# Insect abundance in managed forests benefits from multi-layered vegetation

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## Abstract

Retention forestry intends to promote biodiversity by retaining deadwood and tree-related microhabitats. Simultaneously, production forests undergo major structural changes by conversion into near-natural forests. As insect biomass is declining, it is important to understand how insect communities respond to management-related changes in forest structure. While some structural elements, such as deadwood, are studied extensively, three-dimensional forest structure is often neglected. Terrestrial laser scanning offers new approaches to quantify three-dimensional structure but their suitability has not been evaluated with field-based insect surveys.

To test how insect communities respond to forest structure, we examined insects from window traps from 122 sites in the Black Forest. For total insect abundance and for the seven most abundant taxa, we related deadwood, microhabitats, various conventional stand properties and novel remote sensing-based indices for vegetation structure to total and taxon-specific abundances. Additionally, we assessed the influences of these structural elements on community composition.

Total insect abundance and abundances of most taxa were positively related to multi-layered stands, as derived from remote sensing techniques. Furthermore, each taxon responded to some additional forest structural elements. Higher tree diameter, canopy gap fraction and share of deciduous trees increase abundances of the predominantly herbivorous taxa Heteroptera, Sternorrhyncha and Auchenorrhyncha. Community composition was influenced by mean tree diameter and share of deciduous trees. Neither tree-related microhabitats nor deadwood diversity had a detectable effect on insect abundance.

We conclude that more elements of forest structure than previously acknowledged are related to insect populations. In particular, multi-layered forest stands have higher insect abundances in the midstorey. The current conversion in continuous-cover forestry in Europe from even-aged, often conifer-dominated forests to uneven-aged, mixed species stands can therefore increase the abundance of a wide range of insect taxa and is possibly one strategy to halt insect decline in forests.

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# Introduction

While strictly protected reserves are valuable for biodiversity conservation, they are not sufficient to preserve biodiversity in the wider landscape (Bengtsson et al., 2003). For instance, abundance and biomass of insects have decreased significantly in the past decades in open land and forests (Seibold et al., 2019). Insects play important roles in ecosystems, not least as food resources for vertebrates. Thus, conservation strategies need to be integrated into land use practices (Gustafsson et al., 2012) but this can only be achieved efficiently if patterns and drivers of species diversity and abundance are understood (Schuldt et al., 2018).

Species richness generally increases with habitat area (*sensu* MacArthur & Wilson, 1967). Following the habitat-heterogeneity hypothesis, larger habitat area should allow the co-existence of more species as more niches become available (MacArthur & Wilson, 1967; Tews et al., 2004). Thus, guidelines to increase biodiversity in managed forests recommend increasing structural heterogeneity to provide more (diverse) niches (Gustafsson et al., 2012). In addition to species richness, abundance is another important dimension of biodiversity (Lyashevska & Farnsworth, 2012). The more-individuals hypothesis (Srivastava & Lawton, 1998), for example, connects greater population densities with higher species diversity via reduced extinction risks (Yee & Juliano, 2007; but see Storch et al., 2018).

For many insects, vegetation structure may determine habitat heterogeneity, and their populations are influenced by altered structure, e.g. due to management (Perner & Malt, 2003). Production forests are structurally distinct from old-growth forests in terms of tree species composition, age class distribution, vertical vegetation and canopy structure (Hale et al., 1999). Additionally, structural elements that are typical for old-growth forests such as high quantities of deadwood and of tree-related microhabitats (TreMs, e.g. cavities) are missing in production forests (Hale et al., 1999; Larrieu et al., 2018). Consequently, many forest-dwelling species that depend on these structural elements as feeding or reproduction habitats (Grove, 2002; Müller et al., 2014) have been declining (Seibold et al., 2015b).

Retention forestry aims to increase habitat heterogeneity by retaining structural elements for biodiversity beyond harvesting cycles to integrate conservation goals into forest management (Bauhus et al., 2009). Depending on the prevailing management system, retention forestry is implemented differently. In clear-cutting systems typical for most boreal forests, small areas covered with trees are retained while the retention of deadwood and habitat trees (i.e. trees with TreMs) is more common in continuous-cover forestry in temperate forests of Central Europe (Gustafsson et al., 2020). Additionally, continuous-cover forests currently undergo major structural conversions with regard to tree species composition, age structure and vegetation layering (Bauhus et al., 2013).

While the effects of forest structure on biodiversity, especially with regard to retention, are relatively well studied for saproxylic (i.e. deadwood-dependent) insects (e.g. Fedrowitz et al., 2014; (Seibold et al., 2015a)), much less is known how insects in general, including also non-saproxylic taxa, are influenced by management-related changes in forest structure. Although there is a number of studies from boreal forests (e.g. Deans et al., 2005; Hyvärinen et al., 2009; Jokela et al., 2018), they cannot be transferred directly to temperate forests as the prevailing management regimes differ. We are aware of only few studies in European temperate, continuous-cover forests that comprehensively tested effects of various elements of forest structure other than retention elements or broad management systems on multiple insect taxa simultaneously (Penone et al., 2019; Schall et al., 2018). For example, Schall et al. (2018) compared forest biodiversity between different management systems, but without testing the various structural elements separately.

Data on forest structure is crucial for understanding forest biodiversity (Gustafsson et al., 2012) and remote sensing techniques may provide objective and time-efficient measures for three-dimensional forest stucture. Airborne laser scanning, for example, has been successfully used to explain the relationship between canopy structure and arthropod diversity (Müller et al., 2018). In contrast, structural indices from ground-based terrestrial laser scanning (TLS) describe the vegetation structure below the canopy (e.g. Ehrbrecht et al., 2017, 2016) but, to our knowledge, have never been used in combination with field-based insect surveys.

Thus, our study had two aims: (1) Investigating the relationships between management-related structural elements and major insect taxa in a temperate, continuous-cover forest; (2) Exploring whether structural indices derived from TLS are measuring properties that are relevant for insects. For this purpose, we sampled flying insects in the understorey of a continuous-cover forest in Central Europe that differed in forest structure with regard to deadwood and TreMs (i.e. targeted by retention to increase habitat heterogeneity) and in general stand characteristics. The latter included tree species composition, tree size, canopy cover and three-dimensional vegetation structure that may serve as proxies for resource availability and habitat quality. We related these structural elements to total insect abundance and to the most abundant insect taxa separately. Additionally, we assessed whether the same structural elements influence insect community composition.

