







Forest structure and heterogeneity increase diversity and alter composition of host–parasitoid networks

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Abstract

1. Antagonistic host–parasitoid interactions can be quantified using bipartite and metanetworks, which have the potential to reveal how habitat structural elements relate to this important ecosystem function.
2. Here, we analysed the host–parasitoid interactions of cavity-nesting bees and wasps, as well as their abundance, diversity and species richness with forest structural elements from 127 forest research plots in southwestern Germany.
3. We found that parasitoid abundance, diversity and species richness all increase with host abundance, a potential mediator between parasitoids and forest structure. Both parasitoid abundance and diversity increased with stand structural complexity, possibly mediated by the abundance of hosts. In addition, parasitoid abundance increased with increasing standing deadwood and herb cover.
4. The bipartite networks of host–parasitoid interactions showed higher connectance with increasing standing deadwood, herb cover and host abundance. Analyses of interactions within the host–parasitoid metanetwork revealed that increasing host abundance and decreasing canopy cover diversify the suites of interactions present at the plot level.
5. These results demonstrate that forest structural elements can improve the stability and resilience of host–parasitoid networks by promoting parasitoids and diversifying interactions in ecological networks.

KEYWORDS

ecological networks, ecosystem functions, forest conservation, Hymenoptera, remote sensing

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INTRODUCTION

Parasitism can be quantified and visualised as a network of directed bipartite interactions (Dormann et al., 2009; Thierry et al., 2019) between parasitoids and their hosts. Bipartite networks can quantify and visualise parasitism at varying spatial and temporal scales (Mora et al., 2020; Torné-Noguera et al., 2020) and along environmental gradients (Fisogni et al., 2022). In so doing, it is possible to test the importance of habitat components on parasitism using indices quantified from individual networks. Connectance, for example, is calculated by dividing the linkage density by the number of species present with a high value indicative of a generally well-connected network, which has been associated with higher robustness (Estrada, 2007). Parasitism can be further visualised across whole host–parasitoid communities using metanetworks (Librán-Embíed et al., 2021), which quantify the co-occurrence of interactions. Thus, metanetworks have the potential to evaluate the prevalence of interactions at large spatial scales and across multiple sites and habitats (Grainger & Gilbert, 2016), where previous approaches have examined spatially or temporally isolated interaction networks (Hagen et al., 2012). Additionally, modelling of metanetwork interaction indices accounts for the spatial distributions of species (Emer et al., 2018; Li et al., 2020), revealing interactions that link distinct networks and thus support ecological functions at large spatial scales.

Parasitism is a grouping of life history strategies characterised by species living in close association with their hosts to utilise them or their resources for survival (Gullan & Cranston, 2014). A subset of parasitic species are parasitoids and kleptoparasites (parasitoids hereafter), which, though having slightly different strategies, typically result in the death of hosts to complete their lifecycles (Sedivy et al., 2013), making them functionally similar. Parasitism is an important ecosystem function, regulating populations of hosts (Lynch et al., 1998), which may be pests (Menalled et al., 2003; Mills, 2010), pathogen vectors (Plowright et al., 2017) or invasive species (Chabert et al., 2012; Duan et al., 2013). The top-down regulation of host populations by species at a high trophic position has important effects on host population dynamics (Hassell, 2001), thus cascading effects on the biotic and abiotic resources that hosts utilise (Tan et al., 2020; Vidal & Murphy, 2017). In addition, parasitoids are particularly sensitive to bottom-up effects (fluctuations in host populations) (Hassell, 2001; Singh, 2021) and microclimate variation (Kankaanpää et al., 2020; Wenda et al., 2022), making parasitoid interaction networks good proxies for evaluating habitat integrity and quality (Anderson et al., 2011; Grass et al., 2018).

In forests, the structural elements or physical structure characteristics of forest habitat (e.g. tree canopies) influencing parasitism interactions have only generally been described (Eckerter et al., 2022; Laliberté & Tylianakis, 2010; Staab et al., 2016). The structural elements of forests, and more broadly other habitats, can be quantified to allow meaningful investigations of their importance for various aspects of biodiversity (Rappa et al., 2022; Storch et al., 2018). Canopy cover, for example, while varying between the sites, is a characteristic of forest habitat and, thus, can be hypothesised to have a strong influence on forest biota (Fornoff et al., 2021; Gustafsson et al., 2019; Oettel & Lapin, 2021). Forb cover, by contrast, or the

percentage of flowering plant species, is a quantifiable metric of meadow habitats (Jiang & Hitchmough, 2022). The spatial arrangement of forest structural elements can be strongly influenced by management practices such as retention forestry (Gustafsson et al., 2012). Retention forestry emphasises maintaining forest habitat structural elements that would have been removed during timber harvest as a result of traditional management practices (e.g., deadwood removal) (Storch et al., 2020). Unique forest structural elements such as deadwood are important components of forest habitats and can have important influences on parasitism networks via the abundance and species richness of their potential hosts (Eckerter et al., 2021; Rappa et al., 2023), feeding resources (Heimpel, 2019) and microclimates (Laliberté & Tylianakis, 2010). Thus, understanding the potential effects of retention forestry on parasitism via the arrangement of forest habitat structural elements will provide valuable insights into the maintenance of this important ecosystem function (Baho et al., 2017; Holling, 1973).

Most insect species with parasite/parasitoid life history strategies are within the Hymenoptera (bees, ants and wasps) (Gullan & Cranston, 2014), and thus closer examination of these insects is necessary to characterise parasitism as an ecosystem function. Cavity-nesting bees and wasps, as well as their associated parasitoids, can be easily and reliably sampled using trap nests (Staab et al., 2018) and are thus ideal study organisms. Cavity-nesting bees and wasps locate hollow cavities in deadwood or soil exposures and provision resources in a series of cells for their offspring. In forests, cavity-nesting bees and wasps are considered secondary saproxylics, nesting in the deadwood exit holes created by primary saproxylic organisms (Westerfelt et al., 2015), and can thus be useful indicators of forest structure (Eckerter et al., 2021; Rappa et al., 2023). During nest building, or following nest completion, parasitoid species exploit the opportunity to lay their eggs on the resources provisioned and on/within the host egg or larvae. The parasitised cells can then be easily identified by the presence of a parasitoid individual/cocoon or a host cocoon with parasitoid exit holes.

In the present study, we seek to determine if the gradients of the amounts of structural elements prioritised by retention forestry for their importance for biodiversity can influence the stability and resilience of parasitism as an ecosystem function. Here, we follow Rappa et al., 2023, which investigated the importance of forest structural elements for cavity-nesting bees and wasps, which are the hosts of the parasitoids used in the present study.

