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Research article

Host identity, nest quality, and parasitism strategy: influences on body size variation in parasitoid bees and wasps

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Body size determines mobility and fitness across taxa in various ways. Yet, drivers of body size in higher trophic invertebrates, especially parasitoids, including intra- and interspecific variations, are poorly understood due to complex interactions between parasitoid behaviour, the environment and their hosts. We measured the body size of 393 individuals of four parasitoid species (collected from 2220 parasitized brood cells) sampled with trap nests for cavity-nesting bees and wasps in the Southern Black Forest, Germany. We related parasitoid body size to the size of 15 host species and the diameters of their nests along five environmental gradients (proportion of conifers, canopy cover, structural complexity, herb cover and deadwood diameter). Host identity, nest diameter, and to a lesser extent, size differences within host species were primary drivers of parasitoid body size, albeit responses varied among parasitoid species. For instance, when the host black wood borer wasp *Trypoxylon figulus* doubled in size, the ichneumon wasp *Nematopodius debilis* (parasitising the host directly) increased by 37% in size, while the blue cuckoo wasp *Trichrysis cyanea* (parasitising food resources) increased by only 8%. Across host–parasitoid species combinations, parasitoid size correlated weakly with host size, and environmental gradients did not significantly influence host or parasitoid body size. Our findings highlight the primary factors influencing body size, with host identity and nest diameter emerging as influential factors within and between parasitoid species, although not uniformly. In contrast, the relationship between the top trophic level (parasitoids), the lower trophic level (hosts), and host size with environmental gradients were less influential. Considering the environmental variables that directly affect body size, such as microhabitat conditions and biotic interactions, may further clarify the dynamics shaping the variation in body size at higher trophic levels and should be considered in future studies addressing how land management influences multitrophic interactions.

Keywords: body size, host–parasitoid interactions, host suitability, insect fitness, parasitism, temperate forest retention management

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Introduction

Body size is fundamental to fitness-related functions in diverse organisms (Brown et al. 1993, Chown and Gaston 2010) and, often reflects tradeoffs between growth (Peacor et al. 2007, Texada et al. 2020), reproduction (Krishna and Hegde 2003), development time (Gillooly et al. 2002), and foraging strategies (Weise et al. 2010, Hillaert et al. 2018). Larger individuals usually secure more resources, achieve higher fecundity, and have longer lifespans than their smaller counterparts (Kazmer and Luck 1995, West et al. 1996, Greenleaf et al. 2007, Herlin et al. 2019). Despite extensive studies on the ecological role of body size, quantitative data on inter- and intraspecific variation in natural systems, particularly among higher trophic invertebrates, remain limited. In these systems, body size is shaped by complex spatial and temporal factors, including species interactions, resource availability, habitat structure and microclimate (Emmerson and Raffaelli 2004, Komonen et al. 2004, Pincebourde and Woods 2020). Consequently, understanding these determinants offers insights into key ecological processes, such as demography, population, and community dynamics, especially for higher trophic species that drive ecosystem functions.

For higher trophic groups such as parasitoids, host characteristics are particularly influential in determining body size (Harvey 2005). Parasitoids that parasitize multiple host species may prefer certain hosts to others because of their greater suitability and familiarity with the host, which maximize their fitness (Strand and Obrycki 1996, Jones et al. 2015). Hosts that are unsuitable can hinder parasitoid development through defence mechanisms, such as encapsulation, and the lack of shared evolutionary history can result in physiological incompatibility between the host and parasitoid (Mohamed et al. 2003, Martin et al. 2010). Additionally, host species characteristics, such as differences in nutritional content, can further affect the development and size of parasitoids, with higher-quality hosts providing better nutritional content, leading to a larger progeny of parasitoids (Häckermann et al. 2007), which often similarly occurs in other trophic interactions such as plant–pollinator interactions (Elzay and Baum 2021).

In many parasitoid species, host size has been found to be positively correlated with parasitoid size; female parasitoids also produce larger offspring and increase their clutch size when utilizing larger hosts (Arakawa et al. 2004, da Rocha et al. 2007, Sarikaya and Gülel 2011). The static nature of host resources during parasitoid development may explain the close relationship between parasitoid and host size (Fidgen et al. 2000, Harvey et al. 2006). Furthermore, larger hosts are often correlated with richer resource pools and a longer development time that these hosts provide for parasitoid larvae (Sequeira and Mackauer 1992, Jenner and Kuhlmann 2006).

Ecological relationships are often shaped by environmental factors, affecting species interactions across trophic levels, as seen in studies of plant–pollinators or plant–pest dynamics (Ferrenberg 2016, Anderson et al. 2024). Similarly, habitat alterations, such as those from forest management, influence host–parasitoid interactions (Tylianakis et al. 2007, Moiroux et al. 2010). The changes often disrupt foraging resources and success, reducing host size and, in turn, parasitoid size in impacted areas like deforested habitats (Laliberté and Tylianakis 2010). Changes in habitats particularly affect solitary wasp and bee species that nest in wood hollows and cavities (Montagnana et al. 2021). As their habitats change, the availability of suitable nesting sites decreases and the range of cavity sizes or nest diameters is limited (Morato and Martins 2006). Additionally, larger species tend to nest in cavities with larger diameters (Rauf et al. 2022), and variation in nesting cavity diameter influences total offspring rates and diapause time (Rinehart et al. 2024).

In managed forest ecosystems, such as retention forestry, key structural elements such as portions of the original trees (habitat trees) and deadwoods are preserved to maintain biodiversity (Gustafsson et al. 2012, Fedrowitz et al. 2014). Environmental factors, including proportion of coniferous trees, canopy cover, coarse deadwood debris, forest stand structural complexity, and ground herb shape microhabitats and resource availability, and thereby the community composition of various animal groups (Lassau et al. 2005, Rappa et al. 2023, 2024, Rehling et al. 2023, Cordeiro Pereira et al. 2024). These structural elements not only play a key role in influencing host–parasitoid networks in this system (Rappa et al. 2024), but also shape the abundance, diversity, and species richness of cavity-nesting Hymenoptera (Rappa et al. 2023), which served as hosts for the parasitoids in our study. Retention forestry, which mimics natural forest structure, enables studying these dynamics. However, host–parasitoid size interactions have typically been explored in single-species studies (Jenner and Kuhlmann 2006, King and Napoleon 2006, da Rocha et al. 2007), leaving a gap in understanding how both host and environmental factors jointly shape parasitoid size across species. Environmental influences may act directly, through microhabitats on body size of parasitoids, or indirectly, by altering host quality, which is essential for parasitoid growth and survival.

This study investigates how parasitoid body size across multiple species is influenced by host identity, host size, nest quality, and environmental gradients within a retention forestry system. By examining host–parasitoid size relationships across species and environmental factors, this study extends beyond single-species analyses to reveal the combined effects of host and habitat factors on body size variation within an ecological framework. Integrating host factors with environmental gradients enables us to explore how species-specific and habitat characteristics interact to shape parasitoid size variation.

