



Structural elements enhanced by retention forestry promote forest and non-forest specialist bees and wasps

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ABSTRACT

Retention forestry promotes certain forest structural elements to enhance biodiversity. It is unclear however to what extent retention measures are suited to enhance the biodiversity of bees and wasps, and how relationships to structural elements promoted by retention may differ when habitat-based classifications are accounted for. Here, we analyze the abundance, diversity and species richness of forest and non-forest specialist cavity-nesting bees and wasps collected on 127 plots in the southern Black Forest, Germany. Our aim was to use habitat-based classifications, or groupings based on habitat occurrence of cavity-nesting bees and wasps to evaluate the effectiveness and importance of forest structural elements that are prioritized in biodiversity-focused conservation. We found that canopy cover, stand structural complexity and standing deadwood were principally important for abundance, diversity and species richness of bees and wasps, with differing responses among habitat classifications. Forest specialist biodiversity metrics and composition were related to forest structural variables indicating greater feeding and nesting resource availability, namely herb cover, standing deadwood and stand structural complexity. Non-forest specialist biodiversity metrics were related to primarily canopy cover and elevation while community composition was structured by only forest cover and understory species richness. Our results indicate the importance of considering habitat specializations of cavity-nesting bee and wasp communities for meaningful evaluation of retention forestry structural elements. The presence and arrangement of these forest elements can be altered by stand level management practices utilizing the cascading effects of structural changes, such as increasing herb cover and sun exposed standing deadwood via canopy opening, and high stump retention during tree harvesting.

1. Introduction

The presence or absence of resources and abiotic conditions created by certain habitats can spatially restrict the occurrence and density of species, e.g. saproxylic beetles dependent on the creation and decomposition of deadwood in forests (Müller et al., 2015) or specialist bees foraging for pollen in only mature forest canopies (Urban-Mead et al., 2021). In cases where a species' distribution is restricted to a habitat based on extrinsically rare, yet intrinsically common characteristics, it can be referred to as a specialist (Rosenzweig, 1981, Morris, 2003, Fortin et al., 2008). According to this definition, a forest specialist is a species

with a distribution restricted to forest habitat due to the presence of structural and compositional elements such as deadwood (Radu, 2006, Müller and Büttler, 2010) and tree canopy (Meißner et al., 2012, Czerwinski et al., 2014, Haesen et al., 2021, Meeussen et al., 2021), which create a distinct suite of resources and microclimates (Penone et al., 2018). Due to their dependence on exclusively occurring resources, microclimates and habitat connectivity (Sverdup-Thygeson et al., 2017), specialists are disproportionately hindered by habitat loss compared to generalists (Pandit et al., 2009, Ozinga et al., 2012, Nordén et al., 2013, Mangels et al., 2017, Habel et al., 2019a, Habel et al., 2019b, Neff et al., 2021). As a result of this vulnerability to habitat loss, and the

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importance of unique forest resources for numerous other taxa such as deadwood-feeding saproxylic beetles, forest specialists may be good indicators (Travis, 2003, Preston et al., 2008, Bogusch et al., 2020, Magura et al., 2020) for conservation efforts aiming to promote biodiversity via the retention of key forest structural elements, such as standing or lying deadwood. Changes in the abundance, diversity and species richness of forest specialists can thus help clarify the influence of retention forestry on insect biodiversity.

Retention forestry is a globally practiced conservation strategy with the aim of integrating biodiversity conservation into sustainable management (Gustafsson et al., 2012, Fedrowitz et al., 2014, Franklin and Donato, 2020, Pastur et al., 2020). Retention forestry retains structural elements which may otherwise be removed through harvesting. Such elements include deadwood and habitat trees, leading to greater connectivity among special habitats (Storch et al., 2020). While the importance of forest structural and compositional elements on important insect groups such as saproxylic beetles (Müller et al., 2008, Parisi et al., 2019) and moths (Schmidt and Roland, 2006, Root et al., 2016) has been investigated, these relationships have not been explored in great detail using specialist and non-specialist cavity-nesting aculeate Hymenoptera (bees and wasps). Furthermore, the dependence of forest specialist cavity-nesting bees and wasps on unique forest resources (e.g. deadwood nesting substrates) indicates that information on their communities can provide a useful tool for interpreting the effects of forest structural and compositional elements emphasized by retention forestry.

Cavity-nesting aculeate Hymenoptera comprise the solitary bees and wasps, which build their nests in preexisting holes found in deadwood, plant stems, stone walls and a multitude of other structures (Krombein, 1967, O'Neill, 2001, MacIvor, 2016, Staab et al., 2018). This group contains both specialist and non-specialist taxa in numerous habitat types (Westerfelt et al., 2015, da Rocha-Filho et al., 2017, O'Neill and O'Neill, 2018, Falcón-Brindis et al., 2019), and in several functional groups (Mayr et al., 2020), making their abundance, diversity and species richness useful metrics for bioindication (Tschamntke et al., 1998). The life history of cavity-nesting bees and wasps allows for simple and effective sampling of the entire community (Gaimari and Martins, 1996, Tschamntke et al., 1998) using trap-nests (Staab et al., 2018).

In the present study, we test the following hypotheses: 1) The abundance of all cavity-nesting bees and wasps will increase with greater amounts of natural nesting substrates (deadwood) and greater foraging resources (herb cover). We expect the abundance of forest specialists to increase with increasing amounts of forest structural elements such as deadwood, while the abundance of non-forest specialists to increase with structural changes indicative of decreasing amounts of forest habitat such as lower forest cover (proportion of forested area in surrounding 1 km²), and lower canopy cover (proportion of area overhead occupied tree canopies). 2) The diversity and species richness of all cavity-nesting bees and wasps will increase with increasing heterogeneity in forest stands such as higher stand structural complexity measured using the stand structural complexity index (SSCI; Ehbrecht et al., 2017), greater layering of vegetation measured by the effective number of layers (ENL; Ehbrecht et al., 2016), decreasing canopy cover, greater understory species richness and a higher proportion of deciduous tree species admixture. Our hypotheses follow the habitat heterogeneity hypothesis, which predicts that increases in niche availability yield an increase in species richness (Pianka, 1966). We expect the diversity and species richness of forest specialists to respond more strongly than non-forest specialists, to environmental variables characterizing more diverse forest structure which are important elements in the suite of resources within forest habitats. 3) Community composition will be structured by similar environmental variables structuring biodiversity metrics, with different responses between forest and non-forest specialists.

