

Parasitism rate, parasitoid community composition and host specificity on exposed and semi-concealed caterpillars from a tropical rainforest

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Abstract The processes maintaining the enormous diversity of herbivore—parasitoid food webs depend on parasitism rate and parasitoid host specificity. The two parameters have to be evaluated in concert to make conclusions about the importance of parasitoids as natural enemies and guide biological control. We document parasitism rate and host specificity in a highly diverse caterpillar-parasitoid food web encompassing 266 species of lepidopteran hosts and 172 species of hymenopteran or dipteran parasitoids from a lowland tropical forest in Papua New Guinea. We found that semi-concealed hosts (leaf rollers and leaf tiers) represented 84 % of all caterpillars, suffered a higher parasitism rate than exposed caterpillars (12 vs. 5 %) and their parasitoids were also more host specific. Semi-concealed hosts may therefore be generally

more amenable to biological control by parasitoids than exposed ones. Parasitoid host specificity was highest in Braconidae, lower in Diptera: Tachinidae, and, unexpectedly, the lowest in Ichneumonidae. This result challenges the long-standing view of low host specificity in caterpillar-attacking Tachinidae and suggests higher suitability of Braconidae and lower suitability of Ichneumonidae for biological control of caterpillars. Semi-concealed hosts and their parasitoids are the largest, yet understudied component of caterpillar—parasitoid food webs. However, they still remain much closer in parasitism patterns to exposed hosts than to what literature reports on fully concealed leaf miners. Specifically, semi-concealed hosts keep an equally low share of idiobionts (2 %) as exposed caterpillars.

Keywords Lepidoptera · Specialization · Community structure · External feeding · Malesia

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Introduction

Terrestrial food webs of plants, herbivores and their natural enemies harbour much of global biodiversity (Hamilton et al. 2010; Price 2002), including many parasitoids (Godfray 1994; Quicke 1997). Understanding of the mechanisms maintaining this enormous diversity requires quantitative data on host—parasitoid food webs, especially from the tropics where these food webs are poorly known (Godfray et al. 1999). These data are needed to estimate parasitism rates and host specificity of parasitoids, which in turn determine the top-down impact of parasitoids on their herbivorous hosts. Host specificity determines the potential of parasitoids to mediate density-dependent effects on their hosts as well as apparent competition among different host species sharing the same parasitoid species (Morris et al.

2004). Host specificity is also a key parameter for biological control and knowledge of general parasitism patterns from natural habitats can guide biological control programmes (Kidd and Jervis 2005).

Most of our knowledge of parasitoid communities of externally feeding herbivores comes from several large-scale caterpillar-rearing campaigns (Barbosa and Caldas 2004; Gentry and Dyer 2002; Janzen 1995; Le Corff et al. 2000; Sheehan 1994; Stireman et al. 2005; Stireman and Singer 2003). These studies concentrated on macrolepidopteran hosts, which mostly feed exposed on foliage, while paying less attention to microlepidopterans, which feed in semi-concealed situations like leaf rolls or silk webs (with Le Corff et al. 2000 as a notable exception). Microlepidoptera are much less known taxonomically and also often ignored in the community studies focused on adults, such as those using light trapping. The share of semi-concealed caterpillars in natural communities varies greatly between sites and tree species, but overall, semi-concealed caterpillars are at least as common as exposed ones (Table 1).

Hawkins (1994) identified the degree of host concealment as a key parameter for parasitoid communities. Parasitism rate and parasitoid species richness increase with the degree of concealment from exposed feeders through leaf rollers, leaf tiers and case-bearers, reach maximum values in leaf miners and gallers, and then decrease again in even more concealed borers and root-feeders. While the final decrease from leaf miners to borers and root feeders is likely due to decreasing accessibility of hosts to parasitoids, the initial increase from exposed hosts through semi-concealed hosts to leaf miners has been explained by increasing host apprenency and decreasing host defences (Hawkins 1994), or by decreasing competition with predators which can potentially outcompete parasitoids

through asymmetric intra-guild predation on parasitized hosts (Gentry and Dyer 2002; Polis et al. 1989).

The high abundance of semi-concealed caterpillars in herbivore communities, the higher importance of parasitoids as their natural enemies compared with exposed hosts, and the overall bias against their study may lead to a paradoxical situation in which we know the least about the largest parasitoid component of caterpillar-parasitoid food webs. Our ignorance starts with a question as to whether exposed and semi-concealed caterpillars really differ in parasitism rate. The comprehensive meta-analysis by Hawkins (1994) revealed general trends between parasitism rate and host concealment, but did not find a statistically significant difference between exposed and semi-concealed hosts. So far, two studies have shown higher parasitism rates in semi-concealed caterpillars (Connahs et al. 2011; Gentry and Dyer 2002), while Le Corff et al. (2000) found season to be more important than host concealment. Parasitism rate has also been found to depend on host abundance (Stireman and Singer 2003), as parasitoids could specialize on more common species or attack the more common species from their host range, and on the host plant species of the herbivores (Lill et al. 2002).

