the impact of change in $Na^+ K^+$ ATPase capacity upon tissue respiration. In vertebrate liver, a 5.6-fold change in $Na^+ K^+$ ATPase capacity 'drives' a 1.63-fold change in $\dot{V}O_2$, while in vertebrate brain, a 3.78-fold change in $Na^+ K^+$ ATPase 'drives' a 1.63-fold change in $\dot{V}O_2$; thus the ratios of change in metabolic flux capacities/change in $Na^+ K^+$ ATPase capacities, the c_i values, are 0.29 (for liver) and 0.43 (for brain). We do not have global c_i values for whole-body rates, but because $Na^+ K^+$ ATPase activities account for a large percentage of BMR in numerous animals[12,13], the c_i values estimated for the liver and brain are probably fairly representative. In some tissues, such as kidneys, the values may be higher; in some, such as non-working muscles, they may be lower[13]. That is why, in our simulation (Fig. 1), two widely differing c_i values, 0.70 and 0.35, are used to illustrate the effect on overall scaling behaviour.

A second major energy-demand process under BMR conditions is protein synthesis. Previous allometric studies of protein synthesis rates establish $b_i = 0.77$ (refs 27, 28), but experimental studies allowing quantifying c_i coefficients for this process are not abundant. Nevertheless, *in vitro* studies[29] provide a c_i value of 0.11 for protein synthesis in liver slices of amphibians. In humans and rats, whole-organism studies of protein synthesis and metabolism usually find c_i values that are somewhat higher[2]. For our simulation, with the $Na^+ K^+$ ATPase c_i set at 0.70, we selected for protein synthesis a value of $c_i = 0.10$. To complete our simulation, we also included data for three more ATP demand processes: Ca^{2+} ATPase plus urea and glucose biosyntheses. As above, a value of $b_i = 0.86$ ($r = 0.99$) (ref. 22) is our best current estimate for the Ca^{2+} pump, while because of a low contribution to BMR we assume a relatively low value of $c_i = 0.05$. For urea synthesis[28] $b_i = 0.77$ and we selected $c_i = 0.05$. Similarly, for gluconeogenesis[30], $b_i = 0.76$ and we selected $c_i = 0.05$; the latter two c_i values are again similar to the percentage contributions of these processes to BMR[12]. We consider these low estimates to be reasonable, because so far, no studies have found large contributions of ureagenesis or glucogenesis to the control of basal metabolism[3–5,12]. With the $Na^+ K^+$ ATPase c_i value set at 0.7, the values for all the ATP demand processes are then 0.10, 0.05, 0.05 and 0.05 respectively; these double when the $Na^+ K^+$ ATPase c_i value is reduced to 0.30 (Fig. 1b). The two c_i values for protein synthesis bracket the percentage contribution[12] of this ATP demand process to BMR. A summary of these values is given in Fig. 1b.

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Competing interests statement

The authors declare that they have no competing financial interests.

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Host plants influence parasitism of forest caterpillars

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Patterns of association between herbivores and host plants have been thought to reflect the quality of plants as food resources[1,2] as influenced by plant nutrient composition[3], defences[4,5], and phenology[6]. Host-plant-specific enemies, that is, the third trophic level, might also influence the distribution of herbivores across plant species[7–10]. However, studies of the evolution of herbivore host range[11–15] have generally not examined the third trophic level, leaving unclear the importance of this factor in the evolution of plant–insect herbivore interactions[16]. Analysis of parasitoid rearings by the Canadian Forest Insect Survey shows that parasitism of particular Lepidoptera species is strongly host-plant-dependent, that the pattern of host-plant dependence varies among species of caterpillars, and that some parasitoid species are themselves specialized with respect to tree species. Host-plant-dependent parasitism suggests the possibility of top-down influence on host plant use. Differences in parasitism among particular caterpillar–host plant combinations could select for specialization of host plant ranges within caterpillar communities. Such specialization would ultimately promote the species diversification of Lepidoptera in temperate forests with respect to escape from enemies.