2. Materials and methods

2.1. Study region and plots

The study was conducted on 134 1-hectare plots in the southern Black Forest mountain range in Baden-Württemberg, Germany (Lat: 47.9, Long: 8.2). These plots were established in 2016 by the 'Conservation of Forest Biodiversity' (ConFoBi) project (Storch et al., 2020). The Black Forest consists of mixed temperate forest comprised of mainly Norway spruce (*Picea abies* L.), European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.), sycamore maple (*Acer pseudoplatanus* L.), and sessile oak (*Quercus petraea* Matt.). Close-to-nature forest management and conservation initiatives in this region have focused on converting what was previously large swaths of mono-specific Norway spruce stands to more mixed and beech-dominated stands, reflecting the potentially natural vegetation of the area (Standovár and Kenderes, 2003, Gärtner and Reif, 2005). This forest transformation with increasing focus on biodiversity conservation has also placed more emphasis on enhancing forest structure through deadwood and habitat tree retention (Storch et al., 2018, Storch et al., 2020). Plots reflect gradients in numerous forest elements, such as deadwood amounts, stand structural complexity and forest cover (Table 1). The criteria involved in the selection of study plots ensured representativeness of a wide range of conditions found in European montane forests. This is particularly true for environmental variables such as deadwood and the amount of forest at landscape scale. For more detailed information on

Table 1

Environmental variables and summary statistics characterizing the 127 plots used in analyses. None of the variables were excluded on the basis of assumed collinearity ($p > 0.70$) following pairwise analyses and assessment of variance inflation factors. A summary of Spearman's correlations among environmental variables can be found in the supplement, Table S2. A summary of variance inflation factor assessments can be found in the supplement, Table S4.

Variable	Unit	Definition	Range	Mean ± SD
Canopy cover (%)	%	Proportion of area with sunlight blocked by forest canopy	39–92	78 ± 8
Deadwood DBH (lying)	cm	Sum diameter of lying deadwood structures > 7 cm DBH below decay stage 4	0–1682	238 ± 214
Deadwood DBH (standing)	cm	Sum diameter of standing deadwood structures > 7 cm DBH below decay stage 4	0–1832	499 ± 359
Deciduous tree share	%	Sum diameter of standing deadwood structures > 7 cm DBH below decay stage 4	0–96	28 ± 25
Forest cover	%	Proportion of forested area within 1 km ² of plot centers	9–81	61 ± 15
Herb cover	%	Ratio of area on ground with herb layer present	0.14–73.77	35 ± 19
Elevation	m	Average of min and max heights above sea level	443–1334	821 ± 183
Mean effective number of layers (ENL)	–	Mean number of 1 m thick strata with filled 3D voxels indicating presence of vegetation measured across NW-SE transect on each plot	7–27	16 ± 4
Mean Stand structural complexity index (SSCI)	–	Mean index characterizing the diversity of physical characteristics measured across NW-SE transect on each plot	2–12	4 ± 2
Understory species richness	–	Number of plant species identified in the understory (2–5 m)	2–71	31 ± 14

the ConFoBi plot selection, environmental variables measured, and our plot selection within the Black Forest as a model study system, see [Storch et al. \(2020\)](#). A map of the study area can be found in the supplement (Fig. S1).

2.2. Environmental variables

The environmental variables deciduous tree share, elevation and diameters of standing and lying deadwood pieces above 7 cm in diameter were obtained during full inventories conducted in 2017 and 2018. Deadwood can be classified in five decay stages; recently dead or raw wood (I), solid deadwood (II), rotten wood (III), mould wood (IV), and duff wood (V) ([Hunter 1990](#)). The final two deadwood decay stages are similar to mixtures of soil and leaf litter, and are thus unsuitable as substrates for cavity-nesting bees and wasps, which prefer fresh and moderately decomposed deadwood ([Westerfelt et al., 2015](#), [Bogusch and Horák, 2018](#), [Eckert et al., 2021](#)). To account for this, the cumulative diameter of lying and standing deadwood structures at plot level of only decay stages I–III were used, excluding decay stages IV–V. Herb cover and understory species richness were measured from six 5x5 m subplots in 2017 ([Helbach et al., 2022](#)). Forest cover (proportion of forested area in 1 km² around plot centers) was calculated using aerial image data by [Storch et al. \(2020\)](#). The remotely sensed indices effective number of layers (ENL) and stand structural complexity index (SSCI) were derived from terrestrial laser scans at the northwest and southeast corners, and plot centers ([Ehbrecht et al., 2017](#), [Frey et al., 2019](#), [Knuff et al., 2020](#), [Rappa et al., 2022](#)). The SSCI is a measure of geometric complexity of vegetation and structures within a forest stand ([Ehbrecht et al., 2017](#)). It is derived from the points on a vertical scanline of the whole plot. Points on this line are then connected to a polygon which creates a ratio of area to perimeter. The ENL is an index for measuring the vertical heterogeneity of vegetation layering using voxels in 3D space ([Ehbrecht et al., 2016](#)). A high value of the ENL indicates many forest strata occupied by vegetation, a more evenly layered and diverse stand. While the ENL is representing the layering as well as the stand height, the SSCI is capturing the structural heterogeneity and overall shape complexity. The ENL reaches high scores if the forest is high with an even distribution of plant material along the vertical axis. The highest values are reached in an especially high forest where the crown space is densely occupied by multiple or long tree crowns ([Ehbrecht et al. 2019](#)). The SSCI gains especially high values if vegetation objects are recorded close to the scanner as well as far away. Therefore, semi-open stands with multiple forest strata gain the highest values ([Stiers et al. 2018](#)). Mean values for each index were calculated using three values taken along northwest-southeast transects, to generate one value per plot. Mean canopy cover was measured in ImageJ using overhead hemispherical photos taken at each trap location in early Fall 2020. Summary information of the environmental variables is available in [Table 1](#).