# Materials and methods

## Study area

The study was conducted on the sites of the 'Conservation of forest biodiversity' project (ConFoBi, Storch et al., 2020). The sites (100 × 100 m each), of which 122 were included in this study, are located in the southern Black Forest, a low mountain range in southwestern Germany, at elevations between 500 and 1300 m a.s.l. To cover a gradient of structural diversity, sites

**Table 1.** Environmental variables characterising the study sites. For details on measurements, see Materials and methods. TreM: tree-related microhabitats.

| Environmental variables | Unit | Range | | | Median | Mean ± SD | | | Level of measurement |
|---|---|---|---|---|---|---|---|---|---|
| Share of deciduous trees | basal area% | 0 | – | 96 | 10 | 20 | ± | 23 | Site level |
| Mean tree diameter at breast height (DBH) | [m] | 0.1 | – | 0.5 | 0.29 | 0.30 | ± | 0.08 | Site level |
| Canopy gap fraction | % | 0 | – | 41 | 6 | 10 | ± | 11 | Site level |
| Deadwood diversity index | – | 0 | – | 31 | 13 | 14 | ± | 5 | Site level |
| TreM richness | – | 4 | – | 29 | 11 | 12 | ± | 6 | Site level |
| Understory complexity index | – | 1.9 | – | 4.7 | 3.5 | 3.4 | ± | 0.5 | Trap level |
| Stand structural complexity index | – | 1.2 | – | 2.6 | 1.8 | 1.8 | ± | 0.2 | Trap level |
| Effective number of layers (ENL) | – | 4.4 | – | 33.7 | 19.2 | 18.8 | ± | 6.3 | Trap level |
| Mean distance between trap and nearest vegetation | [m] | 2.5 | – | 11.5 | 6.2 | 6.5 | ± | 1.7 | Trap level |
| Standard deviation of distance between trap and nearest vegetation | [m] | 1.3 | – | 4.6 | 3.4 | 3.3 | ± | 0.6 | Trap level |
| Duration of trap exposure | Days | 95 | – | 119 | 109 | 108 | ± | 6 | Site level |

were selected by the number of standing dead trees (i.e. snags) per hectare. All sites are in state-owned forest stands that are managed as continuous-cover forests employing close-to-nature forest management with the following characteristics: the use of site-adapted tree species of the natural forest vegetation; avoidance of large canopy openings such as clear-cuts; the promotion of mixed and structurally diverse forests; the employment of natural processes such as natural regeneration, self-thinning and self-pruning; a silvicultural focus on individual trees rather than stands (Bauhus et al., 2013; Brang et al., 2014). The main management goal is high-quality timber while simultaneously considering other services such as biodiversity or recreation. The dominating tree species are *Picea abies* (L.) H.KARST, *Abies alba* MILL. and *Fagus sylvatica* L. Further details on the study sites are given in Storch et al. (2020).

## Insect sampling

In 2017, we sampled insects continuously from mid-April to mid-August with two modified window traps per site (100 m distance between traps) that were hanging 1.50 m above ground as described in Knuff et al., (2019). We retrieved catches every four weeks, resulting in a total of five sampling periods. Arthropods were stored in 75% ethanol and sorted to order level (with Hemiptera being further separated into Auchenorrhyncha, Sternorrhyncha and Heteroptera). Larvae and non-flying taxa such as spiders were excluded from the dataset. Window traps are activity traps, meaning that numbers of captured individuals do not only depend on true abundance but also on activity (Taylor, 1963). Thus, the abundance measure in our study is activity abundance to which we refer as abundance for simplicity.

## Environmental variables

We assessed structural elements related to forest management to test their relationships with insect abundance:

percentage share of deciduous trees (based on basal area), mean tree diameter at breast height (DBH), canopy gap fraction, an index of deadwood diversity, TreM richness, and remotely-sensed variables of vegetation structure (Table 1).

Share of deciduous trees on the basal area and mean DBH were assessed during full site inventories (all trees above 7 cm DBH) conducted between 2017 and 2018. Basal area was calculated as $BA = pi * (DBH/2)^2$. Canopy gap fraction is the fraction of the area covered by vegetation lower than 3 m, based on normalized surface models from unmanned aerial vehicle image flights. The surface model contains maximum vegetation height for each raster cell. Raster values above 3 m were reclassified with 1, meaning that the area of the raster cell is covered by canopy. Raster values below 3 m were reclassified with 0 (canopy gap). The mean of all raster values is the area covered by vegetation higher than 3 m (canopy cover), its inverse is equivalent to the canopy gap fraction (see Frey et al., 2018 for details). We calculated a deadwood diversity index following Siitonen (2001). Its value is the number of unique deadwood types in terms of tree species, quality, decay class and diameter present at each site, for details see Appendix A. TreM richness is the number of TreM types as classified in Larrieu et al. (2018) which was recorded for the 15 tree individuals per site with the largest crown diameters (see Asbeck et al., 2019 for details).

In addition to these variables measured for the whole site, we included variables of three-dimensional vegetation structure derived from terrestrial laser scanning at the location of each trap because surrounding vegetation differed between traps within the same site. One scan per trap was recorded with a FARO Focus 3D scanner (Faro Technologies Inc., Lake Mary, Florida) that was placed at 1.3 m height at the location of the trap after trap removal. The TLS system records the geometric 3D environment in a detailed point cloud model from which the indices to describe the distribution of the plant material in the forest were computed. This novel approach provides comparable and holistic descriptors of vegetation structure, which neither rely on human
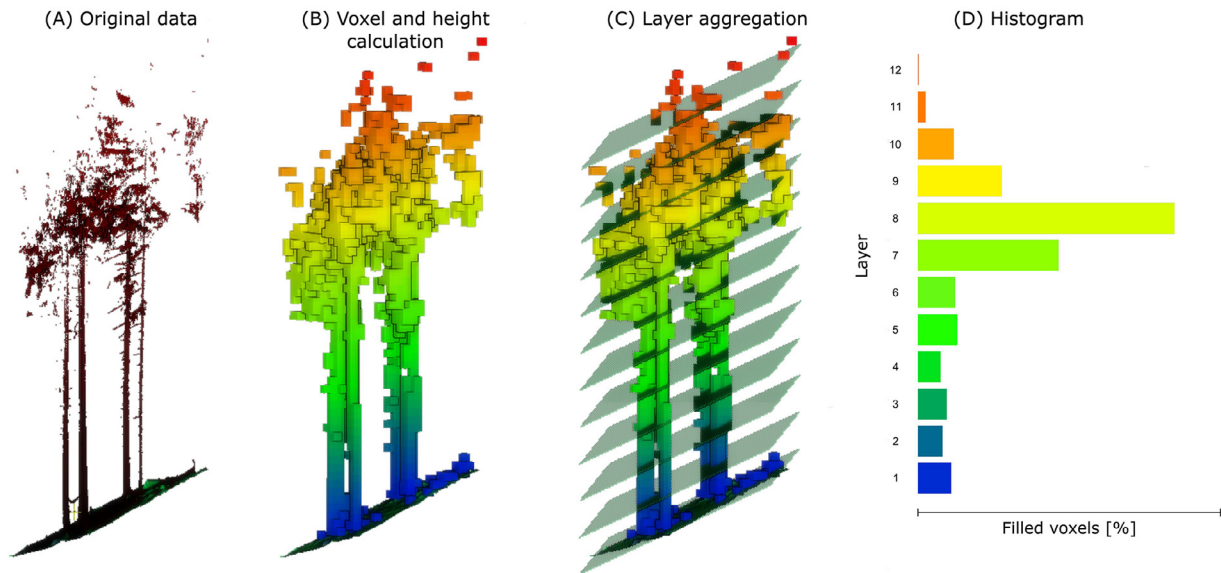
**Fig. 1.** Conceptual illustration of the ENL algorithm (Ehbrecht et al., 2016). (A) Original point cloud from a terrestrial laser scan. (B) Representation of the same data in voxel space. (C) Assignment of the voxels to 1 m thick layers. (D) Final histogram of space filling.

estimation nor on conventional forestry parameters, which often ignore plants other than trees. We calculated the effective number of layers (ENL, Ehbrecht et al., 2016), stand structural (Ehbrecht et al., 2017) and understorey complexity (Willim et al., 2019) and the mean distance and its standard deviation between a trap and the nearest vegetation in any direction (Table 1). As described in the analyses below, ENL was most strongly related to insect abundances, thus we describe the index here. For a description of all other indices, see Appendix B.

