark beetle outbreaks are valuable habitats for many species, making the bark beetle not only an economically important pest, but also an ecosys-

tem engineer species important for biodiversity (Beudert et al., 2015; Przepióra et al., 2020).

A forest manager that has to deal with bark beetles has different possibilities for reacting to a disturbed forest site. The most invasive method is to remove all trees along with the bark beetles (salvage logging), which usually results in a large-scale clear-cut. With most fresh deadwood removed, the carbon storage capacity of a forest is reduced considerably (Dobor et al., 2020). Simultaneously, natural regeneration, microclimatic stability and protective function of deadwood are often reduced (Jonášová & Prach, 2008; Thorn et al., 2014; Leverkus et al., 2021). To keep more deadwood in the forest, other less invasive methods such as gouging or removing the bark from infested trees are suggested (Thorn et al., 2016; Hagge et al., 2019). These methods block the development of bark beetles, which live under the bark, while at the same time, most of the deadwood is kept in the forest and, therefore, can serve as a habitat for many saproxylic species (Fig. 1).



**Fig. 1.** Photographs of the different study sites showing the different post-bark beetle intervention techniques. On the upper left, salvage logged sites (Cz\_F) are illustrated. The upper right picture shows the D\_FS site, with closed canopy spruce forest. On the lower left, site Cz\_S with debarked logs is visible, while the lower right shows the D\_S site, where the bark of logs is gouged.

Here it is investigated how bark beetle disturbance and different interventions after bark beetle outbreaks (removing deadwood vs. bark gouging vs. bark removal) affect moth communities. Moths, a species-rich insect taxon, have often been used as a valuable indicator of habitat characteristics (Uhl et al., 2020; Ellis & Wilkinson, 2021; Fuentes-Montemayor et al., 2022). Post-bark beetle intervention studies often focus on the effects on deadwood-dependent species (Thorn et al., 2016, 2017), while effects on other taxa like herbivorous insects are less well understood. Yet, different interventions might also result in different moth communities: salvage logging might favour the establishment of open habitat species and species feeding on herbaceous plants, whereas debarking (as well as salvage logging) that removes resources like moss and lichen communities growing on the bark, might result in a reduction of moss and lichen feeding species. Compared to other insect species, moths are easy to sample using light trapping and easy to identify as most species are well-described in Central Europe. In addition, the ecology of most species is known, so it is relatively easy to carry out

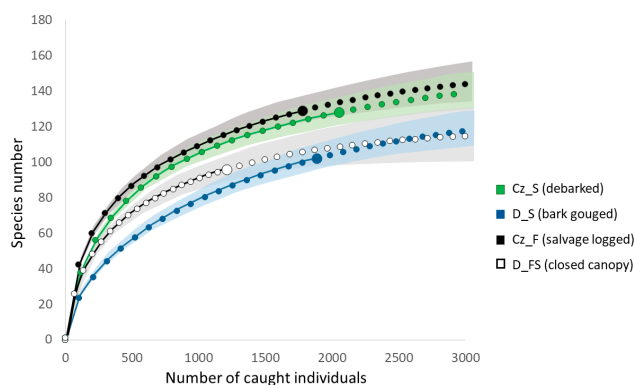
a functional diversity analyses of this taxon (Potocký et al., 2018). The aim was to investigate the following research questions:

1. Are there differences in species richness between undisturbed forest sites and disturbed forest sites with different post-bark beetle interventions?
2. Are there differences in community composition between undisturbed forest sites and disturbed forest sites with different post-bark beetle interventions?
3. Does the occupation of functional niches reflect the typical characteristics of the forests after their structure has been altered by post-bark beetle interventions?