2.3. Insect collection, identification & classification

Solitary cavity-nesting bees and wasps were collected using trap-nests ([Staab et al., 2018](#)) which were exposed on plots between early March and late October 2020. The use of trap-nests is a method which presents artificial cavities to female cavity-nesting bees and wasps for the provision of resources in nest cells for individual offspring, which enter diapause while trapped in the device. At this time, traps are collected, nests opened and individuals reared, allowing for the quantification and identification of each species. Each trap was constructed by fitting hollow reed (*Phragmites australis* Cav.) internodes of ~ 20 cm length into a PVC tube (diameter 11.0 cm). Per side each trap exposed ~ 150 ± 11 SD cavities ranging between 1 ± 0.3 to 10 ± 1.1 mm in diameter. Traps were secured in pairs to ~ 1.5 m high wooden poles halfway between plot centers and the northwest and southeast corners, placed in open ground spaces within a tolerance radius of ~ 5 m, totaling four traps per plot. Each trap was oriented with the available

cavities facing northwest and southeast, to promote nesting via sunlight exposure. After retrieval, internodes occupied with nests were placed in a cooling chamber at ~ 4 °C between late October and late February 2020, to simulate winter diapause. During this time, nests were briefly taken out of the cooling chamber to count the number of brood cells which had been provisioned with resources (abundance), with adults hatched later to determine species identities. Brood cells which could not be reliably identified due to complete hatching of the nest prior to collection (~4%), or when all individuals in a nest died during pupation (~3%), and adult specimens which could not be reliably identified to species level (~1 %), were excluded prior to analyses. Nest building species were separated from parasitoid species, with only the former considered here, as nest building species are more directly affected by the availability of foraging and nesting resources. Species identifications and habitat classification as forest or non-forest specialists were done using the most relevant identification and natural history literature for each taxonomic group (e.g. [Jacobs, 2007](#) for Crabronidae wasps; [Westrich, 2018](#) for bees) (Table S1). A species was considered a forest specialist when the description of its preferred habitat for foraging and nesting included: “forest”, “forest margins”, “woodland”, “open forest” or “forest clearing”. If prey/pollen/nest building resources for a species were to be found in only forests, or if a species’ preferred nest substrates were listed exclusively as “deadwood” and/or “beetle borings”, that species was considered a forest specialist. If a species contained descriptions of other habitats individually, or in combination with terms such as “grassland”, “heathland”, or “sand dunes” it was considered a non-forest specialist. This classification system considers both biotic and abiotic resources necessary for survival ([WallisDeVries, 2014](#)), which is more comprehensive than using only habitat descriptions. *Hylaeus difformis* for example, is a species of cavity-nesting mask bee. In [Westrich et al. 2018](#), this species’ preferred habitat is described as “open forest areas, forest edges and forest clearings”, and it was therefore classified as a forest specialist. Species in our data were compared to taxa-specific red lists to determine conservation statuses included in supplement Table S1.

2.4. Statistical analyses

Species data were pooled per plot prior to calculating abundance, diversity (Shannon index) and species richness. Plots with missing environmental variables at one or both trapping sites (seven plots) were omitted prior to analyses. Sampling completeness was assessed using species accumulation curves and jackknife1 estimation of expected total species richness. Environmental variables were assessed for collinearity using Spearman’s coefficient ([Dormann et al., 2013](#)). According to this procedure, if a pair of variables is determined to be collinear ($p > 0.70$), only one should be retained for analyses. In our data, no pair of variables was found to be collinear (Table S2). Environmental variables were additionally assessed for collinearity using variance inflation factors calculated for all environmental variables included in each model using the “vif” function (R package “car”, [Fox and Weisberg, 2019](#)). While many thresholds are available for assessing collinearity ([Menard, 2001](#), [Vittinghoff et al., 2012](#), [James et al., 2013](#)), we follow [Johnston et al. 2018](#) by using a VIF threshold of > 2.5 for eventual exclusion of environmental variables. In our data, no environmental variables included in any model exceeded this threshold (Table S4). All environmental variables listed in [Table 1](#) were used as fixed effects in models, after being centered and scaled (mean = 0, SD = 1). Moran’s I simulations were conducted on model residuals to test for spatial auto-correlation using the ‘DHARMa’ package ([Hartig, 2022](#)) (Table S3).

Analyses of abundance, diversity and species richness were all conducted for each of the following groups: 1) all cavity-nesting bee and wasp species, 2) forest specialist and 3) non-forest specialist bee and wasp species. Negative binomial generalized linear models (GLM) were used to analyze abundance, linear models to analyze diversity and negative binomial GLM’s to analyze species richness. Negative binomial

models were chosen to analyze abundance and species richness to account for possible overdispersion. All analyses were conducted in R, version 4.2.1 (R Core Team, 2022).

Solitary bee and wasp community composition was analyzed using the 'metaMDS' function (R package *vegan*, Oksanen et al., 2022) with 1,000 permutations. The ordination was made using 'bray' dissimilarities on 3 axes to reduce stress while ensuring ordination and fitting of environmental variables could still be consistently and reliably interpreted. This representation is very similar to a 2-dimensional ordination, and thus only the first two dimensions are shown. All fixed effects included in Table 1 were fitted post-hoc to the scores of the first two ordination axes using the 'envfit' function with 1,000 permutations.

3. Results

In total, 4,889 nests were collected containing 14,957 brood cells provisioned by 57 species (Table S1), representing 86 % of expected total richness (Figure S2). Of these, 36 species (63 %) were forest specialists, representing 3,147 (64 %) nests and 9,684 (65 %) of provisioned brood cells. The five most common species by abundance were: *Trypoxylon figulus* (~29 %), *Deuteragenia subintermedia* (~16 %), *Passaloecus insignis* (~8 %), *Ancistrocerus trifasciatus* (~8 %) and *Hylaeus difformis* (~5 %). The lowest four of these five were considered forest specialists in our data, while the most abundant species collected was considered a non-forest specialist.

Of the species collected, seven were red-listed as at least threatened (~2 % of individuals collected), with three species listed as endangered. The most common red-listed species, *Osmia leaiana* (13 nests, 112 individuals), was found in only four sites which contained relatively open canopies and varying amounts of deadwood. *Megachile ligniseica* (3 nests, 12 individuals), a rare and endangered species of leaf-cutter bee was found on only two sites. The remaining five red-listed species were: *Ampulex fasciata* (3 nests, 9 individuals), *Ancistrocerus scoticus* (5 nests, 9 individuals), *Discoelius zonalis* (22 nests, 69 individuals), *Symmorphus fuscipes* (2 nests, 7 individuals), and *Symmorphus murarius* (21 nests, 44 individuals).