To assess the influence of forest structural elements on parasitism as an ecosystem function, we tested the following hypotheses: 1) parasitoid abundance, species richness and diversity will increase with structural elements in forest habitats, namely standing/lying deadwood, herb cover and canopy cover as these are the most important resources for the foraging and nesting of their hosts (Rappa et al., 2023), which differ from parasitoids that are primarily limited by host availability. Furthermore, we hypothesise that the environmental variables structuring parasitoid communities will differ from those structuring host communities because of differing resource requirements, such as the predatory nature of some host species. 2) The weight and diversity of the bipartite host–parasitoid interaction networks will increase with the increasing forest structural elements that influence the amount of foraging and

nesting resources available to hosts (e.g., greater herb cover) but also the diversity of resources following the habitat-heterogeneity hypothesis (e.g., forest strata occupied by vegetation, greater stand structural complexity and understorey species richness) (Cramer & Willig, 2005; MacArthur & MacArthur, 1961). 3) The arrangement of host–parasitoid interactions will be determined by forest structural elements that have the potential to create stand-level heterogeneity via more diverse foraging and nesting resources (e.g., canopy cover and stand structural complexity). Heterogeneity of structural elements at the stand level has the potential to influence species richness via increased available niches and, thus, may diversify the suites of interactions that co-occur. We additionally employ a metanetwork approach to identify the most important interactions in promoting the stability of host–parasitoid networks, which we expect to involve host general parasitoids because these species have greater niche breadth. We further expect that parasitoid biodiversity metrics, community composition and host–parasitoid interactions will be significantly influenced by host abundance. The results of these analyses will present what is to our knowledge, the first metanetwork analysis of parasitoid bees and wasps, as well as the first simultaneous use of bipartite and metanetworks.

METHODS

Study region and plot selection

The present study was conducted on 134 1-ha plots, established in 2016 by the ‘Conservation of Forest Biodiversity’ (ConFoBi) project in the southern Black Forest mountain range (Baden-Württemberg, Germany) (Storch et al., 2020). The Black Forest is mixed-deciduous, consisting of mainly planted 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.). The transition from timber-focused to close-to-nature forest management has focused on enhancing structure through deadwood and habitat tree retention (Storch et al., 2018; Storch et al., 2020), and reflecting the potentially natural beech-dominated vegetation of the area (Gärtner & Reif, 2005; Standovár & Kenderes, 2003). Initial plot selection focused on deadwood amounts and forest cover at the landscape as the two primary gradients. The high number of plots, large spatial extent of the study area and heterogeneity in the Black Forest have resulted in gradients of numerous environmental variables. For more detailed information on the ConFoBi plot selection and the Black Forest as a study system, as well as additional environmental variables measured, see Storch et al. (2020). For a map of the study area, please see Figure S1.

Forest structural elements and environmental variables

Variables characterising the environment were chosen based on their potential influence on feeding and nesting resources of cavity-nesting bees and wasps, following Rappa et al. (2023). Deciduous tree share

(proportion of deciduous tree species), elevation and diameter at breast height of standing and lying deadwood pieces above 7 cm in diameter were obtained during full plot-level inventories conducted in 2017 and 2018. Typically, five stages are applied to classify deadwood according to decay: recently dead or raw wood (I), solid deadwood (II), rotten wood (III), mould wood (IV) and duff wood (V) (Hunter, 1990). Cavity-nesting bees and wasps, the host species for parasitoids in our study, prefer fresh and/or moderately decomposed deadwood (Bogusch & Horák, 2018; Eckerter et al., 2021; Westerfelt et al., 2015), as nest building requires stable substrates. To account for this, the cumulative diameter of lying and standing deadwood at plot level of only decay stages I–III was used, excluding decay stages IV and V, in which substrates become soft and unsuitable. Herb cover and understorey species richness were measured from six 5 m × 5 m subplots in 2017 (Helbach et al., 2022). Forest cover (proportion of forested area in 1 km² around plot centres) was calculated using the aerial image data by Storch et al. (2020). The remotely sensed indices stand structural complexity index (SSCI) and effective number of layers (ENL) were derived from terrestrial laser scans at northwest and southeast corners, as well as plot centres (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; Stiers et al., 2018). The ENL is an index for measuring the vertical heterogeneity of vegetation layering using voxels in 3D space (Ehbrecht et al., 2016; Ehbrecht et al., 2019). 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 (Rappa et al., 2023). Summary information of the environmental variables is available in Table 1. Further explanation of the remotely sensed indices can be found in Supporting Information.

Insect collection, identification and categorisation

Insects were collected during the spring/summer of 2020 using trap nests, which present hollow cavities within reed (*Phragmites australis* Cav.) internodes packed into polyvinyl chloride tubes (Krombein, 1967; Staab et al., 2018). Traps were secured in pairs to ~2 m high wooden poles, which were placed between the plot centre points and the northwest (NW) and southeast (SE) corners, totalling four traps per plot, each with cavities facing in the NW and SE directions. Traps were deployed in early March–April and collected mid-late October to sample the full breadth of phenologies. When occupied with nests, internodes can be easily opened, allowing for the quantification of cells with provisioned resources (abundance) and parasitised cells. From the number of provisioned and parasitised cells, the parasitism rate or the proportion of provisioned cells that were parasitised can be calculated. This sampling method allows highly detailed host–parasitoid interaction data to be gathered (Krombein, 1967) as the interactions can be directly inferred. After collection, nests were removed from traps and refrigerated at ~4°C

TABLE 1 Environmental variables and summary statistics characterising the 127 plots used in analyses, following exclusion of plots deficient of remotely sensed indices (seven plots).

Variable	Unit	Definition	Range	Mean \pm SD
Canopy cover (%)	%	Proportion of area with sunlight blocked by forest canopy	39–92	78 \pm 8
Deadwood DBH (lying)	cm	Sum diameter of lying deadwood structures >7 cm DBH below decay stage 4	0–1682	238 \pm 214
Deadwood DBH (standing)	cm	Sum diameter of standing deadwood structures >7 cm DBH below decay stage 4	0–1832	499 \pm 359
Deciduous tree share	%	Percentage of trees by count in plot that are deciduous species	0–96	28 \pm 25
Forest cover	%	Proportion of forested area within 1 km ² of plot centres	9–81	61 \pm 15
Herb cover	%	Ratio of area on ground with herb layer present	0.14–73.77	35 \pm 19
Elevation	m	Average of min and max heights above sea level	443–1334	821 \pm 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 \pm 4
Mean stand structural complexity index (SSCI)	-	Mean index characterising the diversity of physical characteristics measured across NW–SE transect on each plot	2–12	4 \pm 2
Understorey species richness	-	Number of plant species identified in the understorey (2–5 m)	2–71	31 \pm 14

Note: None of the variables were excluded on the basis of assumed collinearity ($\rho > 0.70$) following pairwise analyses. A summary of Spearman's correlations among environmental variables can be found in Table S1.

Abbreviations: DBH, diameter at breast height; NW, northwest; SE, southeast.

for 8–24 weeks to simulate winter diapause. While refrigerated, nests were opened to quantify the abundance of hosts (cells provisioned) and parasitoids (parasitised cells). Nests were then exposed to room temperature to facilitate the hatching of individuals, which were subsequently collected for morphological identification, using current taxonomic literature (e.g., Jacobs, 2007 for Crabronidae). Individuals who could not be identified at species level (~8% of host cells, ~12% of parasitised cells) were excluded before analyses. Following identification, species were categorised according to habitat specialisation as forest and non-forest specialists (hosts) (Rappa et al., 2023) and according to host specificity as general and specific (parasitoids). More detailed information regarding trap construction, and insect identification and categorisation can be found in Supporting Information.