The taxonomic composition of parasitoid communities of semi-concealed hosts is expected to lie somewhere between that of exposed caterpillars and leaf miners. While parasitoid communities of exposed caterpillars are composed of ichneumonid wasps, braconid wasps and tachinid flies with only a small proportion of chalcidoid wasps (Barbosa et al. 2004; Gentry and Dyer 2002; Hawkins 1994; Le Corff et al. 2000), leaf miner parasitoids are mostly chalcidoid wasps with fewer braconid and ichneumonid wasps (Askew and Shaw 1979; Hawkins 1994; Hespenheide 1991; Salvo et al. 2011). There is also a

Table 1 Proportion of semi-concealed caterpillars in communities of externally leaf-feeding Lepidoptera in a set of studies that appeared to sample all caterpillars without major bias

Dataset	% Semi-concealed individuals in the community	Habitat	Note
Novotny et al. (2006)	32	Temperate forest	Czech Republic, 14 tree spp., min. 8 %, max. 65 %
Novotny et al. (2006)	28	Temperate forest	Slovakia, 8 tree spp., only beating method
Murakami et al. (2005)	61	Temperate forest	Japan, 1 tree sp.
Murakami et al. (2007)	43	Temperate forest	Japan, 10 tree spp., min. 14 %, max. 93 %
Le Corff and Marquis (1999)	76	Temperate forest	Missouri, USA, 2 oak spp., min. 67 %, max. 84 %
Novotny et al. (2006)	69	Tropical forest	Papua New Guinea, 18 tree spp., very variable between species
Diniz and Morais (1997)	65	Tropical savanna	Brazil, 9 shrub and tree spp., min. 61 %, max. 95 %

The complement to 100 % is the proportion of caterpillars feeding exposed. *min.* minimum, *max.* maximum

considerable shift in parasitoid life history strategies between exposed and leaf-mining caterpillars. Almost all parasitoids of exposed caterpillars are endoparasitic koinobionts which live inside the host while keeping it alive, while two-thirds of the parasitoids of leaf-mining caterpillars are ectoparasitic idiobionts which feed from outside on the host killed by ovipositing females (Askew and Shaw 1979; Hawkins 1994; Le Corff et al. 2000; Sheehan 1991). Semi-concealed hosts are therefore expected to have a larger share of idiobiont parasitoids than exposed hosts. As idiobionts are generally less host specific than koinobionts (Askew and Shaw 1986), parasitoids of semi-concealed hosts are expected to be less specialized than parasitoids of exposed hosts. The analysis of parasitoid community structure requires a survey of all parasitoid taxa, but Hymenoptera and Diptera are commonly studied separately in caterpillar—parasitoid community studies.

Parasitoid host specificity is an important parameter for understanding herbivore—parasitoid food webs, estimating their diversity, and potentially guiding biological control programs. However, a rigorous comparison of parasitoid host specificity requires analysis of a broad range of potential hosts so that parasitoid host ranges are not underestimated. This is probably why no host-specificity comparison between parasitoid groups attacking external leaf-chewing Lepidoptera has been published. The closest to this was a meta-analysis of the complete range of parasitoids, but limited to one superfamily of mostly semi-concealed hosts (Tortricoidea; Mills 1992). From parasitoids of caterpillars in that study, braconid wasps were the most specialized, followed by ichneumonid wasps and the least specialized tachinid flies. This agrees with the traditional view of tachinid flies being more generalist than hymenopteran parasitoids, because of the ability of tachinid larvae to form respiratory funnels while staying inside the host so that they do not have to adapt so closely to the inner environment of the host (Belshaw 1994; Eggleton and Gaston 1992). Recent studies of morphology, DNA barcodes and ecology have shown that both Tachinidae and Microgastrinae (the largest subfamily of Braconidae) are more specialized than previously thought because of historically overly broad species concepts (Smith et al. 2006, 2007, 2008), but the single Hymenoptera subfamily studied was still more host specific than the Tachinidae.

In this study, we analyse a quantitative community dataset of exposed and semi-concealed caterpillars and their parasitoids from a tropical rainforest. We first test whether parasitism rate is influenced by host feeding mode, expecting higher parasitism rates in semi-concealed hosts, and if host abundance and host plant identity also influence parasitism rates. Then we test whether there is a difference between exposed and semi-concealed caterpillars in parasitoid community size and composition, expecting larger

parasitoid communities on semi-concealed hosts with community structure intermediate between that of exposed hosts and leaf miners in terms of parasitoid taxonomy and life history (proportion of koinobionts vs. idiobionts). Further, we test whether exposed and semi-concealed caterpillars differ in parasitoid host specificity, expecting higher host specificity in exposed caterpillars due to a presumed higher proportion of more specialized koinobionts. Finally, we test if parasitoid groups differ in host specificity, i.e. in number or taxonomic relatedness of the host species attacked. We expect hymenopteran parasitoids to be more host specific than dipteran parasitoids. We repeat the last analysis which is the one most likely to be influenced by species concept with species delineations from initial parasitoid morphotyping to test robustness of the result.

Materials and methods

The fieldwork took place within a 10 × 20-km area encompassing a mosaic of primary and secondary forests near Ohu, Baitabag and Mis villages (145°41–7'E, 5°08–14'S, 0–200 m), Madang Province, Papua New Guinea. The average annual rainfall in the Madang area is 3,558 mm, with a moderate dry season from July to September and mean air temperature of 26.5 °C, which varies little throughout the year (McAlpine et al. 1983). The herbivorous insects show little seasonality in the area [median presence of species was reported to be 11 months by Novotny et al. (2002)]. All external leaf-feeding Lepidoptera including leaf rollers and leaf tiers (which together make up >95 % of all larval external leaf chewers on site; Novotny et al. 2002) were collected by field assistants from a selection of 38 locally common tree species from both early and late stages of forest succession (Leps et al. 2001). This selection covered major lineages of angiosperms, viz. magnoliids, monocots, core eudicots, rosids I and II, basal asterids and asterids I (APG 2009). The samples from focal tree species comprised 1,500 m² of leaf area on each of 18 tree species, 3,000 m² on 19 tree species and 4,500 m² on one tree species. The sampling spanned 4–16 months per tree species during 2002–2004 (see Table S1 for a list of tree species and corresponding sampling effort and sampling period). The variable sampling effort is due to merging of two datasets with identical sampling methods (Novotny et al. 2002, 2007) to maximize overall sample size. The number of tree inspections (a particular tree sampled at a particular time) exceeded 1,000 per tree species for each 1,500 m² sampled. Combined data were used for most analyses, but sampling effort was standardized to 1,500 m² of leaves for comparisons between tree species. Only the caterpillars which fed on leaves of the tree species from which they were collected were kept, and