Here, we test the hypothesis that a caterpillar's host plant influences the identity of its parasitoid enemies and its probability of being parasitized. Our analysis includes a broad range of forest tree species and their associated caterpillar and parasitoid species in southern Ontario and Quebec, Canada, taking advantage of the extensive data set generated by the Canadian Forest Insect Survey[17] (CFIS). Because parasitoids almost always kill their hosts, evidence of host-plant-specific parasitism indicates that members of the third trophic level can influence the suitability of host plants for herbivore

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species. In so doing, they can potentially select for traits that influence host plant use by herbivores.

We selected 15 focal caterpillar species from six families of Lepidoptera represented by a large number of records (around 21,000 total rearing records and more than 4,600 parasitism events). Parasitism levels varied significantly among these herbivores. Across all host plants, parasitism differed among families of Lepidoptera ($\chi^2_{1,5} = 245.2$; $P < 0.0001$), ranging from 11% in the Pyralidae to 27% in the Gelechiidae, and among species ($\chi^2_{1,14} = 810.0$; $P < 0.0001$), ranging from 7 to 39%. This variation presumably represents the outcome of ecological and evolutionary interactions between host caterpillars and their parasitoids, but host plant characteristics may also mediate these interactions[18,19]. Because the caterpillar species in our sample share many host plants, we examined how both host plant species and host caterpillar species contributed to variation in rate of parasitism. Our analysis included 17 host plant genera, representing 10 families of plants and including both angiosperms and gymnosperms. To our knowledge, only two other studies[20,21] have examined host-plant-specific parasitism in taxonomically diverse assemblages of herbivores. Both studies showed significant host plant effects, but were limited to only two host plant species. Rearings of individual caterpillar species were generally low (despite several years of intensive collecting) and consequently, host plant effects on parasitism could only be assessed for caterpillars grouped into families or ecological guilds.

In this study, the host plant strongly influenced the level of parasitism experienced by individual species of herbivores. Across the 15 caterpillar species, parasitism was one-third higher on individuals reared from angiosperms (21%) than from gymnosperms (16%) (Wald $\chi^2_{1,1} = 89.5$; $P < 0.0001$). Parasitism differed among host plant families ($\chi^2_{1,7} = 368.1$; $P < 0.0001$), ranging from 16% in Pinaceae to 35% in Salicaceae, and among host plant genera ($\chi^2_{1,16} = 626.9$; $P < 0.0001$), ranging from 8% in *Pinus* spp. to 48% in *Salix* spp. (Fig. 1). Significant host plant effects were also found when caterpillar species were examined individually (Table 1); these host-plant effects were temporally stable (for example, non-significant year × host plant interactions) for three of the five species with sufficient data for analysis. Thus, host plant identity had a large influence on parasitism levels for both the entire assemblage and for individual caterpillar species.

To separate the effects of caterpillar species from host plant species on variation in parasitism level, we isolated four completely filled portions of the host plant and herbivore data matrix suitable for two-way contingency analysis (Table 2). We based these statistical tests on four subsets of Lepidoptera species × host plant genus, including two for gymnosperm-feeders and two for angiosperm-feeders. In each case, we were able to estimate the main effects of host plant and caterpillar species as well as the host caterpillar × host plant interaction on parasitism level.

Significant herbivore and host plant effects were accompanied by highly significant host plant × herbivore species interactions in all data subsets (Table 2). This study is the first to demonstrate both

