

Why Are There So Many Species of Herbivorous Insects in Tropical Rainforests?

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While recent progress has been made in understanding mechanisms of tree species coexistence in tropical forests, a simple explanation for the even more extensive diversity of insects feeding on these plants has been missing. We compared folivorous insects from temperate and tropical trees to test the hypothesis that herbivore species coexistence in more diverse communities could reflect narrow host specificity relative to less diverse communities. Temperate and tropical tree species of comparable phylogenetic distribution supported similar numbers of folivorous insect species, 29.0 ± 2.2 and 23.5 ± 1.8 per 100 m² of foliage. Host specificity did not differ significantly between community samples, an indication that food resources are not more finely partitioned among folivorous insects in the tropics than in temperate forests. These findings suggest that the latitudinal gradient in insect species richness could be a direct function of plant diversity, which increased sevenfold from our temperate to tropical study sites.

Large numbers of herbivore species in the tropics relative to temperate communities might reflect differences in (i) host plant species diversity, (ii) numbers of herbivore species per host, and/or (iii) host specificity, the number of plant species hosting each insect species. The tropical maximum in plant species richness is well documented. For instance, the number of plant species per 10,000 km² is 5–10 times higher in tropical than in temperate areas (1) while woody plant species richness per hectare is on average six times higher in the tropics compared to temperate forests (156.8 ± 63.6 and 25.2 ± 19.7 species with diameter at breast height ≥ 10 cm; fig. S1). However, latitudinal differences in host specificity and numbers of insect species per host plant species are more difficult to assess (2, 3).

A recent proliferation of quantitative studies on tropical insect herbivores that include feeding and rearing experiments (4–9) has not been matched by comparable

activity in temperate forests (10, 11), perhaps because patterns of host use are believed to be well documented for temperate herbivores. Much qualitative data on host associations of herbivores accumulated during the past two centuries, particularly in Great Britain and Central Europe, is not directly comparable to recent, quantitative studies in the tropics (12). A temperate–tropical comparison of herbivore communities is further complicated by differences in the phylogenetic diversity of the vegetation. Temperate forests are dominated by a relatively small number of woody plant lineages compared to the tropics (13).

We compared temperate and tropical communities of folivorous insects using identical sampling protocols and phylogenetically comparable sets of local tree species (14). All externally feeding folivorous insects were hand collected from the foliage of 14 woody plant species in a lowland floodplain forest in Moravia, Central Europe and 14 species in a lowland hill forest in Madang, Papua New Guinea. Caterpillars (Lepidoptera) were also collected from eight woody species in an oak-hawthorn forest in Slovakia, Central Europe and compared with caterpillars from eight tree species in Papua New Guinea (Madang). Samples of tree species from the local vegetation included both close relatives (i.e. congeneric species) and distantly related plant lineages (i.e. multiple families and orders) at each site (table S1). Molecular phylogenetic relationships among species sampled at each locality were compiled from the recent literature and branch lengths were estimated from the large subunit of ribulose-1,5-bisphosphate carboxylase oxygenase (rbcL) gene sequences. The diverse vegetation of lowland New Guinea provided an opportunity to select subsets of tree species with phylogenetic patterns closely matching those of temperate forest tree communities (Fig. 1). Highly concordant and correlated branch lengths permitted the comparison of host specificity and herbivore community structure given a nearly identical phylogenetic distribution of food plants. Controlling for the

effect of vegetation phylogenetic diversity enabled a direct comparison of herbivore specificity between these different tropical and temperate communities.

Adult herbivores were experimentally tested for feeding, and larvae were reared to adults. Our analysis included 26,970 feeding records of herbivorous insects representing 850 species (Appendices S1 and S2). Folivorous communities included larval and adult feeders of Lepidoptera, Coleoptera, Hymenoptera and orthopteroids (Orthoptera and Phasmatodea). Larval Lepidoptera dominated both temperate and tropical communities, followed by adult Coleoptera, whereas larval Coleoptera were of marginal importance (Fig. 2).

Although Hymenoptera were limited to temperate samples and orthopteroids were only encountered in the tropics, tree species in both regions supported similar overall species diversity of leaf chewing insect species per unit area of foliage (Table 1). The occurrence of more speciose assemblages of insect herbivores in tropical forests compared to temperate forests therefore cannot be attributed to finer partitioning of foliar resources among herbivore species feeding on the same plant species. Comparable overall species diversity of herbivores resulted from opposing trends in species diversity of larval and adult folivores, being maximally diverse in Central Europe and New Guinea, respectively. Despite considerable differences in the taxonomic composition of tropical and temperate communities, overall estimates of herbivore species diversity per host plant are of similar magnitude in tropical forests (4–7, 15) and temperate forests (10, 16). The absence of a latitudinal trend in the ratio of butterfly to plant species is also consistent with this observation (17).

