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Original Articles

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ABSTRACT

Forest canopies host an abundant but often neglected diversity of arthropods, which requires careful attention in times of ongoing biodiversity loss. Yet, how tree species composition interacts with canopy structure in shaping arthropod communities remains largely unknown. Here, by combining mobile laser scanning and insecticidal fogging with a machine learning algorithm, we studied which canopy architectural properties affect canopy arthropod communities in monospecific and mixed stands of broadleaved European beech and the coniferous Norway spruce and non-native Douglas fir in Germany. Evaluating the abundances and ecological guild diversity of ∼ 90,000 arthropods and 27 partly novel high-resolution structural variables, we identified vegetation volume and tree species identity as weak predictors of arthropod abundance and ecological guild diversity. In contrast, structural heterogeneity, i.e. structural complexity, vertical layering and variability of canopy gaps—which were highest in coniferous stands—were strong positive drivers. Despite this, arthropod ecological guild diversity was lower in non-native Douglas fir. Mixed stands had intermediate arthropod abundance and ecological guild diversity. Our study shows that habitat heterogeneity and tree species-identity are closely interlinked in shaping associated canopy arthropod communities. Positive effects of habitat heterogeneity on arthropod ecological guild diversity were often uncoupled from resource availability, and the key role of our novel intra-canopy gap indices suggests that they should be considered as indicators in future research on forest heterogeneity-diversity relationships. Broadleaf-conifer mixtures may be suitable to mediate negative tree-species identity effects when adapting forests to global change.

1. Introduction

Arthropods are a key component of forest biodiversity, supporting ecosystem services such as pest control, regulation of herbivory or prey provision (Maleque et al., 2006). However, much of this arthropod diversity is located in the understudied canopy (Wardhaugh, 2014, Floren et al., 2022), limiting our understanding of how it is affected by natural or management-induced changes in forest structure and tree species composition. As biodiversity is declining in forests (Seibold et al., 2019, Ulyshen and Horn, 2023), such knowledge is urgently needed to adapt forests to global environmental changes while securing forest functioning (Wildermuth et al., 2023a).

Canopy traits such as leaf biomass, branch density and structural complexity are important drivers of associated arthropod diversity (Nakamura et al., 2017, Sallé et al., 2021). Canopy biomass and vegetation density define the available resource amount and habitat space (Neves et al., 2013), supporting canopy arthropod abundance and diversity (Müller et al., 2018, Knuff et al., 2020). Further, vertical stratification and horizontal heterogeneity of forest structures lead to spatial differences in temperature, humidity and light availability (Sallé et al., 2021, Xing et al., 2023). These microclimatic conditions shape various habitats for arthropods and increase their abundance and diversity (Zeller et al., 2023).

Providing diverse habitats and shelter from predation or competition pressure, structurally complex vegetation often hosts more diverse arthropod communities (Stein and Kreft, 2015, Rappa et al., 2023, Wildermuth et al., 2023a). However, the underlying drivers of positive heterogeneity-diversity relationships are controversially considered as either direct, with new niches allowing establishment of new species (*habitat-heterogeneity hypothesis*; Tews et al., 2004) or indirect, via increasing numbers of similar habitats which increase arthropod abundances (*more-individuals hypothesis*; Müller et al., 2018). The *more-individuals hypothesis* postulates that complex vegetation structure increases resource availability (i.e. energy), supporting higher arthropod abundances, and thus, more species reach viable population sizes (Müller et al., 2018, Storch et al., 2018). To approach this unresolved ecological question, the description of canopy habitats should cover all three spatial dimensions (Acebes et al., 2021). The advent of Light Detection and Ranging (LiDAR) enabled the three-dimensional rendering of structural characteristics (Seidel et al., 2011). LiDAR allows for rapid, precise depiction of scanned 3D structures on high spatial extent (Kane et al., 2010). Analyses of LiDAR data found canopy structure to be closely linked to arthropod abundances and diversity (Müller et al., 2018). Yet, previous LiDAR studies on structural dependencies of canopy arthropods mostly used airborne laser scanning, the coarse resolution of which cannot depict habitat structures below the tree crown in detail (Hilker et al., 2010).

Irrespective of their architecture, tree species shape associated arthropod communities, e.g. via nutrient quality (Tobisch et al., 2023). Disentangling such tree species effects from general structural dependencies is thus a major challenge for biodiversity research in canopies (Nakamura et al., 2017). Moreover, it remains unclear how mixing tree species alters canopy structural complexity and its habitat suitability for arthropods. This becomes relevant when considering that natural and management adaptations to global environmental changes lead to altered tree species compositions and introduction of new tree species (Löf et al., 2019). In Central Europe, recent diebacks of Norway spruce (*Picea abies* (L.) H.KARST.) call for alternative management strategies, such as planting drought-resistant species like non-native Douglas fir (*Pseudotsuga menziesii* (MIRBEL) FRANCO). Admixing Douglas fir with European beech (*Fagus sylvatica* L.), a native deciduous species with high conservational value, is considered a promising approach to adapt forests to environmental change (Thurm and Pretzsch, 2016). Further, such mixtures might increase canopy structural complexity via architectural complementarity (Fotis et al., 2018). However, negative effects of non-native tree species on native tree populations and arthropod communities are a potential threat (Gossner and Ammer, 2006, Thurm and Pretzsch, 2016, Wildermuth et al., 2023c). To understand whether negative effects of non-native tree species on native arthropod communities are driven by a reduction of adapted arthropod species (Berthelot et al., 2023) or by structural differences between tree species, we need to shed light on how non-native tree species interact with native ones in influencing canopy structure and associated arthropod communities.

However, canopy-associated arthropod communities are complex and arthropods of differing mobility or feeding niche have different structural requirements and thus, their responses to habitat heterogeneity may vary (Heidrich et al., 2020). Flying arthropods may require

different gap structures than non-flying taxa (Dial et al., 2006), and primary consumers such as herbivorous arthropods were shown to depend more on tree species identity and its specific resources, whereas secondary consumers such as predatory arthropods are strongly driven by tree structural architecture (Wildermuth et al., 2023a,c). Yet, commonly used activity-based traps capture only a fraction of the community (Floren, 2010, Floren et al., 2022).

Here, we addressed these shortcomings by sampling arthropods with insecticidal knockdown and using mobile laser scanning to quantify stand structure in 20 pure and mixed plots of native European beech, native Norway spruce and non-native Douglas fir in Germany. To disentangle the roles of structure and tree species identity in driving abundance and ecological guild diversity of canopy arthropods, we applied a machine-learning analysis with *a posteriori* variable selection to consider 27, partly novel scan-based structural properties as linear or non-linear predictors. This component-wise boosting algorithm (Bühlmann and Hothorn, 2007) allows for simultaneous selection of model terms and estimation of model parameters. The novel structural properties analyzed describe gap sizes and distribution within the canopy (*intra-canopy gaps*). Considering the coverage of multiple ecological arthropod guilds with varying mobility and feeding habits and therefore different structural requirements, we hypothesized that (1) structural heterogeneity, especially intra-canopy structure, rather than tree volume, drives canopy arthropod ecological guild diversity and abundance (*habitat-heterogeneity hypothesis*), with particularly pronounced effects for secondary consumers. Moreover, we expected that (2) tree species identity and non-nativeness strongly influence canopy arthropod abundance and diversity—particularly for primary consumers—but arthropods also respond to structural features independent of tree species. Finally, we hypothesized that (3) mixed-species plots promote structural complexity and hence increase arthropod ecological guild diversity.

