



# The positive effects of canopy openness across post-disturbance management on insect diversity

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## ABSTRACT

Forests across Europe are experiencing higher rates of tree mortality while many insect populations are declining, but the links between these two ecological changes are not well understood. While pulses of tree mortality from natural disturbances can enhance structural complexity through canopy openings and deadwood accumulation – both key elements for high value insect habitats – post-disturbance tree removal may reduce habitat quality. We systematically investigated the impact of natural disturbances and post-disturbance logging on total insect diversity across major European forest types, comparing triplets of undisturbed, disturbed, and cleared forest patches. Using metabarcoding and a newly developed phylogeny, we quantified taxonomic and phylogenetic diversity (standardized by sample coverage along Hill numbers) for 21,218 insect OTUs from 347 families and 19 orders. Disturbances and post-disturbance clearing increased taxonomic diversity by up to 12 % in disturbed and 26 % in cleared patches compared to undisturbed patches. However, phylogenetic diversity increased only for rare species. Spaceborne data identified canopy openness as the primary driver of this increase, but responses varied by feeding guilds, with parasitoids and fungivores showing the strongest diversity increase. Overall, our findings show that current post-disturbance logging of small-scale disturbances in Central Europe amplifies canopy openings created by natural disturbances. This leads to a positive response of insect diversity shortly after disturbance, yet effects vary among feeding guilds and phylogenetic lineages. Our combination of innovative spaceborne and metabarcoding information provides new insights into the complex impacts of increasing tree mortality on insect diversity in Central European forests.

## 1. Introduction

### 1.1. Natural disturbances and insect decline are an increasing challenge

A prominent impact of ongoing climate change are more frequent and severe drought events in temperate regions (Spinoni et al., 2018), which can cause more frequent natural disturbances in forest ecosystems (Gazol and Camarero, 2022). In Europe, Norway spruce forests (*Picea abies* (L.) Karst.) are particularly susceptible to drought (Thom et al.,

2023). Ongoing drought stress often leads to bark beetle infestations, which can occur at high severities and can cover large areas (Senf and Seidl, 2021; Potterf et al., 2025). However, increasing tree mortality can be observed also in other major forest types of Europe, such as in pine (*Pinus sylvestris* L.), oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) forests (Bose et al., 2020; Haavik et al., 2015; Thom et al., 2020). At the same time, climate change and land-use changes are driving insect declines in North America and Europe (van Klink et al., 2020). Concerns over biodiversity loss and ecosystem functions have spurred political

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action (Felgentreff et al., 2023) and intensified research (Haase et al., 2023; van Klink et al., 2024; Hallmann et al., 2017; Didham et al., 2020). However, the causes of insect decline remain unclear and likely involve multiple interacting factors (“death by a thousand cuts”; (Wagner et al., 2021)), including land use (Uhler et al., 2021), climate change (Beaumont et al., 2011; Harvey et al., 2023), and unfavourable weather conditions over many years (Müller et al., 2024). However, it remains unclear how insect decline is affected by increasing disturbances. Insect declines are known to occur in forests as well as agricultural areas, yet tree mortality seems to buffer these negative trends in temperate forests (Seibold et al., 2019).

### 1.2. Natural disturbances change ecosystems

Natural disturbances (i.e. pulses of tree mortality) have distinct impacts on forest ecosystems. They can lead to increased structural diversity (Senf et al., 2020; Svoboda et al., 2010), open canopies (Thorn et al., 2020), an accumulation of dead wood resources (Mayer et al., 2022; Svoboda et al., 2010) and an increase in ground vegetation (Zehetgruber et al., 2017). Hence, naturally disturbed forests are of high conservation value, fostering conditions which resemble unmanaged forests (Bässler and Müller, 2010; Müller et al., 2008; Procházka et al., 2020; Donato et al., 2012; Swanson et al., 2011), shaped by post-disturbance legacies like dead and dying trees as well as by a new cohort of regenerating trees (Kortmann et al., 2018; Winter et al., 2017).

Nevertheless, in Central Europe, most forest disturbances are actively managed – typically through salvage logging or clearing – for economic reasons and pest control (Müller et al., 2019). Such management alters disturbance legacies by removing dead and dying trees and can further disturb the forest floor due to the use of heavy machinery. In some cases, it increases disturbance severity through the extensive removal of trees (Leverkus et al., 2021; Lindenmayer and Noss, 2006), while also influencing the structure and composition of post-disturbance tree regeneration (Seidl et al., 2024). Consequently, post-disturbance logging is considered an additional disturbance following a natural event (Leverkus et al., 2018; Lindenmayer et al., 2017).

Both natural disturbances and post-disturbance management shape species communities and assembly patterns in disturbed forests in different ways (Thorn et al., 2018; Thorn et al., 2016; Georgiev et al., 2022). Many studied taxa, such as Hymenoptera, hoverflies, saproxylic beetles, and Hemiptera, generally respond positively to natural forest disturbances (Viljur et al., 2022). In contrast, salvage logging is often expected to have negative effects on insect communities (Thorn et al., 2018), though different taxonomic groups exhibit varying thresholds of logging intensity at which species richness declines (Thorn et al., 2020). How species or taxa respond to disturbance and salvage logging depends on their habitat requirements and life history (Beudert et al., 2015; Kortmann et al., 2024; Thorn and Seidl, 2016; Viljur et al., 2022). Ultimately, we would expect that the response of insect communities to post-disturbance clearing is negative if communities are mainly resource-driven, like saproxylic species, and that the response is positive if communities are mainly light-limited (Thorn et al., 2014). Especially if naturally disturbed patches are small, post-disturbance logging should lead to more intense canopy opening and hence could promote light demanding species.

### 1.3. Metabarcoding to analyse insect diversity

Insects are an exceptionally diverse class of species. To identify this vast number of species across all families, metabarcoding has become an increasingly popular tool for studying insect communities. Currently, metabarcoding is the only method that allows the inclusion of understudied and “dark” taxa, adding further depth to ecological analyses (Kortmann et al., 2022; Leroy et al., 2022; Morinière et al., 2019). While metabarcoding allows the comprehensive identification of communities, a key limitation is its lack of reliable abundance estimates (Liu et al.,

2020). However, recent advances have improved the standardized analysis of metabarcoding data, including the use of phylogenetic diversity metrics (Kortmann et al., 2025).

Recently, a controlled experiment across 11 sites in broadleaved forests dominated by beech in Germany found that insect diversity was highest in canopy gaps containing dead trees (Rothacher et al., 2025). However, it remains unclear whether these experimental results mirror real-world conditions in disturbed forests across major Central European forest types (Jochum et al., 2020). Specifically, we expect that the size and severity of canopy openings and post-disturbance clearing are not independent and hence interact to influence insect diversity. To address this question, we conducted insect sampling using Malaise traps in a replicated natural experiment with triplets of three treatments, undisturbed forest, disturbed forest, and cleared forests after disturbance, across stands dominated by spruce, pine, oak, and beech (Seidl et al., 2024).

Given the natural variability in disturbance size and severity, we used satellite-derived canopy openness values to quantify changes in light availability across treatments. Building on previous experimental findings by Rothacher et al. (2025), we hypothesized that disturbed forests without post-disturbance clearing would show the strongest positive effects on overall insect diversity. At the same time, we expected that particularly non-feeding insects (in their adult stage), predators, and phytophagous insects to also benefit from clearing due to increased light availability in comparison to undisturbed forests. In terms of phylogenetic diversity, we anticipated higher values in disturbed patches, driven by the combined effects of increased deadwood and light. In contrast, we expected similar or lower phylogenetic diversity in cleared patches, where positive responses may be limited to a narrower range of taxa.