Temperate trees supported a higher overall density of folivores than tropical trees (Table 1). Lepidoptera and Coleoptera larval densities tended to be higher on temperate trees but only the density of Hymenoptera larvae was significantly different. The relatively low abundance of larvae on tropical foliage is attributed to high predation, particularly by ants, in the tropics (18, 19). Predation pressure at our study sites was 18 times higher on tropical trees as measured by the proportion of live insect baits attacked by predators (mostly ants) during 30 minutes of exposure on the foliage ($28 \pm 27\%$ in the tropics and $1.6 \pm 0.1\%$ on temperate vegetation; table S2).

The two most important taxon-guilds in terms of species numbers and abundance, namely Lepidoptera larvae and Coleoptera adults, as well as the entire folivorous community, showed no difference in host specificity between temperate and tropical trees (Fig. 2). Lepidoptera larvae on temperate trees in Slovakia were less host-specific than those on the tropical trees, but the mean difference in host range was small (fig. S2), averaging a single host per herbivore in tropical

samples versus two hosts per herbivore in temperate samples. The similarity of folivorous communities on any pair of hosts decreased as the phylogenetic distance of hosts increased. The slope of the relationship was not significantly different between temperate and the tropical tree species, also suggesting a common pattern of host specificity (Fig. 3).

Our findings reject the hypothesis that greater host specificity of tropical herbivores accounts for the greater insect species diversity. Other studies also suggest that there is no difference in host specificity between temperate and tropical communities of insect herbivores. Fiedler (20) found no such difference in butterflies, although particular lineages may be more (e.g. Lycaenidae: Polyommataini) or less (e.g. Papilionidae) (21) specialized in the temperate than tropical regions. Bark beetles (Coleoptera: Curculionidae) (22) and treehoppers (Hemiptera: Membracidae) (23) were more specialized in temperate than tropical regions, whereas a community of temperate caterpillars (10) exhibited lower host specificity than reported from the tropics (6, 8). However, none of these studies has controlled for the phylogenetic diversity of the vegetation.

There are a few caveats to our conclusions. In particular, our species diversity estimates per 100 m² of foliage may not be representative of those for larger areas of foliage as tropical communities are known to include numerous rare species that can be detected only with large sample sizes (24). The upper canopy foliage, which was under sampled in this study, can provide additional microhabitats for specialized herbivores, particularly in the tropics (25). Tropical vegetation can also include additional resources that are rare or absent in temperate forests, such as woody climbing plants (7).

Despite these caveats, our analysis suggests that the latitudinal gradient in species diversity of herbivorous insects is to a large extent driven by the parallel increase in plant diversity (fig. S1). There was a sevenfold increase in plant diversity from our temperate to tropical study sites with 21 tree species per hectare with diameter at breast height ≥ 5 cm in Moravia, compared to 152 species in Madang (26). Our sample of 14 tree species represented 85% of the standing timber in a temperate forest, whereas a phylogenetically comparable subset of tropical forest represented less than 20% of the local vegetation. Greater phylogenetic diversity of tropical vegetation compared to temperate forests rather than greater host specificity of tropical herbivores is the more probable explanation for the extraordinary diversity of tropical insect communities.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/1129237/DC1

Materials and Methods

Figs. S1 and S2

Tables S1 and S2

References

Appendices S1 and S2

27 April 2006; accepted 13 June 2006

Published online 13 July 2006; 10.1126/science.1129237

Include this information when citing this paper.

Fig. 1. Phylogenetic relationships and molecular divergence of temperate and tropical trees selected for the comparison of insect herbivore communities. Temperate and tropical plant species spanning the continuum between close relatives and distantly related lineages were paired to control for differences between communities in the phylogenetic distribution of plant resources. Branching order and branch lengths were matched as closely as possible between the temperate and tropical sets of tree species from different clades. **(A)** Phylogenies of 14 tree species from Moravia and Papua New Guinea with branch lengths proportional to the number of nucleotide substitutions in *rbcL* sequences. **(B)** The correlation of molecular phylogenetic distances between ancestral and descendant nodes for 14 pairs of temperate and tropical tree species was significantly different from chance expectations ($P < 0.05$). **(C)** Phylogenies of eight tree species from Slovakia and Papua New Guinea with branch lengths proportional to the number of nucleotide substitutions in *rbcL*. **(D)** The correlation of molecular phylogenetic distances between ancestral and descendant nodes for eight pairs of temperate and tropical tree species ($P < 0.001$).