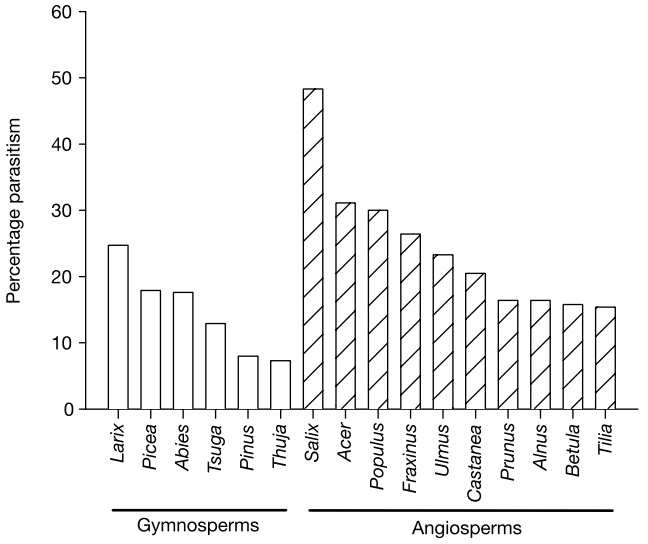

Figure 1 Overall parasitism of 15 focal taxa on 17 host plant genera in two divisions.

that the overall risk of parasitism for a caterpillar assemblage depends upon the identity of the host plant and that the pattern of risk across host plants differs among caterpillar species. Thus, the view that the natural enemies associated with a host plant are a part of its general arsenal of plant defences against herbivores[22] requires elaboration: where one caterpillar species is put at risk, another may find refuge.

The host plant–parasitoid matrix is a complex pattern of 'enemy-reduced' and 'enemy-packed' space (Fig. 2). Here, we designate a host plant as enemy-reduced space for a particular parasitoid species if potential host species of caterpillars reared from that plant have fewer parasitoids than expected. In contrast, potential hosts on enemy-packed plants produced more parasitoids of that particular species than expected. Part of the complex pattern of enemy-reduced and enemy-packed space reflects the heterogeneous nature of the parasitoid community. Our sample yielded 118 species of parasitoids from ten families. Of 39 parasitoid species reared ten or more times, three were restricted to caterpillars found on a single host plant genus and one was a hyperparasitoid; these parasitoids are not included in Fig. 2. The remaining 35 species of parasitoids were reared from caterpillar hosts with broader host plant distributions, allowing us to estimate enemy-reduced and enemy-packed space.

Of the 35 species examined (Fig. 2), most parasitoids exhibited unique, largely non-overlapping patterns of enemy-reduced and enemy-packed space. Six parasitoid species were recovered from individuals of single caterpillar host species collected from a single host plant genus; in each case, individuals of these hosts feeding on other plant genera were free of attack, and in some instances, these

Table 1 Host-plant-specific parasitism levels for six gymnosperm-feeding caterpillar species

	Host plant genus						All years combined			Host plant × year	
Caterpillar species	*Abies*	*Larix*	*Picea*	*Pinus*	*Thuja*	*Tsuga*	*N*	χ^2	*P*	χ^2	*P*
Acleris variana	0.10	–	0.28	–	–	–	775	36.04	0.0001	4.45	0.49
Caripeta divisata	0.15	0.21	0.12	0.29	–	–	388	5.22	0.1560	–	–
Dioryctria abietivorella	0.19	–	0.10	0.13	–	–	1413	5.99	0.0500	1.36	0.82
Lambdina fiscellaria	0.16	0.13	0.08	0.14	–	0.10	1269	15.49	0.0038	7.78	0.45
Nepytia canosaria	0.14	–	0.08	0.15	0.07	0.15	1236	13.01	0.0112	33.15	0.0001
Semiothisa granitata	0.22	0.30	0.29	0.19	–	0.32	2101	11.19	0.0245	24.73	0.0033

Values are proportion of successfully reared larvae that were parasitized. *N* is the number of total rearings (all years combined) of each species and statistics reported are from categorical analyses. To examine temporal variation in host plant effects, the host plant × year interaction was also examined for a subset of years with sufficiently large samples (>30 rearings per host plant per year).