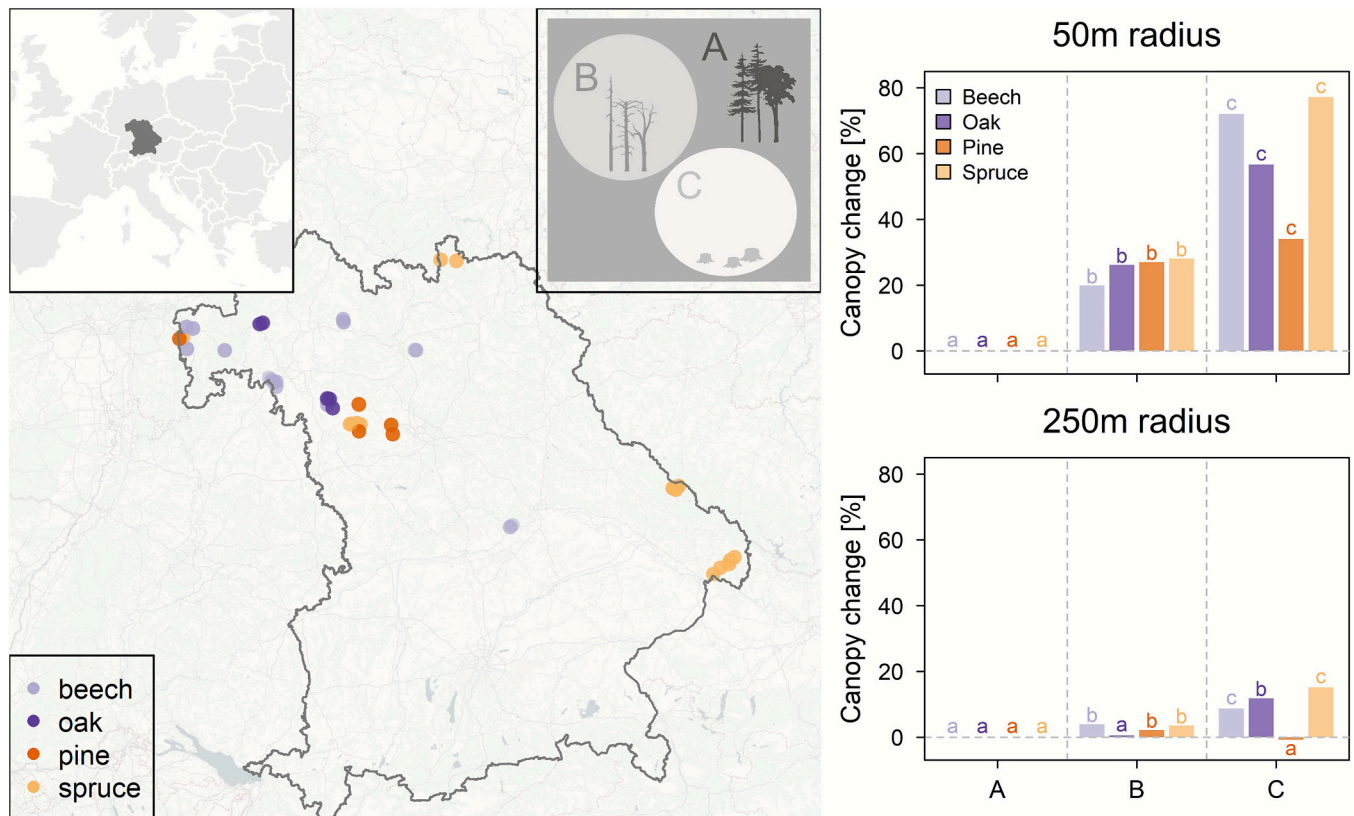
## 2. Methods

### 2.1. Study design

We focused on forests that experienced moderate- to high-severity tree mortality from drought and bark beetles in 2018 and 2020 (for details see Seidl et al. (2024)). Sites were selected in which tree mortality in 2018–2020 exceeded 300 % of the mean rate of canopy opening between 1986 and 2015. Within 40 sites of high tree mortality, triplets of patches were selected (Fig. 1), including (i) a disturbed patch that was unmanaged (standing and downed deadwood remaining on site), (ii) a disturbed patch that was managed (salvage-logged, often planted), and (iii) an undisturbed reference patch, representing the composition and structure prior to the onset of mortality in 2018. The patches within a triplet were located in close proximity to each other (mean distance 372 m), in order to ensure constant site conditions. The minimum patch size requirement was 625 m<sup>2</sup>, with the smallest side of the patch exceeding 25 m. The elevation range of the sites was from 128 m to 971 m asl. Average patch size was 6558 m<sup>2</sup>, and thus close to the long-term average of disturbance patch size in Germany of 7300 m<sup>2</sup> (Senf and Seidl, 2021). All sites were located in Bavaria, Germany.

### 2.2. Remote sensing

For each of the 120 patches we extracted information on total canopy cover for the sampling year 2022 from parameters of forest structure derived from spaceborne remote sensing data. A combined modelling of multispectral and radar data joined with samples from a LiDAR system (Light detection and ranging) was used to describe forest total canopy cover at 10 m spatial resolution in 2022 (Kacic et al., 2023). We used a 50 m (local) and 250 m (neighbourhood) radius around each patch centre to extract the mean value for total canopy cover in close proximity to the patch centre and within a larger radius. In the following, the inverse of total canopy cover was calculated to characterize reduced canopy cover, which is named canopy openness in the following.



**Fig. 1. Study area (Bavaria, southern Germany) and the 40 study sites.** Our sites included four major forest types: Norway spruce (*Picea abies* (L.) Karst.) forests ( $n = 17$  sites | 51 patches), Scots pine (*Pinus sylvestris* L.) forests ( $n = 5$  | 15), European beech (*Fagus sylvatica* L.) forests ( $n = 13$  | 39), and forests dominated by oak species (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.,  $n = 5$  | 15). Each site comprised a triplet of patches, A) undisturbed forest, B) disturbed forest and C) disturbed and cleared forest. Right panels show the change in canopy openness (i.e. inverse of total canopy cover) in disturbed (B) and cleared (C) patches in comparison to undisturbed patches (A) within a 50-m and a 250-m radius, derived from remote sensing. Lower case letters indicate significant differences between the management categories.

### 2.3. Insect sampling and identification

On each patch, we installed a Malaise trap based on the Townes Malaise trap model with black roof and a slightly smaller size than the Townes model (Uhler et al., 2021). Traps were operated from the beginning of May until the end of July in 2022. Traps were equipped with collection bottles filled with ethanol (70 %) to ensure high DNA quality for metabarcoding. Bottles were exchanged biweekly with slight variations in individual sampling periods. This resulted in a total of six completed samples on each patch. Excluding some malfunctions, we collected a total of 702 samples. We separated the captured arthropods of each sample in two size classes using a sieve (mesh size: 8 mm) to avoid underrepresentation of small specimens with relatively low biomass during metabarcoding. Species identification was performed using CO1-5P (mitochondrial cytochrome oxidase 1) metabarcoding. DNA metabarcoding followed the laboratory and bioinformatics pipelines as reported in (Hausmann et al., 2020). A detailed description of the metabarcoding and bioinformatic procedures can be found in Supplement 1 (Metabarcoding).

### 2.4. Statistical analyses

In our 702 insect samples, we identified 21,218 OTUs from 347 families and 19 orders. All statistical analyses were conducted in R 4.3.1 (R Core Team, 2023) following the data processing protocol outlined by Kortmann et al. (2025). Sequencing errors were removed using a statistical approach, and the final read frequency distribution per sample was used to assess sample completeness.

To estimate standardized taxonomic and phylogenetic diversity

along Hill numbers, we used iNEXT.3D (Chao et al., 2021). Phylogenetic diversity calculations were based on a phylogeny combining metabarcoding sequence data with a backbone phylogeny for insect families (see Supplement 1 (iNEXT calculations) for details). Feeding guilds were assigned at the family level using published classifications along the backbone phylogeny (Rainford and Mayhew, 2015) (see Supplement Table S1.1).

### 2.5. Generalized additive models

We used generalized additive models (GAMs) from the *mgcv* package to assess the effects of disturbance and forest type on taxonomic and phylogenetic diversity along Hill numbers. Diversity values were modelled with a negative binomial error term, including disturbance categories (undisturbed, disturbed-unmanaged, and disturbed-managed) and forest type (spruce, beech, oak, pine) as predictors. To account for seasonality, we included a smoothed spline for sampling date and an offset for sampling length, along with site- and patch-specific random effects (smooth term for random effects (bs="re"). Analyses were repeated separately for different feeding guilds.

Additional GAMs with a binomial error term tested effects of the same predictors (disturbance category, forest type, sampling date and length, site and patch) on sample coverage, while models incorporating canopy openness (from remote sensing) instead of treatment categories were used to analyse the effect of disturbance severity in more detail. Since Malaise traps capture highly mobile insects, we considered canopy openness within both local and neighbourhood surroundings. These models used a negative binomial error term and included canopy openness, forest type, sampling date, sampling period length, and site-

and patch-specific random effects. We build separate models for either local or neighbourhood surroundings. Finally, GAMs tested differences in local and landscape canopy openness between forest types and disturbance categories, incorporating site- and patch-specific random effects, using a Gaussian error term (Müller et al., 2024).

To illustrate how canopy openness differs among forest types following disturbance and clearing, we calculated changes in canopy cover between undisturbed and disturbed patches, as well as between disturbed and cleared patches within each site. Since changes in canopy openness were rather subtle in the neighbourhood surrounding, we focused only on the local surrounding in this step. These differences were then plotted against the corresponding changes in insect diversity. Canopy cover changes were expressed as percentage point differences, for example, an increase from an openness of 40 % to 50 % canopy cover was coded as 10 percentage point change. Changes in insect diversity were calculated as percent increases or decreases relative to the undisturbed or disturbed patches, respectively. To test the impact of canopy cover changes we calculated linear models with percentage point change and elevation as predictors for changes in taxonomic and phylogenetic diversity (Fig. 4).