## METHODS

Moth communities at four different forest sites in the Bavarian Forest and Šumava National Parks were sampled. The forests at all four sites consisted mainly of spruce trees. One site (D\_FS) was unaffected by bark beetles and therefore characterized by its closed canopy and sparse understory vegetation. The other three sites were affected by bark beetle outbreaks and, therefore, were treated with different post-bark beetle managements (Fig. 1). At one site (Cz\_F) all the infested trees were removed. As a result,





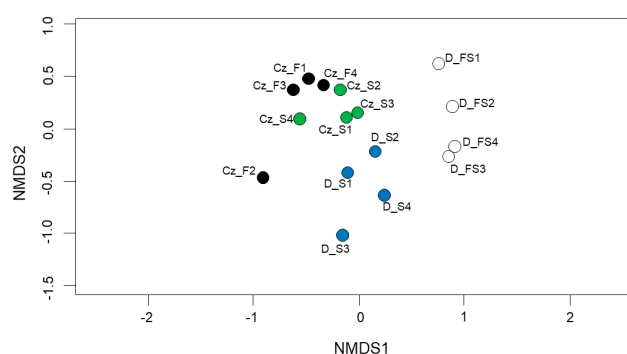
**Fig. 2.** Species extrapolation curves for the four study sites: undisturbed forest (white) and post-disturbance forest subjected to salvage logging (black), debarking (green) and bark gouging (blue). The end of solid lines indicates the actual number of individuals and species caught. Dashed lines indicate extrapolations. The shaded background indicates the upper and lower limits of the estimates.

this former forest was more like open grass or heathland. At the forest sites Cz\_S and D\_S, in contrast, deadwood was kept in the forest and the trees only treated by either gouging the bark (D\_S) or removing the bark (Cz\_S) (Fig. 1). Bark gouging is defined as a disruption of the bark every 16 mm, with a width of 14 mm and a depth of 9 mm, using a mechanical bark-gouging device (Hagge et al., 2019). So, in contrast to full bark removal, the bark phloem is only interrupted by long and standardized gouges. Clear-cut areas were not very large. The soils at the three disturbed forest sites were humid and the dense understory vegetation mainly dominated by *Vaccinium myrtillus* and grasses such as *Calamagrostis villosa*.

Moths were sampled in 2021 by using automated light traps, powered by a 12 V dry battery pack and equipped with two 18 W light tubes (one black light and one white black light tube). In total, four plots per forest site were sampled at subsequent nights when conditions were favourable, i.e. not rainy, windy or extremely cold. In order to obtain a sample of the whole moth community that can be found throughout one vegetation period, the four plots were sampled once in May, June, August and finally September. The sampling started at dusk. The moths were caught in a container and euthanized immediately by the chloroform atmosphere within. The next morning, moths were collected and brought to the lab for identification, which was done to species level using faunal monographs, such as Segerer & Hausmann (2011) and Steiner et al. (2014).

For the data analysis, the R workspace (R Core Team, 2021) was used. To address research question 1, all individuals recorded at a particular forest site were pooled across the four plots and seasons. Species diversity per forest site was calculated using the iNEXT package (Hsieh et al., 2016). Species richness was always extrapolated to 2.5 times the smallest sample size (3000 individuals), to standardize sample size and make the values for the different forest sites comparable.

For research question 2, non-metric multidimensional scaling (NMDS) in the vegan package (Oksanen et al., 2020) was used. This analysis is based on square-root transformed species



**Fig. 3.** Non-metric multidimensional scaling (NMDS) for the moth communities at undisturbed (white), salvage logged (black), debarked (green) and bark gouged (blue) plots (Stress = 0.12). Calculations are based on a Bray-Curtis dissimilarity.

community data with Bray-Curtis dissimilarity. Subsequently, a permutation test was used to test if there is a difference between the study sites. To calculate differences between each of the four study sites, the first and second NMDS axis were extracted and used as a response in linear models, whereas the study sites served as a predictor. Based on these models, a posthoc test with the 'glht' function of the multcomp package (Hothorn et al., 2008) was performed.