To address these relationships, we tested three main hypotheses (Fig. 1): 1) parasitoid size is significantly influenced by the identity of the host, and increases with host size (interspecific level); 2) the size of parasitoids increases with nest quality (i.e. nest diameter) and host quality (i.e. the size of hosts at the intraspecific levels); 3) retention forest structures, including proportion of coniferous trees, canopy

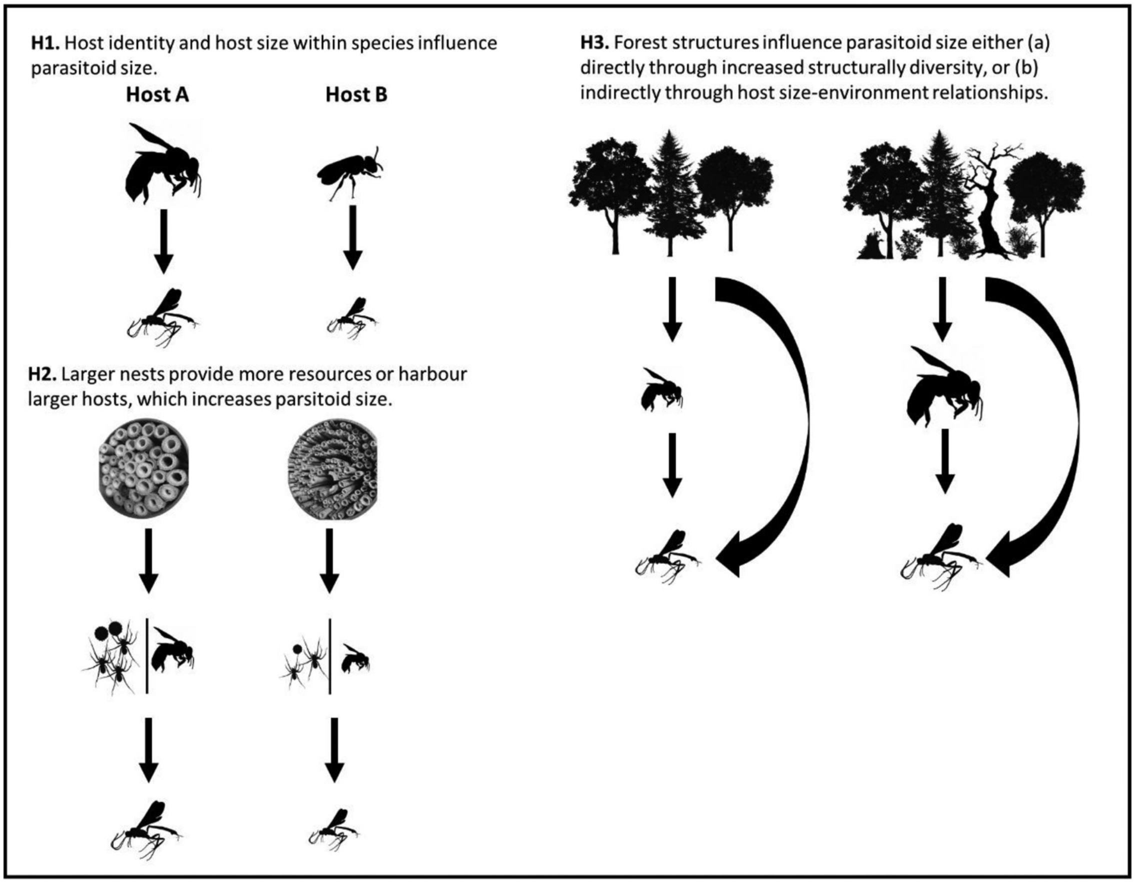

Figure 1. A conceptual diagram of mechanisms influencing variation in parasitoid body size based on our three hypotheses.

cover, stand structural complexity index (SSCI), standing deadwood diameter, and herbaceous cover, directly or indirectly increase parasitoid size through changes in the environment and host size dynamics. Given their role in regulating insect populations, parasitoids contribute substantially to ecosystem stability. Understanding how biotic interactions and environmental gradients shape body size in these higher trophic invertebrates provides key insights into ecological processes, with implications for conservation and ecosystem resilience in changing environments.

Material and methods

Study area

The study was conducted in the southern part of the Black Forest, Baden-Württemberg, Germany, as part of the Research Training Group 2123 – Conservation of Forest Biodiversity 'ConFoBi' (Storch et al. 2020). This part of the Black Forest consists of mixed temperate forests within a low mountain range, spans roughly 5000 km^2 (75% forests) and rises from 120 to 1493 m a.s.l. Norway spruce *Picea abies* accounts for about 42.8% of trees in the forest and is especially prevalent in the northern and eastern regions as well as at higher elevations. In the southern and western regions of the Black Forest, silver fir *Abies alba* and European beech *Fagus sylvatica* comprise greater proportions of forest stands (18.5 and 15.3%, respectively). The forest has been managed under a close-to-nature forest management system since the 1990s. However, an increasing focus on conserving biodiversity led to the introduction of a retention forest program in 2010 (ForstBW 2016), requiring state-owned forests and encouraging private forests to integrate deadwood and habitat tree groups – around 15 trees per 3 ha – into their management strategies (ForstBW 2016).

In the Black Forest, 134 one-ha plots (mean distance between plot centres is 750 m) were distributed across strictly protected forest reserves, and multi-functional forests actively managed by the State Forest Service (Fig. 2). The selection of study plots was guided by two design gradients: 1) landscape-scale forest connectivity, determined by the percentage of forest within a 25 km^2 area surrounding the plot centres and 2) retention-related forest structure at the plot level, including the richness of habitat tree species and deadwood per hectare. This approach ensured the representation of a broad spectrum of conditions prevalent in European montane forests. Plots were pre-selected based on criteria such as topography, forest stand age, absence of water bodies, and human infrastructure (Storch et al. 2020) to minimise variation due to