reared until the adult Lepidoptera or its parasitoid emerged, or the caterpillar died. Caterpillars were assigned to morphospecies prior to rearing, because linking of a reared parasitoid with its host depends on previous identification of the host caterpillar. The caterpillar morphospecies were verified by rearing, as far as possible. A host caterpillar morphospecies was considered reliable and used for the further analysis if at least five caterpillars of that morphospecies on a given host plant were reared to adult moths, and at least 95 % of all reared adults belonged to a single lepidopteran species.

The identification of adult Lepidoptera was based on extensive dissection of genitalia and reference to type specimens, together with extensive DNA barcoding: 80 % of host species barcoded and >10,000 sequences of background host fauna (Craft et al. 2010; Miller et al. 2003). Higher classification follows Holloway et al. (2001) with the exception of splitting Crambidae from Pyralidae. Lepidopteran species were assigned to a semi-concealed (leaf rollers, tiers, web spinners, shelter builders) or exposed (freely foraging caterpillars) feeding mode according to field observations of the caterpillars (Table S2). These two guilds together are referred to as “external leaf chewers”. Host community phylogeny was constructed from DNA barcodes using maximum likelihood and constraining family monophyly (Fig. S1). One species with no DNA barcode sequence (*Brenthia* sp. CHOR016) was substituted with a congener. All branches were transformed to equal length.

All parasitoids were sorted and preliminarily morphotyped by J. H. Microgastrinae and Cardiochilinae (Braconidae) were identified by J. B. W., Tachinidae by H. S., and the remaining groups were identified by other taxonomists, listed in the acknowledgments. A selection of the parasitoid specimens (32 %) based on preliminary morphotyping was DNA barcoded (with 64 % success), and any identifications in conflict with DNA barcodes were re-examined. DNA barcodes were obtained for 87 (51 %) of the 172 parasitoid species. Only 21 of the 172 parasitoid species have been formally described (e.g. Quicke et al. 2012); the other species are putative assessments by the taxonomists. We divided parasitoid species into groups based on combination of their ecology and taxonomy (Table S3). Within Hymenoptera, the monophyletic sister groups Braconidae and Ichneumonidae (Belshaw et al. 1998; Whitfield 2003), with no clear differences in ecology, were analysed separately as the two largest taxa. In Diptera: Tachinidae, there is a clear split in ecology within our dataset, with Exoristinae: Goniini possessing specialized “microtype” eggs which are placed on vegetation and later ingested by the host (hereafter “indirectly ovipositing Tachinidae”) and Dexiinae: Voriini, Tachininae: Siphonini (*Ceromya* and *Peribaea*) and the rest of Exoristinae which

oviposit directly on the host (“directly ovipositing Tachinidae”). As defined here, indirectly ovipositing Tachinidae are probably monophyletic and directly ovipositing Tachinidae paraphyletic (Tachi and Shima 2010). Rare groups which could not have been analysed separately were also included in Hymenoptera vs. Diptera comparisons {Chalcidoidea, Bethylidae, Tachinidae: Blondeliini which inject eggs into hosts with a piercing structure, and some Tachinidae: Siphonini [*Actia* and *Siphona* (*Aphantorhaphopsis*)] which lay well-developed eggs in the host vicinity}. Parasitoid life history categories (endo/ectoparasitoid, koino/idiobiont, hyperparasitoid) were determined for higher parasitoid taxa using published data (Gauld and Bolton 1996; Gauld 1984; Gibson et al. 1997; Goulet and Huber 1993; Hanson and Gauld 1995).

Parasitism rate was quantified as proportion of parasitized caterpillars (analogous to prevalence in parasitology). Parasitoid host-specificity analysis disregards the number of conspecific parasitoids emerging from the same caterpillar. This allows joint analysis of solitary and gregarious parasitoids (only 3 % of successful rearings resulted in more than one adult parasitoid in our study, but these rearings accounted for 17 % of all parasitoid individuals reared). Parasitism rates recorded in rearing surveys are often considered to be underestimates of real parasitoid impact on host populations because the hosts are removed from possible later parasitism at the time of collection (Gentry and Dyer 2002; Stireman et al. 2005). Therefore, collection of only older instars has been previously proposed to give better estimates of parasitism rate. However, the possible biases are complex, and can skew parasitism rate estimates in both directions (Van Driesche 1983). Specifically, parasitized hosts can have longer development, greater mortality in earlier developmental stages (Cornell and Hawkins 1995; Hawkins et al. 1997), and the hosts sampled for rearing are removed from the impact of other natural enemies as well as parasitism, all of which can lead to over-recording of parasitized individuals. We therefore sampled all caterpillar instars found. The impacts parasitoids have on hosts can be safely judged only from life table studies (Van Driesche 1983), but we believe that biologically consistent datasets like ours permit at least relative comparisons.