2. Methods

2.1. Study site

The study was carried out in the managed Solling forest, North-West Germany (N51.666, E9.569). We sampled canopy arthropods and LiDAR data from 20 plots, comprising four replicates of five stand types: Monocultures of (1) European beech (*Fagus sylvatica*), (2) Douglas fir (*Pseudotsuga menziesii*), and (3) Norway spruce (*Picea abies*), as well as mixtures of beech and (4) Douglas fir, and (5) spruce. Minimum distance between plots was 100 m (mean: 1066 ± 619 m). The landscape consists of a mosaic of various stand types, from which we selected our sampling plots, depending on the suitability for canopy fogging (see Appendix: Fig. A1). The average tree age across plots was 50.3 ± 6.3 years (Appendix: Table A1). We centered the collection of arthropods around 4–6 trees in each plot, with equal tree proportions in mixed plots (Fig. 1).

2.2. Arthropod sampling

We collected canopy arthropods using knockdown insecticidal fogging between May 31st and July 3rd, 2021, with each plot being sampled once. Insecticidal fogging is considered the most effective approach to sample canopy arthropods across different forest types (Pedley et al., 2016, Floren et al., 2022). Whilst 19 plots were sampled within two weeks to keep the influence of seasonality to a minimum, one plot had to be fogged on July 3rd due to unfavorable weather conditions. Sampling of all plots took place during early morning hours under windless, dry and cloudless conditions, ensuring ideal conditions for the insecticide to rise up and for the arthropods to drop down. Using a Swingfog SN 50 fogger (Swingtec, Isny, Deutschland), we applied 1 % natural pyrethrum to the targeted tree canopies of each plot for 5–10 min. We placed four white tarps (collecting sheet), each measuring 2x3 m, underneath the target canopies, raising them ~ 1 m above the ground to prevent ground-dwelling arthropods from entering (Floren, 2010).
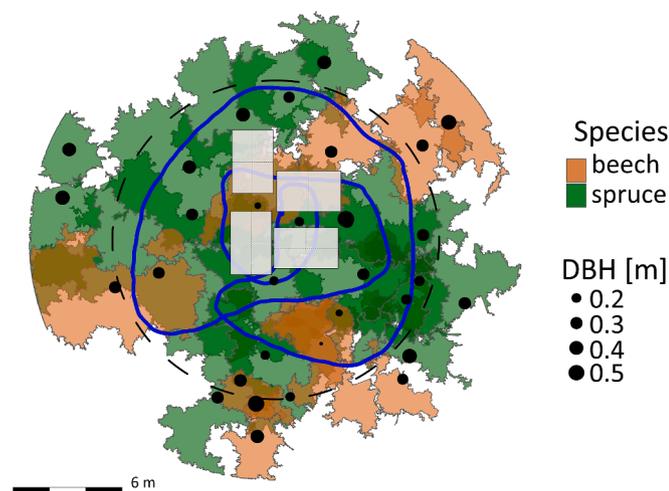
Fig. 1. Illustration of a forest stand cropped at 15 m around the center of the fogging area. The blue line indicates the scanning trajectory. The scanning range is 100 m from each point of view. The dashed circle indicates the nine-meter radius around the fogging and scanning center for the calculation of the canopy metrics. Black circles indicate tree stems position, with their size proportional to their Diameter at Breast Height (DBH). Projected canopy areas are colored according to the tree species (beech or spruce). White rectangles indicate an example of the position of the collecting sheets.

The collecting sheets were divided into four subsamples of 1.5 m^2 to enable subsequent reduction of the sample size, which can comprise arthropod abundances of up to 5,000 individuals per tarp. For two hours after fogging, we collected arthropods from the tarps and stored them in 70 % ethanol. The following analysis is based on arthropods collected from three random subsamples per tarp, resulting in 18 m^2 collecting area in each plot. One Douglas fir plot was excluded from subsequent analysis due to inadequate fogging.

To understand ecological relationships, such as heterogeneity-diversity relationships, it is important to consider ecological groups, i.e. guilds considering movement and feeding strategies beyond taxonomic classifications (Heidrich et al., 2023). We therefore counted 12 higher arthropod taxa and, if needed and within our expertise, we split them further into ecological guilds (Table 1). For example, while Arachnida and Auchenorrhyncha are themselves relatively similar in

Table 1
Overview of the considered ecological guilds, and their dominant mobility types and feeding guilds. In case of the mobility type, "dominant" refers to the ability to fly of most species within the ecological guild, but it does not necessarily describe the preferred movement strategy.

Ecological guild	Dominant mobility type	Dominant feeding guild
Lepidoptera (caterpillars)	non-flying	Herbivores
Sternorrhyncha		
Symphyta (larvae)		
Auchenorrhyncha	flying	
Coleoptera (herbivorous)		
Coleoptera (palynivorous)		
Lepidoptera (adult)		
Thysanoptera		
Coleoptera (fungivorous)	flying	Various
Coleoptera (omnivorous)		
Coleoptera (saproxylic)		
Diptera		
Heteroptera		
Hymenoptera (adult)		
Psocoptera		
Arachnida	non-flying	Carnivores
Coleoptera (carnivorous)	flying	
Mecoptera		
Neuropteroidea		

terms of feeding guild and movement strategy, and thus can be distinguished as different ecological guilds, taxonomic groups such as Coleoptera and Lepidoptera had to be divided into several subgroups because of very different lifestyles, i.e. movement and feeding strategies between lower taxa or developmental stages. To address the diversity of beetle feeding strategies (Biaggini et al., 2007), Coleoptera were identified to family level and assigned the following feeding guilds (Rappa et al., 2022): herbivores, palynivores, fungivores, saproxylics, omnivores and carnivores. Saproxylics were defined following Rappa et al. (2022) as deriving nutrition from the consumption of decaying or dead wood (e.g. Cerambycidae; see Appendix: Table A2 for the assignment of beetle families to their feeding guilds). This grouping resulted in a total of 19 ecological guilds.

2.3. Canopy structure

The vegetation structure of each plot was assessed from 3D point clouds. Four days after the fogging, we scanned the plots using a mobile laser scanner (Zeb-Horizon; 300,000 pts/sec.; accuracy: 1–3 cm; range: 100 m; Geoslam Ltd.). The scanning trajectory was centered around the fogging area (Fig. 1).

To decrease the computation time and homogenize the point density within the point cloud, we subsampled the point-cloud by removing points closer than 0.5 cm to each other (Weiser et al., 2022). Then, we normalized the point heights with ground point heights, eliminating terrain differences between plots (Roussel et al., 2020). We classified non-empty voxels of 50 cm side length as vegetation voxels and calculated the *total vegetation volume* as the sum of their volume (Atkins et al., 2018). We defined *intra-canopy gaps* (*ICG*) as three-dimensional formations of contiguous empty voxels, for which we measured height distribution (*mean* and *CV* of height), *total* and *mean ICG volume*. The minimum intra-canopy gap size was one voxel (50 cm side length). The empty volume below the canopy (*below volume*) was the largest continuous 3D gap.

Canopy height, effective number of layers and vertical diversity ratio of each plot were calculated on rasters. Rasters were produced by cropping the 3D point cloud in quadrats of 50x50 cm, and measuring each variable on each quadrat. The value found for the quadrat was attributed to the raster cell of corresponding coordinates. For each variable, we calculated the average and coefficient of variation (CV) of the values of all quadrats of a plot, giving the variable mean value as well as its spatial variability for each studied area.