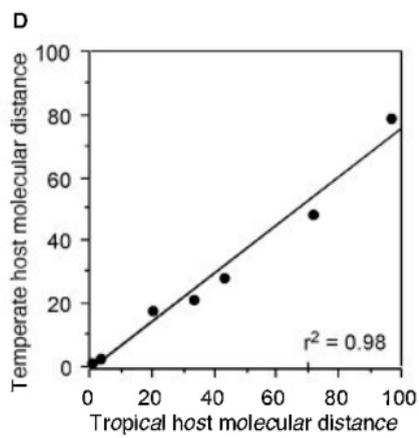
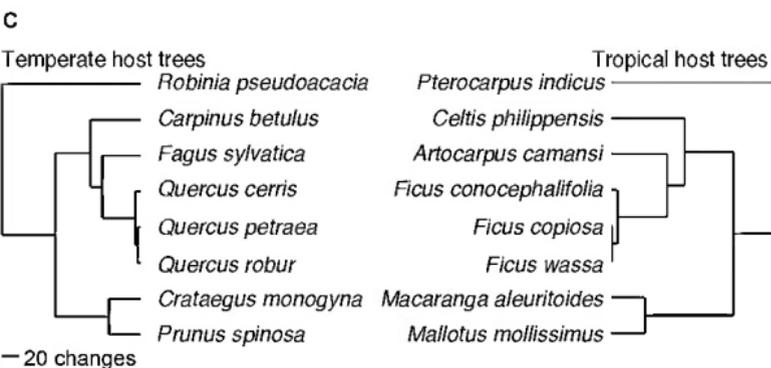
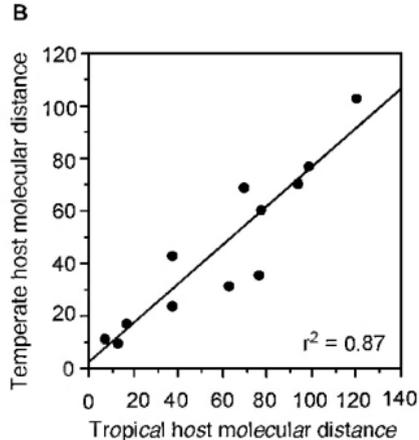
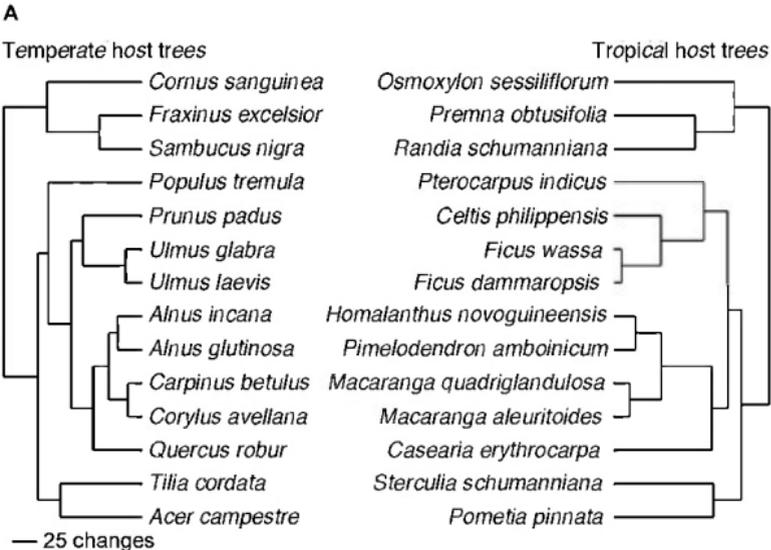
Fig. 2. Host specificity of folivorous insects on temperate **(A)** and tropical **(B)** trees. The number of hosts among the 14 studied tree species (Fig. 1A) is shown for larvae (L) and adults (A) from Lepidoptera, Hymenoptera, Coleoptera and Orthopteroids. The number of hosts was not significantly

different between temperate and tropical folivores, Lepidoptera larvae and Coleoptera adults (Mann-Whitney test, $P > 0.05$).