Overall, 62 % of parasitoid rearings could be assigned to host species, 13 % to host genus and 8 % to host family. The remaining 17 % could not be assigned, either because less than five moths were reared from a given combination of caterpillar morphospecies and tree species (9 % of rearings), the parasitoid emerged from the caterpillar before it was morphotyped (4 %), or there was <95 % confidence in the identification of caterpillar morphospecies (4 %). We used only the rearings assigned to host species for species-level analyses.

Data analysis

We first checked whether exposed and semi-concealed caterpillars differ in rearing success. Bigger difference in rearing success indicates more room for rearing bias, but even a large difference does not mean the presence of bias (see “**Discussion**”). We compared rearing success between lepidopteran species whose caterpillars are easily identifiable (their caterpillar morphospecies produce 95 % or more adults of a single species) with at least 30 caterpillars collected (because rearing success is a proportion and tends to be erratic at low sample sizes) by Wilcoxon rank test.

The difference in parasitism rate between exposed and semi-concealed hosts was evaluated on the level of the entire community, on the level of host plant species and on the level of host species. For the entire community we used a χ^2 -test with caterpillar feeding mode and parasitized (yes/no) as factors on the entire dataset. For the test across tree species we used a Wilcoxon rank test of combined parasitism rate of exposed or semi-concealed caterpillars, paired by tree species. For the test across host species we used a Wilcoxon rank test on host species with at least 30 successful rearings, since parasitism rate is a proportion and tends to be erratic in small sample sizes. We repeated the host species-level analysis using phylogenetically independent contrasts, with host feeding mode coded as 0 (exposed) and 1 (semi-concealed) and parasitism rate square-root arcsin transformed. We further performed analogous tests for the effect of caterpillar feeding mode on partial parasitism rate caused by Hymenoptera and Diptera, removing host species with no parasitism by the given parasitoid order. This resulted in more conservative tests, because the lack of parasitism is hard to distinguish from low sampling.

Correlation between host species abundance and its parasitism rate was computed using logistic regression with quasibinomial distribution for species with at least 30 successful rearings. The effect of host tree species on herbivore parasitism rates was evaluated for the 16 most common herbivore species with more than one host tree species using a two-way contingency table for each species with host tree and parasitized (yes/no) as factors (according to Lill et al. 2002) and applying Bonferroni correction for the number of tests made.

For parasitoid community size, we first checked for correlation with the number of parasitoid rearings by a general linear model (GLM) with a Poisson distribution. Because parasitoid community size significantly correlated with number of rearings we used rarefaction down to five parasitoid rearings (to include as many host species as possible), followed by a Wilcoxon rank test to test for difference in parasitoid community size on exposed and semi-concealed hosts.

The difference in proportion of endoparasitic koinobionts between parasitoids attacking primarily exposed and semi-concealed hosts was tested using a contingency table with life history (endoparasitic koinobiont: yes/no) and host feeding mode as factors. This analysis included all parasitoid species with hosts identified to species level. Difference in the parasitoid taxonomic composition between exposed and semi-concealed hosts was tested by contingency table with host feeding mode and parasitoid group as factors. We further tested if parasitoid groups differ in proportion of species attacking exposed or semi-concealed hosts or both. This is a very similar analysis to the previous one, but from the viewpoint of parasitoids. Further, in the previous analysis, parasitoid species which attack both host feeding mode groups appear in both exposed and semi-concealed feeding modes. Both analyses include all parasitoid species from the four parasitoid groups with hosts identified to species level.

We tested for difference in parasitoid host specificity between parasitoids attacking primarily exposed and semi-concealed hosts using a multinomial log-linear model with parasitoid host-specificity category (species specialist, family specialist, feeding mode specialist, generalist) as a response, and number of parasitoid rearings and primary host feeding mode as predictors. We assessed significance of feeding mode by comparing a model with number of parasitoid rearings with a model with both predictors using a likelihood ratio test (to account for a variable number of rearings). Here and in the following analyses we included only parasitoid species with two or more rearings because a parasitoid reared only once cannot be classified for host specificity.

The difference in the number of species, genera and families attacked between parasitoid groups was analysed using GLM with Poisson distribution with number of parasitoid rearings and parasitoid group as predictors. The significance was assessed by comparing a model with number of parasitoid rearings with a model with both predictors using a χ^2 -test.

We analysed specificity of the parasitoid groups on hosts using a multinomial log-linear model with host-specificity category as a response and number of parasitoid rearings and parasitoid group as predictors. We included number of parasitoid rearings in a null model and tested significance of adding the parasitoid group using a likelihood ratio test. We further tested for differences between parasitoid groups in specificity to the host tree by multinomial log-linear model with tree host specificity category (species specialist, family specialist, generalist) as a response and number of parasitoid rearings, host specificity category, and parasitoid group as predictors. We included the first two predictors in a null model and tested significance of adding parasitoid group using a likelihood ratio test. We repeated

the last two analyses with species delineations from initial parasitoid morphotyping by J. H. to test robustness of the results.

Results

The dataset

In total, 39,094 caterpillars were collected from the 38 focal tree species (129–1,231 caterpillars per 1,500 m² of leaves; mean = 637). The overall rearing success was 33 %, resulting in 11,570 adult lepidopteran hosts and 1,516 hymenopteran or dipteran parasitoids (overall parasitism rate of 12 %). A total of 266 host species from 29 families of Lepidoptera were reared, with Crambidae, Noctuidae, and Tortricidae being the most speciose, and Crambidae, Choreutidae, and Geometridae the most abundant (Table S2). Semi-concealed caterpillars represented 58 % of all species and 84 % of all individuals, the rest being exposed caterpillars. A total of 172 parasitoid species were reared, mostly from Braconidae, Tachinidae and Ichneumonidae (Table S3).