Statistical analyses

Comprehensive information, biodiversity metrics and species composition

Plots with missing environmental variables (seven plots) were omitted before all analyses. Environmental variables were assessed for collinearity using Spearman's coefficient (R package 'ggpubr') (Dormann et al., 2013; Kassambara, 2020). Following this procedure, if a pair of variables share a coefficient greater than 0.70, only one should be retained for analyses. In our data, no pair of environmental variables was found to be collinear (Table S1).

Species data (hosts and parasitoids) were pooled per plot, before calculating abundance, Shannon diversity and species richness, yielding one data point per plot for each metric. Sampling completeness was

assessed with species accumulation curves using the 'specaccum' function (R package 'vegan') (Oksanen et al., 2022) for hosts and parasitoids, with jackknife1 estimators of expected total species richness of each (Figure S2). In addition, an accumulation curve of host–parasitoid interactions was calculated, with jackknife1 estimation of the expected total number of bipartite interactions estimated (Figure S3). To analyse the influence of environmental variables on overall parasitoid biodiversity metrics, abundance and species richness were each analysed using negative binomial generalised linear models, diversity was analysed using a linear model and parasitism rate was analysed using a binomial generalised linear mixed model (GLMM), with parasitism represented as successes and failures of brood cells due to parasitoids at plot level. An observation-level random effect was included in the GLMM, analysing parasitism rate to account for overdispersion. All environmental variables listed in Table 1 were included in each model, with the addition of log-transformed ($\log_{10}[x + 1]$) host abundance at the plot level as a covariate. Host availability is the most limiting resource for parasitoids (Pitcairn et al., 1990; Vogel et al., 2021), and thus host abundance is potentially highly influential for parasitoid biodiversity metrics as well as bipartite and metanetwork interactions.

To test the influence of environmental variables on species composition, NMDS (Non-metric MultiDimensional Scaling) was performed for hosts and parasitoids using the 'metaMDS' function (R package 'vegan') with 1000 random starting draws each. Ordinations were made using 'Bray–Curtis' dissimilarities on three axes to reduce stress while ensuring ordination, and fitting of environmental variables could still be reliably interpreted. Procrustes errors of the first two axes of host and parasitoid ordinations were compared separately to ordinations with two axes using the 'protest' function. The representation of the first two axes in three-dimensional ordinations

was similar to two-dimensional ordinations (Table S3), and thus, only the first two dimensions are displayed in Figure S5. All environmental variables listed in Table 1 were fitted post hoc to the scores of the first two ordination axes of each ordination using the ‘envfit’ function with 1000 permutations.

Bipartite networks

Weighted bipartite networks were calculated at plot level, with network properties quantified with several indices using the ‘bipartite’ package (Dormann et al., 2009), calculated for each plot-level network. The pooled bipartite network was calculated across all sites to examine the diversity of interactions sampled. While numerous indices are available to characterise bipartite networks (Almende et al., 2021; Dormann et al., 2009), weighted connectance, linkage density, link diversity and specialisation ($H2'$) were chosen to test the relationship between the host–parasitoid network structure and environmental variables. Models of connectance and linkage density tested whether the environmental variables listed in Table 1 potentially influence the weight of interactions between the parasitoids and host species. Models of link diversity and specialisation ($H2'$) tested whether environmental variables diversified and compartmentalised networks. Indices were calculated for only networks with more than one host–parasitoid interaction (one parasitised cell or one interaction). Preliminary analyses were conducted using values from all 90 networks where meaningful indices could be calculated (four models), and later excluding networks with fewer than 10 parasitised cells, analysing values from the resulting 68 networks (four models). Each index in both sets of analyses was analysed using linear models, including log-transformed host abundance at plot level as a covariate. To test if host–parasitoid networks and thus interaction indices differed significantly from chance (and are thus not random), we calculated Patefield null models using 1000 random model runs each and compared null indices with observed indices (Blüthgen et al., 2006; Dormann et al., 2009). Additional information about host–parasitoid interactions (Table S7) and bipartite network indices can be found in Supporting Information.

Metanetwork

The metanetwork was constructed using a data frame of unique host–parasitoid interaction co-occurrences. Each unique pair of interactions was used as a node and the frequency of its co-occurrence with another interaction as the edge connecting them (Figure 5). At the centre, or core of a metanetwork are the most central nodes (host–parasitoid interactions) that co-occur with the largest number of other interactions. The metanetwork indices interaction degree (a measure of centrality) and interaction closeness (a measure of distal branching) were calculated for each host–parasitoid interaction throughout the metanetwork using the ‘igraph’ package (Csardi & Nepusz, 2006). While many indices are available for interactions within the metanetwork (R package ‘igraph’) (Csardi & Nepusz, 2006), interaction degree

and closeness were chosen to measure the centrality and distal branching of interactions (Librán-Embú et al., 2021). A high value of interaction degree indicates a high number of uniquely co-occurring interactions, and thus a more central node forming a greater part of the metanetwork core. Closeness measures how many steps are required to reach another node from a given node. While also used to infer interaction centrality, a high value of closeness does not indicate a greater connection to other interactions but fewer steps necessary to reach all other interactions. Importantly, a low value of closeness indicates an interaction that is far from the metanetwork core. The indices were applied to each interaction in the plot-level dataset, resulting in groups of values of interaction degree and interaction closeness for each plot. To model the similar and repeated interaction degree (one model) and closeness (one model) values, where the number of interactions varied between the plots, GLMMs were calculated including the log-transformed ($\log[x + 1]$) number of interactions as an offset and plot as a random term, as well as log-transformed host abundance at plot level as a covariate. Modelling interaction degree tests the influence of environmental variables on the co-occurrence of interactions, and thus the potential to connect plot-level networks with shared function (e.g., standing deadwood promoting frequently occurring interactions). Modelling interaction closeness determines which environmental variables have the potential to diversify suites of interactions, appearing as unique. To compare the indices calculated for interactions in the metanetwork with indices calculated from bipartite networks, mean values for interaction degree and closeness were taken for each plot and then compared to bipartite network indices using Spearman’s correlation coefficients (Table S12). Additional information regarding metanetwork construction, detailed description of the metanetwork core and the selection of interaction indices can be found in Supporting Information.

Residuals of four models of biodiversity metrics, eight models of bipartite indices and two models of metanetwork interaction indices were tested for spatial autocorrelation using Moran’s I calculations, performed using the ‘testSpatialAutocorrelation’ function (R package ‘DHARMA’) (Hartig, 2022), respectively. No model residuals exhibited spatial autocorrelation (Table S11).