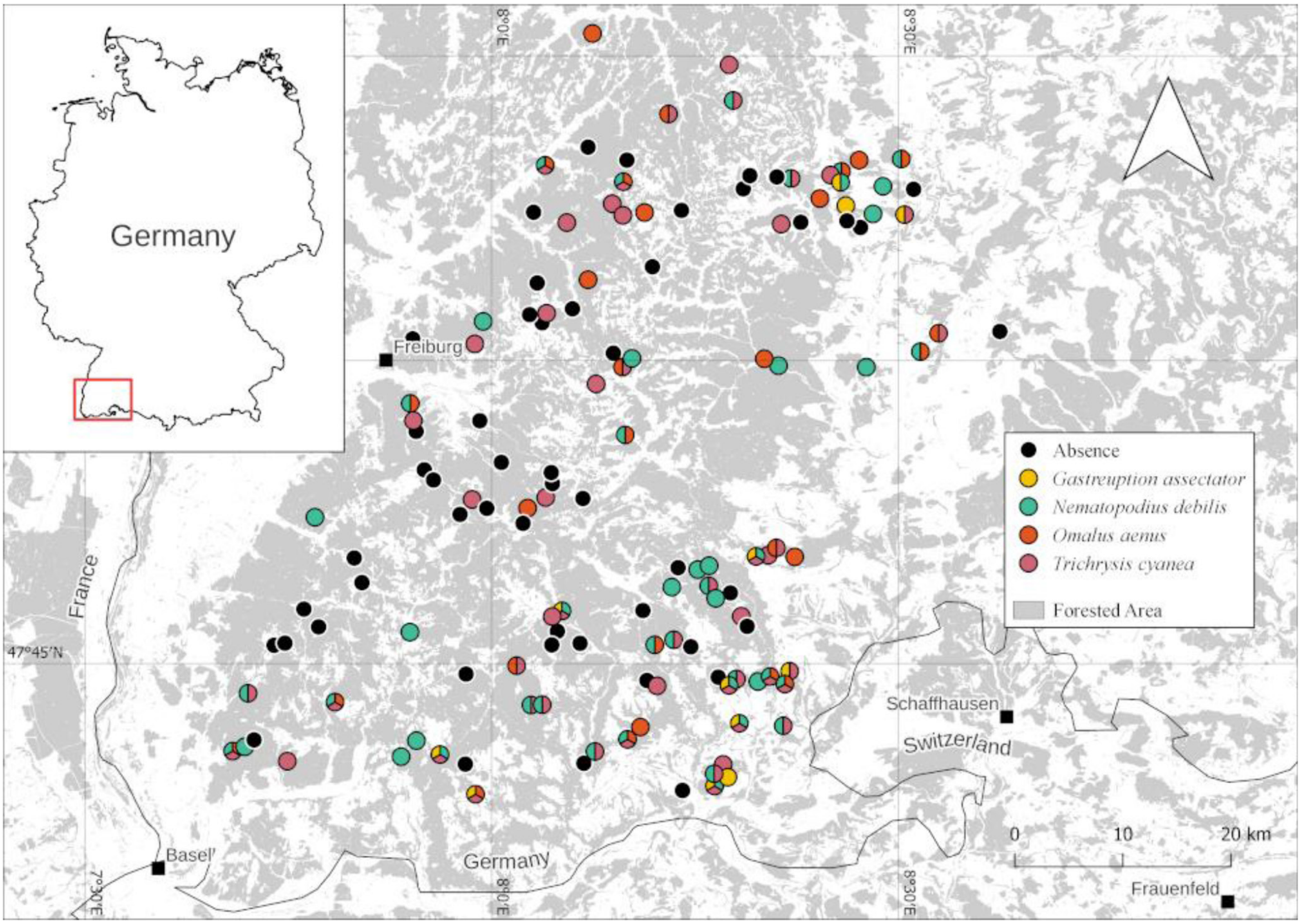

Figure 2. Map of the 134 ConFoBi research plots sampled in the Southern Black Forest, Baden-Württemberg, Germany. Points correspond to plot geolocations: latitude and longitude of plot centres. Colour represents the plots where parasitoid species occurred and were collected, with colours assigned among species. Figure credit: Jan Feigl.

confounding factors. Further verification was conducted to confirm the absence of forest operational activities, such as harvesting and road construction, during the ConFoBi funding periods.

Study species

The wild carrot wasp *Gasteruption assectator* (Gasteruptiidae) parasitizes solitary bees that nest in cavities (Johansson and van Achterberg 2016). The larvae of *G. assectator*, also known as predator-inquiline, initially consume the host larva of the yellow-faced bee *Hylaeus* spp., and subsequently feed on the host's provisions (similar to idiobiont kleptoparasitoid behaviour), such as pollen and nectar (Bogusch et al. 2018). This species is commonly found across Europe and thrives in a wide range of habitats, from agricultural landscapes to forest ecosystems (Bogusch et al. 2018).

Ichneumon wasp *Nematopodius debilis* (Ichneumonidae) is an idiobiont ectoparasitoid species found in the nest of crabronid wasp species (*Trypoxylon* spp.) specialised in hunting spiders. The adult female paralyses the host during oviposition; subsequently, the parasitoid larva consumes the host and develops from outside its body. This species is distributed across Europe, but there is a lack of information on the specific habitat types in which it occurs (Broad et al. 2018).

Two cuckoo wasp species, *Omalus aeneus* and *Trichrysis cyanea*, both members of the Chrysididae family, typically parasitize solitary wasps (Paukkunen et al. 2015, Wiesbauer 2020). *Omalus aeneus* and *T. cyanea* are kleptoparasitoids, meaning the parasitoid larvae appropriate the host's food resources (Wiesbauer 2020). Although they share similar parasitism types, each species targets distinct groups of host species. In our study, *O. aeneus* parasitized two species from the genus *Passaloecus* spp. (Crabronidae), while *T. cyanea* parasitized a broader range of hosts, including four species from the genus *Trypoxylon* spp. (Crabronidae), and two species from the genus *Deuteragenia* spp. (Pompilidae). Both species are distributed across central Europe in various habitats, from forests to open areas, such as agricultural landscapes, parks and gardens (Paukkunen et al. 2015, Wiesbauer 2020).

It is important to note that, while all host and parasitoid species involved in this study are broadly distributed across the Palaearctic region according to the Global Biodiversity Information Facility (GBIF), specific information on their native, non-native, endemic, or invasive status within our study area is not available. Based on their broad distribution, these species are likely native to the Palaearctic region, but precise information on their origin is lacking.

Collection, identification, and measurements of parasitoids and their hosts

Solitary cavity-nesting bees and wasps were collected using trap nests between March and October 2020. Each trap nest was constructed using hollow reed internodes of *Phragmites australis*. The lengths of the hollow reeds were approximately 20 cm and were fitted into a PVC tube with a diameter of about 11 cm. Each trap exposed an average of 150 cavities per trap side, with a wide diameter ranging between 1 and 10 mm. Traps were attached in pairs on 1.5 m high wooden poles, placed in open ground spaces halfway between plot centres and the northwest and southeast corners (within a radius of approximately 5 m), totalling four traps per plot. Each trap was oriented facing southeast and northwest, to promote nesting via sunlight exposure. After being occupied with nests, traps were removed and refrigerated at ~ 4°C during October–February to simulate winter diapause. Nests were then exposed to room temperature, and hatched bees, wasps and parasitoids were collected for species determination. Species identifications were done with identification keys for each taxonomic group (Dahl et al. (2007) for host species and Bogusch et al. (2018) for parasitoid species; also see Rappa et al. 2023, 2024). The parasitoid and host specimens used in this study are a subset of specimens used in previous investigations on solitary bees and wasps by Rappa et al. (2023, 2024). The authors investigated the importance and effectiveness of structural elements within forest ecosystems in enhancing biodiversity conservation through retention forestry practices.