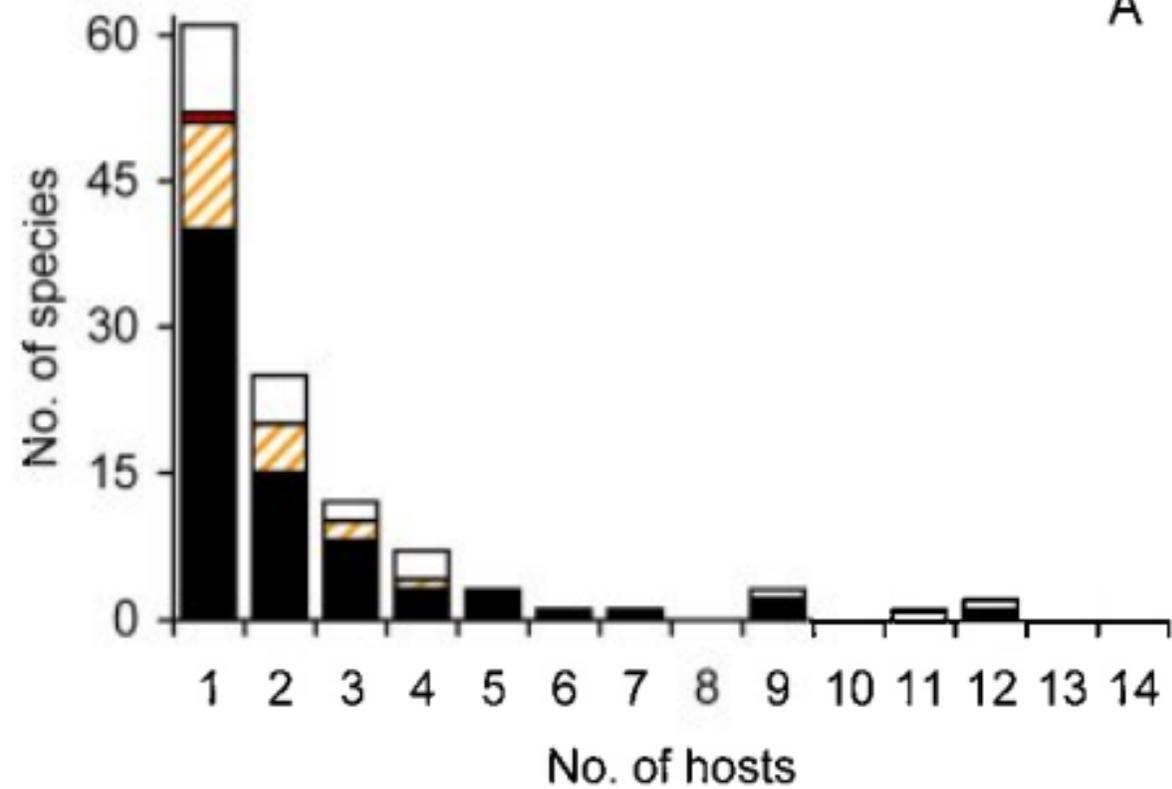
Fig. 3. Similarity of folivorous communities between pairs of host species versus the phylogenetic distance between the hosts in a temperate (crosses) and a tropical (dots) forest. Herbivore similarity was estimated as the proportion of shared species according to the Chao-Sorensen index (27); phylogenetic distance was estimated from Fig. 1A as the absolute number of pairwise differences in rbcL sequences from trees listed in Table S1. The negative correlation between community similarity and phylogenetic distance was significant in both data sets ($P < 0.05$, Mantel test).

Table 1. Numbers of insect species and individuals per unit area of foliage in larval and adult taxon-guilds of folivorous insects reared from temperate and tropical trees. The average (S.E.) values for the density of species and individuals were calculated for insect herbivores from N species of study trees. Rows 1– 8 refer to the Moravia–New Guinea comparison, row nine to the Slovakia–New Guinea comparison. The temperate-tropical differences were tested by t-test (* denotes $P < 0.05$). Comparative analyses accounting for the statistical non-independence of tree species yielded results identical to t-tests (supporting online text).