Using the "lidR" R package (Roussel et al., 2020, R Core Team, 2022), we produced a canopy height raster (canopy height model, CHM) and calculated *mean canopy height*, *CV of canopy height* and the *rumple index*, i.e. the ratio between canopy surface and corresponding ground surface area (LaRue et al., 2018). The *Rumple index* is close to one for smooth canopy surfaces and increases with roughness. Considering two meters as minimum canopy height (Brokaw, 1982), we calculated the *canopy cover, number of horizontal canopy gaps, mean horizontal gap area, CV of horizontal gap area* and *total horizontal gap area* using the R package "ForestGapR" (Silva et al., 2019). The minimum size for horizontal canopy gaps corresponded to the raster resolution (50x50 cm).

Using horizontal layers of 50 cm thickness, we produced rasters of the effective number of layers of dimension 0, 1 and 2 (*ENL*; Fig. 2; Ehbrecht et al., 2016), and of the vertical diversity ratio (*VDR*; Müller et al., 2018). Using the proportion of the number of vegetation points in each layer compared to the total number of vegetation points in a given column, we calculated the dimension 0 ENL as the number of non-empty layers, the dimension 1 *ENL* as the exponential Shannon index and the dimension 2 *ENL* as the inverse Simpson index, representing the weighted diversity of vertical vegetation layers in a forest column (Table 2). The *vertical distribution ratio* (*VDR*) is the difference between the maximum and median vegetation height normalized by the maximum vegetation height (Müller et al., 2018). The higher the *VDR*, the higher is the spreading in height of the vegetation layers.
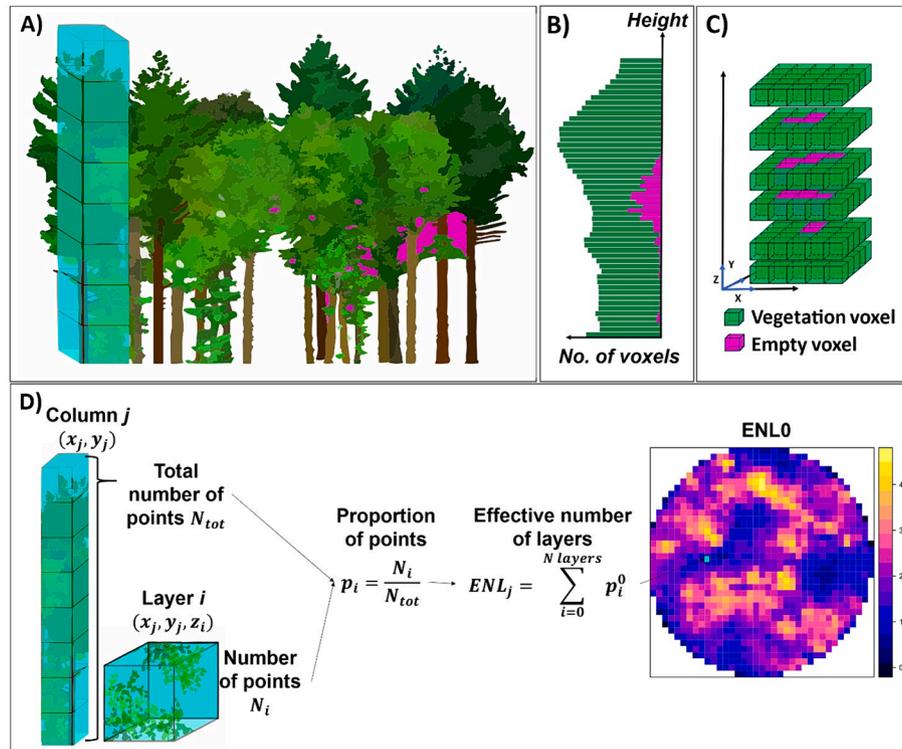
Fig. 2. Illustration of the concept and methods used to calculate the structural variables. A) Transversal view of the forest stand, B) distribution in height of the vegetation voxels used to calculate *mean* and *focal vegetation height*, C) identification of intra-canopy gaps. For each height layer, empty voxels are identified and connected to their neighbours, and then connected vertically into 3D gaps, D) the raster production of *ENL* at the stand scale. For a column of voxels (xj, yj), the *ENL* is derived from the proportion of points pi of each voxel. We produce a spatial raster of *ENL* with each cell being attributed the *ENL* value of the respective voxel column.

Structural complexity was assessed with the *box-dimension*, a fractal index of vegetation structural complexity (Mandelbrot, 1982, Seidel, 2018). The 3D point cloud was fitted in boxes of successively decreasing size, starting with a single box containing all points, and dividing box-volume by eight at each iteration until reaching the smallest box size (lower cut-off), here of 10 cm side length. At each step, we counted the number of non-empty boxes depending on their size. The *box-dimension* corresponds to the slope of the linear regression between the logarithm of the number of non-empty boxes against the logarithm of the inverse size of the corresponding box relative to the original box (Appendix: Fig. A2). Algorithmic details are presented in Arseniou et al. (2021). Analyzing increasing radii around the sampling area, *box-dimension* reached a constant from nine meters radius on. Therefore, all presented structural variables were based on cropped point clouds of nine meters radius around the sampling area center.

2.4. Statistical analysis

2.4.1. Diversity indices

We calculated arthropod richness, Shannon-Wiener diversity and evenness (*richness, SW-index* and *evenness* hereafter) based on the number of ecological guilds (*ecological guild diversity*: n = 19; referred to as diversity hereafter) per subsample and averaged the values on collection sheet level. We further added a diversity analysis only based on the grouping according to taxonomic order or suborder (n = 12; see section 2.2.), to test for differences or loss of information when only considering higher taxonomic groups without consideration of differing ecology within taxa.

2.4.2. Component-wise boosting

We performed regression model estimation with machine learning, i. e. component-wise gradient descent boosting (Bühlmann and Hothorn,

2007), using the package "mboost" (Hothorn et al., 2020). By its iterative algorithm, component-wise boosting allows simultaneous selection of relevant model terms and estimation of model parameters (Kneib et al., 2009).

Component-wise boosting includes regression estimators for each covariate("base-learners"). All variables were first scaled by subtracting the empirical mean and dividing by the empirical standard deviation of the sample. We included two base-learners per covariate, separating linear and non-linear effect components. All base-learners (each representing one degree of freedom) compete in explaining the variation in a sample of *y* by the magnitude and functional form of their effect. As long as explaining variation in *y* improves the prediction of the response (i.e. "out-of-bag observation units"), the iterative algorithm proceeds. This is called reducing the "out-of-bag predictive risk", short "risk". For each model, we used 20-fold cross-validation to set the number of boosting iterations as the point of maximum risk reduction (*early stopping*; Afshartous and De Leeuw, 2005). After the boosting, only selected (informative) base-learners were included in the final models (Mayr and Hofner, 2018). Final model performance was assessed with pseudo R^2 values, which are adapted for boosting approaches (Maloney et al., 2012). Variable importance values (calculated with the *varimp* function) show the percentage of risk reduction by each of the base-learners introduced in each model. We aggregated contributions of linear and non-linear effect components of a variable.