The abundance, diversity and species richness of all species and of both habitat-based classifications decreased with increasing canopy cover and increasing elevation (Table S5). Total abundance ($z = 4.283$, $p < 0.001$), forest specialist ($z = 3.677$, $p < 0.001$) and non-forest specialist ($z = 2.530$, $p = 0.011$) abundances all increased with increasing amounts of standing deadwood (Fig. 1e). Forest specialist diversity also increased with standing deadwood ($t = 2.292$, $p = 0.024$) (Fig. 2b), as well as stand structural complexity ($t = 3.321$, $p = 0.001$) (Fig. 2a). The abundance of forest specialists decreased with lying deadwood DBH ($z = -2.229$, $p = 0.026$) (Fig. 1c) while the abundance of non-forest specialists decreased with deciduous tree share ($z = -2.131$, $p = 0.033$) (Fig. 1a). Total and forest specialist abundances both increased with increasing herb cover ($z = 2.302$, $p = 0.021$, $z = 2.414$, $p = 0.016$) (Fig. 1b). Each metric tested, except for non-forest specialist diversity, increased significantly with increasing stand structural complexity (Table S5). Diversity of all species increased with understory species richness ($t = 2.324$, $p = 0.022$).

The richness of all three groups tested decreased with both canopy cover and elevation (Table S5) while increasing with both standing deadwood and stand structural complexity (Table S5). Only total species richness increased with understory species richness ($z = 2.157$, $p = 0.031$) while only non-forest species richness decreased with forest cover ($z = -2.097$, $p = 0.036$) (Fig. 3). A summary of models and their coefficients is available in the supplement (Table S5). Moran's I tests found no significant spatial autocorrelation in any model residuals (Table S3).

NMDS and post-hoc fitting of environmental variables revealed significant influences from canopy cover ($R^2 = 0.151$, $p < 0.001$), elevation ($R^2 = 0.072$, $p = 0.011$) herb cover ($R^2 = 0.065$, $p = 0.027$), SSCI ($R^2 = 0.073$, $p = 0.007$) and understory species richness ($R^2 = 0.064$, $p =$

0.021) on community composition of all species (Fig. 4) (Table S6). Ordination of forest specialist communities showed significant structuring from variables similar to the ordination of all species, namely canopy cover ($R^2 = 0.184$, $p < 0.001$), elevation ($R^2 = 0.056$, $p = 0.032$), SSCI ($R^2 = 0.056$, $p = 0.033$) and understory species richness ($R^2 = 0.081$, $p = 0.008$). Additionally, deciduous tree share was significant ($R^2 = 0.053$, $p = 0.038$) (Fig. 5a, Table S7). Non-forest specialist communities were structured by only forest cover ($R^2 = 0.061$, $p = 0.044$) and understory species richness ($R^2 = 0.071$, $p = 0.027$) (Fig. 5b, Table S8).

4. Discussion

4.1. Overall bee and wasp biodiversity

Most cavity-nesting bees and wasps in Central Europe nest in sun exposed sites (Westerfelt et al., 2015, Staab et al., 2018, Eckerter et al., 2022), indicating canopy cover may be a mediator of also forest-specialist bees and wasps, which have often been considered to prefer more shaded nesting sites. Canopy-packing by deciduous tree species (Jucker et al., 2015, Zheng et al., 2022), where tree canopies together grow to occupy as much of the open canopy as possible, may therefore potentially explain the observed decrease in non-forest specialists (less tolerant of shaded conditions) with increasing deciduous tree share. While no larger trends in our data can support this, it may be locally possible and potentially influenced communities on only a few plots thusly. Many taxa including birds (Przepióra et al., 2020), bats (Tena et al., 2020) and numerous insect groups (Bouget and Duelli, 2004, Lachat et al., 2016, Sebek et al., 2016, Perry et al., 2018) benefit from increased canopy openness in forests, and therefore forest specialist bees and wasps may be indicative for other communities.

While not a forest structural variable, elevation was important for explaining our data considering the varying relationships it shares with different insect communities (Hodkinson, 2005), most importantly the truncation of insect flight periods due to colder temperature and shorter seasons (Hoiss et al., 2012, Perillo et al., 2017). The reduction of insect activity due to elevation is observed in the elevation gradient of our study plots as every biodiversity metric decreased.

4.2. Abundance

Abundance was hypothesized to increase with both lying and standing deadwood via the availability of nesting substrates (Westerfelt et al., 2015, Eckerter et al., 2021), but this was confirmed for only standing deadwood, and contradicted by the decrease in forest specialist abundance with lying deadwood. This could be due to very large amounts of deadwood covering the forest floor, reducing the growth of resource-providing vascular plants and creating flight barriers to foraging bees and wasps (compare Staab et al., 2022). While it has been observed that lying deadwood of later decay stages has a positive effect on the abundance and richness of vascular plants (Čečko et al., 2015), our study included only early deadwood decay stages. Our data cannot support any conclusions regarding the relationship between lying deadwood and herb cover or understory richness, but we assume that the covering of the forest floor and the prevention of understory plant growth occurred on only those plots with very high lying deadwood amounts. This reduction in plant growth, combined with flight barriers created by deadwood in such amounts could possibly be an explanation for the observed decrease of forest specialist abundance. The use of deadwood by cavity-nesting bees and wasps is secondary, following the use by primary saproxylics (Parisi et al., 2018, Dufour-Pelletier et al., 2020), which create cavities corresponding to body size (Gillespie et al., 2017), which are subsequently utilized by bees and wasps for nesting. The presence of a large community of cavity-nesting bees and wasps then possibly signifies the presence of a similarly large (in terms of abundance and variation in body size) community of saproxylics. It is