Parasitism rate

Rearing success was not significantly different between semi-concealed (mean = 41 %) and exposed (31 %) lepidopteran species ($n = 31/9$ spp., Wilcoxon rank test, $W = 192$, $P = 0.092$). Parasitism rate was significantly correlated with host feeding mode for the entire community and across tree species (Table 2), with semi-concealed hosts suffering higher parasitism rates than exposed hosts (Fig. 1). However, the relationship was not significant in herbivore species-level analyses (Table 2). Parasitism rate caused by Hymenoptera was also significantly higher in semi-concealed hosts, but parasitism rate by Diptera did not differ with host feeding mode (Table 2; Fig. 1).

Overall parasitism rate was not correlated with host species abundance ($P = 0.48$, $F_{1,37} = 0.504$), neither were partial parasitism rates caused by Hymenoptera and Diptera ($P = 0.059$ and 0.15, $F_{1,33} = 3.837$ and $F_{1,26} = 2.264$, respectively). The four most common herbivore species feeding on more than one host tree had significantly different parasitism rates on different host trees ($P < 0.0005$; Bonferroni corrected threshold of significance = 0.003), while a further 12 species which were analysed did not significantly differ in parasitism on their host trees.

Parasitoid community size and composition

The number of parasitoid species per host strongly positively correlated with the number of parasitoid rearings

($P < 0.001$, *explained deviance* = 0.589, $z_{1,49} = 6.402$). The rarefied number of parasitoid species did not differ between semi-concealed and exposed hosts (exposed, mean 2.4 parasitoid species; semi-concealed, 2.2 spp., $n = 22/5$, Wilcoxon rank test, $W = 49$, $P = 0.73$).

Almost all parasitoids (157 of the 172 species or 91.5 %) were endoparasitic koinobionts. A further nine species (5 %) included the three remaining combinations of endo/ectoparasitism and idio/koinobiontism. Only two species were clear hyperparasitoids (1 %) and the biology of a further four species (2.5 %) remained unknown. The obvious and possible hyperparasitoids together constituted only 0.5 % of all parasitoid rearings and only a single specimen of a possible hyperparasitoid species was included in species-level analyses. The proportion of endoparasitic koinobionts was not significantly different between parasitoid species attacking primarily exposed and semi-concealed hosts ($P = 0.43$).

Exposed and semi-concealed hosts significantly differed in parasitoid community composition (Fig. 2a; $P = 0.002$), with semi-concealed Lepidoptera hosting mostly Braconidae, and exposed Lepidoptera hosting mostly directly ovipositing Tachinidae species. This trend was the same when examined with the number of parasitoid rearings from exposed and semi-concealed hosts (Fig. 2b; $P < 0.001$).

Parasitoid specificity to host feeding mode

Most of the parasitoid species attacked semi-concealed hosts (73 %), further 18 % attacked exposed hosts, and only seven species (9 %) attacked both groups of hosts, with all the overlaps being marginal (constituting only one or two individuals from the less common host feeding mode). There was a significant interaction between parasitoid group and feeding mode of the hosts they attack (semi-concealed, exposed or both; Fig. S2, $P = 0.001$). While Braconidae, Tachinidae with microtype eggs and Ichneumonidae attack mostly semi-concealed caterpillars, Tachinidae laying eggs directly on hosts attack semi-concealed and exposed caterpillars with similar intensity (36 vs. 41 %), and had also the highest share of parasitoid species attacking hosts from both feeding-mode groups (23 %). Parasitoids attacking primarily semi-concealed hosts were more host specific than those attacking primarily exposed hosts ($P = 0.0006$; Fig S3).

Host specificity of parasitoid groups

Parasitoid species attacked on average 1.8 (maximum 5) host species, 1.6 (maximum 4) host genera and 1.4 (maximum 3) host families. The number of species, genera and families attacked did not differ between parasitoid groups ($P > 0.8$ in all cases). Parasitoid group was significantly

Table 2 Tests of difference in parasitism rate between exposed and semi-concealed hosts. Parasitism rate for exposed/semi-concealed hosts is given together with the tests

	Parasitism rate (%)	Parasitism rate by Hymenoptera (%)	Parasitism rate by Diptera (%)
Overall (mean, χ^2 -test)	5/12 ***	1/8 ***	4/4 n.s.
Across host species (median, Wilcoxon rank test; Fig. 1)	4/9 n.s.	2/5 *	3/4 n.s.
Across host species (phylogenetic independent contrasts)	n.s.	n.s.	n.s.
Across tree species (median, Wilcoxon rank test)	4/13 **	Not tested	Not tested

For the test across tree species we combined parasitism rate of exposed or semi-concealed caterpillars on each tree species and used a test paired by tree species. See “Materials and methods” for more detail on the analyses