### 3. Results

Insect samples in disturbed and cleared patches had significantly lower sample coverage than those in undisturbed forests. After standardization for a coverage of 99 %, results of the generalized additive models showed higher taxonomic diversity in disturbed and cleared forests compared to undisturbed forests (Fig. 2). In disturbed forests, taxonomic diversity was significantly higher than in undisturbed sites for  $q = 0$  ( $t = 3.784$ ;  $p < 0.001$ ). In cleared forests disturbance-induced changes in taxonomic diversity were significant for  $q = 0$  and  $q = 1$  ( $t = 7.704$ ;  $p < 0.001$  and  $t = 3.883$ ;  $p < 0.001$ ). Generally, diversity responses were more pronounced in cleared than in disturbed forests (Fig. 1).

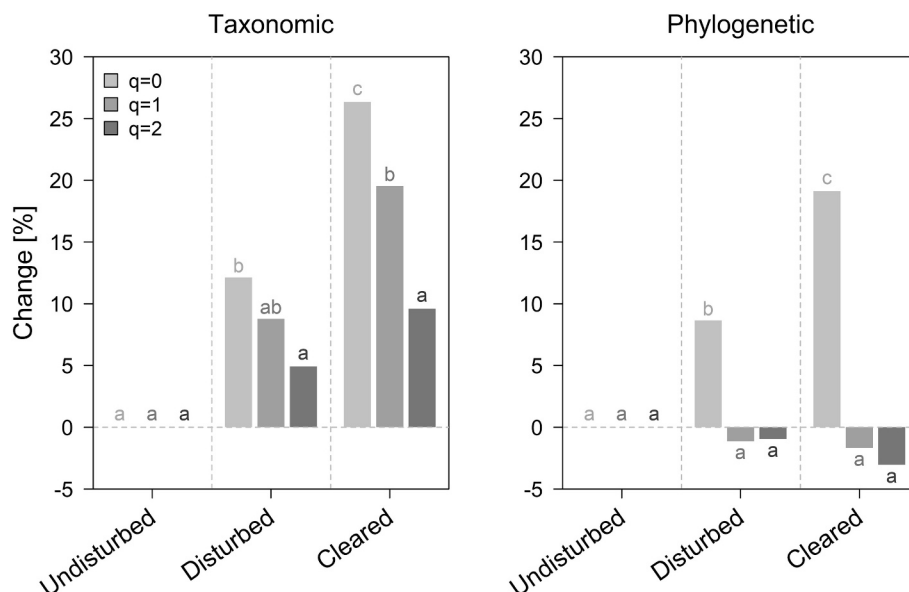
Phylogenetic diversity was significantly higher in disturbed and cleared patches compared to undisturbed for  $q = 0$  ( $t = 3.254$ ;  $p = 0.005$  and  $t = 6.888$ ;  $p < 0.001$ ). In contrast, for  $q = 1$  and  $q = 2$  phylogenetic diversity did not differ significantly from the undisturbed reference in disturbed and cleared patches. Detailed model results can be found in

Supplement 1 Table S1.2.

Results at the level of different feeding guilds were similar to those of the entire dataset. One notable difference was that the phylogenetic diversity of parasitoids increased for  $q = 1$  in disturbed and cleared patches, in contrast to other feeding guilds and the full dataset (Fig. 3).

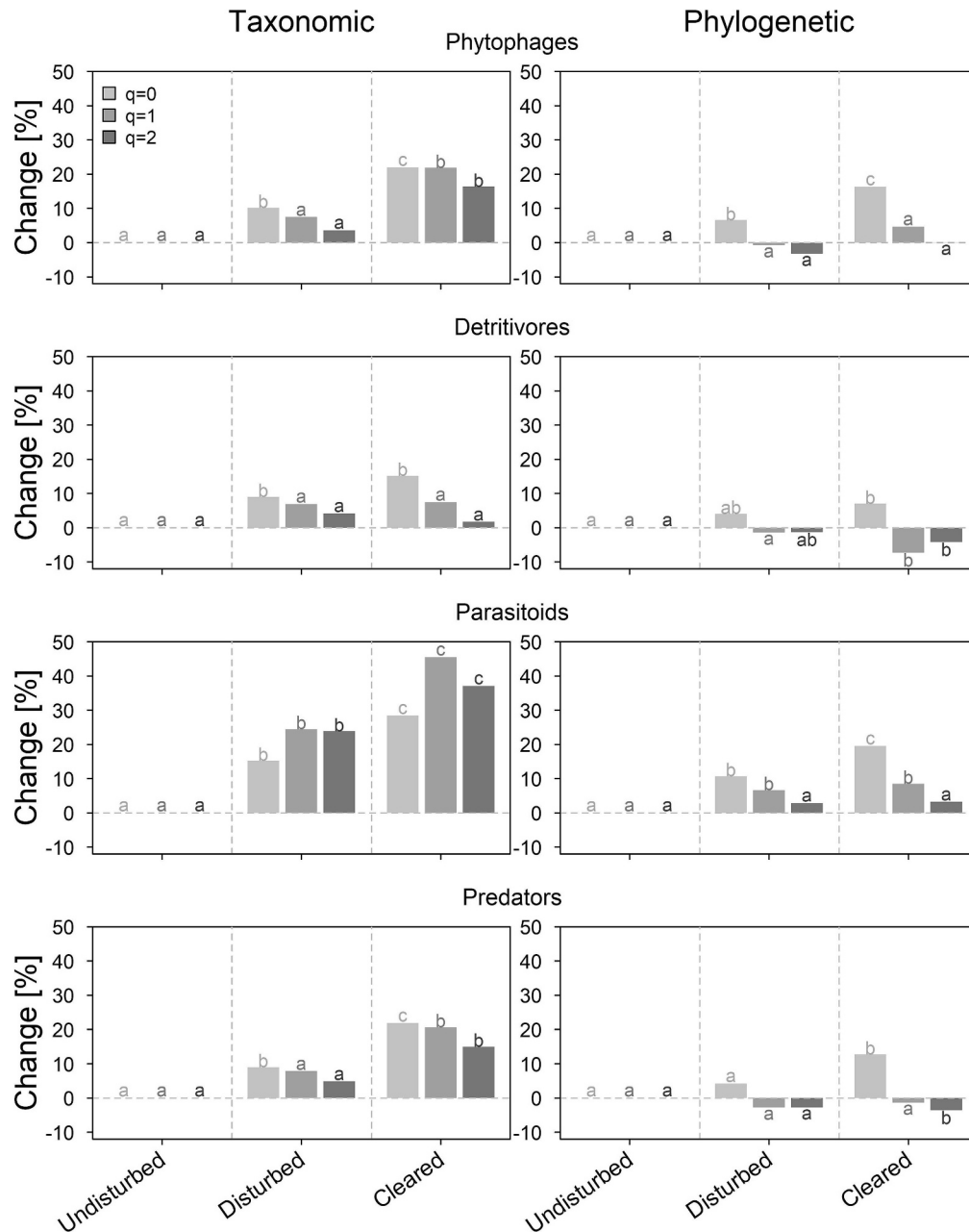
Results of the GAMs with canopy openness and forest type as predictors indicated clear differences in the effect of canopy openness between forest types for both local and neighbourhood surroundings. Oak-dominated forests had the lowest values in canopy cover, but disturbance severity was moderate with canopy openness remaining  $< 60$  % even after disturbance (Supplement Fig. S1.3 and S1.4). While pine forests were also open and had moderate disturbance severity, beech and spruce forests had closed canopy before disturbance and experienced high disturbance severity. Increasing canopy openness only significantly affected taxonomic and phylogenetic diversity in beech and spruce forest types. Especially a disturbance-induced increase in canopy openness in spruce forests in a 250 m radius around the sampling location had significantly positive effects on taxonomic and phylogenetic diversity. In contrast, phylogenetic diversity for  $q = 1$  decreased significantly with increasing canopy openness in spruce stands (50 m radius). In contrast, taxonomic and phylogenetic diversity for  $q = 0$  increased with increasing canopy openness in beech stands (50 m radius).

Since the effects of disturbance-induced canopy openings were most pronounced for taxonomic diversity at  $q = 0$  and for phylogenetic diversity at  $q = 2$ , we focused on these metrics in further analyses (Fig. 4). We found that for most patches, increased canopy openness is associated with higher taxonomic diversity, most notably in spruce stands. Still, the positive effects of canopy openness due to clearing (additional canopy opening in cleared compared to disturbed patches) decreased with increasing openness (Fig. 4A, right panel). Negative effects of disturbance on taxonomic diversity were observed only in oak and pine patches (Fig. 4A, left panel). However, oak and pine patches generally exhibited positive responses in phylogenetic diversity (Fig. 4B, right panel). The additional canopy opening caused by clearing led to a range of changes in both taxonomic and phylogenetic diversity (Fig. 4A and B, right panels). In some cases, however, the effects of disturbance and clearing on canopy cover were small (Fig. 4).