The body size (measured as body length) of both parasitoids and their hosts were measured from the top of the head to the end of the abdomen, excluding the ovipositor protrusion, as the metric for body size in this study. Each parasitoid that emerged from a trap was measured. Similarly, only hosts that emerged from similar nests (not from other nests in the same trap) as the parasitoids were measured. Severely damaged specimens were excluded from the measurements to enhance data reliability and ensure accuracy. Variables such as intertegular distance (ITD) and forewing length were difficult to measure for nearly one third of our samples in our case due to damage incurred during the pinning preparation process, such as being stabbed by pins, being over glued, or having folded wings. As a consequence, we did not include these variables in our measurements.

We measured a total of 393 individual parasitoid specimens (n = 25 for *G. assectator*, n = 151 for *N. debilis,* n = 45 for *O. aeneus*, and n = 172 for *T. cyanea*) (Supporting information). For the hosts, we were unable to obtain an equal number of measurements as we did for their parasitoids because some hosts had been consumed by the developing parasitoids. *Omalus aeneus* parasitized two crabronid wasp species: *Passaloecus insignis* (n = 24) *and P. corniger* (n = 1); *T. cyanea* parasitized four species of *Trypoxylon* and two species of *Deuteragenia* wasps , with *Trypoxylon figulus* being the most parasitized host species (n = 85) (Supporting information). There were three bee species from the genus *Hylaeus* that were parasitized by *G. assectator* (Supporting information), only one individual being available for the measurement of body size. *Nematopodius debilis* parasitized five *Trypoxylon* species, with *T. clavicerum* (n = 17) and *T. figulus* (n = 34) being the two dominant hosts parasitized (Supporting information). All measurements were conducted using a Leica stereo microscope M165 C supported with a Leica Application Suite 3.8 (LAS) imaging software system using a 10× magnification.

Nest quality and forest structures

We selected a variety of nest diameters to have enough choices for the hosts and parasitoids to select their preferred sizes. The quality of the nests, i.e. the diameter of the hollow reeds, was measured with digital callipers. The diameters of the nest entrance (one side of an internode only), each of 383 hollow reeds, were measured. For forest structures, the proportion of coniferous trees was calculated from the inventory basal area of coniferous trees carried out between 2016 and 2018 (Storch et al. 2020). The mean canopy cover was calculated in ImageJ using overhead hemispherical photos obtained at each trap location in early fall 2020. The remotely sensed indices stand structural complexity index (SSCI), were obtained from terrestrial laser scanners performed at the northwest and southeast corners, as well as the centres of the plots. Diameters at breast height (DBH) of standing deadwood above 7 cm in diameter were obtained during plot-level inventories in 2017 and 2018. There were five decay stages applied in the classification of deadwood following Hunter (1990): i) recently dead or raw wood, ii) solid deadwood, iii) rotten wood, iv) mould wood, and v) duff wood. As the host species for parasitoids in our study preferred fresh and/or moderately decomposed deadwood, only decay stages i–iii were used to calculate the cumulative diameter of standing deadwood at plot level. Herbaceous covers were estimated from 5 × 5 m subplots during 2017.

Statistical analyses

We analysed the relationship between parasitoid body size as a response variable, and host identity and nest diameter as fixed factors, with study plot as random factor using linear mixed-effects models (type III sums of squares). For a subset of host–parasitoid interactions, in which we had at least 10 replicates (for two host species in *N. debilis*, and for one host species in each of *O. aeneus* and *T. cyanea*), we also tested if differences in the body size of host individuals explained variance in the body size of parasitoids. Here, we used nest diameter, host size and, in the case of *N. debilis*, host identity and the interaction of host identity and size, as fixed factors in the analysis. Because *G. assectator* fed on host larvae, we did not perform this analysis, as we could not obtain data on the size of larvae from any host species that *G. assectator* parasitized (Supporting information). We used separate models for each parasitoid species because 1) parasitoid species parasitized different host species, 2) parasitoid species and parasitoid–host combinations strongly differed in their number of replicates, and 3) data on the length of hosts could not be collected for all host–parasitoid species combinations (e.g. *G. assectator* and its hosts). Together, these factors led to a strong context-dependency of the studied host–environments effects on parasitoids and the associated underlying data structure, making it impossible to analyse all four parasitoid species in one global model.

In addition, one host species *T. figulus* was parasitised by *N. debilis* and *T. cyanea* simultaneously. Here, we investigated if relationships between the size of *T. figulus* and the two parasitoids differed between the parasitoid species. We used a linear mixed effect model with the size of both parasitoids as response variables, with the identity and size of *T. figulus* and its interaction as a fixed factor, and the study plot as a random factor.

To test the relationship between the size of the four parasitoid species and their 15-host species, we averaged the size values of hosts and parasitoids at the species level. This resulted in a total of eleven host–parasitoid size combinations, as data for some parasitoid–host combinations could not be retrieved. We adjusted body sizes of parasitoids for differences between the parasitoid species and their host combinations using a linear mixed intercept model, with parasitoid species as a random variable and parasitoid body size as a response variable. The residuals from this model were then used in a standard major axis regression (SMA) with parasitoid and host body sizes as dependent variables.

To test for host–environment interaction effects on parasitoid size, we averaged values of body length for host and parasitoid individuals at the plot level. First, we analysed relationships between forest variables (stand structural complexity, canopy cover, standing deadwood diameter and herb cover) and host body length using linear models. Then, we tested relationships between parasitoid length and the forest variables. Because differences in nest quality and host size explained differences in the size of parasitoids, we also included host-related factors at the plot level (nest diameter, host identity, host size and its two-way interactions) as fixed factors in these models. In *T. cyanea*, *O. aeneus* and *G. assectator*, host size and nest diameter were correlated at the plot level, and the host–environment interactions could only be analysed for one host species. Therefore, we included only host size as a co-variable in their respective models (Supporting information). Note that we did not find effects of sex on the parasitoid–host interactions, nor differences in the sex ratios across forest variables. Consequently, the sex variable was excluded from all our analyses.

The linear mixed models were performed using the R package 'glmmTMB' (Brooks et al. 2017). To study the assumptions of homogeneity and normality of residuals and to check for overdispersion, we used the R package 'DHARMa' (Hartig 2024). We further used Wald-χ^2 test from the R package 'car' (Fox and Weisberg 2019) to assess the statistical significance of each term in the model. For the standard major axis regression, we used the R package 'lmodel2' (Legendre 2018). All analyses were conducted using R (ver. 4.2.1) within the RStudio environment (www.r-project.org).

Results

Host identity, nest diameter and host size

Of the four parasitoid species, *G. assectator* was the largest parasitoid species (9.55 ± 1.20 mm; mean ± SD), *N. debilis* (8.54 ± 1.18 mm) and *T. cyanea* (6.35 ± 0.79 mm) were intermediate, and *O. aeneus* was the smallest (5.15 ± 0.78 mm) (Supporting information). The number of observations per host species varied across parasitoid species, with *G. assectator* ranging from 2 to 10 observations per host, *N. debilis* from 1 to 79 observations, *O. aeneus* from 9 to 39 observations, and *T. cyanea* from 1 to 155 observations. This range reflects the variability in the sample sizes for each host–parasitoid interaction.