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. $P > 0.05$

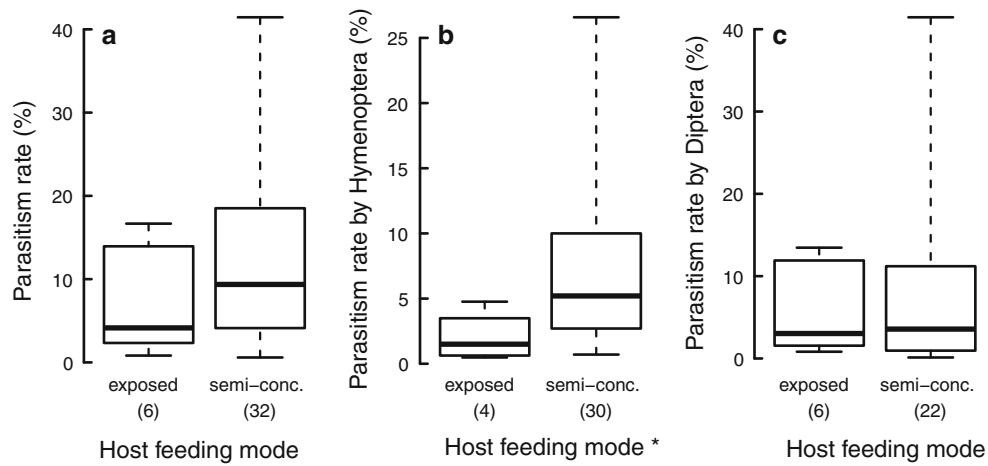


Fig. 1 Parasitism rates per herbivore species **a** overall, **b** by Hymenoptera, and **c** by Diptera, categorized by caterpillar feeding mode (exposed or semi-concealed). The box shows the first to third quartile with the median as a horizontal line, the whiskers show range. Significance of feeding mode in the Wilcoxon rank test ($P < 0.05$) is

indicated by an asterisk. The number of host species in each category is in parentheses. Host species with zero parasitism rate in one of the feeding mode categories were not included in evaluation of Hymenoptera and Diptera parasitism rates

associated with host-specificity category (Fig. 3; $P = 0.006$). Parasitoid groups did not differ significantly in host-tree-specificity category after accounting for number of rearings and parasitoid host specificity ($P = 0.30$). Ichneumonidae attacked hosts on average on 1.6 tree species, both directly and indirectly ovipositing Tachinidae on 1.8 tree species, and Braconidae on two tree species. We repeated the last two analyses with species delineations from initial parasitoid morphotyping by J. H. to test robustness of the results. Only 2 % of parasitoid specimens changed identification between the initial morphotyping and the final species concept, but this affected a further 32 % of specimens by removing or adding specimens to species they belonged to and thus possibly affecting the host-specificity estimate for the given species. The number of parasitoid species entering the analysis also increased from 57 to 59 between the initial morphotyping and the final species concept. However, the influence on the overall result of host-specificity analysis was minimal, with only slightly different P -values ($P = 0.007$, 0.46).

Discussion

How does host feeding mode affect parasitism?

Semi-concealed hosts suffered higher parasitism rates than exposed hosts. The overall difference was high, but the species-level test was significant only for hymenopteran parasitoids, pointing to high variability of parasitism rate between host species. The observed non-significant phylogenetically corrected test was expected, because host feeding mode is a strongly conserved trait. The host species are therefore clearly not phylogenetically independent points, but clustered by feeding mode. Interestingly, the difference in parasitism rate was due to hymenopteran parasitoids, as dipterans parasitize both host groups with the same intensity. Semi-concealed hosts, therefore, seem to be preferred by parasitoids which are able to reach them either by ovipositor in the case of Hymenoptera or microtype eggs in the case of Diptera. This is most likely due to one of the following effects or their combination: (1) parasitoids may

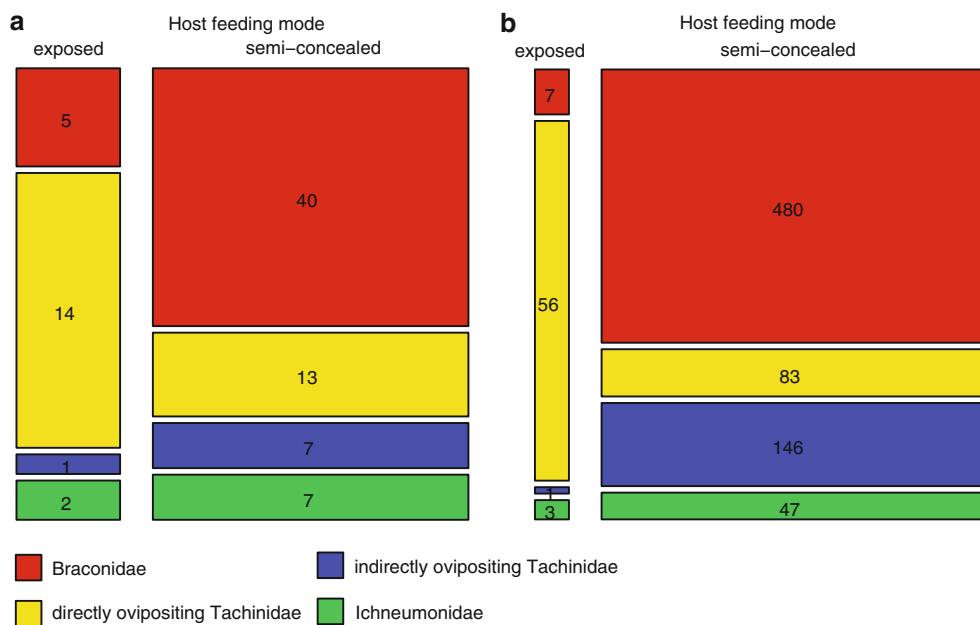


Fig. 2 Mosaic plot of parasitoid community composition on exposed and semi-concealed lepidopteran hosts for **a** number of parasitoid species, **b** number of parasitoid rearings. The width of the columns shows the relative number of parasitoid species/rearings on exposed and semi-

concealed hosts, and the colour sections within each column the relative number of species/rearings from each parasitoid group (significantly different between exposed and semi-concealed hosts; two-way contingency table, $P = 0.002$ and $P < 0.001$) (colour figure online)