The ENL is an index for vertical vegetation layering (Ehbrecht et al., 2016) and similar to the foliage height diversity index (MacArthur & MacArthur, 1961) but without being subject to observer-bias (Fig. 1). Higher values indicate vertically more evenly layered vegetation components (corresponding to multi-layered stands). The ENL algorithm (Fig. 1) considers the 3D space in voxels with 0.1 m edge length for the entire area covered by the scan and checks which of these voxels contain at least one point from the laser scan. These are marked as filled. Then the ratio between filled and available voxels is summarized in 1 m thick layers. This results in a histogram of the space filled with plant material in the layers (Fig. 1). The diversity between the layers is calculated using the inverse Simpson index, which gives the final index value.

## Statistical analysis

We related the environmental variables to insect abundances, both to total insects and separately to the most abundant taxa (Table 2), with generalized linear mixed-effects models (GLMM) using negative-binomial error distribution to account for overdispersion (lme4 package, Bates et al., 2015). Prior to analyses, samples from mid-April to mid-August were pooled per trap. Some traps and sites were excluded from analysis because of missing data points in the environmental variables resulting in a dataset of 238 traps from 122 sites.

**Table 2.** Response variables (on trap level) used for the GLMMs. Total insects include adults of all flying taxa (see Appendix D: Table 2 for all taxa).

| Abundance of | Range | Median | Mean ± SD | Sum |
|---|---|---|---|---|
| Total insects | 200 – 3618 | 766 | 838 ± 460 | 199,490 |
| Auchenorrhyncha | 0 – 47 | 9 | 11 ± 9 | 2696 |
| Coleoptera | 39 – 1083 | 169 | 198 ± 131 | 47,030 |
| Diptera | 37 – 2779 | 266 | 351 ± 336 | 83,513 |
| Heteroptera | 0 – 63 | 7 | 10 ± 9 | 2351 |
| Hymenoptera | 12 – 530 | 64 | 80 ± 66 | 19,056 |
| Lepidoptera | 0 – 36 | 8 | 10 ± 7 | 2294 |
| Sternorrhyncha | 1 – 852 | 86 | 118 ± 118 | 28,181 |

We tested for collinearity between all environmental variables (Table 1) which was assumed when two variables were correlated with Spearman's $r_s > 0.7$ (following Dormann et al., 2013). The highest correlation coefficients were among variables on trap level (with maximum $r_s = 0.67$ between understorey complexity index and mean distance between trap and vegetation). Although they were below the threshold, we condensed all trap-level variables to linear combinations using principal component analysis (PCA) to reduce the number of environmental variables and, thus, to keep GLMMs parsimonious. We used the axis scores of the first two PCA-axes, which cumulatively explained 70% of the inertia, as variables in the GLMMs. PC2 axis reflects ENL, whereas PC1 axis reflects all other TLS-based metrics (see Appendix C: Fig. 1).

All variables (see Table 1) were centred and scaled (mean = 0, SD = 1) to allow comparison of coefficients among variables. As we could not operate all traps for identical periods of time due to logistic constraints, we included the duration of trap exposure (ln-transformed) as co-variate. We added site identity as random effect to account for the hierarchical data structure with two traps nested in each site. Model assumptions were checked and confirmed using the DHARMa package (Hartig, 2018).

The relationship between the environmental variables and the composition of insect taxa among sites was analysed with distance-based redundancy analysis (db-RDA; function 'capscale' in the vegan package, Oksanen et al., 2018) based on Bray-Curtis dissimilarity. For this, we pooled the data per site and omitted sites from which we only had data from one trap, resulting in 116 observations. As constraints, we included the same variables (Table 1) as for the GLMMs.

All analyses were conducted with R 3.5.1 (R Core Team, 2018).

## Results

In total, we collected 199,490 adults from 18 taxa (see Appendix D: Table 1). Of those, 93% belonged to the seven most abundant taxa with at least 2200 individuals each (Table 2).

### Relationships between environmental variables and insect abundances

Total abundance and abundances of the separate insect taxa were related to various structural elements (Table 3). Total insect abundance was significantly positively related to ENL, where higher values indicate more evenly layered vegetation (PC2 axis corresponding to ENL; negative-binomial GLMM; parameter estimate: $0.20 \pm 0.03$, $z = 6.21$, $p$

$< 0.001$; Fig. 2A). This variable was also significant for all other taxa except Heteroptera (Table 3, Fig. 2B-D). Furthermore, each taxon responded to a unique combination of forest structural elements.

Relationships of most variables were positive across several taxa. For instance, mean tree diameter was positively related to abundances of the mostly herbivorous taxa Heteroptera ($0.17 \pm 0.07$, $z = 2.34$, $p = 0.02$; Fig. 3A) and Sternorrhyncha ($0.24 \pm 0.06$, $z = 3.84$, $p < 0.001$; Fig. 3B), while Auchenorrhyncha abundance was positively related to the share of deciduous trees ($0.24 \pm 0.06$, $z = 3.83$, $p < 0.001$; Fig. 3C) and to canopy gap fraction ($0.14 \pm 0.05$, $z = 2.51$, $p = 0.01$; Fig. 3D). None of the tested taxa was related to TreM richness. The number of collected insects increased with trap exposure.

### Relationships between environmental variables and insect community composition

The db-RDA analysis indicated that insect community composition, at the coarse taxonomic level analysed, was related to mean DBH (permutation test; $F = 4.3$, df = 1, $p = 0.002$) and share of deciduous trees ($F = 2.4$, df = 1, $p = 0.013$). Trap exposure influenced the insect community as well. However, the environmental variables explained only a relatively small proportion of the variation in taxon composition (constrained inertia = 2.4 versus unconstrained inertia = 16.8; Fig. 4).

## Discussion

### Forest structure

We found that various elements of forest structure influenced insect abundances and taxon composition. The share of deciduous trees and mean DBH did not only increase abundances of herbivorous taxa but also shaped taxon composition. An index for vertical vegetation layering (ENL), which was derived from terrestrial laser scanning, was of particular importance, even for non-herbivorous taxa. To our knowledge, this study is among the firsts to directly link novel TLS-based three-dimensional structural complexity metrics to insect abundance in forests.

Biodiversity is positively correlated with heterogeneity in vegetation structure (Schuldt et al., 2019; Tews et al., 2004) with insect abundance emerging from numerous biological processes (Price, 1991). In our study, forest stands with a well-developed midstorey, as indicated by higher ENL values, haboured higher insect abundances and, hence, probably also higher insect species richness. It should be noted that the scope of this study included sampling of insects in the midstorey only. However, vegetation structure can also affect ground-dwelling insects via altered litter quality and

**Table 3.** Parameter estimates (± standard error) with test statistic (z-value) and corresponding p-values of negative-binomial models with scaled variables for total insect abundance and abundances of insect taxa. Significant p-values (at $p \leq 0.05$) are in bold.