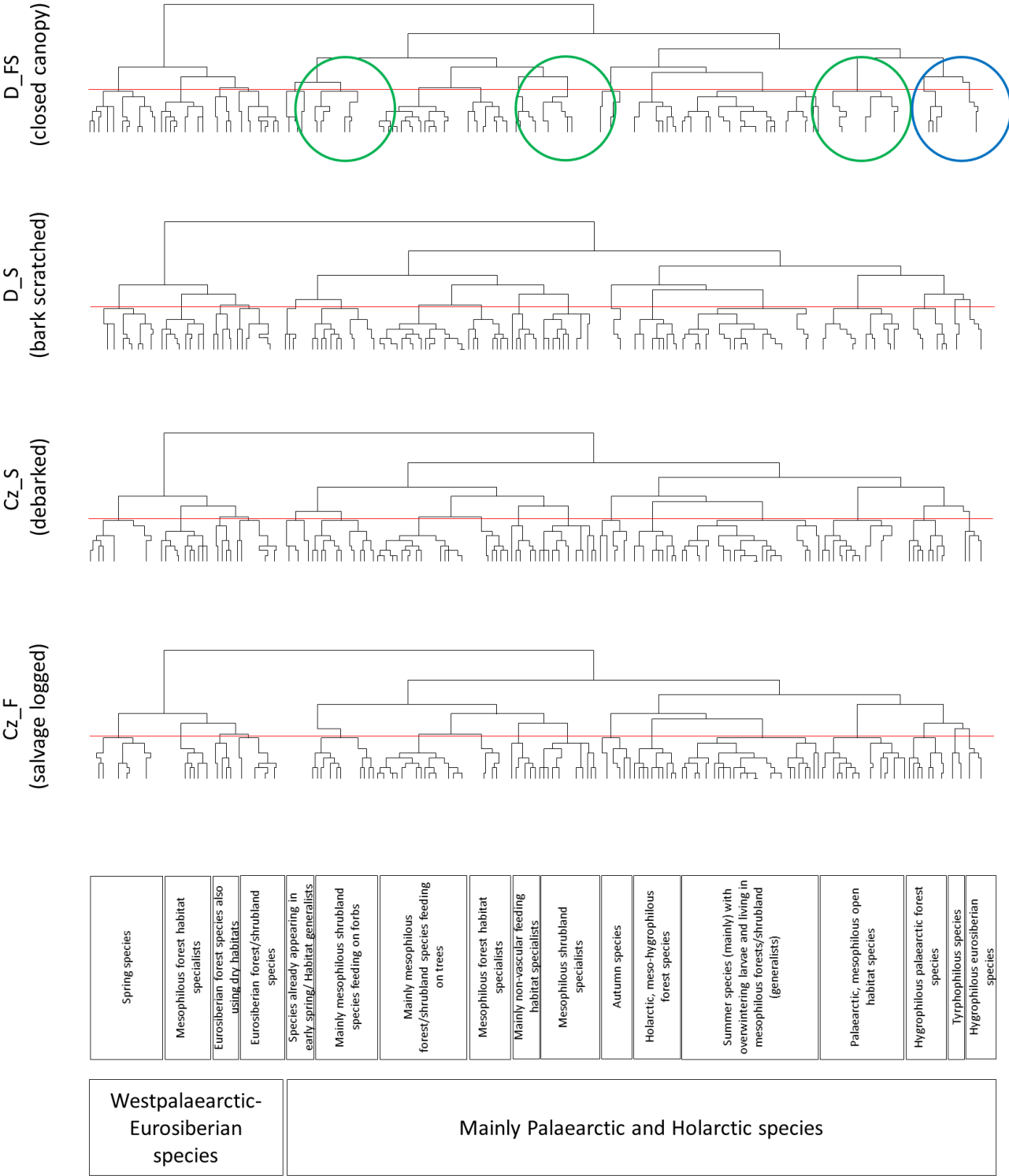
For research question 3, the species trait matrix provided by Potocký et al. (2018) was used. A variety of different traits, describing taxonomic affiliation (taxonomic family), physiological characteristics (wingspan), phenology (overwintering stage, voltinism, seasonality, flight length), larval dietary preferences and behaviour (trophic range, host plant form, host plant part, larval behaviour and appearance), adult behaviour and appearance (adult feeding, adult activity, sexual and seasonal polyphenism) and distributional information (altitudinal range, habitat range, habitat characteristics and latitudinal distribution) were included in this analysis. It was decided to use this mix of different characteristics, in order to obtain the best possible descriptions of the functional niches of the species. Based on the trait matrix, a functional dendrogram with Gower dissimilarity was calculated and functional groups defined by visual inspection of the dendrogram clusters. The functional groups were named based on the traits shared by species within the same cluster. To obtain an insight into how management might alter the functional composition and create new ecological niches, the dendrograms were visually inspected to see which functional niches are occupied at the different forest sites.