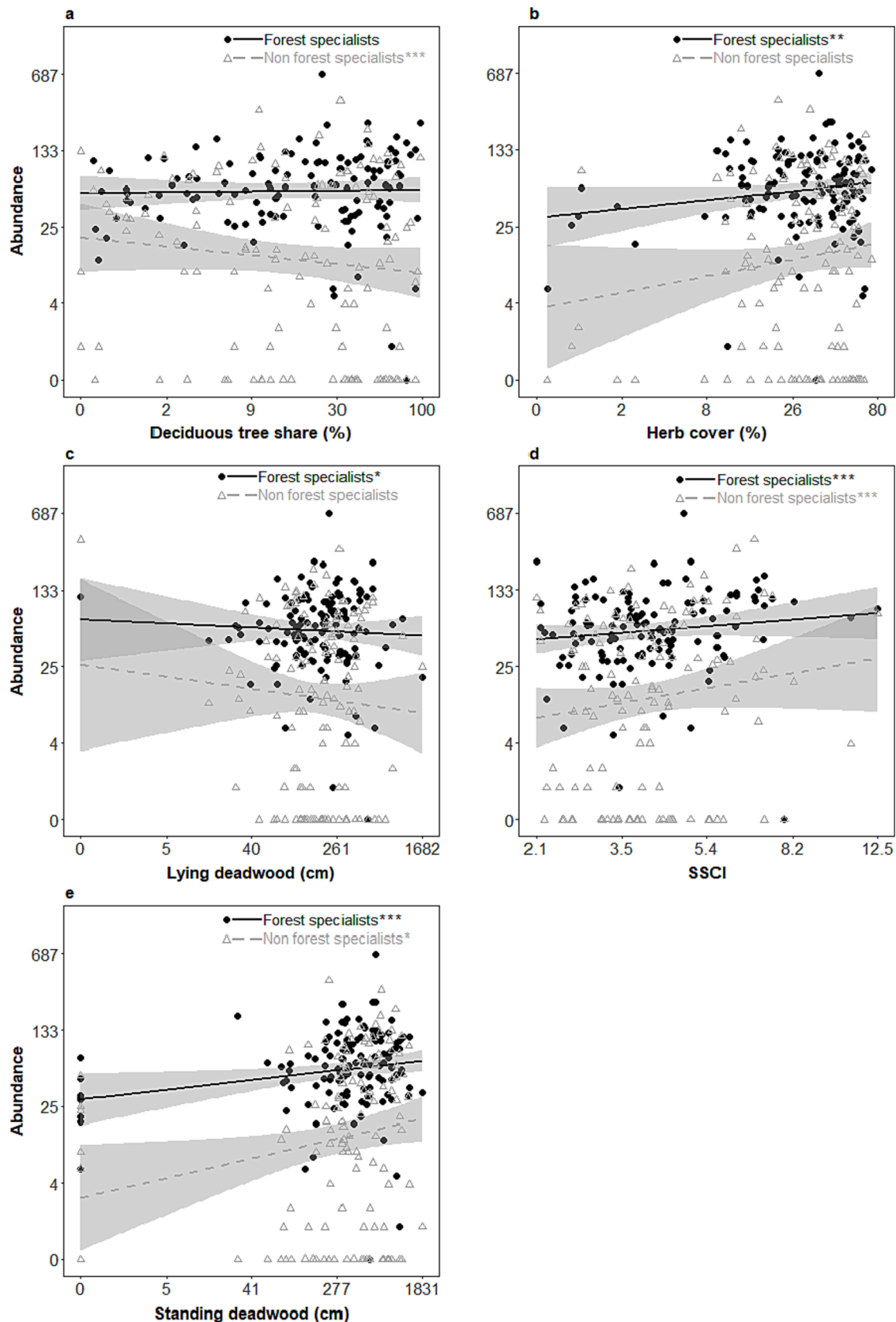


Fig. 1. Abundance of cavity-nesting bee and wasp forest (solid black points) and non-forest specialists (hollow light gray triangles) and significant fixed effects: a) deciduous tree share (%), b) herb cover (%), c) lying deadwood DBH (cm), d) stand structural complexity index (SSCI), e) standing deadwood DBH (cm). All variables were log-transformed ($\log_{10}(x + 1)$) prior to plotting, with real values displayed at axes. Trend lines from generalized linear models are depicted for both forest specialists (solid black) and non-forest specialists (dashed light gray), with 95 % confidence intervals colored in dark gray. Significance is indicated by * in the legend.

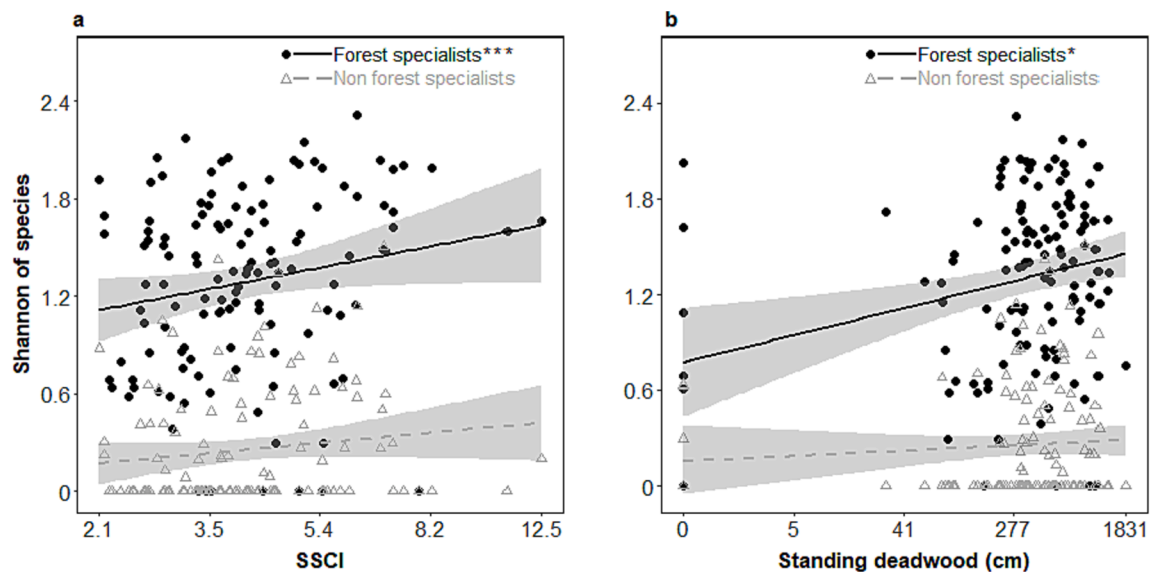


Fig. 2. Diversity of cavity-nesting bee and wasp forest (solid black points) and non-forest specialists (hollow light gray triangles) and significant fixed effects: a) stand structural complexity index (SSCI), b) standing deadwood DBH (cm). Both SSCI and standing deadwood DBH were log-transformed ($\log_{10}(x + 1)$) prior to plotting, with real values displayed at axes. Trend lines from linear models are depicted for both forest specialists (solid black) and non-forest specialists (dashed light gray), with 95 % confidence intervals colored in dark gray. Significance is indicated by * in the legend.