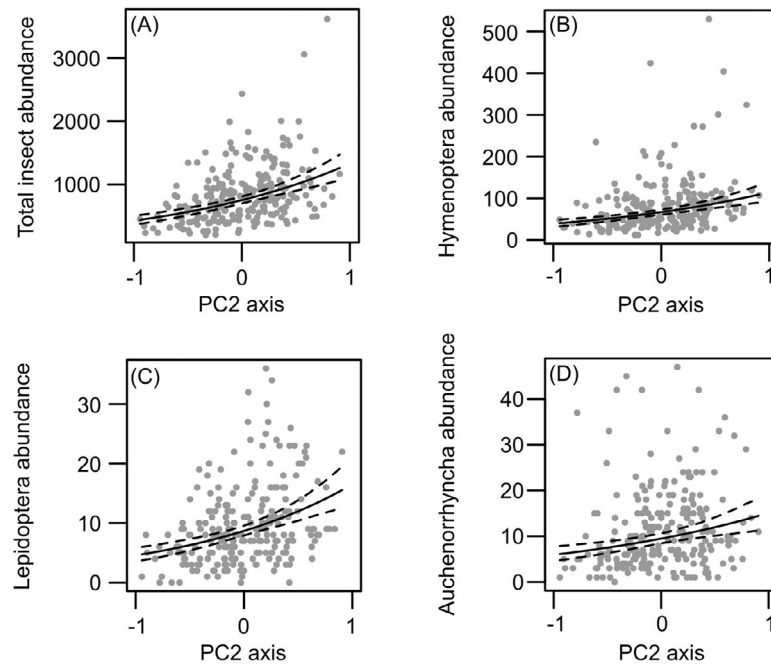| | Total | | Auchenorrhyncha | | Coleoptera | | Diptera | | Heteroptera | | Hymenoptera | | Lepidoptera | | Sternorrhyncha | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Estimate ± SE | z-value p-value | Estimate ± SE | z-value p-value | Estimate ± SE | z-value p-value | Estimate ± SE | z-value p-value | Estimate ± SE | z-value p-value | Estimate ± SE | z-value p-value | Estimate ± SE | z-value p-value | Estimate ± SE | z-value p-value |
| (Intercept) | 6.64 ±0.03 | 193.18 **< 0.001** | 2.29 ±0.05 | 42.60 **< 0.001** | 5.17 ±0.04 | 125.47 **< 0.001** | 5.63 ±0.05 | 130.62 **< 0.001** | 2.06 ±0.06 | 31.69 **< 0.001** | 4.23 ±0.04 | 95.30 **< 0.001** | 2.19 ±0.05 | 47.95 **< 0.001** | 4.55 ±0.05 | 84.47 **< 0.001** |
| Share of deciduous trees | −0.03 ±0.04 | −0.78 0.43 | 0.24 ±0.06 | 3.83 **< 0.001** | 0.07 ±0.05 | 1.49 0.14 | −0.15 ±0.07 | −2.22 **0.03** | 0.02 ±0.08 | 0.24 0.81 | −0.05 ±0.05 | −0.93 0.35 | −0.08 ±0.05 | −1.53 0.13 | 0.08 ±0.07 | 1.15 0.25 |
| Mean DBH | 0.06 ±0.04 | 1.41 0.16 | 0.11 ±0.06 | 1.87 0.06 | 0.03 ±0.05 | 0.70 0.48 | 0.03 ±0.06 | 0.45 0.65 | 0.17 ±0.07 | 2.34 **0.02** | 0.01 ±0.05 | 0.18 0.86 | 0.08 ±0.05 | 1.46 0.14 | 0.24 ±0.06 | 3.84 **< 0.001** |
| Canopy gap fraction | 0.03 ±0.04 | 0.74 0.46 | 0.14 ±0.05 | 2.51 **0.01** | 0.04 ±0.04 | 0.88 0.38 | 0.01 ±0.06 | 0.15 0.88 | 0.09 ±0.07 | 1.42 0.16 | −0.04 ±0.05 | −0.95 0.34 | 0.00 ±0.05 | 0.01 0.99 | 0.05 ±0.06 | 0.94 0.35 |
| Deadwood diversity | 0.07 ±0.04 | 1.64 0.10 | −0.01 ±0.06 | −0.15 0.88 | 0.10 ±0.05 | 2.19 **0.03** | 0.10 ±0.06 | 1.53 0.13 | 0.10 ±0.07 | 1.30 0.19 | 0.02 ±0.05 | 0.29 0.77 | 0.10 ±0.05 | 2.02 **0.04** | −0.02 ±0.06 | −0.35 0.72 |
| TreM richness | −0.04 ±0.04 | −1.07 0.29 | −0.05 ±0.06 | −0.89 0.37 | −0.09 ±0.05 | −1.81 0.07 | −0.07 ±0.06 | −1.03 0.30 | −0.05 ±0.07 | −0.64 0.52 | −0.06 ±0.05 | −1.15 0.25 | −0.09 ±0.05 | −1.72 0.09 | 0.09 ±0.06 | 1.43 0.15 |
| PC1 | −0.03 ±0.03 | −0.98 0.33 | −0.05 ±0.05 | −0.99 0.32 | 0.07 ±0.03 | 2.22 **0.03** | −0.13 ±0.04 | −2.97 **0.003** | 0.00 ±0.15 | −0.01 0.99 | −0.00 ±0.04 | −0.02 0.99 | 0.02 ±0.04 | 0.49 0.63 | 0.10 ±0.04 | 2.16 **0.03** |
| PC2 | 0.20 ±0.03 | 6.21 **< 0.001** | 0.17 ±0.05 | 3.13 **0.001** | 0.17 ±0.04 | 4.67 **< 0.001** | 0.29 ±0.05 | 5.80 **< 0.001** | 0.09 ±0.05 | 1.55 0.12 | 0.20 ±0.04 | 4.89 **< 0.001** | 0.20 ±0.05 | 4.17 **< 0.001** | 0.12 ±0.04 | 2.40 **0.02** |
| Trap exposure | 0.09 ±0.04 | 2.29 **0.02** | 0.01 ±0.06 | 0.11 0.91 | 0.02 ±0.04 | 0.46 0.64 | 0.14 ±0.06 | 2.38 **0.02** | 0.11 ±0.07 | 1.54 0.12 | 0.15 ±0.05 | 3.20 **0.001** | 0.09 ±0.05 | 2.02 **0.04** | 0.02 ±0.06 | 0.34 0.73 |