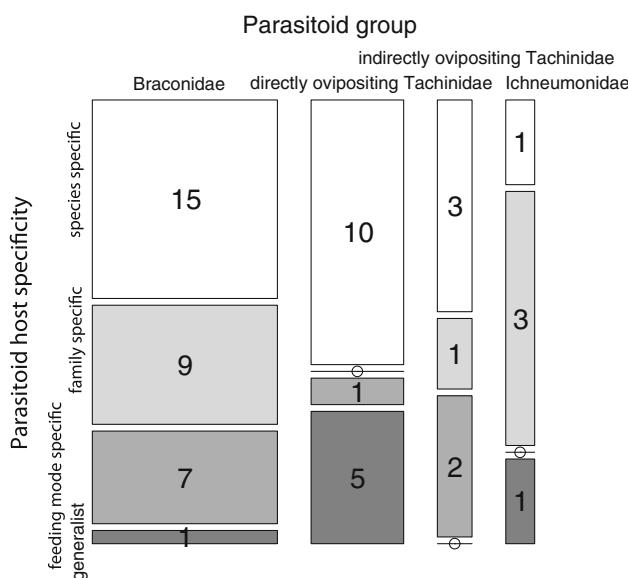


Fig. 3 Mosaic plot of host specificity of parasitoid groups. The width of the columns shows relative number of species in each parasitoid group, and the colour sections within each column show the relative number of species from each host-specificity category. Darker colour indicates a wider host range. Parasitoid groups significantly differ in host specificity ($P = 0.006$, multinomial regression). Only species with two or more parasitoid rearings are included

be deterred by the exposed caterpillar's active defence (Gentry and Dyer 2002), (2) semi-concealed caterpillars could be more apparent to parasitoids due to the conspicuous leaf structures they construct (Gentry and Dyer 2002;

Hawkins 1994), or (3) parasitoids of exposed hosts could be more easily outcompeted by generalist predators through asymmetric intra-guild predation on parasitized hosts (Polis et al. 1989; Tvardikova and Novotny 2012). Host abundance was not significantly correlated with the parasitism rate the host suffered, probably because the parasitoids are too host specific to be able to switch to currently more abundant hosts on the scale of the whole community (Stireman and Singer 2003). However, host abundance may play a role on a finer scale, such as between conspecific herbivore sub-populations feeding on different tree species.

Exposed and semi-concealed hosts differed in parasitoid community composition, with Braconidae dominating communities on semi-concealed hosts and directly ovipositing Tachinidae on exposed hosts. Tachinidae seem to be most successful in exposed hosts, less in semi-concealed ones and only rarely able to parasitize miners (Memmott et al. 1994). Both exposed and semi-concealed hosts harboured few Chalcidoidea parasitoids, while leaf miner parasitoids studied elsewhere are mostly Chalcidoidea (Askew and Shaw 1979; Lewis et al. 2002; Salvo et al. 2011). Semi-concealed hosts can therefore be placed between exposed hosts and leaf miners in terms of taxonomic parasitoid community composition, but closer to exposed hosts. Also, exposed and semi-concealed hosts did not differ in the number of parasitoid species per host, signalling no large difference in parasitoid community size among these two groups. Surprisingly, both exposed and semi-concealed hosts were attacked by very few idiobionts

in the caterpillar stage. Exposed and semi-concealed hosts therefore represent a single resource category for parasitoids judged by life history syndromes, and differ from leaf-mining hosts, which are reported in the literature to be attacked mainly by idiobionts (Askew and Shaw 1979; Hawkins 1994). Contrary to the general expectations, parasitoids of semi-concealed hosts were even more host specific than parasitoids of exposed hosts.

The host feeding-mode barrier between exposed and semi-concealed hosts strongly split the parasitoid community, but some parasitoid species occasionally crossed it. This happened most commonly in directly ovipositing Tachinidae, and might indicate that members of this group attack the more common semi-concealed hosts if they find a way to reach them.

Host specificity of parasitoid groups

The parasitoid groups did not differ significantly in number of host species attacked, but the differences became significant once host relatedness was taken into account. Braconidae were the most specialized, followed by directly and indirectly ovipositing Tachinidae and Ichneumonidae. This is unexpected, as hymenopteran parasitoids have been thought to be much more specialized than Diptera (Sheehan 1994; Stireman et al. 2005). A simple comparison of Hymenoptera and Diptera would be misleading in our study, as there was a large difference in host specificity between the two hymenopteran taxa, Braconidae and Ichneumonidae. Interestingly, host specificity differed more between ecologically similar Braconidae and Ichneumonidae, than between the two Tachinidae groups with different oviposition modes. The unexpected position of Ichneumonidae at the generalist end of the host-specificity spectrum was a reasonably well-supported result, as there were five Ichneumonidae species analysed in the dataset. The analysis was also robust to the species concept, based either on initial morphotyping only or on expert morphotyping and molecular data. This is encouraging, as studies from other sites and biotopes are needed to confirm our host-specificity analysis and they are likely to be very informative even if they do not have the resources to include both morphological and molecular species concept evidence. It also corroborates Kaartinen et al. (2010) and Smith et al. (2011) who showed that added molecular evidence for parasitoids had a low impact on food web parameters.

Like in our study, Braconidae were more host specific than koinobiont Ichneumonidae in Sheehan's (1991) temperate study on Macrolepidoptera. In contrast, Mills's (1992) meta-analysis of Tortricoidea parasitoids reported a slightly broader host range for Braconidae than for Ichneumonidae. Janzen and Gauld (1997) reported high host specificity of Ichneumonidae, but gave no comparison

with other groups. The results on host specificity are surprisingly difficult to compare among studies as the absolute measures, such as numbers of host species, depend on sample size and design of each study, while relative comparisons among different parasitoid groups are not available from many studies focusing on single parasitoid taxa.