Body size of *G. assectator* was related to the identity of its hosts ($\chi^2_{3,18} = 6.65$, $p = 0.083$) and positively related to nest diameter ($\chi^2_{1,18} = 2.74$, $p = 0.097$; Fig. 3a, e, Table 1). Body size of *N. debilis* was related to host identity ($\chi^2_{3,140} = 6.65$, $p = 0.063$) and also increased with nest diameter ($\chi^2_{1,140} = 2.74$, $p = 0.022$; Fig. 3b, f). Body size of *N. debilis* was further positively related to the size of individuals of the host species *T. figulus* ($\chi^2_{1,41} = 13.33$, $p < 0.001$) (Table 1).

In the case of *T. cyanea*, variations in body size were associated with host identity ($\chi^2_{4,154} = 9.04$, $p = 0.06$) and nest diameter ($\chi^2_{1,154} = 6.15$, $p = 0.013$) (Fig. 3c, g). However, body size was not associated with host size ($\chi^2_{1,176} = 1.25$, $p = 0.262$; Table 1), although host size was significantly related to nest diameter ($\chi^2_{1,154} = 20.87$, $p < 0.001$; Fig. 4a–b, Supporting information). Host identity of *O. aeneus* positively related with body length ($\chi^2_{1,35} = 10.93$, $p < 0.001$), whereas nest diameter ($\chi^2_{1,35} = 1.7$, $p = 0.192$) and host size ($\chi^2_{1,15} = 0.01$, $p = 0.896$) did not show significant correlation (Fig. 3d, h, Table 1). In addition, when the host *T. figulus* doubled in size, the body size of *N. debilis* increased by 37% in size, while *T. cyanea* increased by 8% (Fig. 4d, e). At the species level, the size of all four parasitoid species was positively, albeit only weakly related to the size of their hosts (Fig. 5).

Host/parasitoid size and forest structure

We found no evidence that forest structures influenced the size of host individuals (Fig. 6a–e, Table 2, Supporting information). Nest diameter was an important variable that explains the variation in the individual host sizes from the parasitoid *T. cyanea* ($\chi^2_{6,56} = 20.87$, $p = < 0.001$; Fig. 4b, Table 2, Supporting information). Whereas for the hosts of *N. debilis*, the individual sizes were significantly different between host species ($\chi^2_{8,28} = 9.18$, $p = 0.002$) (Supporting information).

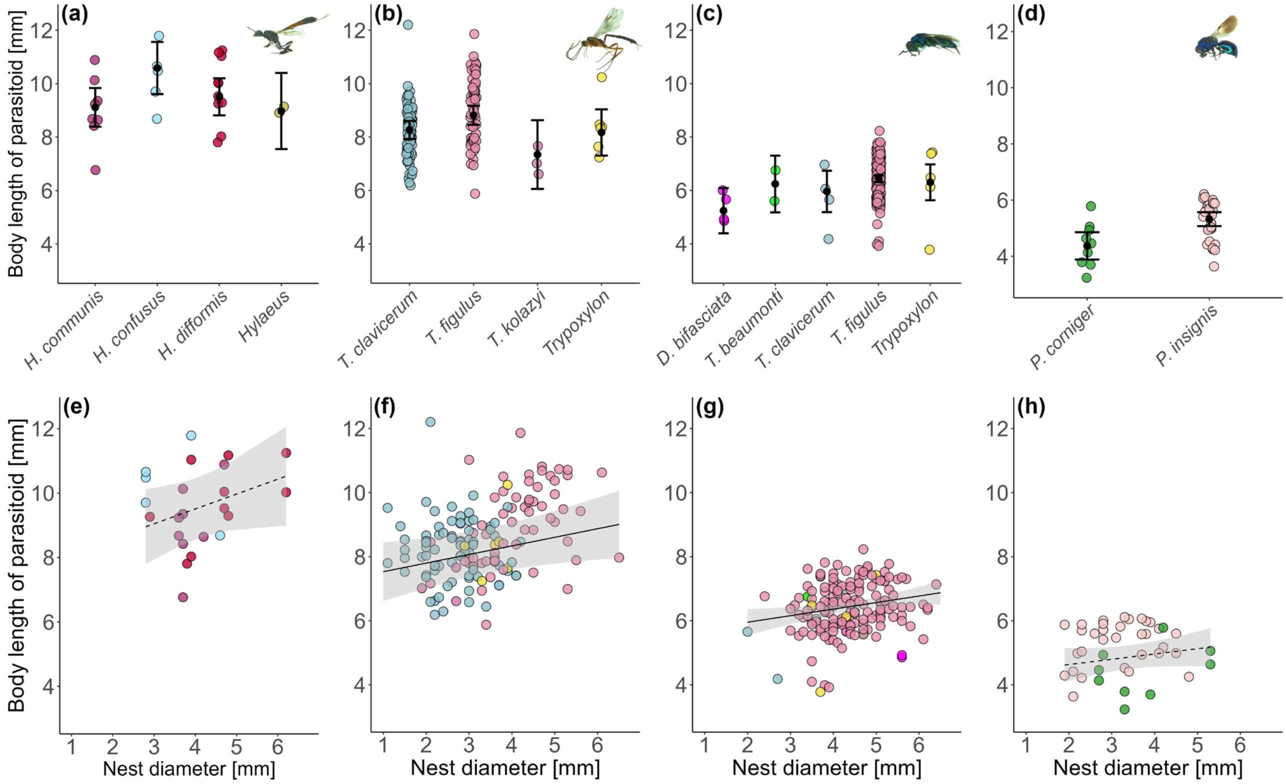

Figure 3. Influence of host identity (a–d) on parasitoid size, and the relationship between nest diameter and parasitoid size (e–g) in *Gasteruption assectator* (a, e), *Nematopodius debilis* (b, f), *Trichrysis cyanea* (c, g), and *Omalus aeneus* (d, h). The dashed regression line indicates non-significant relationships.

Body size of *N. debilis* and *T. cyanea* were positively related to host size (*N. debilis*: $\chi^2_{14,22} = 20.47$, $p < 0.001$; *T. cyanea*: $\chi^2_{6,57} = 5.802$, $p = 0.016$). Additionally, host species also influenced the size of *N. debilis* ($\chi^2_{14,22} = 4.08$, $p = 0.043$), and the interaction between host length and host species was correlated with changes in the size of *N. debilis* ($\chi^2_{14,22} = 4.33$, $p = 0.037$) (Supporting information). However, no evidence of clear associations between forest structures and parasitoid body sizes existed for all parasitoid species (Fig. 6e–h, Supporting information). Additionally, the interactions between host species and forest structure metrics (proportion of coniferous trees, canopy cover, stand complexity (SSCI), standing deadwood diameter (DBH), and herb cover) also did not yield clear correlations (Supporting information).