We grouped our models in i) arthropod abundances and ii) arthropod diversity as response (at the level of collecting sheets; n = 76) with stand type and plot as covariates, iii) structural properties per plot (n = 19) as response with stand type as covariate, iv) arthropod abundances and v) arthropod diversity as response (at the level of collecting sheets) with structural properties, stand type and plot as covariates (for model equations see Appendix: Table A3). We did so to account for unmeasured plot specificities (all models) and to analyze both total stand type effects

Table 2
Structural variables derived from the point cloud with description of their measurement. We further calculated the coefficient of variance (CV) for the following variables: *mean ICG volume, mean horizontal gap area, mean canopy height, median vegetation height, ENL0, ENL1, ENL2, VDR, mean ICG height.*

	Structural property	Unit	Description and calculation	Global point-cloud	Raster cell
Volume	**Total vegetation volume**	m³	Sum of all non-empty voxels	X	
	Below volume	m³	Sum of all empty voxels below the canopy	X	
	Total ICG volume	m³	Total volume of all intra-canopy gaps	X	
	Mean ICG volume	m³	Mean volume of intra-canopy gaps	X	
Area	**Canopy cover**	%	Ratio between number of cells of canopy height above 2 m and total number of cells		X
	Mean horizontal gap area	m²	Mean area of horizontal canopy gaps		X
	Number of horizontal gaps		Number of horizontal canopy gaps	X	X
	Total horizontal gap area	m²	Total area of all horizontal canopy gaps	X	X
Vertical	**Median vegetation height**	m	Median height of the vegetation-voxels	X	
	Focal vegetation height	m	Height of the mode of the vegetation-voxels distribution	X	
	Mean canopy height	m	Mean maximal canopy height	X	
	ENL0		Effective number of layers dimension 0: the number of vegetation layers $ENL_0 = \sum_{i=1}^{N} p_i^0$ With p_i the proportion of points in the layer i		X
	ENL1		Effective number of layers dimension 1 $ENL_1 = \exp\left(-\sum_{i=1}^{N} p_i \bullet \ln(p_i)\right)$ With p_i the proportion of points in the layer i		X
	ENL2		Effective number of layers dimension 2 $ENL_2 = 1/\sum_{i=1}^{N} p_i^2$ With p_i the proportion of points in the layer i		X
	VDR		Vertical Diversity Ratio $VDR = \frac{\max(Height) - median(Height)}{\max(Height)}$		X
	Mean ICG height	m	Mean height of intra-canopy gaps	X	
	Rumple Index		Ratio between canopy surface area and its projected area on the ground		X
3D	**Box-dimension**		Fractal index of structural complexity. Measured as the slope of the linear regression between $\log(N) = D_b * \log\left(\frac{S_0}{S}\right) + \beta$ With N the number of boxes, S the size of the box, S_0 the initial box size and D_b the box dimension	X	

(including structural effects; i, ii), and stand type effects whilst accounting for structural effects by letting stand type and structural covariates compete in explaining the arthropod responses (iv, v). Note that stand type only comprised five levels, whereas structural properties were measured in each plot (n = 19), which gives structural covariates more freedom to explain arthropod responses than stand type in the models iv) and v). Disentangling structural effects from the remaining direct tree species identity effects (e.g. resource quality or resource suitability for local arthropod communities) is thus inherently limited in that tree species identity effects, compared to structural effects, have a competitive disadvantage in the boosting selection due to their categorical nature with five possible values (stand type) and no additional continuous variable for e.g. tree species specific resource quality. Therefore, the variable importance of forest stand type in the models iv) and v) has a tendency of underestimation. The identified effects, however, are independent from the variable importance and remain unaffected by this issue.

As the response variables were arthropod counts, we modeled i) and iv) with a negative binomial distribution (*nbinomial*). In models ii) and v), we modeled the arthropod diversity indices using a gamma distribution. For both distributional models, we applied the logarithmic link function. For the structural variables (iii), we applied a Gaussian distribution (with identity link-function).

For linear relationships, we give the marginal effect sizes corresponding to the two observed extrema (η_{start}, η_{end}). For non-linear effects (hump-shaped or U-shaped relationships), we give marginal effect sizes corresponding to the three extrema ($\eta_{start}, \eta_{opt}, \eta_{end}$) on the response axis. For categorical covariates, we give the marginal effect point estimates. Bootstrap uncertainties for the marginal effect size estimations were calculated by re-sampling from the nested data-structure: plot ID was first sampled, and then the observation units (collecting sheet). This was randomly repeated 25 times ("bootstrapping").

3. Results

In the following, all described differences and effects were selected by the boosting algorithm and can therefore be regarded as informative.

3.1. Arthropod response to stand type

We analyzed a total of 86,261 arthropods. Of the 19 ecological arthropod guilds analyzed, Diptera (22,616), Psocoptera (21,335) and Sternorrhyncha (16,678) were the most abundant (Appendix: Table A4). The average *richness* per collecting sheet was 13.22 ± 0.29, mean *SW-index* was 1.75 ± 0.03 and mean *evenness* was 0.69 ± 0.01.

Models with arthropod responses and stand type and plot as covariates showed mean model performance values of 0.64 (pseudo R²) across all analyzed arthropod guilds (Appendix: Table A5). Total arthropod abundance per collecting sheet was highest in pure spruce stands and lowest in pure beech stands, whilst Douglas fir stands and mixtures hosted intermediate abundances (Fig. 3a). Spruce stands had particularly high numbers of the herbivorous guilds of Sternorrhyncha, larvae of Symphyta, Lepidoptera (caterpillars and adults), Heteroptera, palynivorous Coleoptera and herbivorous Coleoptera. In pure beech stands, most ecological guild abundances were the lowest; only the herbivorous Auchenorrhyncha were most abundant there, and least abundant in pure non-native Douglas fir stands. Douglas fir hosted the most of Neuropteroidea, Diptera and Thysanoptera. Mecoptera and omnivorous Coleoptera were the only ecological guilds with the highest numbers in mixed stands (Appendix: Table A5).

While *richness* was highest in pure and mixed spruce plots, it was lowest in pure beech plots (Fig. 3b). *SW-index* was highest in beech-spruce mixtures and lowest in pure Douglas fir stands (Fig. 3c). Similarly, *evenness* was lowest in pure Douglas fir stands, but highest in pure beech stands (Fig. 3d).
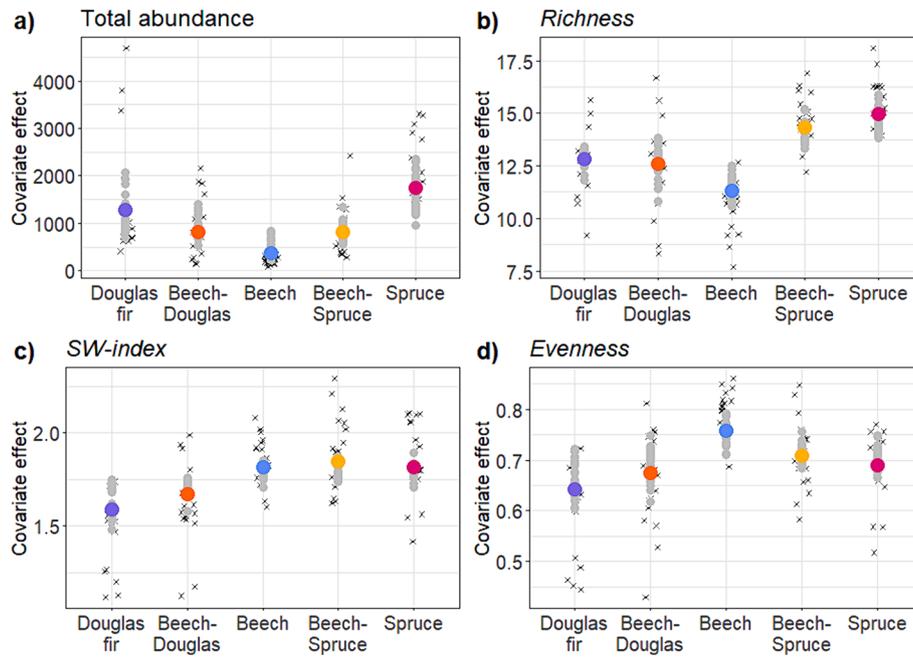
Fig. 3. Marginal effect point estimates of stand type on a) total arthropod abundance, b) *richness* c) *SW-index* (Shannon-Wiener diversity), and d) *evenness*. Bootstrap uncertainties (n = 25) are shown as light grey dots alongside the marginal effect point estimates (colored dots according to stand type). Black crosses are the original datapoints.