interesting that the abundance of all groups increased with SSCI because this structural variable may better approximate the diverse range of nesting substrates used by cavity-nesting bees and wasps such as more standing deadwood and tree microhabitats (Frey et al., 2020), hanging branches (Seidel, 2017), and denser forest stand layering (Ehbrecht et al., 2021). The positive relationships between stand structural complexity and abundance may be further augmented by increased microclimate stability in sun-exposed sites (Ehbrecht et al., 2017) and increased foraging opportunities from higher plant diversity (Ehbrecht et al., 2021).

The importance of greater herb cover is most apparent for our studied taxa, with palynivorous bees and adult wasps feeding on flowering herbs and predatory wasps hunting and provisioning insect herbivores and arachnids, which are more abundant in more developed understories (Hammond and Miller, 1998; Schuldt et al., 2008; Shao et al., 2021). While the abundance of forest specialists was related to herb cover, the abundance of non-forest specialists was not, possibly indicating a stronger link between biotic elements (forest specialists and biotic resources) in forest habitat (Kimberley et al., 2014; Jiménez-Alfaro et al., 2018; Zheng et al., 2022). Similar studies have noted the importance of biotic habitat elements such as pollen producing trees for bees and wasps (Rubene et al., 2015; Urban-Mead et al., 2021), but without close examination of the specific biotic links between specialists (e.g. pollen producing forest specialist plants visited by a single forest specialist bee species). It would therefore be interesting to examine the strength of specialist-specialist interactions as affected by forest structure. In addition, more research is needed to investigate the relationships between insects and plant hosts, to determine if plant habitat specialization is more important than quantity in driving bee and wasp abundance in forests. Furthermore, numerous other insect communities benefit from greater herb cover, such as hoverflies (Fayt et al., 2006), ground beetles (Negro et al., 2014) and flies (Scherber et al., 2014), indicating bee and wasp abundance increases could occur in parallel to, and be representative of other groups.

A synergy between canopy openness, standing deadwood and herb cover may exist through increased light exposure (Vockenhuber et al., 2011; Doerfler et al., 2018; Depauw et al., 2019) and microclimate. These structural elements can be directly influenced by management decisions during harvesting which can increase herb cover (Dormann et al., 2020) and sun exposure to deadwood substrates via single-tree

removal and high stump retention. An interesting next step would be to follow studies practicing deadwood enrichment (Sandström et al., 2019; Eckerter et al., 2021), albeit with new techniques such as high-girdling so the synergy between deadwood creation and increased light exposure can be tested for primary and secondary saproxylic taxa.

4.3. Diversity and species richness

Our hypotheses that diversity and richness increase with increasing diversity of forest structural variables were partially confirmed. Only forest specialist diversity increased with increasing stand structural complexity and standing deadwood, driving the same relationship between diversity of all species and stand structural complexity. This indicates that forest structure is more important for specialist than non-specialist diversity and that species differentially utilize nesting substrates in forests. Forest specialist cavity-nesting bees and wasps benefit more strongly from retention and could potentially be used as indicators for stand structural complexity, which is often difficult to quantify. Spider-hunting wasps in the Genus *Deuteraenia* for example, are highly associated with standing deadwood for nesting, as their nest building strategies involve pulling and dragging paralyzed prey. These wasps are found in predominantly forests compared to more characteristically open habitats such as meadows, or even forest clear cuts. As such the species of this genus can be used to indicate not only deadwood suitable for nesting but intact forest habitat and structural complexity. Such taxa can be used as indicators of high stand structural complexity to indicate the presence of old-growth forest characteristics (Franklin and Pelt, 2004), which are prioritized in biodiversity-focused conservation (Bauhus et al., 2009).

Vertical heterogeneity was unrelated to the diversity or richness of any group tested, indicating the vegetation increasing vertical heterogeneity is less likely to provide resources (such as pollen or prey) or nesting sites to cavity-nesting bees and wasps. The absence of any effect from increased vertical heterogeneity may also indicate that sampling of additional forest strata is necessary as our measure of vertical heterogeneity was not limited in height, and bees and wasps were sampled in only the understory. Similar studies found distinct communities in canopies when compared to the understory (Sobek et al., 2009; Urban-Mead et al., 2021), which may not necessarily share similar relationships with forest structural variables as we observed in understory