## RESULTS

In total, 6933 individuals were caught and assigned to 209 species. Of these, 188 species were used for functional analyses (excluding cryptic species groups that were only determined to genus level due to bad quality and Microlepidoptera, which were not included in the trait database). 30 species were listed either in the German (17 species), Czech (6 species) or both red lists of threatened species (7 species). The Cz\_F plots were inhabited by the most red-

**Table 1.** t-values of the posthoc tests, based on linear models with the first NMDS axis (values before the slash) and the second NMDS axis (values behind the slash) as the response variables and the study site as the predictor. Significant values are marked with asterisks.

	D_FS (closed canopy)	D_S (bark gouged)	Cz_S (bark removed)
D_S (bark gouged)	5.57*** / 2.74		
Cz_S (bark removed)	7.44*** / -0.32	1.88 / -3.05	
Cz_F (salvage logged)	9.88*** / -0.35	4.32** / -3.09	2.44 / -0.04



**Fig. 4.** Functional dendrograms for the four forest sites, based on Gower dissimilarity. The red line indicates the threshold for defining the affiliation of species to functional groups. Boxes contain explanations of the characteristics of each functional group. Green circles highlight a lack of open and shrubland species. The blue circle indicates the lack of species adapted to humid environments.

listed species (20 species), followed by the Cz\_S plots (17 species), D\_S plots (10 species) and D\_FS plots (9 species). Species extrapolation resulted in the highest species richness at the Cz\_F forest site (salvage logged), followed by the Cz\_S forest site (debarked) and the D\_S forest site (bark gouged). D\_FS had the lowest species richness (Fig. 2).

The community composition at disturbed forest sites differed from that at undisturbed sites (Fig. 3, Table 1). There was no significant difference between the composition of the communities recorded at bark gouged (D\_S) and bark removed (Cz\_S) sites, and also the two Czech forest sites showed no significant difference in community composition. Forest site accounted for 47% of the total variation in species composition.

Based on the functional dendrogram, the species separate into two main groups, which are mainly associated with their distributions in either the Westpaleartic and Eurosiberian or Palearctic and Holarctic regions. A lack of grass and herbaceous plant feeding species was recorded at the German D\_FS plots (closed canopy, Fig. 4). In addition, hygrophilous and tyrophilous species were mostly absent at the German plots (D\_FS and D\_S).