3.2. Structural characteristics of stand type

Models with canopy structural responses and stand type as covariate showed mean model performance values of 0.13 (pseudo R^2) across all analyzed canopy structural properties (Appendix: Table A6). Pure beech plots were characterized by an almost closed canopy (*canopy cover*: 99.91 ± 0.05 %, *mean horizontal gap area*: 0.125 ± 0.073 m^2, *CV horizontal gap area*: 0 ± 0), and proportionally, vegetation elements were the highest (*focal vegetation height*; Fig. 4a). Spatial heterogeneity of the vertical diversity ratio (*CV VDR*) was highest in pure beech and lowest in

pure conifer stands (beech: 0.399 ± 0.044, spruce: 0.242 ± 0.037, Douglas fir: 0.292 ± 0.036). *Box-dimension* of pure beech stands was the lowest (Appendix: Table A6).

Coniferous stands had higher mean *numbers of horizontal canopy gaps* than pure beech (Fig. 4b), with the highest *mean horizontal gap area* in Douglas fir (2.59 m^2 ± 1.8). Pure spruce stands had the highest number of vertical effective layers (*ENL0*; Fig. 4c) and the highest diversity in vertical layer spreading (*ENL1*, *ENL2*). Pure and mixed spruce stands had the highest structural complexity (*box-dimension*; Fig. 4d). For most structural variables, mixtures had intermediate values compared to pure
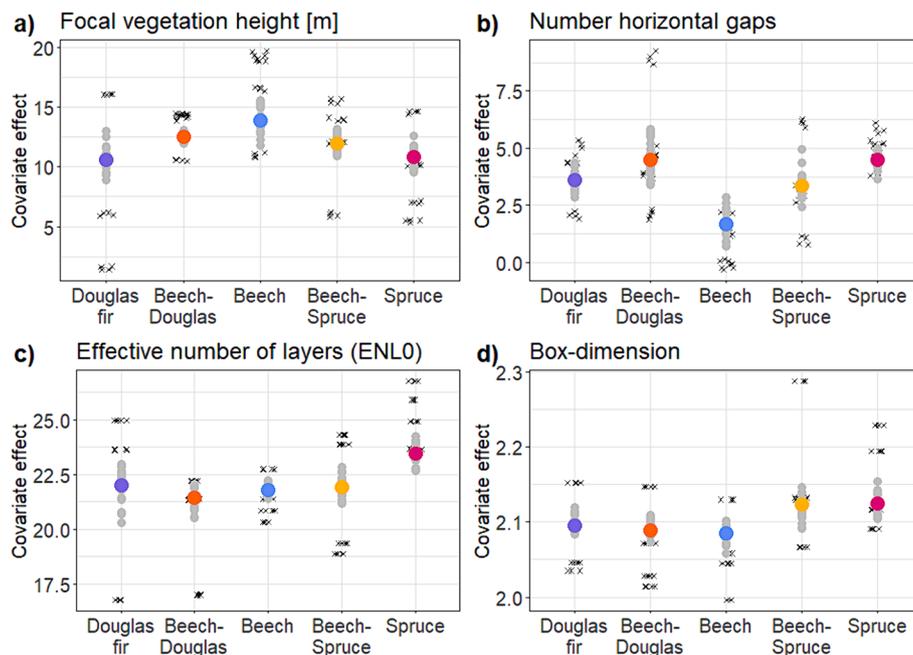
Fig. 4. Marginal effect point estimates of stand type on a) *focal vegetation height* (all non-empty voxels included), b) number of horizontal gaps interrupting the canopy, c) effective number of vertical layers (*ENL0*), and d) *box-dimension* (structural complexity). Bootstrap uncertainties (n = 25) are shown as light grey dots alongside the marginal effect point estimates (colored dots according to stand type). Black crosses are the original datapoints.

stands of the admixed species (Appendix: Table A6).

3.3. Arthropod responses to canopy structure

Models with arthropod abundances and diversity as responses and canopy structure, stand type and plot as covariates showed mean model performance values of 0.65 (pseudo R^2) across all analyzed arthropod responses (Appendix: Tables A7,A8). All 27 structural variables had informative relationships with the abundance of at least one arthropod guild or total arthropod abundance (Fig. 5a). Total arthropod abundance had relationships with 12 of the 27 structural properties and diversity indices had relationships with 16 properties (Appendix: Table A9). Only for the abundance of herbivorous Sternorrhyncha, stand type had similar variable importance (44 %) as structural properties (46 %), whereas for all other arthropod guilds structural properties had higher variable importance than stand type (Fig. 5b, Appendix: Table A7, A8; note that accumulating the variable importances of structural properties increases the underlying degrees of freedom, and see the general remark on lower freedom of stand type in explaining arthropod responses in section 2.4.2.). In the following, we group the structural variables into their spatial dimension and present those in detail which had high explanatory power for most arthropod guilds, and/or overall abundance or diversity. The results from the diversity analysis based on taxonomic groupings largely were the same compared to the results based on a finer ecological grouping and are presented in Appendix: Fig. A3, Table A10.

3.3.1. Responses to volume and area properties

The most important volume and area property was horizontal canopy gap area. *Mean horizontal gap area* related in a hump shape with 10 arthropod guilds (Fig. 5a), total abundance ($\eta_{start} = 613.3, \eta_{opt} = 1800, \eta_{end} = 684$; VImp = 22.92 %) and *richness* ($\eta_{start} = 12.7, \eta_{opt} = 13.6$,

$\eta_{end} = 12.8$; Vimp = 6.62 %). *Total horizontal gap area* showed a hump-shaped relationship with five arthropod guilds (Appendix: Table A9). *Total vegetation volume* only showed a hump-shaped relationship with arthropod *richness* (variable importance (Vimp) = 6.55 %; Fig. 6a,b). Empty volume below the canopy (*below volume*) related negatively with total arthropod abundance (marginal effect size $\eta_{start} = 1280.1, \eta_{end} = 1023$; Vimp = 3.09 %).

3.3.2. Responses to vertical and horizontal properties

Vertical distribution patterns of vegetation and gaps were important drivers for multiple ecological guilds and overall guild diversity. *Focal vegetation height* showed negative relationships with individual abundances of six arthropod guilds (Fig. 5a) and total abundance ($\eta_{start} = 2030.2, \eta_{end} = 746.8$; VImp = 16.75 %), but a positive relationship with *SW-index* ($\eta_{start} = 1.7, \eta_{end} = 1.8$; VImp = 1.28 %) and *evenness* ($\eta_{start} = 0.64, \eta_{end} = 0.75$; VImp = 5.87 %). The effective number of vertical layers (*ENL0*) related positively with eight arthropod guilds (Fig. 5a), *richness* ($\eta_{start} = 13.0, \eta_{end} = 13.5$; VImp = 3.16 %) and *SW-index* ($\eta_{start} = 1.70, \eta_{end} = 1.79$; VImp = 3.54 %), but showed no relationship with total abundance. Abundances of eight arthropod guilds showed positive relationships with *ENL1* (Shannon diversity of *ENL0*; Appendix: Table A9).