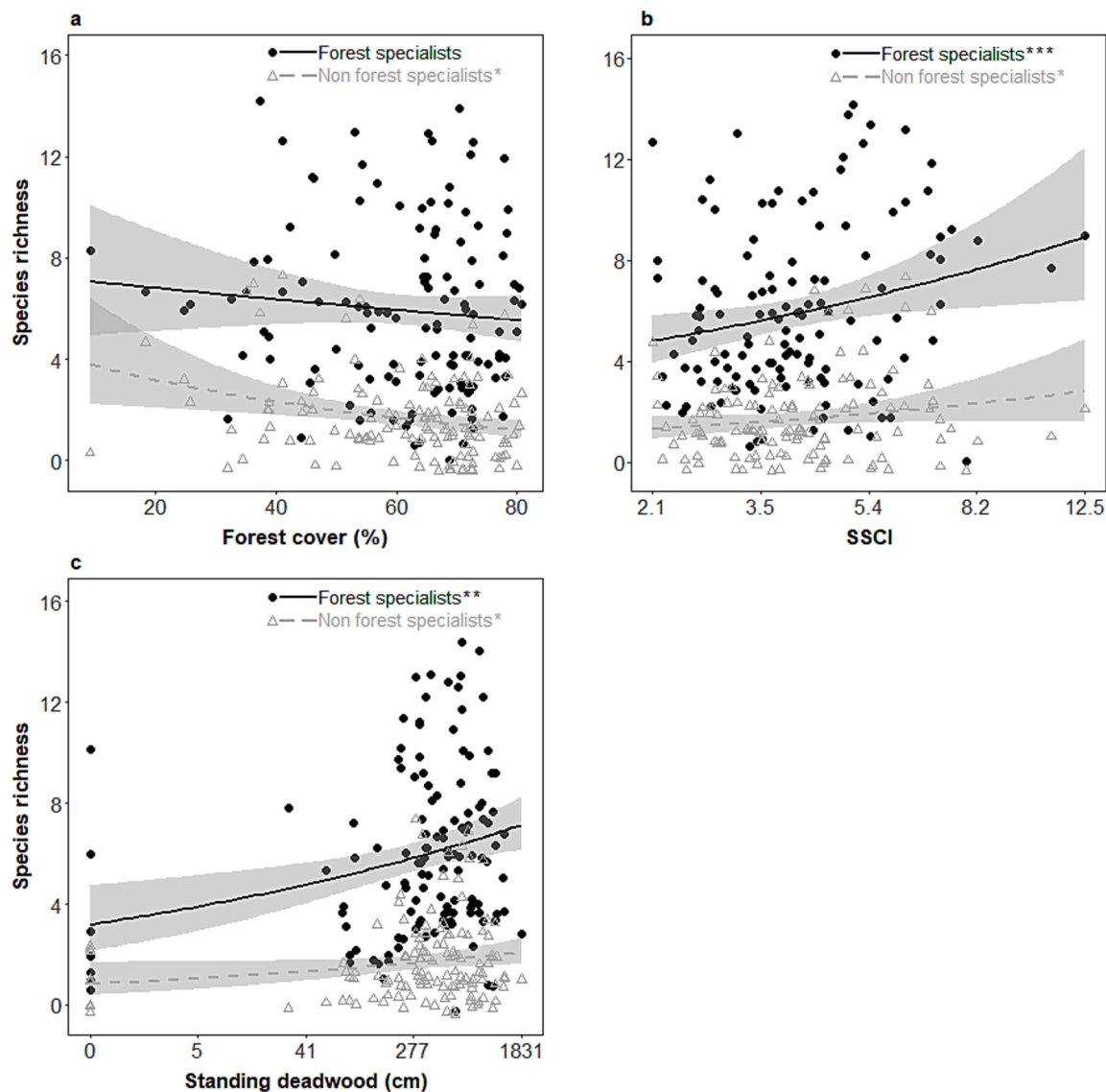


Fig. 3. Species richness of cavity-nesting bee and wasp forest (solid black points) and non-forest specialists (hollow light gray triangles) and significant fixed effects: a) forest cover (%), b) stand structural complexity index (SSCI), and c) standing deadwood DBH (cm). SSCI and standing deadwood DBH were log-transformed ($\log_{10}(x + 1)$) prior to plotting, with real values displayed at axes. Trend lines from negative binomial generalized linear models are depicted for both forest specialists (solid black) and non-forest specialists (dashed light gray), with 95 % confidence intervals colored in dark gray. Significance is indicated by * in the legend.

communities. Sampling of the forest canopy using similar methods, across forest types and with canopy structure quantified would thus allow to disentangle the role of vertical stratification.

While the decrease in non-forest specialist species richness with increasing forest cover in the surrounding of the plot is somewhat unclear, it is possible that it is related to species spillover from non-forest habitats (Brudvig et al., 2009, Löhms et al., 2014, Collado et al., 2019, Blitzer et al., 2012), on plots with low surrounding forest cover. It is important however to note that the minimum forest cover value in our data was 39 %, and thus to fully characterize this potential spillover effect, sampling the full gradient of forest cover would be necessary, including areas with very low surrounding forest cover. Our results nevertheless further emphasize that greater forest cover is needed in conservation efforts seeking to promote only forest specialists, regardless of the other structural elements retained which support all species.

4.4. Community composition

The composition of all species was structured by the same

environmental variables which were significant for individual models of biodiversity metrics, namely canopy cover, stand structural complexity, elevation, herb cover and understory species richness. Canopy cover ordinated against herb cover and understory species richness, indicating that it may structure communities by decreasing activity via changes in biotic and abiotic elements (Muscolo et al., 2014), namely sunlight exposure which has cascading effects on understory plant growth (Dormann et al., 2020). Interestingly, communities from sites with greater canopy cover were almost entirely comprised of forest specialists, despite the negative responses of their individual biodiversity metrics. This indicates that while forest specialist bees and wasps prefer nesting in sun-exposed sites, they are at least tolerant of more shaded conditions. In light of these results, localized reduction of canopy cover (e.g. via single tree felling) can potentially be used as a tool during retention to promote certain specialist taxa via increased light exposure and understory plant growth. Conversely, canopy can be strategically maintained to exclude non-forest specialists from the areas where canopy has been opened.

Composition differed between habitat-based classifications, with

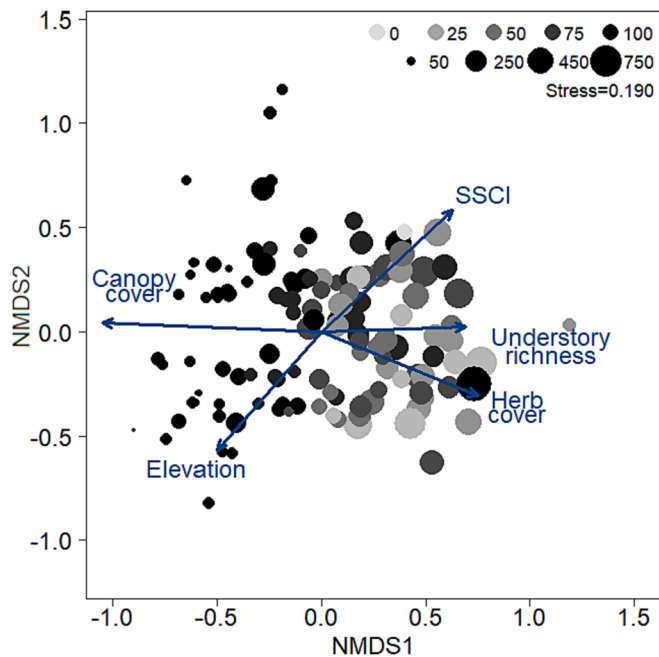


Fig. 4. NMDS ('metaMDS', iterations = 1000) of cavity-nesting bee and wasp species matrix using Bray-Curtis dissimilarities at 0.190 stress. Environmental variables were fitted post-hoc to the scores of the first two ordination axes using the 'envfit' function with 1,000 permutations, with only significant ($p < 0.05$) correlations plotted as arrows. Point color corresponds to the proportion of forest specialists sampled, as a gradient from light gray (0% forest specialist) to black (100% forest specialist). Point sizes correspond to the number of individuals sampled.