RESULTS

Biodiversity metrics and species composition

In total, 2220 parasitised brood cells (from a total of 14,957 provisioned by hosts) from 39 species (Table S2) were collected, representing 85% of the expected total parasitoid species richness (Figure S2). The average parasitism rate of brood cells was 14.52% ($\pm 14.14\%$). Only two obligate hyperparasitoid individuals were collected and, thus, were excluded from our data which had no influence on our results. Abundance, diversity and species richness of parasitoids were all positively related to the abundance of hosts at plot level (Figure S4), whereas abundance ($z = 2.036$, $p = 0.042$) and diversity ($t = 2.284$, $p = 0.024$) were additionally positively related to standing

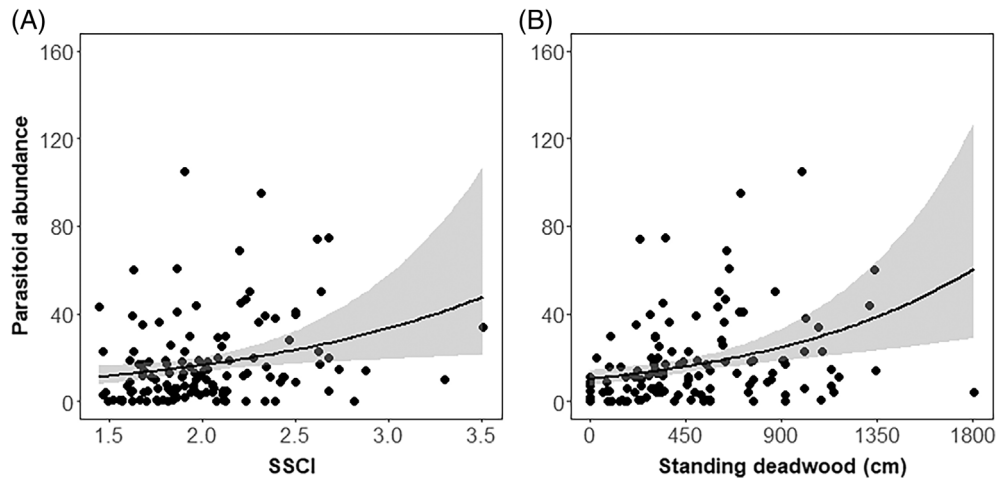


FIGURE 1 Abundance of parasitoids of cavity-nesting bees and wasps and significant fixed effects: (a) stand structural complexity index (SSCI) and (b) standing deadwood cumulative diameter (cm). Trend lines from negative binomial generalised linear models are depicted for abundance in both figures, with 95% confidence intervals coloured in grey.

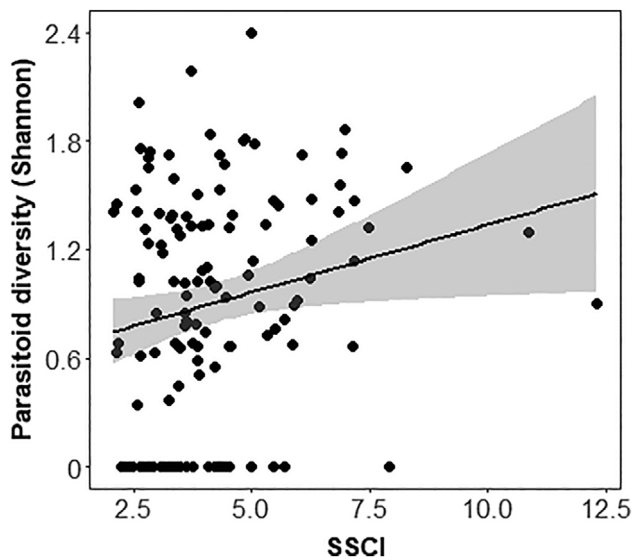


FIGURE 2 Diversity (Shannon) of parasitoids of cavity-nesting bees and wasps and stand structural complexity index (SSCI). Trend line for the linear model of diversity is depicted, with 95% confidence intervals coloured in grey.

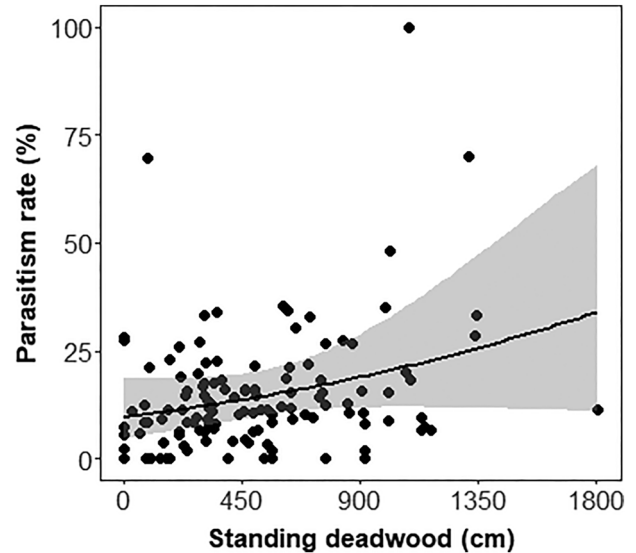


FIGURE 3 Parasitism rate of cavity-nesting bees and wasps and standing deadwood cumulative diameter (cm). Trend line for the binomial generalised linear model (GLM) is depicted with 95% confidence intervals coloured in grey.

structural complexity (Table S4) (Figures 1a and 2). Parasitoid abundance increased with standing deadwood ($z = 3.368$, $p < 0.001$) (Figure 1b). Parasitism rate increased with only increasing standing deadwood ($z = 2.998$, $p < 0.001$) (Figure 3). These results changed little following exclusion of the most common parasitoid species (*Melittobia acasta*) from our data, with parasitoid abundance and diversity no longer increasing with stand structural complexity (Table S13).

Host species composition was structured by canopy cover ($r^2 = 0.157$, $p < 0.001$), SSCI ($r^2 = 0.071$, $p = 0.001$), understorey species richness ($r^2 = 0.063$, $p = 0.019$), herb cover ($r^2 = 0.065$, $p = 0.015$) and elevation ($r^2 = 0.064$, $p = 0.021$) (Table S5 and Figure S5). Parasitoid species composition was structured by only canopy cover ($r^2 = 0.080$, $p = 0.026$) and host abundance ($r^2 = 0.094$, $p = 0.015$) (Table S6 and Figure S5).

Bipartite networks

The pooled host–parasitoid interaction network had a Shannon interaction diversity of 3.453 and specialisation ($H2'$) of 0.567 (Figure 4). Most (83%) of networks including those with fewer than 10 parasitised cells and nearly all (93%) networks excluding those with fewer than 10 parasitised cells differed significantly from chance during null model comparisons and are thus ecologically reliable. In analyses that included networks with fewer than 10 parasitised cells, linkage density ($t = 2.653$, $p = 0.009$) and link diversity ($t = 4.647$, $p < 0.001$) both increased with increasing host abundance (Table S8). Specialisation ($H2'$) decreased ($t = -2.277$, $p = 0.026$) while weighted connectance increased with standing deadwood ($t = 2.116$, $p = 0.038$) and herb cover ($t = 2.297$, $p = 0.024$). Linkage density ($t = -2.467$,