**Fig. 2.** Partial effects of natural disturbance and post-disturbance management on taxonomic and phylogenetic diversity. Changes are in comparison to undisturbed forests and are based on estimates from generalized additive models. Disturbed = tree mortality from drought and bark beetles; Cleared = tree mortality from drought and bark beetles, followed by post-disturbance salvage logging. Letters indicate statistical differences at  $p < 0.05$  between the different disturbance types within each order of  $q$ .





**Fig. 3.** Partial effects of natural disturbance and post-disturbance management on the taxonomic diversity of different feeding guilds. Changes are in comparison to undisturbed forests and are based on estimates from generalized additive models, fit at the level of feeding guilds. Letters indicate statistical differences at  $p < 0.05$  between the different disturbance types within each order of  $q$ .

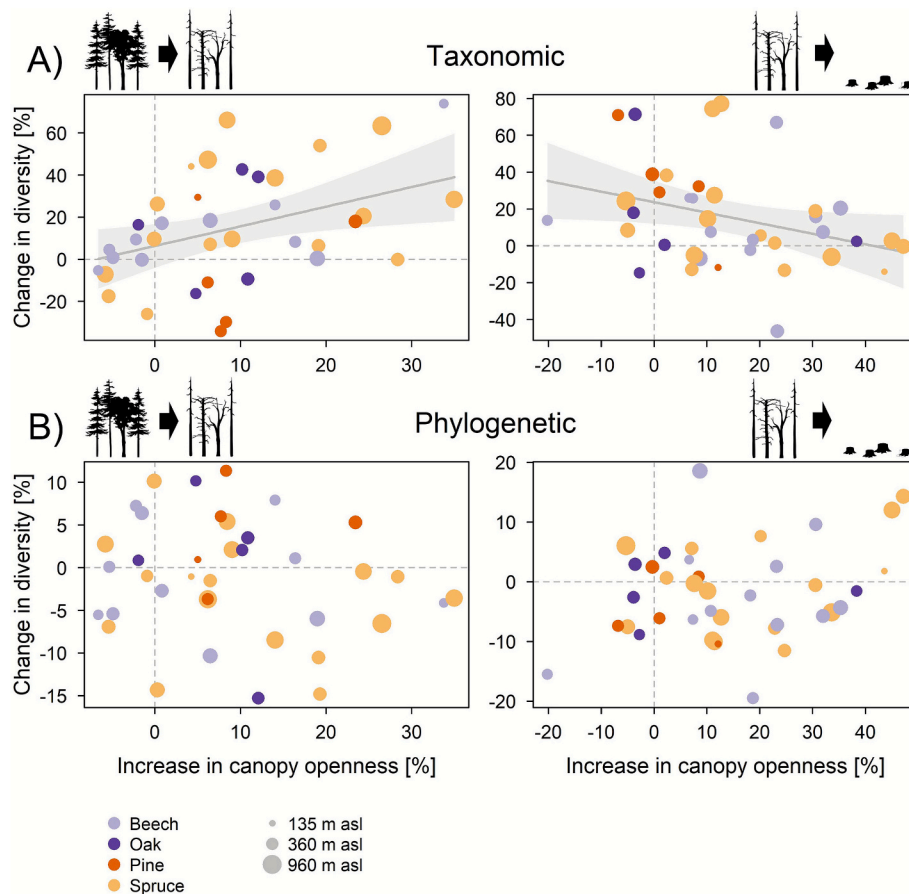
#### 4. Discussion

Our study revealed predominantly positive effects of disturbance and post-disturbance management on taxonomic diversity, with increases of up to 12 % in disturbed patches and up to 26 % in cleared patches compared to undisturbed forests. Conversely, phylogenetic diversity showed only significant increases for rare species (9 % and 19 % in disturbed and cleared patches). Disturbed and cleared patches also had lower sample coverage, suggesting the presence of more undetected species despite standardized sampling efforts, a pattern already observed by Rothacher et al. (2025) under conditions of experimental disturbance. Importantly, we also found that increasing canopy openness, particularly in beech- and spruce-dominated forests, was strongly associated with higher taxonomic insect diversity.

##### 4.1. Taxonomic and phylogenetic diversity

The strong diversity increase in cleared patches in our study contradicts our initial expectations and differs from findings in experimentally disturbed broadleaf forests, where gaps of controlled size with deadwood supported higher diversity than those where trees were removed (Rothacher et al., 2025). Our results also contrast with those of Sire et al. (2022) and (Wang et al. (2021), both of whom reported that climate- or pest-induced dieback did not significantly alter overall insect species richness. Instead, these studies found that canopy opening and associated structural changes primarily drove shifts in community composition, with the strongest responses often observed among rare or habitat-sensitive taxa.

Generally, post-disturbance management, such as salvage logging, is considered detrimental to biodiversity due to deadwood removal and



**Fig. 4.** The effect of changes in canopy cover in the local surrounding on changes in taxonomic (A) and phylogenetic diversity (B). Left panels show changes between undisturbed and disturbed patches and right panels between disturbed and cleared patches. Changes in taxonomic diversity (A) were calculated for  $q_0$  (species richness or rare species) and for phylogenetic diversity (B) for  $q_2$  (the inverse of Simpson's concentration index or dominant species). Points are based on raw data, prediction lines and confidence bands are based on linear models controlled for elevation, showing only significant ( $p < 0.05$ ) effects of canopy cover change.

the additional disturbance it causes, e.g. to the soil and to residual vegetation (Lindenmayer and Noss, 2006; Leverkus et al., 2018; Lindenmayer et al., 2017; Hyvärinen et al., 2006). For saproxylic insects in particular, this expectation has been consistently confirmed (Thorn et al., 2018). However, our study included a broad range of insect taxa across multiple feeding guilds, many of which are also influenced by herb-layer vegetation and light availability, in addition to deadwood resources. These factors may partly explain the observed patterns.

Furthermore, while taxonomic diversity increased, phylogenetic diversity declined among common and dominant species, aligning with experimental findings from beech forests (Rothacher et al., 2025). This suggests that disturbance and especially post-disturbance management may selectively benefit certain evolutionary lineages.

Taken together, these results point to a more nuanced picture of insect diversity responses, potentially shaped by interacting factors such as light conditions, resource heterogeneity, and disturbance scale, which we will explore in the following sections.

#### 4.2. Drivers and effects of disturbance and post-disturbance management

Two of the main resources altered by drought induced disturbances are light and deadwood. Deadwood is consistently abundant in disturbed patches and heavily reduced in cleared patches, while still being considerably higher compared to undisturbed forests (Priewasser et al., 2013). Canopy openness, and thus light availability, vary substantially across disturbed areas, as patch size and disturbance severity differ within and between forest types. To explore this variation further and better understand the underlying processes driving insect responses

to disturbance, we analysed satellite-derived changes in canopy cover at both local and broader spatial scales around each trap. For shade-tolerant species such as spruce and beech, disturbances led to significant increases in light availability. These changes were accompanied by consistently positive responses in taxonomic diversity relative to undisturbed patches (Fig. 4, Fig. S1.3, Fig. S1.4). In contrast, light-demanding tree species like pine and oak already had relatively open canopies before disturbance, and disturbances only moderately increased canopy openness further (Fig. 4). Consequently, the response of taxonomic diversity in oak and pine forests to disturbance was more mixed.

Cleared plots generally exhibited greater canopy openness than those that were disturbed but remained untreated, an effect that likely contributed to the strong positive response of taxonomic insect diversity in these areas (Fig. 4). In our study, canopy openness serves as an indicator of disturbance intensity, as clearing after natural disturbances removes additional canopy cover beyond what the disturbance itself created. This pattern, i.e. higher canopy openness in cleared sites, reflects the amplifying effect of post-disturbance management such as salvage logging. Similar mechanisms may explain global observations that disturbance patches within managed forests are often larger and more severe than those in forests without management (Sommerfeld et al., 2018; Krüger et al., 2025). In many cases, this difference likely arises not from the natural disturbance regime itself, but from management interventions (e.g., salvage logging) that expand or intensify disturbance effects in unprotected, managed forests. Importantly, although this greater openness was associated with higher insect taxonomic diversity in the short term in our study, the long-term ecological

implications of such management-driven canopy alteration remain uncertain and should be carefully considered when balancing biodiversity conservation with post-disturbance interventions.