Table 2 Main effects and interaction effects of host plant and caterpillar species on the incidence of parasitism

Herbivore species	Host plant genus	χ^2 (herbivore)	χ^2 (plant)	χ^2 (herbivore × plant)
Lambdina fiscellaria, *Semiothisa granitata*	*Abies*, *Picea*, *Pinus*, *Tsuga*, *Larix*	31.19***	1.39 NS	24.18***
Acleris variana, *Caripeta divisata*, *Dioryctria abietivorella*, *L. fischellaria*, *Nepytia canosaria*, *S. granitata*	*Abies*, *Picea*	108.45***	2.90 NS	74.55***
Archips cerasivorana, *H. cunea*	*Populus*, *Prunus*, *Salix*	7.34**	107.63***	29.50***
Choristoneura rosaceana, *Hyphantria cunea*, *Orgyia leucostigma*	*Acer*, *Betula*, *Populus*, *Ulmus*	36.27***	37.12***	28.58***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.0001$; NS, not significant.

plants represented enemy-reduced space. The other parasitoid species were either host caterpillar specialists (10 species in total) reared from a single caterpillar host on multiple host plant genera or generalists (19 species) reared from multiple caterpillar hosts and host plant genera. Ten of 17 host plant genera afforded enemy-reduced space against one or more parasitoids, while 13 showed evidence of enemy packing. *Populus* and *Ulmus* exhibited only enemy-reduced space, while *Acer*, *Fraxinus* and *Pinus* exhibited only enemy-packed space. Of the 267 combinations of parasitoids and host plants, 33 (12.4%) exhibited a significantly reduced rate of parasitism and 29 (10.9%) exhibited a significantly increased rate of parasitism compared with expected rates based on the relative abundance of potential hosts. Overall, there is a non-clustered distribution of enemy-reduced and enemy-packed space in this matrix, with similar frequencies of each type of space among the three families of parasitoids ($\chi^2 = 4.90$, $P = 0.26$) and the two plant divisions ($\chi^2 = 5.04$, $P = 0.08$). Thus, the suitability of host plants varies with the particular host plant–caterpillar combination.

The mechanism(s) contributing to these host plant effects are likely to be varied[21] and include: (1) plant-volatile-related differences in parasitoid attraction and/or retention rates[18,23]; (2) variation in the apparency of caterpillars on different host plants[24]; (3)