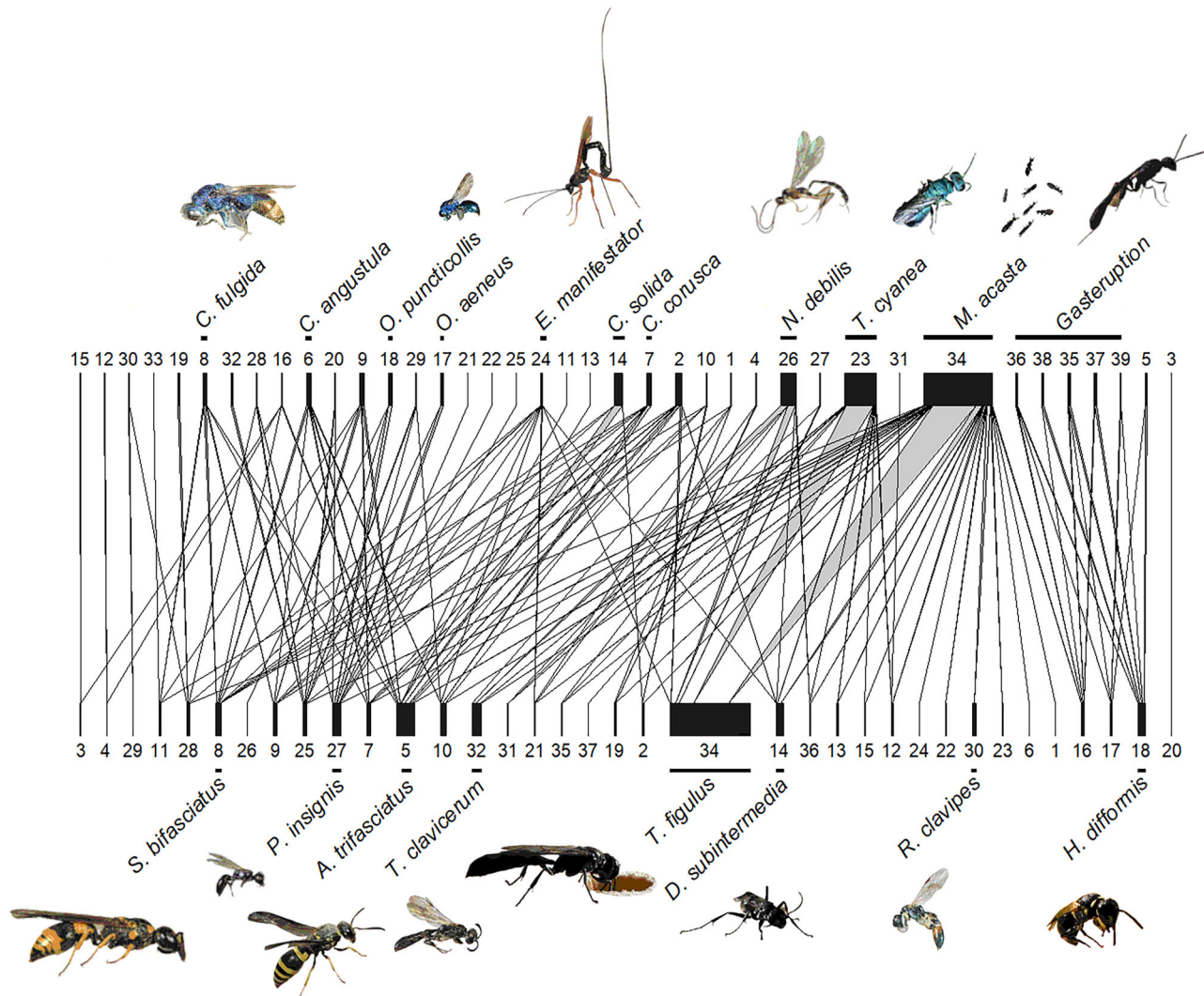


FIGURE 4 Pooled quantitative bipartite host–parasitoid network ($H2' = 0.567$) representing all plots where parasitism was observed. Width of upper bars represents brood cells parasitised by each species. Width of lower bars represents total number of parasitised brood cells for each host species. Arrow width represents the number of interactions (parasitised brood cells) between each parasitoid (above) and host (below) species. Numbers correspond to species listed in Table S7. Species names are listed for the strongest (highest numbers of parasitised brood cells) interactions.

$p = 0.016$) and link diversity ($t = -2.093$, $p = 0.039$) both decreased with increasing canopy cover.

In analyses restricted to networks with more than 10 parasitised cells, both linkage density ($t = -2.215$, $p = 0.031$) and link diversity ($t = -2.168$, $p = 0.034$) decreased with increasing canopy cover (Table S9). Weighted connectance decreased with only host abundance ($t = -3.407$, $p = 0.001$). Specialisation ($H2'$) was not related to environmental variables or host abundance (Table S9).

Metanetwork indices

Both interaction degree ($z = -4.856$, $p < 0.001$) and closeness ($t = -7.338$, $p < 0.001$) decreased with increasing host abundance (Table S10). Interaction closeness increased with increasing canopy cover ($t = 2.188$, $p = 0.032$). Spearman's coefficients revealed weak correlations between interaction degree (0.062 ± 0.039) or closeness (0.066 ± 0.024) with bipartite indices (Table S12). The metanetwork

core was comprised of mostly specific parasitoids parasitising forest specialist hosts (Figure 5 and Table S7).

DISCUSSION

Parasitoid reliance on hosts

The reliance of parasitoids on their hosts results in close and relatively specialised interactions compared with other interaction types such as pollination, which can be characterised as being more general (Fontaine et al., 2009; Soares et al., 2017). Host abundance was the primary determinant of parasitoid biodiversity metrics, particularly parasitoid abundance but also species composition. These results support the more-individuals hypothesis (Srivastava & Lawton, 1998), where an increase in host abundance yields not only an increase in the abundance of parasitoid species but increases in their richness and diversity as well. This has been observed in several studies