## DISCUSSION

More individuals and slightly higher species richness was recorded at all bark beetle-disturbed forest sites. In addition, there were differences between the three post-bark beetle managements, with lower species richness in bark gouged plots than in debarked and especially salvage-logged plots. These differences in species richness, however, are most likely a result of site-specific characteristics, like enhanced habitat diversity in the surroundings of the Czech sites and, therefore, not necessarily an effect of post-bark beetle management on moth diversity. It is more likely, that the area of bark beetle disturbed habitat in the surroundings might contribute to explain the observed pattern. At the Czech sites, more than 20% (on average 25.5%) of the forest within in a 250 m radius around the plots were defined as disturbed forest habitat, while for the German sites, the percentage was always below 15% (on average 6%). Habitat diversity at the Czech sites, therefore, is enhanced by bark beetle activity, while it is rather low at the German sites. The importance of the surrounding habitat structure has also been shown in previous studies, where habitat diversity positively affected moth species richness (Uhl et al., 2020). Disturbed forest sites resulting from bark beetle infestations, therefore, can ameliorate habitat diversity and can serve as a habitat for many different species, many of which are rare and threatened (Müller et al., 2008; Kortmann et al., 2021). 21 out of the 30 recorded red-listed species were exclusively found at disturbed forest sites, making them high-quality habitats. Four red-listed species, however, were only recorded at the closed-canopy forest site, underlining the importance of both types of forest; closed canopy and disturbed open canopy, at the landscape scale (Kortmann et al., 2022). The diversity in different forest structures can be crucial for regional gamma diversity (Schall et al., 2018) and bark beetles here might help to create landscape-scale habitat heterogeneity for many different species (Thorn et al., 2017), underlining the role of bark beetles as keystone species (Müller et al., 2008).

There was a clear difference between the forest moth communities at the four study sites. Especially the closed canopy forest site was characterized by a moth community that strongly differed from that recorded at the other study sites. Sites in the Czech Republic had similar species compositions and also the moth assemblage of the German D\_S plots was not significantly different from the Czech Cz\_S plots, again indicating that the post-bark beetle management is of minor importance for community composition, but bark beetle disturbance itself changes moth communities. It is assumed that bark beetle infestations benefit

moth communities by opening up the canopy. This creates early-successional habitats and enhances habitat diversity, which favours the establishment of different assemblages of moths, irrespective of post-bark beetle management made. In fact, early-successional habitats are known for their high biodiversity and their importance for many specialized species. Previous studies, therefore, stress that early-succession forest stages should be given more consideration, especially in forest areas where biodiversity conservation is the main objective (Swanson et al., 2010).

Forest disturbance especially favoured the establishment of species associated with open and shrubland habitats. Hence, opening the canopy can help create additional niches and microhabitats, which might also be beneficial for rare species like *Lasionhada proxima* (not red-listed in the Czech Republic, but vulnerable in Germany). This species is bound to mountainous habitats and prefers forest edges and open habitats. Similarly, *Pharmacis fusconebulosa* (nearly threatened in the Czech Republic and Germany) profited from bark beetle infestations as it only occurred at disturbed forest sites. At the salvage logged plots of Cz\_F, many rare and endangered species were recorded, like *Litophane lamda* (vulnerable in the Czech Republic, critically endangered in Germany), *Acrionicta menyanthidis* (nearly threatened in the Czech Republic, endangered in Germany) and *Xestia speciosa* (endangered in Germany). All these species are more or less tyrophobic, which indicates that this specific study site is a suitable habitat for species of wet and open habitats. There are some important bog habitats in the surrounding of the Cz\_F site (the peat-bogs “Cikánské slatě” and “Mlynářské slatě”), which might favour the occurrence of bog habitat species in this region. Thus, in the current study, the combination of salvage logging and high-quality bog habitats in the surroundings was beneficial for the establishment of rare and endangered bog habitat species in these plots. So, although salvage logging is not considered to be consistent with the management objectives for protected areas (Thorn et al., 2018), it might help to quickly restore peatlands and open forest habitats (Anderson, 2010). For natural closed-canopy forest habitats, in contrast, salvage logging has negative effects on biodiversity and therefore should be avoided (Thorn et al., 2015).

In conclusion, differences in community composition could not be explained by the different post-disturbance management regimes and are more likely to be a result of the spatial distance between the plots, soil properties and the larger landscape context. Salvage logging in this study did not have a negative effect on biodiversity but favoured, in combination with neighbouring high-quality habitats, the establishment of rare bog habitat species. As it was not possible to disentangle management effects from landscape context effects, further studies are needed to get a better understanding of how post-bark beetle management affects herbivore communities.

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