It is important to note that the positive effects of clearing after disturbance observed here are contingent on the relatively small disturbance patches that are typical for our study area. This is underscored by the observation of the strongest changes in canopy cover within a 50-m radius from the sampling location (Fig. 1 and Fig. S1.3). We also observed that the positive effects of clearing were especially high for relatively small additional canopy openness (Fig. 4 A) right panel). The fact that disturbances in our study are predominantly small is representative for Central Europe, where the average disturbance patch size over the past decades was approximately 0.73 ha (Senf and Seidl, 2021). It is important to note that as climate change intensifies and disturbances potentially become larger, the beneficial effects of salvage logging on insect diversity reported here may change. Furthermore, our findings do not indicate a universally positive effect of post-disturbance clearing but rather highlight that outcomes are highly context-dependent and contingent on the prevailing disturbance regime and forest type.

Positive effects of post-disturbance management on insect diversity were also observed in previous research. A study on post-windthrow insect diversity over 20 years found that salvage logging had minimal impacts on most taxa, except saproxylic beetles, which benefited from unsalvaged sites (Wermelinger et al., 2025). Similarly, a meta-analysis reported significant species richness declines in only eight out of 24 species groups following salvage logging, whereas 13 taxa showed no significant response and three taxa increased in species richness (Thorn et al., 2018). Moreover, prior research suggests that post-disturbance management can accelerate deadwood diversification in early post-disturbance years (Thorn et al., 2014), as managed sites provide a quicker and more varied supply of deadwood compared to natural decay, especially in commercial forests where damaged trees tend to be of uniform age, size and species.

It is also important to recognize that substantial amounts of deadwood often remain in patches that were cleared post-disturbance. For example, windthrown sites in Switzerland retained approximately 70 m<sup>3</sup> ha<sup>-1</sup> of deadwood after clearing, which is considerably more deadwood than in most commercial forests of Central Europe (Priewasser et al., 2013; Müller and Büttler, 2010). The effects of deadwood and light were recently disentangled in a dedicated experiment (Rothacher et al., 2025), but also here the effect of canopy openings was identified as the overall strongest driver of insect diversity.

Still, the positive effects of canopy openings might only last for a limited time after disturbance. Forests in Europe recover their pre-disturbance canopy cover within 30 years (Senf and Seidl, 2022), and local recovery can even be considerably faster (Mandl et al., 2024). Consequently, disturbance effects on insect diversity are subject to change over time. For example, a study in Finland focusing on forest fire and clearing showed that open patches initially had the highest species richness, but that this effect diminished over time with resource depletion. After a decade, disturbed sites that were not cleared exhibited greater species richness than cleared ones (Heikkala et al., 2016). Since changes in forest structures in the early successional phase are extremely dynamic, temporal changes in insect communities do not occur linearly and differ between taxonomic groups with different habitat requirements (Gazzea et al., 2025; Wermelinger et al., 2025). We note that the ecological benefits of post-disturbance legacies, such as standing and downed deadwood, diverse decay stages, and regenerating vegetation (including diverse early-seral plant communities), develop only gradually and were not captured in our study.

#### 4.3. Effects on different feeding guilds

A range of different feeding guilds exhibited consistently positive responses in taxonomic diversity to disturbance, with the most

pronounced increase observed in parasitoids, with common species increasing by 45 % in cleared patches. The strong taxonomic response of parasitoids may reflect enhanced host availability and a subsequent increase in trophic complexity. Similar trends have been documented in boreal forests under various management regimes, that found higher parasitoid richness in early successional forests than old-growth forests (Rodríguez et al., 2019) and in expanded host–parasitoid networks following clear-cutting (Eckerter et al., 2022). Another study from the Italian Alps showed increased species richness and abundance in Tachinidae the following five years after windthrows linking it to higher availability of host species (Gazzea et al., 2025). In contrast, phylogenetic diversity revealed divergent patterns across guilds: while parasitoids, non-feeding insects (as adults), and fungivores maintained or increased their diversity after disturbance, detritivores, predators, and ectoparasites declined, an effect that was particularly strong for common species from these guilds.

Phytophagous insects and predators appeared particularly sensitive to changes in canopy openness. Previous research suggests that taxonomic diversity in these groups increases in open-canopy conditions, likely due to improved access to plant resources (Bouget and Duelli, 2004). In our study, cleared patches exhibited greater canopy openness than disturbed ones, which likely explains the more pronounced increase in taxonomic diversity for these guilds on cleared patches. Supporting this notion, (Seibold et al., 2016a; Seibold et al., 2016b) found that sun exposure was strongly beneficial for phytophagous species especially in the absence of deadwood, likely due to a higher cover of herb layer. This proliferation of herbivores may in turn support a higher abundance of predators through increased prey availability (Bouget and Duelli, 2004). However, the benefits appear taxon-specific, as reflected by the mixed responses in predator phylogenetic diversity (Fig. 3). While literature remains limited on such patterns, studies on damselflies (Shelly, 1982), robber flies (Shelly, 1984), and Vespidae (Shure and Phillips, 1991) hint at similarly nuanced responses to canopy density and resource availability.

Fungivores exhibited significant increases in both taxonomic and phylogenetic diversity in cleared compared to undisturbed patches. One possible mechanism is the response of wood-inhabiting fungi, a key food resource for fungivores, which may benefit from cutting dead trees into several pieces during post-disturbance logging. The resultant diversification in deadwood resources can reduce competitive exclusion, which is a known driver of fungal diversity (Juutilainen et al., 2016; Hottola et al., 2009; Heilmann-Clausen and Christensen, 2004). Our results also align with previous findings showing that Collembola thrive in forest gaps and benefit from understory removal (Perry et al., 2018). Non-feeding insects, in contrast, likely responded to increased canopy openness and the associated rise in temperature, rather than changes in resource availability, given their minimal reliance on feeding during adult life stages.

Overall, these patterns underscore the complex biodiversity responses to disturbance, particularly when considering both taxonomic and phylogenetic dimensions of all insect families. While taxonomic diversity increased across most feeding guilds, phylogenetic diversity revealed more nuanced patterns, suggesting that canopy openings selectively benefit specific evolutionary lineages. Notably, phylogenetic diversity gains were largely restricted to rare species, indicating that among common and dominant taxa only a few lineages benefit from the altered conditions post disturbance. Similar patterns were observed by Sire et al. (2022), who reported that climate-induced forest dieback caused pronounced shifts in insect community composition, with the strongest responses also occurring in rare species. Evidence from controlled experiments with artificial gaps further supports this pattern, as Rothacher et al. (2025) found that phylogenetic diversity increased in both gap types, but again only among rare species. Together, these results underscore the importance of considering both abundance and evolutionary history when assessing disturbance effects and points to the need for further research on the drivers of phylogenetic diversity

across functional guilds.

## 5. Conclusions

Our study offers novel insights into the disturbance response of biodiversity in major Central European forest types, considering a wide range of insect species via a standardized approach for assessing both taxonomic and phylogenetic diversity. By incorporating spaceborne data into our analysis, we were able to analyse the detailed effects of changes in canopy cover after natural disturbance and post-disturbance management, and their respective impacts on insect communities. We found that salvage logging extends natural disturbances in size and severity. Shortly after the event (2–4 years), both natural disturbances and subsequent management increased insect diversity, with canopy opening identified as the primary driver of these gains.

Responses to disturbance differed among feeding guilds, with parasitoids, non-feeding insects, and fungivores showing the most pronounced increase in diversity. Our findings suggest that disturbance acts as filter on species composition, promoting richness within certain phylogenetic lineages.

From a management perspective, these results highlight the importance of scale, forest context, and temporal perspective. In managed forests where sanitation felling is often mandatory, additional clearing after small-scale disturbances may not be as detrimental to insect diversity in the short term as commonly assumed. However, this finding should not be misinterpreted as a general argument for clearing after all disturbances. In larger-scale events, canopy openness is already extensive, and further clearing is unlikely to provide ecological benefits. Moreover, the long-term value of allowing natural disturbance legacies to remain, such as deadwood and structural heterogeneity, remains critical for sustaining forest biodiversity, particularly in protected areas.

Looking ahead, future research should focus on studies that capture both disturbance and post-disturbance management effects across an extended time since disturbance. Rather than relying on long-term monitoring alone, carefully applied space-for-time substitution can provide critical insights into long-term ecological trajectories, without having to wait for decades to obtain relevant data. In the face of accelerating environmental change, such timely and integrative approaches are essential for informing effective conservation management strategies.

## CRedit authorship contribution statement

**Mareike Kortmann:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Conceptualization. **Rupert Seidl:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization. **Niklas Jaggy:** Writing – review & editing, Investigation, Data curation. **Patrick Kacic:** Writing – review & editing, Investigation, Data curation. **Jérôme Morinière:** Writing – review & editing, Methodology, Investigation, Data curation. **Jörg Müller:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

## Declaration of competing interest

Authors declare that they have no competing interests.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111647>.

## Data availability

Data and R code are available at Zenodo <https://doi.org/10.5281/zenodo.17775804>.