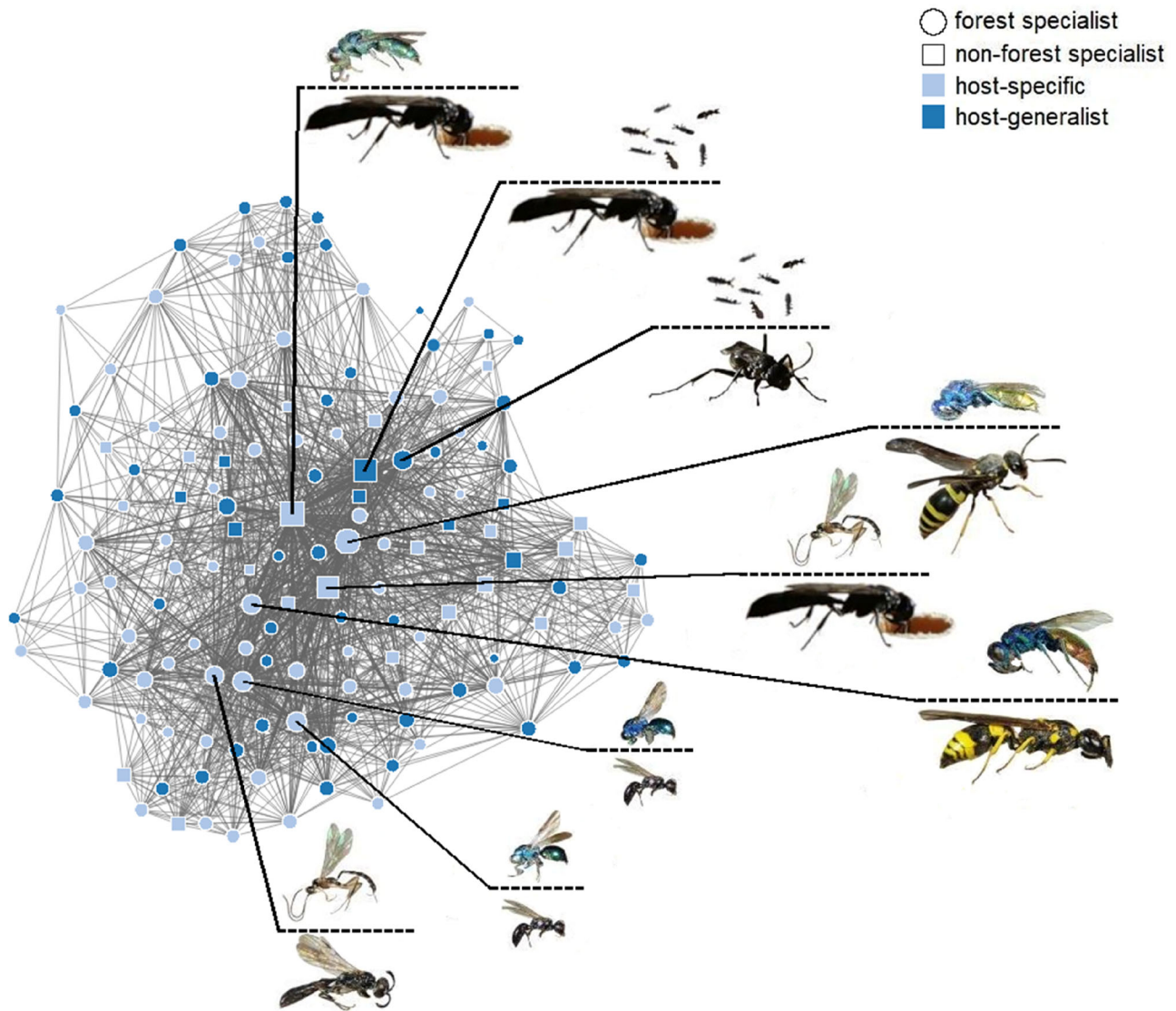


FIGURE 5 Host–parasitoid interaction metanetwork representing all 115 plots where parasitism was observed. Nodes in the metanetwork represent host–parasitoid interactions from local bipartite networks while edges represent co-occurrences with other interactions at plot-level. For each node (interaction) parasitoid species are depicted above dashed lines while hosts are depicted below. Edge width corresponds to the number of local networks where both interactions co-occurred. Point size corresponds to degree, or number of co-occurring interactions, with the most common ‘core’ interactions represented with images. Point shape corresponds to the habitat specialisation of hosts while point colour corresponds to specificity of host utilisation by parasitoids. The host–parasitoid interactions depicted are (from top to bottom): *Trypoxylon figulus*-*Trichrysis cyanea*, *T. figulus*-*Melittobia acasta*, *Deuteraenia subintermedia*-*M. acasta*, *Anicistrocerus trifasciatus*-*C. solida*, *T. figulus*-*Nematopodius debilis*, *Symmorphus gracilis*-*C. corusca*, *Passaloecus insignis*-*Omalus aeneus*, *P. insignis*-*O. puncticollis* and *T. clavicerum*-*N. debilis*. Additional descriptions of the interactions pictured, and the metanetwork core can be found in Supporting Information.

examining parasitoid taxa (e.g., Vogel et al., 2021), as host availability is likely an important component of parasitoids’ ecological niche. Our results, therefore, add further support to the significance of bottom-up influences in trophic interactions (Mehrparvar et al., 2019). The analyses of host biodiversity metrics in Rappa et al. (2023) show that structural components of forest habitat, namely standing deadwood and SSCI, promote greater abundance and species richness of cavity-nesting bees and wasps through increased and more diverse foraging and nesting resources. The potential influences of these relationships were observed in our study of parasitoids at higher trophic levels, with

greater abundance, diversity and species richness. Thus, the retention of forest structural elements can potentially promote this important ecosystem function via bottom-up focused conservation and potentially enhance top-down influences by increasing resilience through redundancy (Sanders et al., 2018; Thierry et al., 2022).

The density-dependent regulation of common host species potentially fosters greater ecosystem stability by buffering competitive exclusion (Brown, 2022), which would occur if a highly abundant species consumes foraging and nesting resources. Under these circumstances, other species with overlapping foraging and nesting

requirements would experience a population decline or a decreased carrying capacity. In our data, the most abundant species *Trypoxylon figulus* built ~28% of all nests collected. Given its highly general habitat tolerance (Jacobs, 2007) and tendency to nest in a wide range of cavity diameters, this species could, if very abundant, occupy potential nest sites before other species could utilise them. This is unless higher host density increases parasitism rate (Wang et al., 2020), thus creating a more stable population dynamic, buffering the exclusion effect. The increase in parasitism rate with greater standing deadwood observed in our data is possibly mediated by higher stability of host nesting substrates and is, thus, an effect of resource stability. This is consistent with studies examining the philopatric tendencies of solitary bees and wasps (Murray et al., 2009; Polidori et al., 2006) and their propensity to nest close to other individuals of the same species, and in close proximity to where they themselves hatched. Additional analyses of parasitism rate from our data, including the abundance of host nests as a covariate cannot support this however (Table S14). Interestingly, parasitism rate was influenced by only standing deadwood in our additional analyses, indicating that it may not be the density or abundance of host nests increasing parasitism rate, but rather the stable presence of hosts as resources, facilitated by stable deadwood structures.

Parasitoid and host species' compositions shared only canopy cover as a significant environmental variable. The activity of many host species included in our study is strongly reliant on sun exposure (Eckerter et al., 2022; Fye, 2012; Hilmers et al., 2018), and most cavity-nesting species tend to prefer sun-exposed deadwood substrates (Bogusch & Horák, 2018). Interestingly, no relationships were observed between parasitoid biodiversity metrics and canopy cover. Following the habitat-heterogeneity hypothesis (Cramer & Willig, 2005; MacArthur, 1972); however, the potential influence of forest structure could possibly be mediated by host abundances. The creation of canopy gaps (e.g., by tree felling) can diversify light conditions and, thus, the communities of photophilic bees and wasps in forests. The resulting increase in host abundance (see also Achury et al., 2023) and thus parasitoid species richness could improve functional resilience of parasitism networks to environmental changes (Evans et al., 2016; Gladstone-Gallagher et al., 2019; Laliberté & Tylianakis, 2010; Standish et al., 2014) such as those resulting in unfavourable microclimates (Bernaschini et al., 2021) via redundancy.

Interaction bipartite networks

Our hypotheses regarding the influence of forest habitat structural elements on networks were only partially confirmed. Among models including indices from all possible networks, only standing deadwood and herb cover are revealed as potentially supporting more stable parasitism networks by increasing connectance. This is partially supported by our finding that parasitism rate increased with standing deadwood, though parasitism rate and connectance differ. However, networks at plots with more standing deadwood exhibited lower specialisation, indicating that parasitoid host range potentially increases with host abundance, or when host populations are denser (Arneberg et al., 1998; Stanko et al., 2006). It is interesting that greater herb

cover increases connectance in our data, considering that nectar foraging by adult parasitoids (Zemenick et al., 2019) is typically overlooked in favour of their more relevant resources (hosts). In addition, it is possible that the abundance of prey items for predatory cavity-nesting wasps (e.g., aphids, spiders) increases with greater herb cover, creating a potentially compounding positive influence on host abundance, and therefore parasitoids (Ziesche & Roth, 2008).