The *CV of horizontal gap area* related in a hump shape with 12 arthropod guilds, and positively with four guilds (Fig. 5a), total abundance and *richness* (VImp = 26.48 %; 22.81 %; Fig. 6c,d). It had particularly high variable importance for predatory arthropods (Appendix: Table A8). The *CV of canopy height* showed negative relationships with total abundance ($\eta_{start} = 1184.6, \eta_{end} = 1025.6$; VImp = 0.92 %) and *richness* ($\eta_{start} = 13.3, \eta_{end} = 13.0$; VImp = 0.66 %).
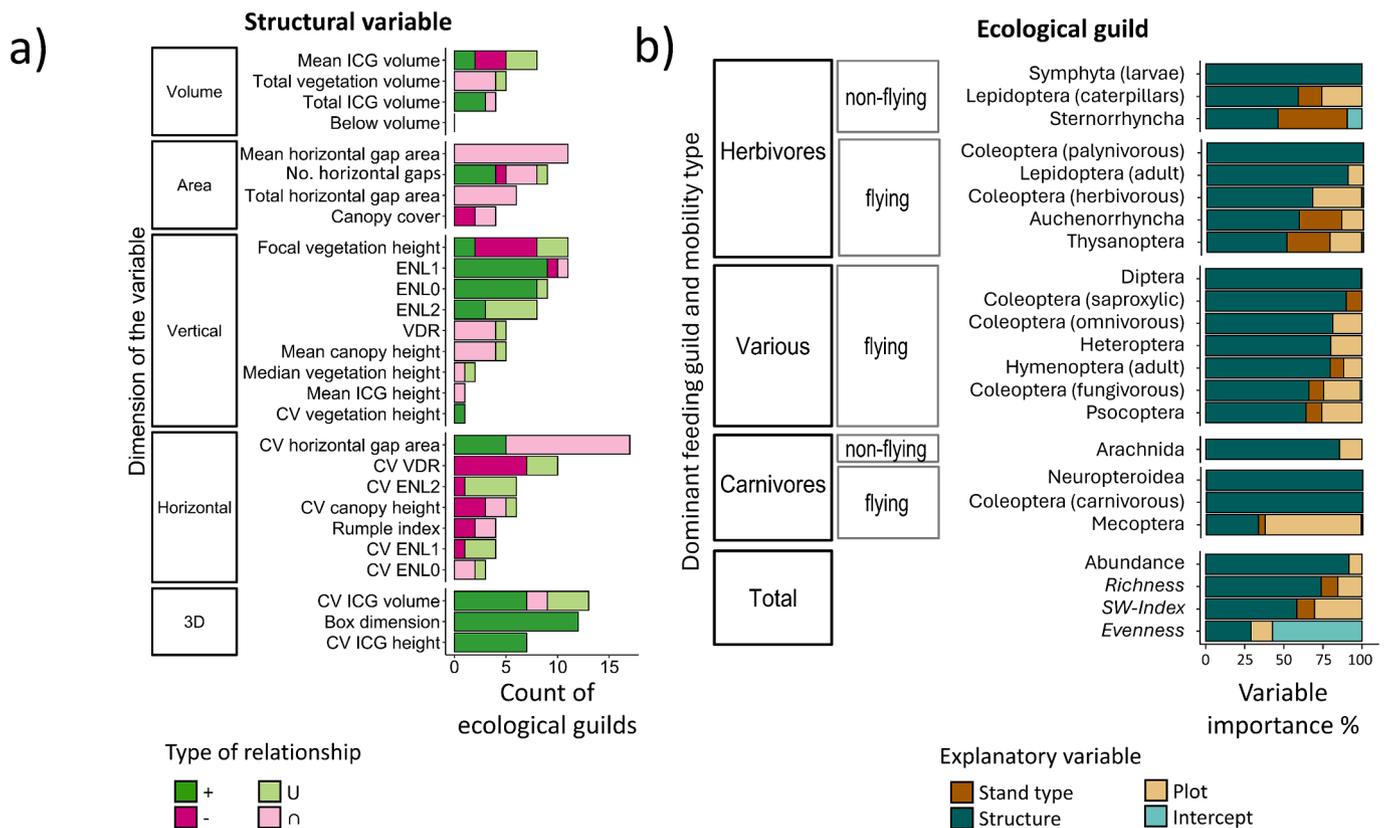
Fig. 5. a) Types and numbers of relationships between canopy structural properties and abundances of ecological arthropod guilds. Structural properties are grouped according to their dimension and sorted in decreasing numbers of significant relationships with arthropod guilds. Relationships are positive (+), negative (-), hump-shaped (∩) or U-shaped (U). Detailed results are provided in Appendix: Table A9. b) Cumulated variable importances (%) of all structural properties per arthropod response, and variable importances of stand type, plot and intercept.
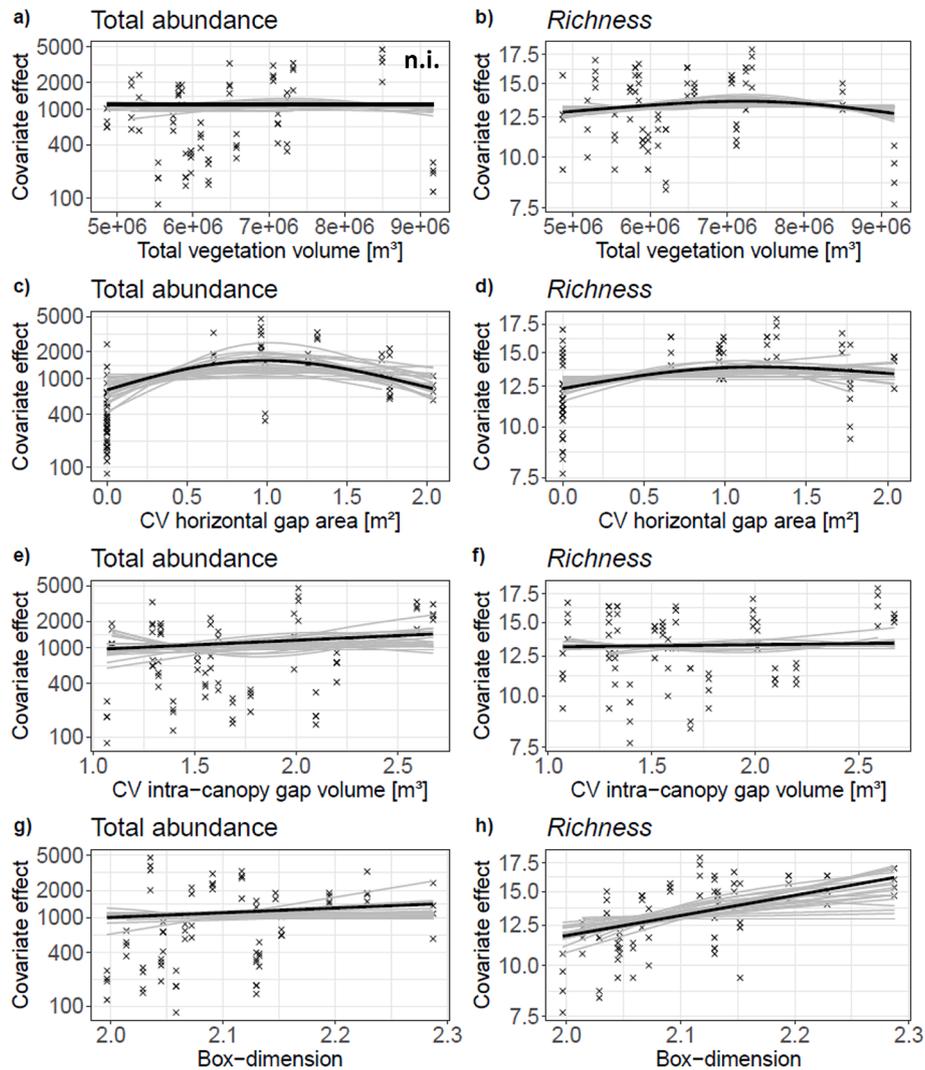
Fig. 6. Relationships between marginal effect sizes of selected structural properties and arthropod abundances and *richness*: a) total vegetation volume (non-empty voxels) and total abundance (variable importance VImp = 0 %, not informative), b) *vegetation volume* and *richness* (VImp = 6.55 %), c) coefficient of variation (CV) of horizontal gap area (interrupting the canopy) and abundance (VImp = 26.48 %), d) *CV horizontal gap area* and *richness* (VImp = 22.81 %), e) CV of intra-canopy gap (*ICG*) volume and abundance (VImp = 4.77 %), f) *CV ICG volume* and *richness* (VImp = 0.9 %), g) *box-dimension* (structural complexity) and abundance (VImp = 3.18 %), and h) *box-dimension* and *richness* (VImp = 28.42 %). Bootstrap uncertainties (n = 25) are shown as light grey lines alongside the marginal effect size estimates (black lines). Black crosses are the original datapoints.