Discussion

Our findings indicate that host and nest size, but not the wider forest environment, affects parasitoid size. We further found that parasitoid species differed in their response to variability in host size within species, explaining why the correlation between parasitoid and host size across species was generally weak. Additionally, no significant correlations were found between various forest structures and host or parasitoid size.

Host-driven factors

The trends observed in our study suggest that host identity might be an important factor in determining parasitoid size, potentially extending beyond the size of the host. Although not all host identity influences were statistically significant, the observed patterns imply that host suitability may play a critical role. Some studies on generalist parasitoid species have reported significant variation in offspring size among different host species (Brodeur et al. 1996, Häckermann et al. 2007), supporting the notion that parasitoids are adapted to specific hosts in ways that optimize their development. According to the optimization theory (Roff 1992), animals tend to choose resources that best enhance their fitness and that of their offspring.

Host suitability may not be restricted solely to the nutritional value of the host, but rather to a combination of factors including physiological compatibility, nutritional value, foraging behaviour, and detectability cues that collectively influence the ability of the parasitoid to acquire and utilize the host (Vinson and Iwantsch 1980, Rivers and Denlinger 1995, Brodeur et al. 1996, 1998). Physiologically suitable hosts (e.g. the ability to suppress the host immune system) may support optimal conditions for parasitoid development (Harvey et al. 2012), while nutritionally rich hosts offer essential resources for their maturation (Chown and Gaston 2010). Additionally, hosts that emit clear detectability cues,

Table 1. Relationship between parasitoid size (measured by body length) and host identity, nest diameter, and host size effect on parasitoid size. Wald-chi square (χ^2) tests were used to assess the statistical significance of each term in the model. Significant relationships ($p < 0.05$) are displayed in bold.

Response variable	Fixed effect	χ^2	df	Pr(> χ^2)	Species figure
Gasteruption assectator	Host identity	6.65	3	0.083	
Length	Nest diameter	2.74	1	0.097	
	Host length	–	–	–	
Nematopodius debilis	Host identity	6.65	3	0.063	
Length	Nest diameter	2.74	1	**0.022**	
	Host length	13.33	1	**< 0.001**	
Omalus aeneus	Host identity	10.93	1	**< 0.001**	
Length	Nest diameter	1.70	1	0.192	
	Host length	0.01	1	0.896	
Trichrysis cyanea	Host identity	9.04	4	0.060	
Length	Nest diameter	6.15	1	**0.013**	
	Host length	1.25	1	0.262	

such as chemical signals (Fatouros et al. 2008) or colour (Ferreira Santos de Aquino et al. 2012), are more likely to be effectively parasitized, leading to better offspring growth. By selecting hosts that offer the best combination of these factors, parasitoids can maximize their fitness, resulting in variations in body size across different host–parasitoid interactions.

Our analysis indicated that nest diameter positively influenced the size of some parasitoid species feeding on bee and wasp hosts. Specifically, the ichneumon wasp *N. debilis* and the blue cuckoo wasp *T. cyanea* showed significant positive relationships, while the wild carrot wasp *G. assectator* exhibited a trend toward significance, and the cuckoo wasp *O. aenus* did not show a significant relationship. This suggests that nest diameters can be an important factor for certain species, though its influence may vary. While research on nest diameter–body size relationships has mostly been conducted for cavity-nesting bees and wasps (Polidori et al. 2010, Rauf et al. 2022), the pattern generally suggests that larger bees and wasps often nest in cavities with larger diameters. The diameter of the nests influences the number of cells built by female bees and wasps, increases the size and volume of provisions collected relative to smaller nest diameters, and optimizes the body mass of their offspring but not the sex ratio (Fricke 1991, Bosch and Vicens 2006, Seidelmann et al. 2016, Rinehart et al. 2024).

Most parasitoid species in our study feed on the resources provisioned by hosts. Since the size and volume of collected provisions influence the body sizes of bees and wasp offspring, it is reasonable to expect that adult female parasitoids may use the nest diameter factor as a criterion to select higher-quality nests, thereby ensuring the production of a fitter generation. Although our data did not fully confirm the expectation that all parasitoid species would increase in size with larger nest diameters, the overall trend supports the idea that high-quality nests can enhance the growth of emerging parasitoids.

Existing literature often suggests that host size is an important factor in explaining differences in parasitoid size (Cohen et al. 2005, Jenner and Kuhlmann 2006, King and Napoleon 2006, da Rocha et al. 2007). However, our results indicated that host size alone is often a poor predictor of parasitoid size across species. We found only a weak relationship between parasitoid size and host size at the species level, though comparing the 1:1 ratio suggests that smaller hosts can produce larger parasitoids (Fig. 5). Additionally, the fact that only *N. debilis* showed a significant size relationship with its host suggests that its development is more tightly linked to host size compared to other species. Notably, when examining the two parasitoid species *N. debilis* and *T. cyanea*, which share similar hosts, we found different responses to changes in host size (Fig. 4d–e).

The dependency on host size in the ichneumon wasp *N. debilis* can be explained by its life history strategy as an idobiont ectoparasitoid. As an idiobiont ectoparasitoids, *N. debilis* paralyses their hosts to prevent any further development, relying mainly on their hosts as food resources, which makes them highly dependent on the host's initial size for sufficient resources to complete their development. This dependency is also noted in the literature, which highlights that the fixed amount of resources in idiobiont ectoparasitoids makes larger hosts more valuable, thus demonstrating a strong relationship between host and adult size (Fidgen et al. 2000, Harvey