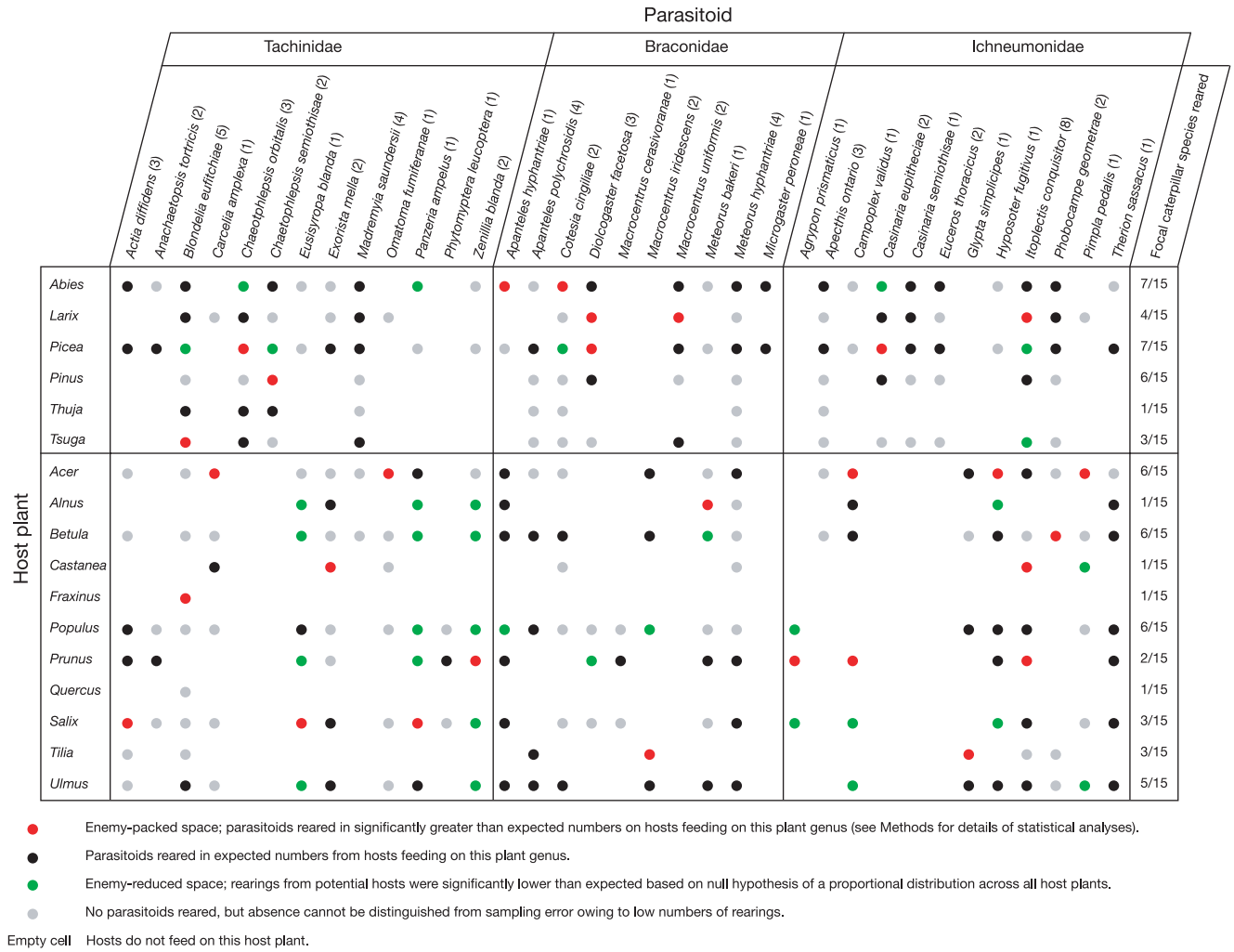

Figure 2 Parasitoid–host plant associations for 35 parasitoid species with hosts that feed on more than one host plant genus. For each parasitoid species, the number of host plants examined reflects the combined diet breadth of the focal caterpillar species that are potential hosts. The average cell size (±1 s.e.m.) is 544 ± 64.5 and ranges from 31 to 6,652. The number of focal caterpillar species that are host to each parasitoid is shown in parentheses.

density-dependent foraging by parasitoids (if host abundances also vary with host plant); (4) host-plant effects on caterpillar resistance to parasitism[25,26]; and (5) the presence and/or abundance of other herbivore species on the host plants (that is, apparent competition via shared natural enemies)[10,27]. As found previously[21], there was no relationship in this study between risk of parasitism and the abundance of a caterpillar species on a particular host plant, either for all 15 caterpillar species together ($r^2 = 0.0002$, $N = 62$, $F_{1,60} = 0.012$, $P = 0.91$) or for each species individually (mean $r^2 = 0.10 \pm 0.025$, $N = 5$–8, $P = 0.30$–0.92 for the seven most polyphagous species), suggesting that future research should focus on other possible mechanisms.

These results demonstrate that a caterpillar's host plant, a fundamental aspect of its niche, influences the vulnerability of that insect to its natural enemies. The strong influence of host plant on the risk of attack by parasitoids suggests that the third trophic level should be considered a potentially important selective force in the evolution of herbivore diet breadth. Given a suite of 'suitable' host plants that nevertheless vary in quality with respect to caterpillar growth and development in the absence of enemies, we predict that selection by the third trophic level could favour either increased or decreased host plant specialization, depending on how the risk of parasitism varies with food quality among host plants[28]. Regardless of that relationship, our data suggest that the third trophic level, in addition to host plant quality, should be considered as a contributing factor influencing the diversification of herbivore faunas. □