**Fig. 2.** Relationships between PC2 axis (corresponding to vertical layering of vegetation, i.e. ENL) and abundances of total insects and of exemplary taxa ($n = 238$ samples). Higher values of PC2 axis correspond to vertically more evenly layered vegetation (multi-layered stands). Shown are bootstrapped model predictions (solid lines) with 95% confidence interval (dashed lines) for the respective bivariate relationships.
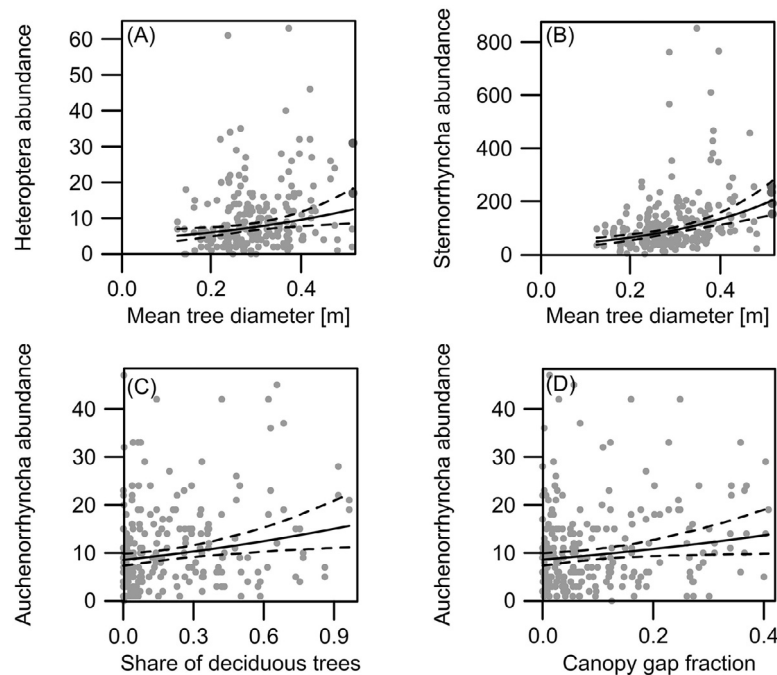


**Fig. 3.** Relationships between selected environmental variables and abundances of selected taxa ($n = 238$ samples). Shown are the bootstrapped model predictions (solid lines) with 95% confidence interval (dashed lines) for the respective bivariate relationships.

light regime due to differences in amount of litter source and shading from the midstorey and canopy (Jacob et al., 2009; Yi & Moldenke, 2005). Flight paths and dispersal height of canopy-dwelling insect may be influenced by the midstorey as well (Ulyshen, 2011 and references therein).

The evenly layered vegetation (as indicated by higher values of ENL) was either related to smaller trees as in uneven-aged forests or to shrubs in the midstorey. In the first case, insects benefit from higher resource availability, while in the second case, increased habitat heterogeneity through an
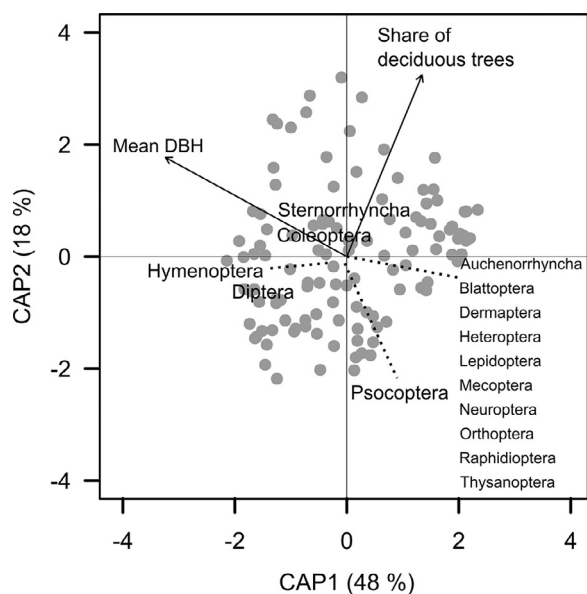
**Fig. 4.** Distance-based redundancy analysis biplot of insect abundances. Ordination shows similarity of insect communities at each site (dots) constrained by structural variables (arrows, only significant relationships are shown). Scores of insect taxa are plotted as text labels. Hymenoptera, Psocoptera and the taxa listed on the right were all situated very close to the centre as indicated by the stippled lines. Percentages in axis labels indicate explained variation.

increase in resource diversity would promote insects (e.g. Fornoff et al., 2019; Schuldt et al., 2019). In both cases, bottom-up effects increase abundances of both herbivores and other trophic groups. Parasitoids, for example, which accounted for the majority of captured Hymenoptera, benefit from the higher abundances and diversities of herbivores as hosts (Scherber et al., 2010; Sobek et al., 2009).

Our finding that, besides ENL, mean DBH was significantly related to the abundance of several herbivorous taxa may support the importance of vegetation further. Although larger trees characterized by a higher mean DBH tend to have more microhabitats (Asbeck et al., 2019), mean DBH and TreM richness were only weakly correlated (Pearson; $r = 0.17$, $p < 0.05$). Thus, the relationship between mean DBH and insect abundance is probably driven only to a small extent by habitat heterogeneity related to TreMs. Instead, mean DBH was positively correlated to basal area ($r = 0.97$, $p < 0.001$) and thus likely represents higher resource availability for herbivores as larger trees have more foliage (Leidinger et al., 2019; Reemer, 2005). Accordingly, many insect taxa are more abundant in zones of higher vegetation density (Fuentes-Montemayor et al., 2013; Schroeder et al., 2009). This is in line with our finding that herbivorous taxa such as Sternorrhyncha, Auchenorrhyncha and Lepidoptera, which feed on plant sap or green plant tissue, were more abundant in sites with higher mean DBH and ENL.

Species identities of plants also structure arthropod communities because for insect specialists, the occurrence of their host plants is prerequisite (Knuff et al., 2019; Schaffers et al., 2008; Sobek et al., 2009). However, the plants surrounding a host plant may alter the detectability of that plant by herbivores resulting in associational resistance or susceptibility (Barbosa et al., 2009; Hambäck et al., 2014) depending on their degree of specialisation (Andow, 1991; Root, 1973). Notably, plant species composition does not only affect abundances of herbivores (Leidinger et al., 2019; Sobek et al., 2009; Vehviläinen et al., 2007), but also predatory arthropods (Vehviläinen et al., 2008), parasitoid Hymenoptera (Fraser et al., 2007) and even overall arthropod abundance (Schowalter & Ganio, 1999).

Our findings support the importance of tree identity. Coniferous and deciduous tree species harbour distinct insect communities (Brändle & Brandl, 2006), which explains the change in composition with the share of deciduous trees in our study. Depending on the taxon, abundance either increased (Auchenorrhyncha) or decreased (Diptera) with share of deciduous trees. Penone et al. (2019) found the same relationships for corresponding trophic groups in other temperate, continuous-cover forests in Germany. In their study, arthropod herbivores (including Auchenorryhncha) were negatively associated with share of conifers. In addition, they found positive relationships for arthropod carnivores and decomposers. As many Diptera belong to these trophic groups, this is also in line with our results. Hence, Penone et al. (2019) found the same, contrasting effects of tree species composition on different trophic groups as we did.

## Retention elements: deadwood and tree-related microhabitats

Deadwood plays a major role for the conservation of forest biodiversity in retention forestry in continuous-cover forests as many forest arthropod species depend for at least parts of their life cycle on deadwood (Stokland et al., 2012). Whether non-saproxylic species also benefit from deadwood retention, is still a matter of debate (Gao et al., 2015). Among ground-dwelling arthropods, for example, only Coleoptera increased with experimental deadwood enrichment (Ulyshen & Hanula, 2009). In our study, abundances of Coleoptera and Lepidoptera were positively correlated with deadwood diversity. For Lepidoptera, deadwood may provide shelter and serve as moisture source or temperature buffer (Ulyshen et al., 2011). However, the effect of deadwood on non-saproxylic insects is inconsistent across taxa (Binkenstein et al., 2018; Seibold et al., 2015a) and many non-saproxylic insect groups may not benefit from increased deadwood availability and diversity because of different habitat requirements.