## References

- Bässler, C., Müller, J., 2010. Importance of natural disturbance for recovery of the rare polypore *Antrodia citrinella* Niemelä & Ryvarden. *Fungal Biol.* 114, 129–133.
- Beaumont, L.J., Pitman, A., Perkins, S., Zimmermann, N.E., Yoccoz, N.G., Thuiller, W., 2011. Impacts of climate change on the world's most exceptional ecoregions. *Proc. Natl. Acad. Sci. USA* 108, 2306–2311.
- Beudert, B., Bässler, C., Thorn, S., Noss, R., Schröder, B., Dieffenbach-Fries, H., Foullois, N., Müller, J., 2015. Bark beetles increase biodiversity while maintaining drinking water quality. *Conserv. Lett.* 8, 272–281.
- Bose, A.K., Gessler, A., Bolte, A., Bottero, A., Buras, A., Cailleret, M., Camarero, J.J., Haeni, M., Hereš, A.-M., Hevia, A., Lévesque, M., Linares, J.C., Martínez-Vilalta, J., Matías, L., Menzel, A., Sánchez-Salguero, R., Saurer, M., Vennetier, M., Ziche, D., Rigling, A., 2020. Growth and resilience responses of scots pine to extreme droughts across Europe depend on predrought growth conditions. *Glob. Chang. Biol.* 26, 4521–4537.
- Bouget, C., Duelli, P., 2004. The effects of windthrow on forest insect communities: a literature review. *Biol. Conserv.* 118, 281–299.
- Chao, A., Henderson, P.A., Chiu, C.-H., Moyes, F., Hu, K.-H., Dornelas, M., Magurran, A.E., 2021. Measuring temporal change in alpha diversity: a framework integrating taxonomic, phylogenetic and functional diversity and the iNEXT.3D standardization. *Methods Ecol. Evol.* 12, 1926–1940.
- Didham, R.K., Basset, Y., Collins, C.M., Leather, S.R., Littlewood, N.A., Menz, M.H.M., Müller, J., Packer, L., Saunders, M.E., Schönrögge, K., Stewart, A.J.A., Yanoviak, S.P., Hassall, C., 2020. Interpreting insect declines: seven challenges and a way forward. *Insect Conserv. Diversity* 13, 103–114.
- Donato, D.C., Campbell, J.L., Franklin, J.F., 2012. Multiple successional pathways and precocity in forest development: can some forests be born complex? *J. Veg. Sci.* 23, 576–584.
- Eckerter, T., Braunisch, V., Pufal, G., Klein, A.M., 2022. Small clear-cuts in managed forests support trap-nesting bees, wasps and their parasitoids. *For. Ecol. Manag.* 509, 120076.
- Felgentreff, E.S., Buchholz, S., Straka, T.M., 2023. From science to society to practice? Public reactions to the insect crisis in Germany. *People and Nature* 5, 660–667.
- Gazol, A., Camarero, J.J., 2022. Compound climate events increase tree drought mortality across European forests. *Sci. Total Environ.* 816, 151604.
- Gazzea, E., Conti, L., Rossi, E., Cerretti, P., Mei, M., Panicia, D., Battisti, A., Marini, L., 2025. High temporal Beta-diversity of pollinators in early successional forests after Windthrow. *Ecol. Evol.* 15, e71571.
- Georgiev, K.B., Bässler, C., Feldhaar, H., Heibl, C., Karasch, P., Müller, J., Perlik, M., Weiss, I., Thorn, S., 2022. Windthrow and salvage logging alter  $\beta$ -diversity of multiple species groups in a mountain spruce forest. *For. Ecol. Manag.* 520, 120401.
- Haase, P., Bowler, D.E., Baker, N.J., Bonada, N., Domisch, S., García Marquez, J.R., Heino, J., Hering, D., Jähnig, S.C., Schmidt-Kloiber, A., Stubbington, R., Altermatt, F., Álvarez-Cabria, M., Amatulli, J., Angeler, D.G., Archambaud-Suard, G., Jorrín, I.A., Aspin, T., Azpiroz, I., Bañares, I., Ortiz, J.B., Bodin, C.L., Bonacina, L., Bottarin, R., Cañedo-Argüelles, M., Csabai, Z., Detry, T., Eyto, E. de, Dohet, A., Dörflinger, G., Drohan, E., Eikland, K.A., England, J., Eriksen, T.E., Evtimova, V., Feio, M.J., Ferréol, M., Flourey, M., Forcellini, M., Forio, M.A.E., Fornaroli, R., Friberg, N., Fruget, J.-F., Georgieva, G., Goethals, P., Graça, M.A.S., Graf, W., House, A., Huttunen, K.-L., Jensen, T.C., Johnson, R.K., Jones, J.I., Kiesel, J., Kuglerová, L., Larrañaga, A., Leitner, P., L'Hoste, L., Lizée, M.-H., Lorenz, A.W., Maire, A., Arnaiz, J.A.M., McKie, B.G., Millán, A., Monteith, D., Muotka, T., Murphy, J.F., Ozolins, D., Paavola, R., Paril, P., Peñas, F.J., Pilotto, F., Polásek, M., Rasmussen, J.J., Rubio, M., Sánchez-Fernández, D., Sandin, L., Schäfer, R.B., Scotti, A., Shen, L.Q., Skuja, A., Stoll, S., Straka, M., Timm, H., Tyufekchieva, V.G., Tziortzis, I., Uzunov, Y., van der Lee, G.H., Vannevel, R., Varadinova, E., Várbró, G., Velle, G., Verdonschot, P.F.M., Verdonschot, R.C.M., Vidinova, Y., Wiberg-Larsen, P., Welti, E.A.R., 2023. The recovery of European freshwater biodiversity has come to a halt. *Nature* 620, 582–588.
- Haavik, L.J., Billings, S.A., Guldin, J.M., Stephen, F.M., 2015. Emergent insects, pathogens and drought shape changing patterns in oak decline in North America and Europe. *For. Ecol. Manag.* 354, 190–205.
- Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., Kroon, H. de, 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* 12, e0185809.
- Harvey, J.A., Tougeron, K., Gols, R., Heinen, R., Abarca, M., Abram, P.K., Basset, Y., Berg, M., Boggs, C., Brodeur, J., Cardoso, P., Boer, J.G. de, Snoo, G.R. de, Deacon, C., Dell, J.E., Desneux, N., Dillon, M.E., Duffy, G.A., Dyer, L.A., Ellers, J., Espíndola, A., Fordyce, J., Forister, M.L., Fukushima, C., Gage, M.J.G., García-Robledo, C., Gely, C., Gobbi, M., Hallmann, C., Hance, T., Harte, J., Hochkirch, A., Hof, C., Hoffmann, A.