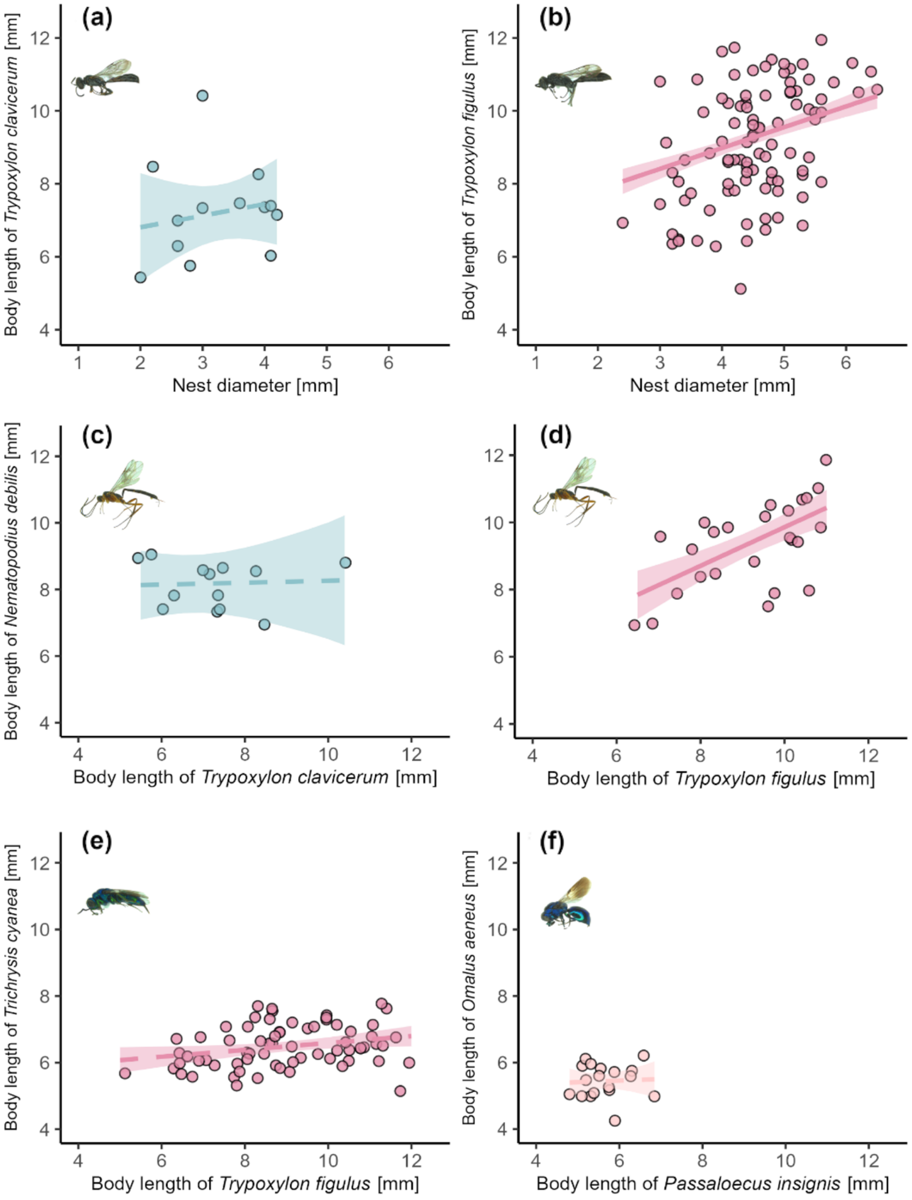

Figure 4. Relationship between the size of different hosts (a, b) and nest diameter, and the relationship between the size of parasitoid species and their hosts (c–f). *Nematopodius debilis* (9.28 ± 0.27 mm) and *Trychrisis cyanea* (6.47 ± 0.18 mm), two parasitoid species that parasitize similar host species showed different responses in size when their host *Trypoxylon figulus* doubled in size (d, e). All axes are scaled the same (a and b, c–f). The dashed regression line indicates non-significant relationships.

2005, Harvey et al. 2006, Kishani Farahani et al. 2016). This strong dependency between host and adult size observed in *N. debilis* highlights the species-specific impact of host resources on body size, a pattern consistent with other idiobiont parasitoids.

In contrast, larvae of kleptoparasitoid species, such as *T. cyanea*, *O. aeneus*, and *G. assectator*, rely on provisions collected by their hosts and may exploit hosts already parasitized by other parasitoid species (Torreta 2015, Winterhagen 2015, Polaszek and Vilhemsen 2023). This kleptoparasitic strategy may introduce a complex dynamic into the development of these parasitoids, as competition with other parasitoids or reliance on pre-provisioned resources may reduce the predictability of size outcomes. As a result, the development of kleptoparasitoid individuals may depend more on the quantity and quality of host provisions than on host size itself, leading to a potentially weaker correlation between host size and parasitoid size. The contrasting body size pattern found in *N. debilis* and *T. cyanea* highlights the adaptive diversity among parasitoids, where distinct life history strategies shape body size responses in relation to food resources.

Direct studies on the effect of host provision on kleptoparasitoids are lacking, and the variability in food resources, both in terms of quantity and quality, may be crucial in driving

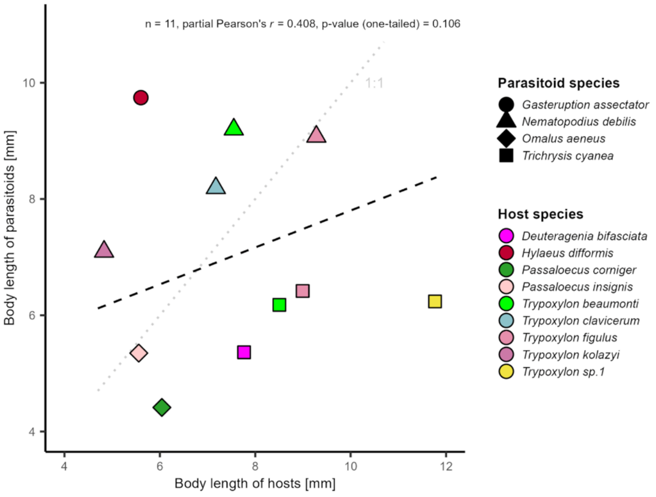

Figure 5. Correlation between parasitoid body length and host body length across eleven host–parasitoid interactions. The shape of the points represents different parasitoid species and the colour represents different host species. The black dashed line indicates the correlation between parasitoid and host body lengths (partial Pearson's r = 0.408, p = 0.106, one-tailed). The grey dotted line represents the 1:1 ratio, illustrating that smaller hosts can produce larger parasitoids, although the overall correlation strength is weak.

the development of this parasitoid group. Additionally, the importance of host identity and nest quality in determining parasitoid size found in our study, suggests that the multifaceted nature of the influencing factors, including the quantity and quality of host provisions and host species suitability, may explain the lack of correlation between host size within host species and parasitoid size observed in *T. cyanea*, *O. aeneus*, and *G. assectator*. Future research on the quantity and quality of host provisions could offer further insights into the development patterns of kleptoparasitoids and clarify the drivers behind observed size variability.