TreMs were not related to abundances of any of the insect taxa in our study even though they are conceived as promising habitat-based surrogates for forest biodiversity (Larrieu et al., 2018) and play a major role in retention forestry in our study area. Generally, relationships between TreMs and insects appears to be relatively weak (Gao et al., 2015; Paillet et al., 2018). TreMs might play a role in the protection of specific species associated with a particular TreM, e.g. beetles that are specialised on tree hollows with wood mould (Schauer et al., 2018), but not in promoting insect abundance in general.

## Remotely-sensed structural complexity metrics in an ecological context

To our knowledge, this study is among the firsts (but see Schuldt et al., 2019) to use TLS-based structural complexity metrics in relation to insect abundance. TLS measurements are highly sensitive and allow objective descriptions of three-dimensional vegetation structure, which might make them promising monitoring proxies in place of direct insect sampling. The ENL index for vertical vegetation layering was related to abundances of most insect taxa. This is ecologically plausible, as multi-layered vegetation likely supports more insects (see above). The importance of vertical vegetation structure for arthropods (Müller et al., 2018; Tanabe et al., 2001) is corroborated by studies that used both remote sensing techniques and classical methods such as the foliage height diversity index (MacArthur & MacArthur, 1961). Thus, TLS-based indices will likely prove to measure ecologically relevant structural properties and may become useful tools in biodiversity monitoring.

## Implications for forest management

Increasing insect abundance is no conservation goal *per se*, but it might become important for forest management as the insect decline in forests (Seibold et al., 2019) may lead to food deprivation in conservation-relevant vertebrates (Bowler et al., 2019). In this regard, our study provides several insights that are relevant for silviculture in continuous-cover forests because the structural elements that we studied are largely controlled by management (Bauhus et al., 2013).

TreMs are considered important indicators for the ecological value of retention trees (Kraus et al., 2016), but our results suggest that they do not have a measurable impact on insect abundance. As the species communities associated with different TreMs have very distinct life histories (e.g. Schauer et al., 2018), the conservation value of TreMs is likely limited to specific species (Paillet et al., 2018). Forest-dwelling insect species have widely differing habitat requirements and management-related structural elements

that equally promote all taxa are unlikely (Gao et al., 2015). Nevertheless, we found that a well-developed midstorey, as intended by continuous-cover forestry, was positively related to insect abundance across taxa and trophic groups. Thus, the current conversion in temperate European forests to uneven-aged, mixed species stands could help to halt insect decline in forests as far as abundance is concerned.

However, the conversion may not result in homogenisation of stand structure on landscape-scale as Schall et al. (2018) point out. They found higher regional diversity in even-aged as compared to uneven-aged forests which they attributed to larger between-stand heterogeneity of structure, light conditions and microclimate among the different age-classes (Schall et al., 2018). Our study underpins the notion that variability in different structural elements is important for biodiversity as we related many of the elements they mention (e.g. canopy gap fraction as proxy for light conditions) to insect abundance and found that each taxon responds to a unique set of structural elements.

## Conclusions

We conclude that more elements of forest structure than previously acknowledged influence insect populations. Each taxon responded to a unique set of forest structural elements. Abundances of species and taxa are the result of numerous biological processes in response to varying habitat requirements. Thus, the same habitat characteristic will evoke different responses in different organisms and it is unlikely that a single structural element is beneficial for all insect taxa. Nevertheless, our study demonstrates that multi-layered forest stands with increased habitat heterogeneity have higher insect abundances. Although it is unclear how this translates to species diversity on different spatial scales, the current conversion in continuous-cover forestry in Europe from even-aged, often conifer-dominated forests to uneven-aged, mixed species stands can increase the abundance of a wide range of insect taxa in the midstorey and is possibly one strategy to halt insect decline in forests.

## Declaration of Competing Interest

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

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## Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2020.09.002.

## References

Andow, D. A. (1991). Vegetational diversity and arthropod population response. *Annual Review of Entomology*, *36*(1), 561–586. doi:10.1146/annurev.ento.36.1.561.

Asbeck, T., Pyttel, P., Frey, J., & Bauhus, J. (2019). Predicting abundance and diversity of tree-related microhabitats in Central European montane forests from common forest attributes. *Forest Ecology and Management*, *432*, 400–408. doi:10.1016/j.foreco.2018.09.043.

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., & Szendrei, Z. (2009). Associational resistance and associational susceptibility: Having right or wrong neighbors. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 1–20. doi:10.1146/annurev.ecolsys.110308.120242.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. doi:10.18637/jss.v067.i01.

Bauhus, J., Puettmann, K. J., & Kuehne, C. (2013). Close-to-nature forest management in Europe: does it support complexity and adaptability of forest ecosystems? In C. Messier, K. J. Puettmann, K. D. Coates (Eds.), *Managing forests as complex adaptive systems: Building resilience to the challenge of global change* (pp. 187−213). New York: Routledge.

Bauhus, J., Puettmann, K., & Messier, C. (2009). Silviculture for old-growth attributes. *Forest Ecology and Management*, *258* (4), 525–537. doi:10.1016/j.foreco.2009.01.053.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., et al. (2003). Reserves, resilience and dynamic landscapes. *Ambio*, *32*(6), 389–396. doi:10.1579/0044-7447-32.6.389.

Binkenstein, J., Klein, A.-. M., Assmann, T., Buscot, F., Erfmeier, A., Ma, K., et al. (2018). Multi-trophic guilds respond differently to changing elevation in a subtropical forest. *Ecography*, *41*, 1013–1023. doi:10.1111/ecog.03086.

Bowler, D. E., Heldbjerg, H., Fox, A. D., Jong, M.d., & Böhning−Gaese, K. (2019). Long−term declines of European insectivorous bird populations and potential causes. *Conservation Biology*, *33*(5), 1120–1130. doi:10.1111/cobi.13307.

Brändle, M., & Brandl, R. (2006). Is the composition of phytophagous insects and parasitic fungi among trees predictable. *Oikos*, *113*, 296–304.

Brang, P., Spathelf, P., Larsen, J. B., Bauhus, J., Boncina, A., Chauvin, C., et al. (2014). Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. *Forestry*, *87*, 492–503. doi:10.1093/forestry/cpu018.

Core Team, R. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Deans, A. M., Malcolm, J. R., Smith, S. M., & Bellocq, M. I. (2005). Edge effects and the responses of aerial insect assemblages to structural-retention harvesting in Canadian boreal peatland forests. *Forest Ecology and Management*, *204*(2−3), 249–266. doi:10.1016/j.foreco.2004.09.015.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., et al. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. doi:10.1111/j.1600-0587.2012.07348.x.

Ehbrecht, M., Schall, P., Ammer, C., & Seidel, D. (2017). Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. *Agricultural and Forest Meteorology*, *242*, 1–9. doi:10.1016/j.agrformet.2017.04.012.