No.	Taxon	Guild	Species/100m ² foliage		t-test	Individuals/100m ² foliage		t-test	N
			Temperate	Tropical		Temperate	Tropical		
1	Lepidoptera	Larvae	19.9 (1.9)	9.1 (1.3)	*	66.6 (13.5)	36.7 (5.9)	n.s.	14
2	Hymenoptera	Larvae	1.8 (0.4)	0 (0)	*	3.8 (1.1)	0.0 (0.0)	*	14
3	Coleoptera	Larvae	0.1 (0.1)	0.3 (0.1)	n.s.	6.4 (6.3)	2.7 (2.7)	n.s.	14
4	Coleoptera	Adults	5.5 (0.7)	9.5 (0.7)	*	42.9 (12.7)	24.4 (2.6)	n.s.	14
5	Orthopteroids	Adults	0.0 (0.0)	4.2 (0.4)	*	0.0 (0.0)	7.5 (1.3)	*	14
6	All	Larvae	23.5 (2.1)	9.4 (1.3)	*	84.4 (13.4)	40.4 (6.1)	*	14
7	All	Adults	5.5 (0.7)	13.7 (0.9)	*	42.9 (12.7)	31.9 (3.1)	n.s.	14
8	All	All	29.0 (2.2)	23.5 (1.8)	n.s.	127.2 (15.6)	75.2 (5.8)	*	14
9	Lepidoptera	Larvae	19.3 (3.6)	9.2 (2.0)	*	82.5 (18.0)	45.5 (5.9)	n.s.	8

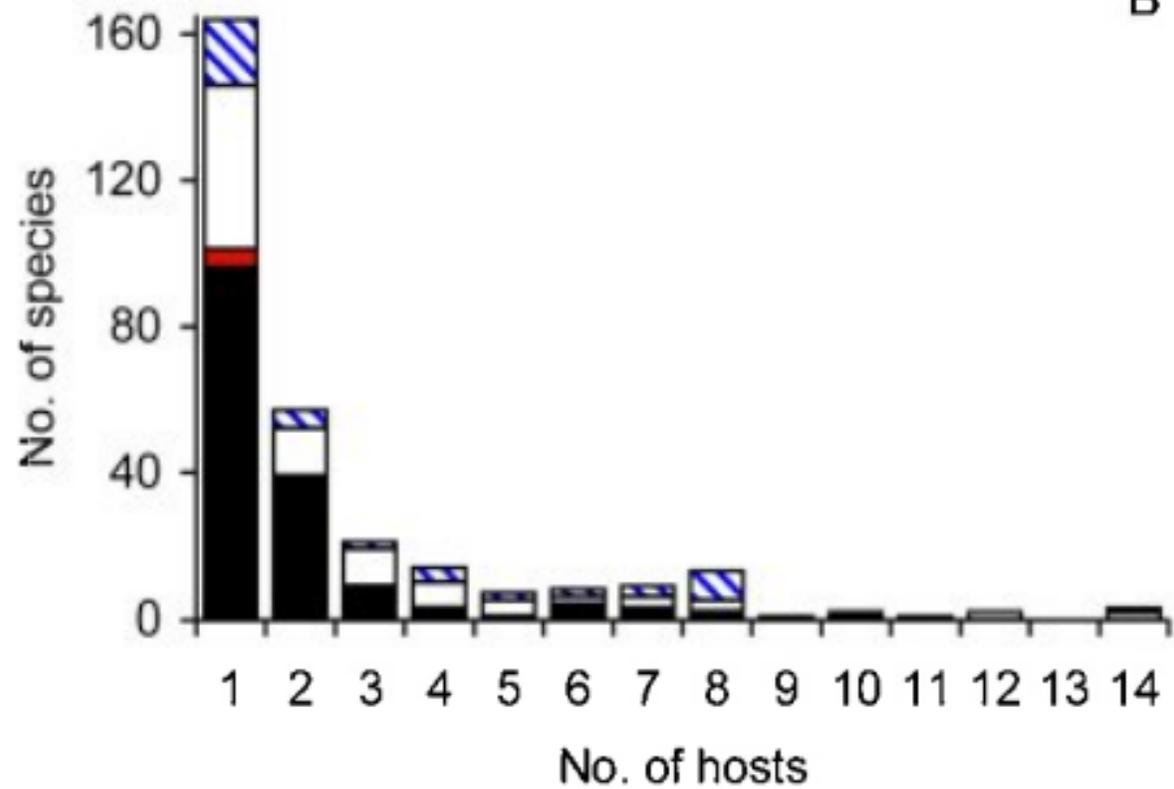


A



■ Lep - L ▨ Hym - L ■ Col - L □ Col - A ▨ Ort - A

B



■ Lep - L ▨ Hym - L ■ Col - L □ Col - A ▨ Ort - A