Host/parasitoid size and forest structure

Contrary to our hypotheses, the structural variables associated with retention forestry did not strongly influence the body size or the sex ratio of the parasitoids or their hosts. This finding contrasts with previous research (Blake et al. 1994, Sorvari and Hakkarainen 2007, Grab et al. 2019, Elzay and Baum 2021), which reported a significant influence of habitat structure on insect body size and sex ratio. Our inclusion of environmental variables was based on evidence from prior studies (Rappa et al. 2023, 2024), which demonstrated that factors such as the proportion of coniferous trees, canopy cover, deadwood, and structural complexity influence host diversity, abundance and host–parasitoid network dynamics. We hypothesised that similar indirect

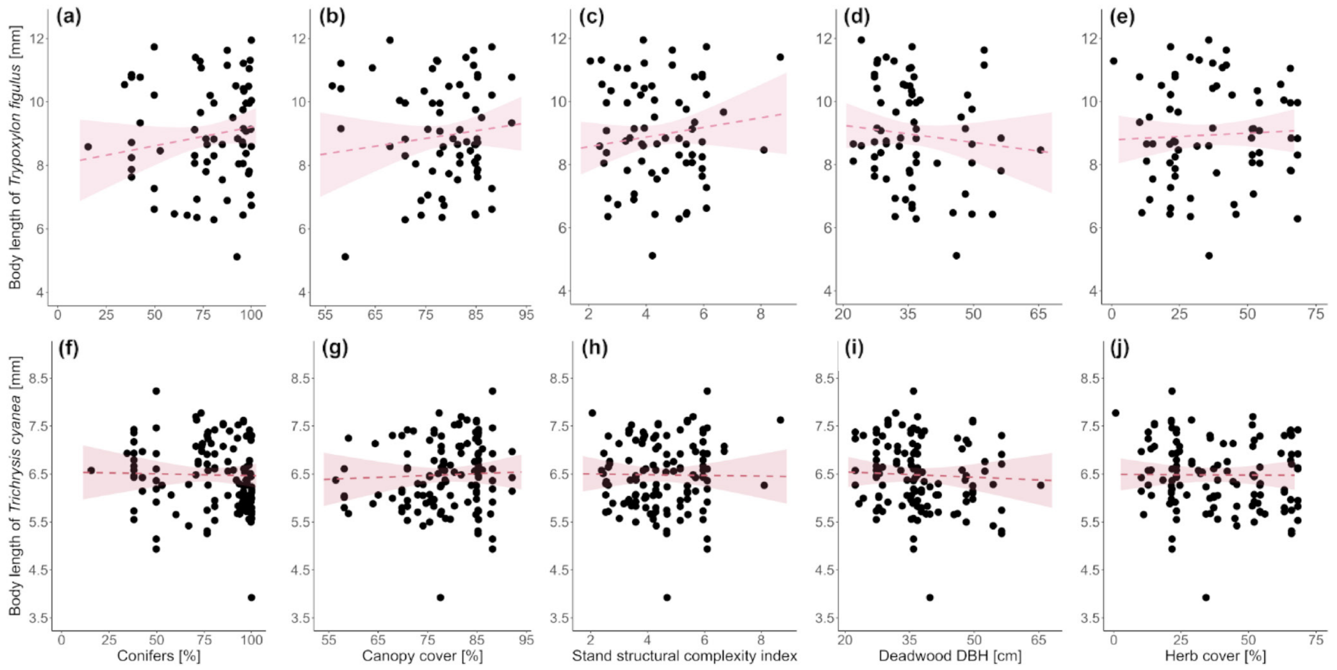

Figure 6. The relationship between characteristics of proportion conifers (a, f), canopy cover (a, e), stand structural complexity index (SSCI) (c, h), diameter at the breast height of standing deadwood (DBH) (d, i), herb cover (e, j) and, body length of host (a–e) and the parasitoid species (f–j), exemplified in the interactions between *Trichrysis cyanea* (parasitoid) and *Trypoxylon figulus* (host). The lack of significant environmental relationships between forest variables and host and parasitoid sizes were similar for the rest of the host–parasitoid along the five environmental gradients (*Gasteruption assectator* only parasitoid size response*,* *Nematopodius debilis* with *Trypoxylon clavicerum* and *T. figulus,* and *Omalus aeneus* with *Passaloecus insignis;* see the Supporting information). The dashed regression line indicates non-significant relationships.

Table 2. The relationship between characteristics of proportion of coniferous trees, canopy cover, stand structural complexity index (SSCI), diameter at the breast height of standing deadwood (DBH), herb cover and body length of host and the parasitoid species, exemplified in the interactions between *Trichrysis cyanea* (parasitoid) and *Trypoxylon figulus* (host). The lack of significant environmental relationships between forest variables and host and parasitoid sizes were similar for the rest of the host–parasitoid along the five environmental gradients (*Gasteruption assectator, Nematopodius debilis* with *Trypoxylon clavicerum* and *T. figulus,* and *Omalus aeneus* with *Passaloecus insignia;* see the Supporting information). Wald-chi square (χ^2) tests were used to assess the statistical significance of each term in the model. Significant relationships ($p < 0.05$) are displayed in bold.

Response variable	Fixed effect	χ^2	df	Pr(> χ^2)
Body length of host				
Trypoxylon figulus	Proportion conifers	1.661	1	0.197
	Canopy cover	0.518	1	0.069
	SSCI	0.304	1	0.421
	Standing deadwood DBH	0.436	1	0.496
	Herb cover	0.308	1	0.470
	Nest diameter	20.879	1	**< 0.001**
Body length of parasitoid				
Trichrysis cyanea	Proportion conifers	0.037	1	0.847
	Canopy cover	0.004	1	0.708
	SSCI	0.207	1	0.939
	Standing deadwood DBH	0.238	1	0.620
	Herb cover	0.005	1	0.781
	Host length	5.802	1	**0.016**

effects of forest habitat structure might extend to parasitoid traits, such as body size, by influencing host quality. Although our findings did not support this hypothesis, they reveal a context-dependent relationship, suggesting that habitat complexity may shape species interactions in indirect or subtle ways that vary across ecological settings. Consequently, incorporating these environmental factors remains significant, as it enhances our understanding of how habitat composition influences species traits across multiple trophic levels.

One possible explanation for the lack of a significant relationship observed in our study may be the spatial scale at which the data were collected. Finer-scale measurements might better capture microhabitat variations that influence body size and sex ratio. Additionally, other unmeasured environmental factors or biotic interactions, such as competition pressure, might play a more substantial role in shaping parasitoid traits, as parasitoids tend to adjust their body size when parasitising similar hosts (Iwao and Ohsaki 1996, Cusumano et al. 2015).

Our findings add to the growing literature questioning the impact of forest structure on insect body size in managed ecosystems. While forest management practices may not directly alter body size – a key fitness trait – indirect effects and other environmental variables may still be influential. This study highlights how biotic factors and environmental gradients shape life-history traits, with species-specific responses to host quality driving variation even without strong habitat effects. Using parasitoids as a model, we contribute insights into how trophic interactions and environmental conditions jointly affect trait variation and ecosystem stability, with implications for conservation in managed forests. Future research would benefit from long-term studies incorporating finer-scale environmental variables and experimental habitat manipulations to deepen our understanding of subtle environmental effects on body size.

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Author contributions

Riko Fardiansah: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Resources (equal); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Finn Rehling**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Supervision (lead); Validation (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (lead). **Nolan J. Rappa**: Data curation (equal); Investigation (supporting); Resources (lead); Writing – review and editing (equal). **Carsten F. Dormann**: Formal analysis (supporting); Supervision (supporting); Validation (supporting); Writing – review and editing (equal). **Alexandra-Maria Klein**: Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (lead); Methodology (supporting); Supervision (equal); Validation (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rfj6q57m6 (Fardiansah et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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