Ehbrecht, M., Schall, P., Juchheim, J., Ammer, C., & Seidel, D. (2016). Effective number of layers: A new measure for quantifying three-dimensional stand structure based on sampling with terrestrial LiDAR. *Forest Ecology and Management*, *380*, 212–223. doi:10.1016/j.foreco.2016.09.003.

Fedrowitz, K., Koricheva, J., Baker, S. C., Lindenmayer, D. B., Palik, B., Rosenvald, R., et al. (2014). Can retention forestry help conserve biodiversity? A meta-analysis. *Journal of Applied Ecology*, *51*(6), 1669–1679. doi:10.1111/1365-2664.12289.

Fornoff, F., Klein, A.-. M., Blüthgen, N., & Staab, M. (2019). Tree diversity increases robustness of multi-trophic interactions. *Proceedings of the Royal Society B-Biological Sciences*, *286*,(1898) 20182399. doi:10.1098/rspb.2018.2399.

Fraser, S. E. M., Dytham, C., & Mayhew, P. J. (2007). Determinants of parasitoid abundance and diversity in woodland habitats. *Journal of Applied Ecology*, *44*(2), 352–361. doi:10.1111/j.1365-2664.2006.01266.x.

Frey, J., Kovach, K., Stemmler, S., & Koch, B. (2018). UAV photogrammetry of forests as a vulnerable process: A sensitivity analysis for a structure from motion RGB-image pipeline. *Remote Sensing*, *10*(6), 912. doi:10.3390/rs10060912.

Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J. M., & Park, K. J. (2013). Fragmented woodlands in agricultural landscapes: The influence of woodland character and landscape context on bats and their insect prey. *Agriculture, Ecosystems & Environment*, *172*, 6–15. doi:10.1016/j.agee.2013.03.019.

Gao, T., Nielsen, A. B., & Hedblom, M. (2015). Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecological Indicators*, *57*, 420–434. doi:10.1016/j.ecolind.2015.05.028.

Grove, S. J. (2002). Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics*, *33*(1), 1–23. doi:10.1146/annurev.ecolsys.33.010802.150507.

Gustafsson, L., Baker, S. C., Bauhus, J., Beese, W., Brodie, A., Kouki, J., et al. (2012). Retention forestry to maintain multifunctional forests: A world perspective. *Bioscience*, *62*(7), 633–645. doi:10.1525/bio.2012.62.7.6.

Gustafsson, L., Bauhus, J., Asbeck, T., Augustynczik, A. L. D., Basile, M., Frey, J., et al. (2020). Retention as an integrated biodiversity conservation approach for continuous-cover forestry in Europe. *Ambio*, *49*, 85–97. doi:10.1007/s13280-019-01190-1.

Hale, C. M., Pastor, J., & Rusterholz, K. A. (1999). Comparison of structural and compositional characteristics in old-growth and mature, managed hardwood forests of Minnesota, U.S.A. *Canadian Journal of Forest Research*, *29*(10), 1479–1489. doi:10.1139/x99-076.

Hambäck, P. A., Inouye, B. D., Andersson, P., & Underwood, N. (2014). Effects of plant neighborhoods on plant−herbivore interactions: Resource dilution and associational effects. *Ecology*, *95*(5), 1370–1383. doi:10.1890/13-0793.1.

Hartig, F. (2018). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.2.0.*

Hyvärinen, E., Kouki, J., & Martikainen, P. (2009). Prescribed fires and retention trees help to conserve beetle diversity in managed boreal forests despite their transient negative effects on some beetle groups. *Insect Conservation and Diversity*, *2*(2), 93–105. doi:10.1111/j.1752-4598.2009.00048.x.

Jacob, M., Weland, N., Platner, C., Schaefer, M., Leuschner, C., & Thomas, F. M. (2009). Nutrient release from decomposing leaf litter of temperate deciduous forest trees along a gradient of increasing tree species diversity. *Soil Biology and Biochemistry*, *41*(10), 2122–2130. doi:10.1016/j.soilbio.2009.07.024.

Jokela, J., Juutilainen, K., Korpela, L., Kouki, J., Kuntsi, S., Koivula, M., et al. (2018). Cross-taxon congruence and relationships to stand characteristics of vascular plants, bryophytes, polyporous fungi and beetles in mature managed boreal forests. *Ecological Indicators*, *85*, 137–145. doi:10.1016/j.ecolind.2017.10.036.

Knuff, A. K., Staab, M., Frey, J., Helbach, J., & Klein, A.−. M. (2019a). Plant composition, not richness, drives occurrence of specialist herbivores. *Ecological Entomology*, *44*, 833–843. doi:10.1111/een.12767.

Knuff, A. K., Winiger, N., Klein, A.−. M., Segelbacher, G., & Staab, M. (2019b). Optimizing sampling of flying insects using a modified window trap. *Methods in Ecology and Evolution*, *10*, 1820–1825. doi:10.1111/2041-210X.13258.

Kraus, D., Bütler, R., Krumm, F., Lachat, T., Larrieu, L., Mergner, U., et al. (2016). Catalogue of tree microhabitats - Reference field list. *Integrate+ Technical Paper.*

Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., et al. (2018). Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. *Ecological Indicators*, *84*, 194–207. doi:10.1016/j.ecolind.2017.08.051.

Leidinger, J., Seibold, S., Weisser, W. W., Lange, M., Schall, P., Türke, M., et al. (2019). Effects of forest management on herbivorous insects in temperate Europe. *Forest Ecology and Management*, *437*, 232–245. doi:10.1016/j.foreco.2019.01.013.

Lyashevska, O., & Farnsworth, K. D. (2012). How many dimensions of biodiversity do we need. *Ecological Indicators*, *18*, 485–492. doi:10.1016/j.ecolind.2011.12.016.

MacArthur, R. H., & MacArthur, J. W. (1961). On bird species diversity. *Ecology*, *42*(3), 594–598.

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton: Princeton University Press.

Müller, J., Brandl, R., Brändle, M., Förster, B., Araujo, B. C.de, & Gossner, M. M. (2018). LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. *Oikos (Copenhagen, Denmark)*, *127*(6), 814–824. doi:10.1111/oik.04972.

Müller, J., Jarzabek-Müller, A., Bussler, H., & Gossner, M. M. (2014). Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity. *Animal Conservation*, *17*(2), 154–162. doi:10.1111/acv.12075.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2018). *Vegan: Community Ecology Package. R package version 2.5−2.*

Paillet, Y., Archaux, F., Puy, Du, S., Bouget, C., Boulanger, V., Debaive, et al. (2018). The indicator side of tree microhabitats: A multi-taxon approach based on bats, birds and saproxylic beetles. *Journal of Applied Ecology*, *55*, 2147–2159. doi:10.1111/1365-2664.13181.

Penone, C., Allan, E., Soliveres, S., Felipe-Lucia, M. R., Gossner, M. M., Seibold, S., et al. (2019). Specialisation and diversity of multiple trophic groups are promoted by different forest features. *Ecology Letters*, *22*, 170–180. doi:10.1111/ele.13182.