Why were caterpillar-parasitizing Braconidae more host specific than Ichneumonidae, even though they are sister groups with otherwise similar biology? Gauld (1988) hypothesized that koinobiont endoparasitism arose in Braconidae on coleopteran or lepidopteran hosts, while in Ichneumonidae it probably arose mainly on symphytan hosts. In the most recent phylogeny, the monophyletic Ichneumonidae: Ophioniformes (which contain the majority of Lepidoptera-attacking koinobiont Ichneumonidae) also have symphytan parasitoids near the base of the clade (Quicke et al. 2009). Therefore, we hypothesize that more generalist species or lineages of koinobiont Ichneumonidae managed to switch from symphytan to lepidopteran hosts, and they have kept their broader host ranges since. More detailed Ichneumonoidea phylogeny, as well as more intensive and comprehensive studies of parasitoid host ranges would be needed to evaluate this hypothesis. A supporting argument is that Ichneumonidae are more useful for the biological control of Symphyta than of Lepidoptera (Greathead 1987), and are therefore possibly more host specific in Symphyta. Another, but even less understood factor that could influence host specificity in Ichneumonoidea are endosymbiotic viruses which help parasitoids to overcome the host immunity system and are probably parasitoid-species specific (Whitfield 1994; Whitfield and O'Connor 2011). Many of the most common braconid parasitoids (Microgastrinae, Cardiochilinae) harbour these viruses, but functionally similar viruses are present also in some Ichneumonidae.

Implications for biological control

Our study has several general implications for biological control, as the caterpillar stage is the most vulnerable, and its parasitoids are much more specialized than parasitoids of eggs and pupae. Semi-concealed hosts are likely to be more amenable to biological control by parasitoids than exposed hosts, because their parasitoids are more specialized and cause higher parasitism rates. Braconidae are candidates for the control of semi-concealed hosts, because they prefer this host group and are highly host specific. Directly ovipositing Tachinidae seem to be the parasitoids best suited for the control of exposed hosts, as they are the only group which prefers them, but the species should be carefully tested as we found some to be host specific while others were broad generalists. Finally, biological control with the more generalist Ichneumonidae is likely to be less

efficient and potentially risky for the environment due to non-target effects (Kidd and Jervis 2005).

Methodology

More than half of the caterpillars collected for our study died while being reared. This is probably similar in other studies, although rearing success is often not reported (but see Stireman and Singer 2003). Rearing failure opens room for bias in the data if parasitoids have a higher or lower chance of emerging from their hosts than they would have in nature. There is no evidence in favour of or against rearing bias in our study, and a strong systematic bias would be needed to influence our findings (e.g. very low rearing success of parasitized-exposed caterpillars). In the future, molecular methods can be used alongside rearing for the evaluation of possible bias and to salvage host-parasitoid interaction data from hosts which die during rearing (Hrcek et al. 2011). Considering other mortality agents with similar biology to insect parasitoids (Eggleton and Gaston 1990), we have not detected significant parasitism by nematodes ($\sim 1\%$ of caterpillars were parasitized by nematodes among ~ 300 individuals from various species we dissected; J. H., personal observation).

As usual in other parasitoid community studies (Memmott et al. 1994; Sheehan 1994), the recorded parasitoid community on hosts is not complete, and further sampling would inevitably bring more species and interactions. It is even more difficult to fully describe the host range of a parasitoid compared to describing the parasitoid complex of a host, because for the former a broad sampling of potential host species is necessary (Shaw 1994; Whitfield and Wagner 1988). In a rainforest food web, there may be an order of magnitude higher number of potential host species for parasitoids than potential host plant species for herbivores (Novotny et al. 2010). Unsurprisingly, herbivore host specificity is better known than that of parasitoids in tropical food webs. Species concept of both the hosts and the parasitoids has a strong potential to influence all species-level analyses in this study and especially the host-specificity estimates, if there are differences between host and parasitoid groups in our ability to identify the species. Such bias is hard to quantify, but double morphotyping (by J. H. and by experts), together with molecular evidence does not signal any systematic bias.

Our study was restricted to larval parasitoids. Egg parasitoids (e.g. Trichogrammatidae) and pupal parasitoids (mostly Ichneumonidae and Chalcidoidea) were not sampled and are considerably more difficult to study. We can expect these parasitoids to be mostly idiobionts (Askew and Shaw 1986), and therefore more generalist than the larval parasitoids studied here. From Mills's (1993) results on exophytic Tortricidae, we can expect that we are thus

missing about one-third of species of the whole parasitoid community on the studied hosts.

Conclusion

We show that host feeding mode is a crucial factor for parasitism in externally leaf-feeding Lepidoptera, with semi-concealed hosts experiencing higher parasitism rates, having more specialized parasitoids and having a different parasitoid community structure with more Braconidae and indirectly ovipositing Tachinidae and fewer directly ovipositing Tachinidae. However, exposed and semi-concealed caterpillars remain much closer to each other in parasitism patterns than they are to internally feeding leaf miners studied elsewhere, because they are attacked mainly by koinobionts, while leaf miners are attacked mainly by idiobionts. Semi-concealed hosts should be given at least the same attention as exposed hosts in future caterpillar-parasitoid studies, as they tend to harbour the majority of parasitoids in local caterpillar-parasitoid food webs. Unexpectedly, we found that Braconidae and Tachinidae were more host specific than Ichneumonidae, but this result should be tested by replicated studies in both temperate and tropical forests.

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