3.3.3. Responses to three-dimensional properties

Variation of intra-canopy gap size and position, and particularly structural complexity (*box-dimension*) were important positive drivers of canopy arthropod abundance and *richness*. The *CV of ICG volume* and *height* showed positive relationships with the abundance of six, respectively seven arthropod guilds, including the non-flying spiders in both cases (Appendix: Table A9). *CV of ICG volume* further related positively with total abundance (VImp = 4.77 %; Fig. 6e) and *richness* (VImp = 0.9 %; Fig. 6f). *Box-dimension* related positively with 11 arthropod guilds (Fig. 5a), total abundance (VImp = 3.18 %; Fig. 6g) and *richness* (VImp = 28.42 %; Fig. 6h), but showed a hump-shaped relationship with *SW-index* ($\eta_{start} = 1.73, \eta_{opt} = 1.77, \eta_{end} = 1.73$; VImp = 2.38 %).

4. Discussion

We show that ground-based LiDAR and our novel structural indices can help identifying key relationships between canopy structure and arthropod communities. Structural heterogeneity within and beyond tree-identity, rather than sheer vegetation volume drove arthropod communities. Arthropod abundances and ecological guild diversity were better explained by tree structure (74 % mean total risk reduction, i.e. variable importance) than by tree species identity effects (8 %). In particular, canopy structural complexity and heterogeneity of gap structures contributed up to 50 % to the variable importance within our machine learning approach. In the following, we discuss i) which structural properties were key drivers of arthropod abundance and diversity, and what mechanisms may be active behind the observed relationships, ii) possible causes why vegetation volume turned out a weak predictor, and iii) how the observed structural effects related to tree species identity and in which cases tree species identity may have been the better predictor. Notably, only half of the canopy structural properties assessed here differed significantly between forest stand types, and our models explaining structural properties with stand type presented low pseudo R^2 values. Therefore, impacts of canopy structure on arthropod responses as elaborated below, can be regarded as independent of stand type in most cases.

4.1. Importance of habitat heterogeneity

Structural complexity (*box-dimension*), vertical layering (*ENL0,*

ENL1) and heterogeneity in size and position of gap structures were key predictors of arthropod responses with foremost positive relationships (increasing total abundance by up to ~ 500 individuals and ecological *richness* by up to ~ 5 guilds per collecting sheet). Arthropod abundance and ecological *richness* increased with *box-dimension*, which had a variable importance ~ 30 % for *richness* (Appendix: Table A7). This underlines that structurally complex forests promote arthropod diversity (Rappa et al., 2023, Wildermuth et al., 2023a) by providing multiple spatial and climatic niches and decreasing competition pressure (*habitat-heterogeneity hypothesis*; Tews et al., 2004, Stein and Kreft, 2015). Alternatively, as *box-dimension* increases with higher vegetation space filling, it could be regarded as a measure of resource availability, which increases arthropod abundance and—indirectly—diversity (*more-individuals hypothesis*; Müller et al., 2018). Yet, whilst vertical layering of vegetation had linear positive relationships with half of the arthropod guilds and *richness*, it had no effects on overall abundance. This partly corroborates that multi-layered forests promote arthropod abundances and diversity (Müller et al., 2018, Knuff et al., 2020) by increasing spatial separation of habitats (Stein and Kreft, 2015), but the fact that vertical layering did not increase total abundance and eight ecological guilds contradicts the *more-individual hypothesis*. Moreover, this underlines that arthropods of differing ecology show idiosyncratic responses to different measures of habitat heterogeneity (Swart et al., 2020). The hump-shaped relationship between *box-dimension* and *SW-index* further indicates that specific arthropod guilds might be more promoted at high levels of structural complexity than others.

Further, the widespread positive effects of intermediate to strong gap size variation (inter- and intra-canopy gaps), and linear positive effects of variability in height distribution of intra-canopy gaps (see the methods for the description of these novel indices) on arthropod abundances and *richness* provide more support for habitat heterogeneity as major driver of canopy arthropod abundance and diversity (Heidrich et al., 2020). Variable importance of horizontal gap size variation was particularly high for predatory arthropod guilds such as Arachnida, carnivorous Coleoptera and Neuropteroidea, whereas tree species identity had almost no identifiable effect on these guilds. This supports past studies showing that secondary consumers are strongly driven by tree structure and less dependent on tree-specific resources than primary consumers such as herbivores (Mupepele et al., 2014, Wildermuth et al., 2023a,c). We interpret decreasing abundances and *richness* at very high levels of gap size variation as *area-heterogeneity tradeoffs*, with extreme heterogeneity fragmenting local populations, eventually leading to increased local stochastic extinction rates (Allouche et al., 2012). Although effects of gap size variability on arthropod *richness* did not exceed more than two ecological guilds and showed low variable importance, we emphasize that these guilds are on a coarse ecological level, comprising multiple species. Therefore, the gain or loss of one ecological guild may concern crucial ecological functions provided by entire communities. High variability of canopy heights had a similar (but weak) negative effect, possibly due to harsh climatic conditions in exposed canopy tops of those trees which overtower the others (Gossner and Ammer, 2006, McCaig et al., 2020).

Arachnida in particular responded positively to both variation in intra-canopy gap size and height. As arachnids would be excluded from e.g. flight interception trap sampling, this highlights the importance of comprehensively sampling canopy arthropods with insecticidal fogging and considering different ecological guilds with different movement strategies (Floren, 2010, Heidrich et al., 2023). Thus, intra-canopy gap properties, although only assessable with ground-based laser scanning (Hilker et al., 2010), should be considered in future studies.

Regarding the debate as to whether positive heterogeneity-diversity relationships are direct (*habitat-heterogeneity hypothesis*; Tews et al., 2004, Stein and Kreft, 2015), or indirect via increasing abundances (*more-individuals hypothesis*; Müller et al., 2018, Storch et al., 2018), our study is limited in its conclusions, because the presented diversity indices are calculated at ecological guild level (n = 19), preventing

species-abundance correlations. Yet, the selected ecological guilds represent all major canopy arthropod functional groups and higher taxa, and previous research showed that order-level analyses of arthropod diversity can be a surrogate for local species diversity (Biaggini et al., 2007). Although we cannot resolve diversity on the species level and some guilds may have more species (e.g. Hymenoptera) than others (e.g. Mecoptera), we accounted for the abundances of each guild with the Shannon-Wiener diversity (*SW-index*). In the future, expanding the scope to species-level arthropod analyses may add higher resolution to our understanding of relationships between intra-canopy structures and forest biodiversity.