- A., Kingsolver, J.G., Lamarre, G.P.A., Laurance, W.F., Lavandero, B., Leather, S.R., Lehmann, P., Le Lann, C., López-Urbe, M.M., Ma, C.-S., Ma, G., Moiroux, J., Monticelli, L., Nice, C., Ode, P.J., Pincebourde, S., Ripple, W.J., Rowe, M., Samways, M.J., Sentis, A., Shah, A.A., Stork, N., Terblanche, J.S., Thakur, M.P., Thomas, M.B., Tylianakis, J.M., van Baaren, J., van de Pol, M., van der Putten, W.H., van Dyck, H., Verberk, W.C.E.P., Wagner, D.L., Weisser, W.W., Wetzal, W.C., Woods, H.A., Wyckhuys, K.A.G., Chown, S.L., 2023. Scientists' warning on climate change and insects. *Ecol. Monogr.* 93.
- Hausmann, A., Segerer, A.H., Greifenstein, T., Knubben, J., Morinière, J., Bozicevic, V., Doczkal, D., Günter, A., Ulrich, W., Habel, J.C., 2020. Toward a standardized quantitative and qualitative insect monitoring scheme. *Ecol. Evol.* 10, 4009–4020.
- Heikkala, O., Martikainen, P., Kouki, J., 2016. Decadal effects of emulating natural disturbances in forest management on saproxylic beetle assemblages. *Biol. Conserv.* 194, 39–47.
- Heilmann-Clausen, J., Christensen, M., 2004. Does size matter? *For. Ecol. Manag.* 201, 105–117.
- Hottola, J., Ovaskainen, O., Hanski, I., 2009. A unified measure of the number, volume and diversity of dead trees and the response of fungal communities. *J. Ecol.* 97, 1320–1328.
- Hyvärinen, E., Kouki, J., Martikainen, P., 2006. Fire and green-tree retention in conservation of red-listed and rare deadwood-dependent beetles in Finnish boreal forests. *Conservation biology: the journal of the Society for Conservation Biology* 20, 1711–1719.
- Jochum, M., Fischer, M., Isbell, F., Roscher, C., van der Plas, F., Boch, S., Boenisch, G., Buchmann, N., Catford, J.A., Cavender-Bares, J., Ebeling, A., Eisenhauer, N., Gleixner, G., Hölzel, N., Kattge, J., Klaus, V.H., Kleinebecker, T., Lange, M., Le Provost, G., Meyer, S.T., Molina-Venegas, R., Mommer, L., Oelmann, Y., Penone, C., Prati, D., Reich, P.B., Rindisbacher, A., Schäfer, D., Scheu, S., Schmid, B., Tilman, D., Tschantke, T., Vogel, A., Wagg, C., Weigelt, A., Weisser, W.W., Wilcke, W., Manning, P., 2020. The results of biodiversity-ecosystem functioning experiments are realistic. *Nature ecology & evolution* 4, 1485–1494.
- Juutilainen, K., Mönkkönen, M., Kotiranta, H., Halme, P., 2016. The role of novel forest ecosystems in the conservation of wood-inhabiting fungi in boreal broadleaved forests. *Ecol. Evol.* 6, 6943–6954.
- Kacic, P., Thonfeld, F., Gessner, U., Kuenzer, C., 2023. Forest structure characterization in Germany: novel products and analysis based on GEDI, Sentinel-1 and Sentinel-2 data. *Remote Sens.* 15, 1969.
- Kortmann, M., Buse, J., Hilszczański, J., Jaworski, T., Müller, J., Thorn, S., Roth, N., 2024. Bark-beetle disturbance severity only moderately alters forest affinity of arthropod communities. *Insect Conserv. Diversity* 17, 579–588.
- Kortmann, M., Chao, A., Chiu, C.-H., Heibl, C., Mitesser, O., Morinière, J., Bozicevic, V., Hothorn, T., Rothacher, J., Englmeier, J., Ewald, J., Fricke, U., Ganuza, C., Haensel, M., Moning, C., Redlich, S., Rojas-Botero, S., Tobisch, C., Uhler, J., Zhang, J., Steffan-Dewenter, I., Müller, J., 2025. A shortcut to sample coverage standardization in metabarcoding data provides new insights into land-use effects on insect diversity. *Proc. Biol. Sci.* 292, 20242927.
- Kortmann, M., Heurich, M., Latifi, H., Rösner, S., Seidl, R., Müller, J., Thorn, S., 2018. Forest structure following natural disturbances and early succession provides habitat for two avian flagship species, capercaillie (*Tetrao urogallus*) and hazel grouse (*Tetrastes bonasia*). *Biol. Conserv.* 226, 81–91.
- Kortmann, M., Roth, N., Buse, J., Hilszczański, J., Jaworski, T., Morinière, J., Seidl, R., Thorn, S., Müller, J.C., 2022. Arthropod dark taxa provide new insights into diversity responses to bark beetle infestations. *Ecological applications: a publication of the Ecological Society of America* 32, e2516.
- Krüger, K., Senf, C., Hagge, J., Seidl, R., 2025. Setting aside areas for conservation does not increase disturbances in temperate forests. *J. Appl. Ecol.* 62, 1271–1281.
- Leroy, B.M.L., Seibold, S., Morinière, J., Bozicevic, V., Jaworek, J., Roth, N., Vogel, S., Zytynska, S., Petercord, R., Eichel, P., Weisser, W.W., 2022. Metabarcoding of canopy arthropods reveals negative impacts of forestry insecticides on community structure across multiple taxa. *J. Appl. Ecol.* 59, 997–1012.
- Leverkus, A.B., Buma, B., Wagenbrenner, J., Burton, P.J., Lingua, E., Marzano, R., Thorn, S., 2021. Tamm review: does salvage logging mitigate subsequent forest disturbances? *For. Ecol. Manag.* 481, 118721.
- Leverkus, A.B., Lindenmayer, D.B., Thorn, S., Gustafsson, L., 2018. Salvage logging in the world's forests: interactions between natural disturbance and logging need recognition. *Glob. Ecol. Biogeogr.* 27, 1140–1154.
- Lindenmayer, D., Thorn, S., Banks, S., 2017. Please do not disturb ecosystems further. *Nature ecology & evolution* 1, 31.
- Lindenmayer, D.B., Noss, R.F., 2006. Salvage logging, ecosystem processes, and biodiversity conservation. *Conservation biology: the journal of the Society for Conservation Biology* 20, 949–958.
- Liu, M., Clarke, L.J., Baker, S.C., Jordan, G.J., Burridge, C.P., 2020. A practical guide to DNA metabarcoding for entomological ecologists. *Ecological Entomology* 45, 373–385.
- Mandl, L., Viana-Soto, A., Seidl, R., Strith, A., Senf, C., 2024. Unmixing-based forest recovery indicators for predicting long-term recovery success. *Remote Sens. Environ.* 308, 114194.
- Mayer, M., Rosinger, C., Gorfer, M., Berger, H., Deltedesco, E., Bässler, C., Müller, J., Seifert, L., Rewald, B., Godbold, D.L., 2022. Surviving trees and deadwood moderate changes in soil fungal communities and associated functioning after natural forest disturbance and salvage logging. *Soil Biol. Biochem.* 166, 108558.
- Morinière, J., Balke, M., Doczkal, D., Geiger, M.F., Hardulak, L.A., Haszprunar, G., Hausmann, A., Hendrich, L., Regalado, L., Rulik, B., Schmidt, S., Wägele, J.-W., Hebert, P.D.N., 2019. A DNA barcode library for 5,200 German flies and midges (Insecta: Diptera) and its implications for metabarcoding-based biomonitoring. *Mol. Ecol. Resour.* 19, 900–928.
- Müller, J., Bußler, H., Goßner, M., Rettelbach, T., Duelli, P., 2008. The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species. *Biodivers. Conserv.* 17, 2979–3001.
- Müller, J., Büttler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *Eur J Forest Res* 129, 981–992.
- Müller, J., Hothorn, T., Yuan, Y., Seibold, S., Mitesser, O., Rothacher, J., Freund, J., Wild, C., Wolz, M., Menzel, A., 2024. Weather explains the decline and rise of insect biomass over 34 years. *Nature* 628, 349–354.
- Müller, J., Noss, R.F., Thorn, S., Bässler, C., Leverkus, A.B., Lindenmayer, D., 2019. Increasing disturbance demands new policies to conserve intact forest. *Conserv. Lett.* 12.
- Perry, K.I., Wallin, K.F., Wenzel, J.W., Herms, D.A., 2018. Forest disturbance and arthropods: small-scale canopy gaps drive invertebrate community structure and composition. *Ecosphere* 9.
- Potterf, M., Fröhbrodt, T., Thom, D., Lemme, H., Hahn, A., Seidl, R., 2025. Hotter drought increases population levels and accelerates phenology of the European spruce bark beetle *Ips typographus*. *For. Ecol. Manag.* 585, 122615.
- Priewasser, K., Brang, P., Bachofen, H., Bugmann, H., Wohlgemuth, T., 2013. Impacts of salvage-logging on the status of deadwood after windthrow in Swiss forests. *Eur J Forest Res* 132, 231–240.
- Procházka, J., Černý, L., Čížková, P., Kletečka, Z., Dvořák, V., 2020. Rediscovery of the Rare Saproxylic Beetle *Peltis Grossa* (Linnaeus, 1758). *Trogossitidae*, in the Šumava National Park and its occurrence in surrounding area. *Silva Gabreta, Coleoptera*, pp. 33–49.
- R Core Team, 2023. R: A Language and Environment for Statistical Computing.
- Rainford, J.L., Mayhew, P.J., 2015. Diet evolution and clade richness in Hexapoda: a phylogenetic study of higher taxa. *Am. Nat.* 186, 777–791.
- Rodriguez, A., Pohjoismäki, J.L., Kouki, J., 2019. Diversity of forest management promotes parasitoid functional diversity in boreal forests. *Biol. Conserv.* 238, 108205.
- Rothacher, J., Seidl, R., Thom, D., Kortmann, M., Chao, A., Chiu, C.-H., Heibl, C., Hothorn, T., Mitesser, O., Mori, A.S., Morinière, J., Pierick, K., Wild, C., Wild, N., Müller, J., 2025. The impact of tree mortality and post-disturbance management on insect diversity in temperate forests: insights from a replicated experiment. *J. Appl. Ecol.* 62, 1878–1888.
- Seibold, S., Bässler, C., Baldrian, P., Reinhard, L., Thorn, S., Ulyshen, M.D., Weiß, I., Müller, J., 2016a. Dead-wood addition promotes non-saproxylic epigeal arthropods but effects are mediated by canopy openness. *Biol. Conserv.* 204, 181–188.
- Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M.D., Müller, J., 2016b. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *J. Appl. Ecol.* 53, 934–943.
- Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarli, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Naus, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574, 671–674.
- Seidl, R., Potterf, M., Müller, J., Turner, M.G., Rammer, W., 2024. Patterns of early post-disturbance reorganization in central European forests. *Proc. Biol. Sci.* 291, 20240625.
- Senf, C., Mori, A.S., Müller, J., Seidl, R., 2020. The response of canopy height diversity to natural disturbances in two temperate forest landscapes. *Landsc. Ecol.* 35, 2101–2112.
- Senf, C., Seidl, R., 2021. Mapping the forest disturbance regimes of Europe. *Nat. Sustainability* 4, 63–70.
- Senf, C., Seidl, R., 2022. Post-disturbance canopy recovery and the resilience of Europe's forests. *Glob. Ecol. Biogeogr.* 31, 25–36.
- Shelly, T.E., 1982. Comparative foraging behavior of light- versus shade-seeking adult damselflies in a lowland Neotropical Forest (Odonata: Zygoptera). *Physiol. Zool.* 55, 335–343.
- Shelly, T.E., 1984. Comparative foraging behavior of Neotropical robber flies (Diptera: Asilidae). *Oecologia* 62, 188–195.
- Shure, D.J., Phillips, D.L., 1991. Patch size of forest openings and arthropod populations. *Oecologia* 86, 325–334.
- Sire, L., Yáñez, P.S., Wang, C., Bézier, A., Courtial, B., Cours, J., Fontaneto, D., Larrieu, L., Bouget, C., Thorn, S., Müller, J., Yu, D.W., Monaghan, M.T., Herniou, E. A., Lopez-Vaamonde, C., 2022. Climate-induced forest dieback drives compositional changes in insect communities that are more pronounced for rare species. *Communications biology* 5, 57.
- Sommerfeld, A., Senf, C., Buma, B., D'Amato, A.W., Després, T., Díaz-Hormazábal, I., Fraver, S., Frelich, L.E., Gutiérrez, Á.G., Hart, S.J., Harvey, B.J., He, H.S., Hlásny, T., Holz, A., Kitzberger, T., Kulakowski, D., Lindenmayer, D., Mori, A.S., Müller, J., Paritsis, J., Perry, G.L.W., Stephens, S.L., Svoboda, M., Turner, M.G., Veblen, T.T., Seidl, R., 2018. Patterns and drivers of recent disturbances across the temperate forest biome. *Nat. Commun.* 9, 4355.
- Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P., Dosio, A., 2018. Will drought events become more frequent and severe in Europe? *Int. J. Climatol.* 38, 1718–1736.
- Svoboda, M., Fraver, S., Janda, P., Bače, R., Zenáhlíková, J., 2010. Natural development and regeneration of a central European montane spruce forest. *For. Ecol. Manag.* 260, 707–714.
- Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J., 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Front. Ecol. Environ.* 9, 117–125.
- Thom, D., Buras, A., Heym, M., Klemmt, H.-J., Wauer, A., 2023. Varying growth response of Central European tree species to the extraordinary drought period of 2018–2020. *Agric. For. Meteorol.* 338, 109506.