Perner, J., & Malt, S. (2003). Assessment of changing agricultural land use: Response of vegetation, ground-dwelling spiders and beetles to the conversion of arable land into grassland. *Agriculture, Ecosystems & Environment*, *98*(1−3), 169–181. doi:10.1016/S0167-8809(03)00079-3.

Price, P. W. (1991). Evolutionary theory of host and parasitoid interactions. *Biological Control*, *1*(2), 83–93. doi:10.1016/1049-9644(91)90107-B.

Reemer, M. (2005). Saproxylic hoverflies benefit by modern forest management (Diptera: Syrphidae). *Journal of Insect Conservation*, *9*(1), 49–59. doi:10.1007/s10841-004-6059-9.

Root, R. B. (1973). Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs*, *43*(1), 95–124.

Schaffers, A. P., Raemakers, I. P., Sýkora, K. V., & ter Braak, C. J. F. (2008). Arthropod assemblages are best predicted by plant species composition. *Ecology*, *89*(3), 782–794.

Schall, P., Gossner, M. M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., et al. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *Journal of Applied Ecology*, *55*(1), 267–278. doi:10.1111/1365-2664.12950.

Schauer, B., Steinbauer, M. J., Vailshery, L. S., Müller, J., Feldhaar, H., & Obermaier, E. (2018). Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest. *Biodiversity and Conservation*, *27*(4), 853–869. doi:10.1007/s10531-017-1467-9.

Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., et al. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, *468*(7323), 553–556. doi:10.1038/nature09492.

Schowalter, T. D., & Ganio, L. M. (1999). Invertebrate communities in a tropical rain forest canopy in Puerto Rico following hurricane Hugo. *Ecological Entomology*, *24*, 191–204.

Schroeder, B., Buddle, C. M., & Saint-Germain, M. (2009). Activity of flying beetles (Coleoptera) at two heights in canopy gaps and intact forests in a hardwood forest in Quebec. *The Canadian Entomologist*, *141*(5), 515–520. doi:10.4039/n09-022.

Schuldt, A., Assmann, T., Brezzi, M., Buscot, F., Eichenberg, D., Gutknecht, J., et al. (2018). Biodiversity across trophic levels drives multifunctionality in highly diverse forests. *Nature Communications*, *9*(1), 2989. doi:10.1038/s41467-018-05421-z.

Schuldt, A., Ebeling, A., Kunz, M., Staab, M., Guimarães-Steinicke, C., Bachmann, D., et al. (2019). Multiple plant diversity components drive consumer communities across ecosystems. *Nature Communications*, *10*(1), 1–11. doi:10.1038/s41467-019-09448-8.

Seibold, S., Bässler, C., Brandl, R., Gossner, M. M., Thorn, S., & Ulyshen, M. D. (2015a). Experimental studies of dead-wood biodiversity — A review identifying global gaps in knowledge. *Biological Conservation*, *191*, 139–149. doi:10.1016/j.biocon.2015.06.006.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., et al. (2015b). Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology*, *29*(2), 382–390. doi:10.1111/cobi.12427.

Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., et al. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, *574*(7780), 671–674. doi:10.1038/s41586-019-1684-3.

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, *49*, 11–41.

Sobek, S., Gossner, M. M., Scherber, C., Steffan-Dewenter, I., & Tscharntke, T. (2009a). Tree diversity drives abundance and spatiotemporal β-diversity of true bugs (Heteroptera). *Ecological Entomology*, *34*(6), 772–782. doi:10.1111/j.1365-2311.2009.01132.x.

Sobek, S., Scherber, C., Steffan-Dewenter, I., & Tscharntke, T. (2009b). Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest. *Oecologia*, *160*(2), 279–288. doi:10.1007/s00442-009-1304-2.

Srivastava, D. S., & Lawton, J. H. (1998). Why more productive sites have more species: An experimental test of theory using tree−hole communities. *The American Naturalist*, *152*(4), 510–529.

Stokland, J. N., Siitonen, J., & Jonsson, B. G. (2012). *Biodiversity in dead wood*. New York: Cambridge University Press.

Storch, D., Bohdalková, E., & Okie, J. (2018). The more-individuals hypothesis revisited: The role of community abundance in species richness regulation and the productivity-diversity relationship. *Ecology Letters*, *21*(6), 920–937. doi:10.1111/ele.12941.

Storch, I., Penner, J., Asbeck, T., Basile, M., Bauhus, J., Braunisch, V., et al. (2020). Evaluating the effectiveness of retention forestry to enhance biodiversity in production forests of Central Europe using an interdisciplinary, multi-scale approach. *Ecology and Evolution*, *10*, 1489–1509. doi:10.1002/ece3.6003.

Tanabe, S.-. I., Toda, M. J., & Vinokurova, A. (2001). Tree shape, forest structure and diversity of drosophilid community: Comparison between boreal and temperate birch forests. *Ecological Research*, *16*, 369–385.

Taylor, L. R. (1963). Analysis of the effect of temperature on insects in flight. *Journal of Animal Ecology*, *32*(1), 99–117. doi:10.2307/2520.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., et al. (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, *31*(1), 79–92. doi:10.1046/j.0305-0270.2003.00994.x.

Ulyshen, M. D. (2011). Arthropod vertical stratification in temperate deciduous forests: Implications for conservation-oriented management. *Forest Ecology and Management*, *261*(9), 1479–1489. doi:10.1016/j.foreco.2011.01.033.

Ulyshen, M. D., & Hanula, J. L. (2009). Responses of arthropods to large-scale manipulations of dead wood in Loblolly pine stands of the Southeastern United States. *Environmental Entomology*, *38*(4), 1005–1012.

Ulyshen, M. D., Klooster, W. S., Barrington, W. T., & Herms, D. A. (2011). Impacts of emerald ash borer-induced tree mortality on leaf litter arthropods and exotic earthworms. *Pedobiologia*, *54*(5−6), 261–265. doi:10.1016/j.pedobi.2011.05.001.

Vehviläinen, H., Koricheva, J., & Ruohomäki, K. (2007). Tree species diversity influences herbivore abundance and damage: Meta-analysis of long-term forest experiments. *Oecologia*, *152*(2), 287–298. doi:10.1007/s00442-007-0673-7.

Vehviläinen, H., Koricheva, J., & Ruohomäki, K. (2008). Effects of stand tree species composition and diversity on abundance of predatory arthropods. *Oikos*, *117*(6), 935–943. doi:10.1111/j.0030-1299.2008.15972.x.

Willim, K., Stiers, M., Annighöfer, P., Ammer, C., Ehbrecht, M., Kabal, M., et al. (2019). Assessing understory complexity in beech-dominated forests (*Fagus sylvatica* L.) in Central Europe-from managed to primary forests. *Sensors*, *19*(7). doi:10.3390/s19071684.

Yee, D. A., & Juliano, S. A. (2007). Abundance matters: A field experiment testing the more individuals hypothesis for richness−productivity relationships. *Oecologia*, *153*(1), 153–162. doi:10.1007/s00442-007-0707-1.

Yi, H., & Moldenke, A. (2005). Response of ground-dwelling arthropods to different thinning intensities in young Douglas fir forests of Western Oregon. *Environmental Entomology*, *34*(5), 1071–1080. doi:10.1093/ee/34.5.1071.