The most common interaction in our data involved the highly host general parasitoid species *M. acasta*, which was observed on ~52% of research plots and accounts for 36% of interactions. The importance of generalist species for stabilising networks through redundancy has been well studied (Fornoff et al., 2019). However, networks dominated by one or only a few generalist parasitoids could be overly simple (Dehling, 2018; Poisot et al., 2012) and potentially more vulnerable to disturbances or stochastic changes. For example, a network with only *M. acasta* would be highly robust, and top-down density dependant population regulation would occur for (theoretically) all species. Removal of half the population of *M. acasta* in this case may not collapse the network (Nuwagaba et al., 2017; Vizentin-Bugoni et al., 2019). One potential consequence could be, however, greater vulnerability due to decreased redundancy driven by lower richness, meaning a stochastic effect on this single species could collapse the network. Greater resilience provided by the promotion of generalists may be particularly relevant when networks contain highly general species, which have the potential to parasitise also non-native hosts, as is the case with *M. acasta*. The potential to parasitise non-native hosts may provide a potential buffer against species invasions (Magal et al., 2008), which without population regulation mechanisms could otherwise collapse ecosystems (Hensel et al., 2021; Morales et al., 2013; Reaser et al., 2007; Walsh et al., 2016).

When only networks with more than 10 parasitised cells are considered, similar effects from only host abundance and canopy cover were observed compared with analyses from networks including fewer than 10 parasitised cells. These analyses together highlight the potential importance of considering small networks to reveal trends. The decrease in network connectance with increasing host abundance is possibly due to dilution (Civitello et al., 2015; Okuyama, 2021), especially when considering the observed increase in parasitoid abundance with host abundance. The significance of canopy cover for linkage density and link diversity could potentially indicate that promoting the abundance of only hosts may not be a sufficient measure to foster new interactions within networks. This could then mean that consideration of also forest structure is important for actions meant to promote greater network resilience. The diversification of networks with decreasing canopy cover is a somewhat contrary conclusion to Laliberté and Tylianakis (2010), where networks were homogenised by the removal of forest canopy. Furthermore, it has been found that canopy cover re-establishes communities of cavity-nesting bees, wasps and parasitoids (Fornoff et al., 2021), albeit these studies were conducted in subtropical forests. It is important to acknowledge that in the context of our study; only forests were sampled, and, thus, we have not sampled the full gradient of canopy cover or examined variables unassociated with forests, which would no doubt provide additional insights.

Interaction metanetwork

The metanetwork allowed for the visualisation of parasitism over the entirety of our study area, and revealed which interactions are co-occurring more frequently and potentially bridging distal groups of interactions. For example, the interaction between the spider-hunting wasp *T. figulus* and the gregarious parasitoid *M. acasta* was the most frequent in terms of parasitised cells in the trap nests, yet did not co-occur with other interactions as frequently as the interaction between *T. figulus* and the kleptoparasitoid *Trichrysis cyanea*. This indicates that the latter interaction is potentially more important for connecting distal networks and is a more important feature of parasitism networks in forests.

It was contrary to our expectations that more specific parasitoids comprise more of the metanetwork core than generalists, given that generalists are more frequently encountered due to greater niche breadth (Kassen, 2002; Robinson & Strauss, 2018). Several studies have highlighted the importance of rare or unique parasitoids in stabilising metanetworks (Santos et al., 2020), but the importance of more specific parasitoids in our analyses of metanetwork interactions warrants further study. Moreover, more abundant hosts may support more specialist parasitoids due to the stability of hosts as a resource and sensitivity of specialist parasitoids to fluctuations in host populations (Cagnolo et al., 2009; Holzchuh et al., 2010).

Canopy cover partially confirmed our hypothesis that increasing forest structural heterogeneity would diversify interactions in the metanetwork, manifesting as the distal branches of the metanetwork where unique species are present. The leftmost distal branch, for example, is comprised of interactions, which occurred on very few plots, for example, the leaf-cutter bee *Megachile versicolor* parasitised by the cuckoo bee *Coelioxys inermis*. Interestingly, the host species in these interactions are often forest specialists (Rappa et al., 2023), and thus characteristic among forest biota. This result is contrary to our expectation that removal of canopy cover would foster unique interactions with non-forest species (Fricke & Svenning, 2020), following transformation of forest habitat. These findings indicate that discrimination by host habitat specialisation is necessary to assess the value of forest structures for parasitism networks.

Future research could reveal the impact of habitat structural elements on specialist and non-specialist-based interactions, by sampling research plots across habitats and analysing the interaction values from the resulting metanetwork. Furthermore, analyses of interaction indices extracted from the metanetwork can reveal habitat structural elements with important roles in maintaining the complexity of interactions and thus ecological communities (Mougi & Kondoh, 2012; Xing & Fayle, 2021). The metanetwork approach could be taken yet another step further and include multiple interaction types, and interactions involving multiple actors to more precisely assess the importance of habitat structural elements in structuring multi-trophic interaction networks. For example, using the co-occurrences of both host-parasitoid and plant-pollinator interactions sampled from forests and grasslands, hypothetically revealing the most important habitats for interaction types and more importantly, the interactions which connect them spatially.

CONCLUSIONS

Parasitoid biodiversity in forests is influenced most strongly but not exclusively by the abundance of their hosts. Stand heterogeneity (measured here by canopy cover, and stand structural complexity) may have strong influences on parasitoid abundance, species richness and diversity directly but also via increasing host abundance. Forest structural elements such as deadwood have the potential to enhance ecosystem functions, such as parasitism in the case of our study. This research demonstrates the potential insightfulness of concurrent analyses of bipartite and metanetworks for evaluating interactions and ecosystem functions with important considerations for conservation. Furthermore, the derivation of metanetworks from bipartite interactions necessitates their use in tandem to thoroughly answer research questions.

AUTHOR CONTRIBUTIONS

Nolan J. Rappa: Conceptualisation; investigation; writing – original draft; visualisation; formal analysis; data curation. **Michael Staab:** Methodology; writing – review and editing; supervision; project administration; conceptualisation. **Laura-Sophia Ruppert:** Conceptualisation; writing – review and editing; investigation. **Julian Frey:** Data curation; writing – review and editing; conceptualisation. **Marco A. R. Mello:** Conceptualisation; writing – review and editing; methodology; resources. **Alexandra-Maria Klein:** Conceptualisation; funding acquisition; writing – review and editing; methodology; project administration; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are currently private for peer review, available in Dryad at https://datadryad.org/stash/share/atyeUKm_-Kdi87kz5dyZWDNMyoF7q4rHoMKN7K9e2E.

ETHICS STATEMENT

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

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data. Supporting Information.

Figure S1. Map of the 134 ConFoBi research plots sampled in the southern Black Forest, Baden-Württemberg, Germany. Green points correspond to plot geolocations (latitude and longitude of plot centres). Figure credit: Julian Frey.