Although stand type beyond structural effects only had 10 % variable importance for *richness* (Fig. 5b) and had no effect on total abundance at all, we emphasize that stand type effects may be underestimated due to lower degrees of freedom and fewer data points (five stand types) compared to canopy structural properties (multiple variables, measured in each plot with n = 19). For example spruce plots hosted the highest arthropod abundances and *richness*, including highly abundant primary consumers, i.e. herbivores; and also presented the highest structural complexity and vertical layering. Thus, high arthropod *richness* in spruce stands may be explained by structural complexity, but also partly by tree species-specific plant-herbivore interactions which were not measured in this study (Leidinger et al., 2021, Rappa et al., 2022).

4.2. Empty space, but not vegetation volume, as key driver

Canopy gap properties contributed over 50 % of the total variable importance for abundance and over 30 % for *richness*. This shows the immense importance of gaps for canopy arthropods (for review see Zeller et al., 2023). Horizontal gap size had hump-shaped relationships with total abundance, most arthropod guilds and *richness*, indicating beneficial effects of medium sized gaps (effect sizes were above 1000 individuals and ~ 1 ecological guild per collecting sheet). Forest openings often have positive effects on arthropod abundances and diversity (Eckerter et al., 2022, Achury et al., 2023), potentially due to favorable microclimates, light conditions and superior food quality for herbivores (Ulyshen et al., 2005, Seibold et al., 2016). In our study, negative effects of closed canopies were connected to tree-species identity effects of beech, which had few and small gaps while hosting low arthropod abundances and *richness*. However, the hump-shaped relationship between gap size and arthropod abundance and *richness* indicates negative effects of very large gaps, which were independent of tree species identity. Negative effects of large gaps might reflect limited canopy connectivity and increased predator activity (Dial et al., 2006, Erasmy et al., 2021). In line with our finding on beneficial effects of intermediate canopy gap sizes, moderate forest disturbances and openings have widespread positive legacy effects on overall arthropod diversity in temperate forests (Viljur et al., 2022). Therefore, sanitation logging in disturbed forest should be limited to partially retain positive disturbance legacies (Cours et al., 2023).

Sparse understory, i.e. open space under the canopy (high *focal vegetation height* and *below volume*) decreased arthropod abundances by more than 200 individuals per collecting sheet, but increased *SW-index* and *evenness*. The decrease in abundance highlights the importance of understory habitats for temperate forest arthropods (Weiss et al., 2019). The increase of *SW-index* and *evenness*, however, might be due to tree-species identity effects: beech forests typically have sparse understory, while hosting few, but diverse arthropods with high *evenness* (Ottaviani et al., 2019, Wildermuth et al., 2023a). Conversely, we found no effect of vegetation volume and tree height on total arthropod abundance, while *richness* of ecological guilds responded in a hump shape to increasing vegetation volume. This does not support resource availability as positive linear predictors of arthropod abundance and diversity (Neves et al., 2013). However, because our study investigated stands of similar height and volume, the range of tree sizes may not have been large enough to detect effects of variation in vegetation volume.

4.3. Tree species identity and mixture effects

Beyond the afore-described structural properties, we found tree-species identity effects on arthropod communities, independent of any investigated structural property. For example, the lack of positive effects of vegetation volume may partly be attributed to the fact that non-native Douglas fir stands had the highest (although not significant) vegetation volume but hosted only moderately high arthropod abundances and *richness*. This supports the notion that resources provided by non-native trees cannot sustain the same abundance and diversity of arthropods as resources of native trees (Berthelot et al., 2023, Wildermuth et al., 2024). Moreover, although Douglas fir featured intermediate structural characteristics and arthropod *richness* compared to native beech and spruce, it had the lowest arthropod *SW-index* and *evenness*. This underscores previous studies showing that non-native Douglas fir cannot be regarded as equal replacement for native conifers, when considering associated arthropod diversity (Koppmann-Rumpf et al., 2017, Wildermuth et al., 2023b,c). Native spruce stands harbored particularly high abundances of herbivores including Sternorrhyncha and larvae of Lepidoptera and Symphyta, but also low *evenness*, which might reflect susceptibility to potential pest species (Gossner and Ammer, 2006, Canelles et al., 2021, Wildermuth et al., 2024). In contrast, despite low levels of complexity and arthropod abundances in beech stands, they hosted arthropod communities with high *SW-index* and *evenness*, as previously found in other studies (Gossner et al., 2009, Wildermuth et al., 2023a,c).

Mixed stands comprised intermediate arthropod abundances and *richness*, mitigating tree species effects. Likewise, structural complexity was intermediate in mixed compared to pure stands. Whilst tree species mixtures often mitigate effects of the admixed tree species on ecosystem functioning and arthropod diversity (van der Plas et al., 2016, Wildermuth et al., 2023b,c), our findings contradict previous observations that canopy complexity increased in tree species mixtures compared to monospecific stands (Fotis et al., 2018). Therefore, our results do not support the expectation that mixtures increase canopy arthropod abundance and *richness* via increasing structural complexity. We suggest that the local scale of our sampling plots may have prevented the detection of positive mixture effects, since mixtures of the tree species considered in our study were reported to increase associated diversity foremost at the landscape scale (Wildermuth et al., 2023a,2024). Moreover, local inter-plot and inter-tree architectural variability directly affects measures of structural complexity and thus may have occluded effects of increasing complexity in mixed stands (Ehrecht et al., 2017). However, arthropod *SW-index* was highest in beech-spruce mixtures and abundances of omnivorous beetles increased in mixed stands, indicating some positive mixture effects. We propose that mixtures between native beech and economically important conifers could buffer potentially negative effects of Norway spruce or non-native Douglas fir, safeguarding conservational interests in European forest management (Pretzsch, 2005, Wildermuth et al., 2023c,2024).

5. Conclusions

Our study shows that habitat heterogeneity and tree species identity interact in shaping canopy arthropod communities. Overall arthropod abundance and ecological guild diversity were better explained by tree structure than by tree identity effects. This highlights that canopy arthropod diversity can only be understood and predicted when canopy structures are extensively researched. Our quantification of canopy structure includes novel intra-canopy gap indices, which enable a more comprehensive depiction of the three-dimensional canopy habitat. These intra-canopy gaps were shown to be equally important drivers of arthropod abundances and diversity as gaps interrupting the canopy and should thus be included in future canopy research. Broadleaf-conifer mixtures mediated negative effects of non-native Douglas fir, representing a promising solution for climate change-adapted forest management.

CRediT authorship contribution statement

Benjamin Wildermuth: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Alice Penanhoat:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Holger Sennhenn-Reulen:** Writing – review & editing, Visualization, Software, Methodology, Formal analysis. **Dragan Matevski:** Writing – review & editing, Validation, Methodology, Investigation, Conceptualization. **Jochen Drescher:** Writing – review & editing, Methodology, Conceptualization. **Mélaine Aubry-Kientz:** Writing – review & editing, Supervision, Software, Methodology. **Dominik Seidel:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Andreas Schuldt:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

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 are available from GRO.data at https://doi.org/10.25625/FQLF1O.

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Appendix A. Supplementary data

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