- Thom, D., Seidl, R., 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biol. Rev. Camb. Philos. Soc.* 91, 760–781.
- Thom, D., Sommerfeld, A., Seibald, J., Hagge, J., Müller, J., Seidl, R., 2020. Effects of disturbance patterns and deadwood on the microclimate in European beech forests. *Agric. For. Meteorol.* 291.
- Thorn, S., Bässler, C., Bernhardt-Römermann, M., Cadotte, M., Heibl, C., Schäfer, H., Seibold, S., Müller, J., 2016. Changes in the dominant assembly mechanism drive species loss caused by declining resources. *Ecol. Lett.* 19, 163–170.
- Thorn, S., Bässler, C., Brandl, R., Burton, P.J., Cahall, R., Campbell, J.L., Castro, J., Choi, C.-Y., Cobb, T., Donato, D.C., Durska, E., Fontaine, J.B., Gauthier, S., Hebert, C., Hothorn, T., Hutto, R.L., Lee, E.-J., Leverkus, A.B., Lindenmayer, D.B., Obrist, M.K., Rost, J., Seibold, S., Seidl, R., Thom, D., Waldron, K., Wermelinger, B., Winter, M.-B., Zmihorski, M., Müller, J., 2018. Impacts of salvage logging on biodiversity: a meta-analysis. *J. Appl. Ecol.* 55, 279–289.
- Thorn, S., Bässler, C., Gottschalk, T., Hothorn, T., Bussler, H., Raffa, K., Müller, J., 2014. New insights into the consequences of post-windthrow salvage logging revealed by functional structure of saproxylic beetles assemblages. *PLoS One* 9, e101757.
- Thorn, S., Chao, A., Georgiev, K.B., Müller, J., Bässler, C., Campbell, J.L., Castro, J., Chen, Y.-H., Choi, C.-Y., Cobb, T.P., Donato, D.C., Durska, E., Macdonald, E., Feldhaar, H., Fontaine, J.B., Fornwalt, P.J., Hernández, R.M.H., Hutto, R.L., Koivula, M., Lee, E.-J., Lindenmayer, D., Mikusiński, G., Obrist, M.K., Perlik, M., Rost, J., Waldron, K., Wermelinger, B., Weiß, I., Zmihorski, M., Leverkus, A.B., 2020. Estimating retention benchmarks for salvage logging to protect biodiversity. *Nat. Commun.* 11, 4762.
- Uhler, J., Redlich, S., Zhang, J., Hothorn, T., Tobisch, C., Ewald, J., Thorn, S., Seibold, S., Mitesser, O., Morinière, J., Bozicevic, V., Benjamin, C.S., Englmeier, J., Fricke, U., Ganuza, C., Haensel, M., Riebl, R., Rojas-Botero, S., Rummler, T., Uphus, L., Schmidt, S., Steffan-Dewenter, I., Müller, J., 2021. Relationship of insect biomass and richness with land use along a climate gradient. *Nat. Commun.* 12, 5946.
- van Klink, R., Bowler, D.E., Gongalsky, K.B., Shen, M., Swengel, S.R., Chase, J.M., 2024. Disproportionate declines of formerly abundant species underlie insect loss. *Nature* 628, 359–364.
- van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A., Chase, J.M., 2020. Meta-Analysis Reveals Declines in Terrestrial but Increases in Freshwater Insect Abundances. *Science*, vol. 368. New York, N.Y., pp. 417–420.
- Viljur, M.-L., Abella, S.R., Adámek, M., Alencar, J.B.R., Barber, N.A., Beudert, B., Burkle, L.A., Cagnolo, L., Campos, B.R., Chao, A., Chergui, B., Choi, C.-Y., Cleary, D. F.R., Davis, T.S., Dechnik-Vázquez, Y.A., Downing, W.M., Fuentes-Ramirez, A., Gandhi, K.J.K., Gehring, C., Georgiev, K.B., Gimbutas, M., Gongalsky, K.B., Gorbunova, A.Y., Greenberg, C.H., Hylander, K., Jules, E.S., Korobushkin, D.I., Köster, K., Kurth, V., Lanham, J.D., Lazarina, M., Leverkus, A.B., Lindenmayer, D., Marra, D.M., Martín-Pinto, P., Meave, J.A., Moretti, M., Nam, H.-Y., Obrist, M.K., Petanidou, T., Pons, P., Potts, S.G., Rapoport, I.B., Rhoades, P.R., Richter, C., Saifutdinov, R.A., Sanders, N.J., Santos, X., Steel, Z., Tavella, J., Wendenburg, C., Wermelinger, B., Zaitsev, A.S., Thorn, S., 2022. The effect of natural disturbances on forest biodiversity: an ecological synthesis. *Biol. Rev. Camb. Philos. Soc.* 97, 1930–1947.
- Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R., Stopak, D., 2021. Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences of the United States of America* 118.
- Wang, C., Yang, C., Wang, X., Wu, C., Larrieu, L., Lopez-Vaamonde, C., Wen, Q., Yu, D. W., 2021. The ecological impact of pest-induced tree dieback on insect biodiversity in Yunnan pine plantations. *China. Forest Ecology and Management* 491, 119173.
- Wermelinger, B., Obrist, M.K., Duelli, P., Schneider Mathis, D., Gossner, M.M., 2025. Two decades of arthropod biodiversity after windthrow show different dynamics of functional groups. *J. Appl. Ecol.* 62, 371–387.
- Winter, M.-B., Bässler, C., Bernhardt-Römermann, M., Krah, F.-S., Schaefer, H., Seibold, S., Müller, J., 2017. On the structural and species diversity effects of bark beetle disturbance in forests during initial and advanced early-seral stages at different scales. *Eur J Forest Res* 136, 357–373.
- Zehetgruber, B., Kobler, J., Dirnböck, T., Jandl, R., Seidl, R., Schindlbacher, A., 2017. Intensive ground vegetation growth mitigates the carbon loss after forest disturbance. *Plant Soil* 420, 239–252.