Methods

Database

We entered all data yielding parasitoids and adult moths (1937–1947) from hand-written rearing records provided by the CFIS (now the Forest Insect Disease Survey), Sault Ste Marie, Ontario, Canada. Collection records of caterpillars from each tree species and site include the number of larvae of each species collected, the number of adult moths emerging, and the number of parasitoids, mostly identified to species[17]. Collections were made from host plants that overlap considerably in distribution[29]. Although collections contained several individuals per caterpillar–host plant combination, no single collection contained more than 2% of the total rearings for a caterpillar species; thus, we considered all rearings independent in the analyses. We updated the taxonomy of host plants, herbivores and parasitoids when possible, using the current literature. From this larger data set, we selected 15 focal species having moderate to large numbers of records of parasitized individuals. For these, we entered the additional rearing records from which no parasitoids emerged. The focal taxa, each of which belonged to a different genus, span six families of Lepidoptera (Arctiidae [*Hyphantria cunea*], Gelechiidae [*Anacampsis innocuella*], Geometridae [*Alsophila pometaria*, *Caripeta divisata*, *Erannis tiliaria*, *Lambdina fiscellaria*, *Nepytia canosaria*, *Semiothisa granitata*], Lymantriidae [*Orgyia leucostigma*], Pyralidae (*Dioryctria abietivorella* and Tortricidae [*Acleris variana*, *Archips cerasivorana*, *Choristoneura rosaceana*, *Rhyacionia buoliana* and *Pseudosciaphila duplex*]) and feed on host trees in ten families and seventeen genera, including both angiosperms and gymnosperms. Individual focal taxa varied in diet breadth, from highly restricted (feeding on a single host plant genus) to highly polyphagous (hosts in over 15 plant families).

Data analysis

Data from different sites and years were pooled for analysis. We constructed a $15 \times 17 \times 2$ matrix of the number of parasitized and non-parasitized individuals of each of 15 caterpillar species on each of 17 host plant genera. For a given caterpillar species, we included only host plant genera from which at least 30 individuals (parasitized + non-parasitized) had been reared (cellmean $\pm$ 1 s.e.m. $= 332.3 \pm 96.7$). Using nested sets of categorical models (SAS PROC CATMOD) with proportion parasitism as the response variable, we examined the individual effects of host plant division (angiosperm versus gymnosperm), host plant family (including families with over 100 rearing records), host plant genus (including genera containing over 100 rearing records), herbivore family and herbivore species. To examine the joint and interactive effects of herbivore species and host plant genus, we were restricted to analysing subsets of the matrix (see Table 2) because 75% of the cells in the matrix were empty, owing to variation in the host ranges of different herbivores.

Because parasitism also may depend on a species' relative abundance on a particular host, we regressed parasitism on abundance (log-transformed), using the number of collections made on each host plant genus over the entire CFIS collection period (1933–1957) as an estimate of relative abundance. We did this for the combined set of 15 caterpillar species and for seven species that individually fed on five or more host plants. Proportion parasitism was arcsine square-root transformed before analysis to improve normality.

To examine patterns of parasitism of potential hosts (caterpillar species from which at least one individual had been reared) by individual parasitoid species across host plants (Table 2), we used Monte Carlo $2 \times N$ randomization tests[30] (1,000 randomizations per parasitoid species); when parasitism varied significantly among host plants, we performed Fisher's exact tests[30] comparing parasitism on each host plant to parasitism on all of the other host plants combined (dividing alpha by the number of tests performed). This is analogous to the procedures for subdividing contingency tables used in standard chi-square tests, where expectations are sufficiently large to permit standard approximations. When the Fisher's exact tests were significant, and depending on the directionality of the effect (greater or less than expected), host plants were labelled as enemy-packed or enemy-reduced, respectively, for a particular parasitoid species.

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Competing interests statement

The authors declare that they have no competing financial interests.

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