forest specialist communities structured by more forest variables (namely deciduous tree share, stand structural complexity and canopy cover) while non-forest specialist composition was structured by only forest cover in the area surrounding plots and understory species richness. While this may further indicate potential species-spillover effects, our data cannot test such conclusions without sampling of habitats outside of forests, with forest cover $< 10\%$, or forest research sites with

surrounding habitats quantified with variables complementary to forest cover (e.g. grass cover in surrounding grassland habitats) (Gao, 2006). Similar studies of aculeate Hymenoptera have found community changes across different habitats (Neumüller et al., 2020) and habitat mosaics (Pereira-Peixoto et al., 2014), but have not examined whether such changes have negative impacts on specific communities. Additionally, it would be interesting in the context of forests, to test whether certain structural variables buffer such effects and if the surrounding habitat mosaic influences potential spillover. Importantly, forest specialist communities are more strongly related to forest variables, and therefore must be considered when developing biodiversity-focused forest conservation strategies and assessing their impacts.

5. Conclusions

The biodiversity metrics of forest specialists showed stronger relationships to structural elements such as standing deadwood, which can be augmented through retention practices. Non-forest specialists respond similarly to increasing nesting substrates in terms of abundance, but showed negative relationships to the share of deciduous trees in plots and the surrounding forest cover (1 km radius). Hence the promotion of forest specialist bees and wasps through retention of structural variables such as standing deadwood is most effective in landscapes with high forest cover. All species of cavity-nesting bees and wasps could respond positively to the synergies created by single-tree or selective harvesting, which open forest canopies in a patchy way and increase understory plant growth via light exposure. Additionally, the simultaneous retention of standing dead trees or high-stumps during harvesting create additional nesting resources supporting most cavity-nesting bee and wasp species.

Declarations

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Availability of data and material

Data and material for this work are available upon request to the corresponding author.

Code availability

Codes are available upon request to the corresponding author.

Authors contributions

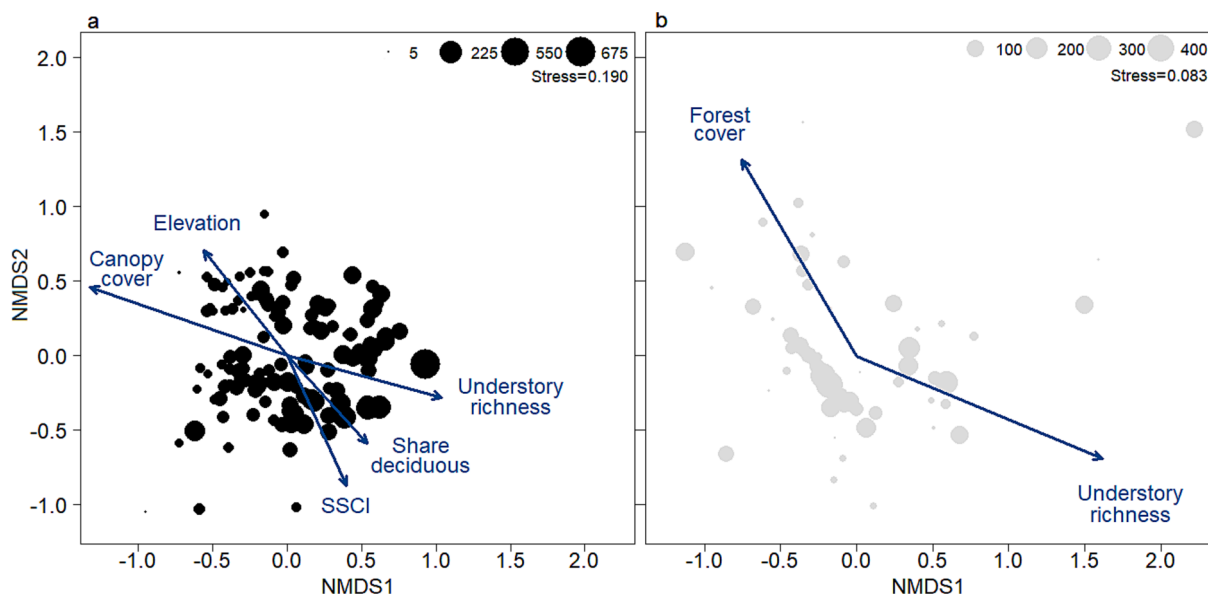


Fig. 5. NMDS ('metaMDS', iterations = 1000) of cavity-nesting bee and wasp forest (a) and non-forest (b) specialist species matrices using Bray-Curtis dissimilarities at 0.190 and 0.083 stress values respectively. Environmental variables were fitted post-hoc to the scores of the first two ordination axes using the 'envfit' function with 1,000 permutations, with only significant ($p < 0.05$) correlations plotted as arrows. Point sizes correspond to the number of individuals sampled.

NJR conceived the research question and hypotheses, conducted data collection, analyses and drafted the manuscript. MS provided conceptual and analytical advisement and reviewed drafts of this work. LSR participated in fieldwork and conceptual development. JF contributed remote sensing data as well as reviewing drafts of the manuscript. JB provided conceptual interpretation of results. AMK and MS designed the research. All authors commented the manuscript.

Ethics approval

NJR reports this work was carried out in compliance with the Guidelines for safeguarding good research practice, laid out by the German Research Foundation (DFG).

Consent to participate

Not applicable.

Consent for publication

NJR grants full consent for the publication of this manuscript.

CRediT authorship contribution statement

Nolan J. Rappa: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Michael Staab:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Laura-Sophia Ruppert:** Conceptualization, Investigation, Writing – review & editing. **Julian Frey:** Data curation, Writing – review & editing. **Jürgen Bauhus:** Conceptualization, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Alexandra-Maria Klein:** Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration, Funding acquisition.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120709>.

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