Figure S2. Species accumulation curves of: a) cavity-nesting bees and wasps and b) their associated parasitoids, collected using 4 trap-nests on each of 127 plots. Plots missing remotely sensed variables (7) were excluded prior to analyses. Observed cumulative species richness is represented in each figure by solid lines, with 95% CI of accumulation curves shown as grey polygons. Total species richness (extrapolated) based on jackknife1 estimators is represented by horizontal lines (solid) with 95% CI (dashed lines). In total, 57 species (86% of expected total richness) of cavity-nesting Hymenoptera and 39 species (85% of expected total richness) of parasitoids were collected.

Figure S3. Host-parasitoid interaction accumulation curve, displaying cumulative parasitism events (one species parasitising another) per each of 115 sampled plots where parasitism was observed. Observed cumulative interactions is represented by solid lines, with 95% CI accumulation curves shown in grey. Total interactions possible (extrapolated) based on jackknife1 estimators is represented by horizontal lines (solid) with 95% CI (dashed lines). In total, 139 interactions (72% of expected total interactions) were observed.

Figure S4. Abundance (parasitised brood cells) (a), diversity (b) and species richness (c) of parasitoids of cavity-nesting bees and wasps and host abundance. Host abundance was log-transformed ($\log(x+1, 10)$) prior to plotting in each figure. Trend lines are depicted for negative binomial generalised linear models (a and c) and a linear model (b), with 95% confidence intervals coloured in grey.

Figure S5. NMDS ('metaMDS', permutations=1,000) of a) cavity nesting bees and wasps and b) their parasitoid species matrices using Bray-Curtis dissimilarities on 3 axes at 0.191 and 0.164 stress respectively. Forest variables were correlated with the scores of each NMDS using the 'envfit' function (permutations=1,000, $p < 0.05$). Plots where only one or no individuals were collected were omitted prior to ordination, resulting in 122 plots used for cavity-nesting Hymenoptera and 97 for their parasitoids respectively.

Table S1. Spearman correlation coefficients (ρ) for all pairwise comparisons of environmental variables. Abbreviations are as follows: DBH, diameter at breast height; ENL, effective number of layers or 1-meter forest strata; SSCI, stand structural complexity index.

Table S2. Parasitoid (including klepto-parasitic) species collected between March-October of 2020 using trap nests, deployed on 134 plots. The total number of nests, genera and host species

parasitised are listed for each parasitoid species. The total abundance (number of parasitised brood cells) is listed for each species. The relevant literature used for identification is listed for each species.

Table S3. Results of Procrustes comparison of 3 to 2 axes ordinations for both host and parasitoid species composition. Procrustes sum of squares is represented as m^2 . Significant p-values (listed in bold) indicate correlation between ordinations.

Table S4. Regression coefficients of models of parasitoid abundance (negative binomial), parasitism rate (binomial), parasitoid species richness (negative binomial) and parasitoid diversity (normal) sampled on 127 plots. Each model included all environmental variables listed in Table 1, with log-transformed host abundance at plot-level included as a covariate. Significant coefficients are displayed in bold. Conditional and marginal R^2 values are listed in parentheses for models of diversity and parasitism rate, while McFadden's pseudo R^2 is listed for models of abundance and parasitoid species richness.

Table S5. Summary results from permutation tests fitting environmental variables to host species NMDS ("metaMDS, 1,000 permutations) using "envfit" function with 1,000 permutations. Significant correlations ($p < 0.05$) are displayed in bold.

Table S6. Summary results from permutation tests fitting environmental variables to parasitoid species NMDS ("metaMDS, 1,000 permutations) using "envfit" function with 1,000 permutations. Significant correlations ($p < 0.05$) are displayed in bold.

Table S7. Parasitoid interactions (parasitoids, corresponding hosts and number of parasitised brood cells) from 115 plots where parasitism was sampled. Corresponding bipartite network numbers for parasitoids and their hosts are listed in parentheses. Corresponding habitat specialisation of hosts and specificity (restriction in host acceptance) of parasitoids are included for each interaction.

Table S8. Regression coefficients of models using bipartite network indices as response variables, excluding networks with single links for which no indices could be calculated, resulting in values from 90 networks being analysed. Models included all environmental variables listed in Table 1 as fixed-effects and log-transformed host abundance at plot-level as a covariate. Weighted connectance (linear), link density (linear) linkage diversity (linear) and network specialisation (linear) were analysed. Number of interactions (parasitised brood cells) among modelled networks ranged from 3-105 (23 ± 20). Conditional and marginal R^2 values are listed in parentheses for each model.

Table S9. Regression coefficients of models using bipartite network indices as response variables, and all environmental variables listed in Table 1 as fixed-effects and log-transformed host abundance at plot-level as a covariate. Weighted connectance (linear), link density (linear) linkage diversity (linear) and network specialisation (linear) were analysed. Bipartite networks which were too small (singleton and doubleton), as well as networks with fewer than ten parasitised brood cells were excluded prior to analyses, resulting in values from 68 networks being analysed. Number of interactions (parasitised brood cells) among modelled networks ranged from 10-105 (27 ± 19). Conditional and marginal R^2 values are listed in parentheses for each model.

Table S10. Regression coefficients of models using indices calculated for each interaction (host parasitised by parasitoid species) throughout metanetwork as response variables. Interaction degree (negative binomial) and interaction closeness (normal) were each modelled with site included as a random term and an offset using the number of observed interactions per site. Indices were calculated for interactions for each site where they were observed. Singleton interactions (those occurring alone at site level) were excluded prior to analyses, resulting in indices calculated from parasitoids collected on 90 plots being modelled. Each model included all environmental variables listed in Table 1, with log-transformed host abundance at plot-level included as a covariate. Conditional and marginal R^2 values are listed in parentheses for each model.

Table S11. Results of Moran's I calculations for assessing potential spatial autocorrelation in model residuals. Moran's I calculations were performed using residuals of bipartite models including and excluding small networks (fewer than 10 parasitised brood cells) separately. Calculations were performed using simulated residuals for mixed-models of interaction degree and closeness. Note: All models' residuals were tested for spatial-autocorrelation using the "DHARMA" package (Hartig 2022).

Table S12. Spearman correlation coefficients (ρ) for all pairwise comparisons of bipartite (rows) and mean metanetwork interaction (columns) indices. Mean values of Spearman's correlation coefficients for interaction degree (0.062 ± 0.039) and interaction closeness (0.066 ± 0.024) showed no correlation to bipartite network indices.

Table S13. Regression coefficients of models of parasitoid abundance (negative binomial), parasitism rate (binomial), parasitoid species richness (negative binomial) and parasitoid diversity (normal) sampled on 127 plots, following removal of the most common parasitoid species *M. Acasta* from the dataset. Each model included all environmental variables listed in Table 1, with log-transformed host abundance at plot-level included as a covariate. Significant coefficients are displayed in bold. Conditional and marginal R^2 values are listed in parentheses for the models of diversity and parasitism rate, while McFadden's pseudo R^2 is listed for models of abundance and parasitoid species richness.

Table S14. Regression coefficients of models of parasitism rate (binomial), sampled on 127 plots. Each model included all environmental variables listed in Table 1, with log-transformed host and nest abundances at plot-level included as covariates. Significant coefficients are displayed in bold. Conditional and marginal R^2 values are listed in parentheses.

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