LETTERS

Host specificity of Lepidoptera in tropical and temperate forests

L. A. Dyer[1], M. S. Singer[2], J. T. Lill[3], J. O. Stireman[4], G. L. Gentry[1], R. J. Marquis[5], R. E. Ricklefs[5], H. F. Greeney[6], D. L. Wagner[7], H. C. Morais[8], I. R. Diniz[8], T. A. Kursar[9,10] & P. D. Coley[9,10]

For numerous taxa, species richness is much higher in tropical than in temperate zone habitats[1]. A major challenge in community ecology and evolutionary biogeography is to reveal the mechanisms underlying these differences. For herbivorous insects, one such mechanism leading to an increased number of species in a given locale could be increased ecological specialization, resulting in a greater proportion of insect species occupying narrow niches within a community. We tested this hypothesis by comparing host specialization in larval Lepidoptera (moths and butterflies) at eight different New World forest sites ranging in latitude from 15° S to 55° N. Here we show that larval diets of tropical Lepidoptera are more specialized than those of their temperate forest counterparts: tropical species on average feed on fewer plant species, genera and families than do temperate caterpillars. This result holds true whether calculated per lepidopteran family or for a caterpillar assemblage as a whole. As a result, there is greater turnover in caterpillar species composition (greater β diversity) between tree species in tropical faunas than in temperate faunas. We suggest that greater specialization in tropical faunas is the result of differences in trophic interactions; for example, there are more distinct plant secondary chemical profiles from one tree species to the next in tropical forests than in temperate forests as well as more diverse and chronic pressures from natural enemy communities.

Ecological theory requires that organisms differ in their use of shared, limiting resources if they are to coexist. The role of resource specialization in fostering biodiversity is thus a central issue in ecology and evolutionary biology. A longstanding hypothesis predicts a direct relationship between ecological specialization and species richness in communities[2]. Specialization reduces interspecific competition and facilitates species coexistence by partitioning niche space[3,4]. Character divergence across generations in response to trophic interactions or competition[5] provides an evolutionary mechanism by which species richness and specialization can increase together[6–8]. Beginning with observations recounted by Darwin[9] and Wallace[10], examples of ecological specialization in tropical organisms have fostered a widespread perception that specificity of interactions is a hallmark of the high-diversity tropics.

Although biotic inventories often confirm the higher species richness of tropical communities than those at higher latitudes[1], few studies have quantified increased ecological specialization along a latitudinal gradient[11]. Novotny *et al.*[12] recently challenged the notion that herbivorous insects are more specialized in the tropics by the use of a quantitative comparison of host specificity of herbivorous insects in tropical forests of Papua New Guinea and those in temperate forests of central Europe. They reported a similar host specificity among temperate and tropical herbivorous insects and concluded that the greater species richness of tropical herbivores is a direct consequence of greater tropical plant diversity rather than increased host plant specialization. The large contribution that herbivorous insects make to global biodiversity[13] as well as the centrality of ecological specialization in theories of biodiversity warrant further comparison of host specificity of tropical and temperate herbivorous insects.

Here we demonstrate a latitudinal gradient in host specificity for the most ecologically dominant group of externally feeding herbivores, larval Lepidoptera, using extensive caterpillar–host-plant data sets from the Americas (Table 1). Any such data set, regardless of size, is incomplete: the most specialized herbivores might not be sampled, cryptic specialist species might not be distinguished, the host plant range of generalist herbivores might be underestimated, and herbivore diets can shift from one community to another[14]. Thus, although thorough collecting efforts involved in generating these data sets are crucial[12], smaller data sets in particular present practical problems for traditional calculations of diet breadth. We address this issue explicitly by analysing the host specificity of herbivores with two measures: first, a direct comparison of taxonomic diet breadth calculated for each herbivore species, which depends heavily on sampling effort, and second, beta diversity (turnover) of herbivores among focal tree species[15], which gives an indirect but more accurate representation of host specificity with limited sampling effort.

We compiled rearing data of field-collected caterpillars from eight sites in North, Central, and South America (Table 1) spanning temperate (southern Canada and Connecticut, USA), subtropical (southern Arizona and southern Louisiana, USA) and tropical forests or woodlands (wet forest in Costa Rica, moist forest in Panama, cloud forest in Ecuador, and cerrado in Brazil). Lists of host plants and caterpillar species used for analyses are provided in Supplementary Information. Externally feeding caterpillars (mostly macrolepidopterans, but including Zygaenoidea and in some cases Pyraloidea) were collected in the field by scanning visually or by beating foliage.

The host plant specificity of forest caterpillars decreased significantly with increasing latitude as measured for plant families ($F_{1,5} = 47.2$, $P = 0.001$, $R^2 = 0.90$), genera ($F_{1,5} = 20.8$, $P = 0.006$, $R^2 = 0.81$; Fig. 1) and species ($F_{1,5} = 14.7$, $P = 0.01$, $R^2 = 0.75$). The latitude–specialization relationship as measured by the number of host plant species per caterpillar species was strengthened slightly

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[1]Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, Louisiana 70118, USA. [2]Department of Biology, Wesleyan University, Middletown, Connecticut 06459, USA. [3]Department of Biological Sciences, George Washington University, Washington, DC 20052, USA. [4]Department of Biological Sciences, Wright State University, Dayton, Ohio 45435, USA. [5]Department of Biology, University of Missouri–St Louis, St Louis, Missouri 63121, USA. [6]Yanayacu Biological Station and Center for Creative Studies, Cosanga, Napo, Ecuador c/o Foch 721 y Juan Leon Mera, Quito, Ecuador. [7]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269, USA. [8]Department of Ecology/Zoology, University of Brasilia, 70910-900, Brasilia, DF, Brazil. [9]Department of Biology, University of Utah, Salt Lake City, Utah 84112-0840, USA. [10]Smithsonian Tropical Research Institute, Panama City, Panama.

Table 1 | Caterpillar rearing databases

Study site	Median latitude	Sampling area (ha)	Rearings	Caterpillars	Host plants	Effort (h)	Years
Canada	47° 15′ N	80,000,000	131,431	28, 280, 653	27, 59, 155	Unknown	20
Connecticut	41° 30′ N	1,437,100	3,158	19, 166, 252	12, 13, 14	Unknown	5
Arizona	32° 13′ N	1,000,000	7,601	20, 136, 184	50, 104, 161	9,000	10
Louisiana	31° 00′ N	500,000	2,300	19, 98, 127	48, 77, 106	5,000	6
Brazil	15° 56′ S	10,000	5,614	43, 264, 565	44, 80, 109	8,000	12
Costa Rica	10° 25′ N	2,400	22,348	29, 223, 509	72, 176, 281	52,000	15
Panama	9° 10′ N	1,600	4,536	30, 384, 401	57, 139, 209	8,000	9
Ecuador	0° 25′ S	30,000,000	24,413	13, 65, 192	53, 110, 177	72,000	6

Rearings include only those portions of the databases used for analyses in this study. Sampling area was estimated for Canada, Louisiana, Arizona and Ecuador, where multiple sites were sampled. Hours of search effort were estimated for Panama but were not estimable for Canada and Connecticut. Number of rearings per host plant species varied from 1 to over 100 for all sites. Numbers of caterpillar or host plant taxa are listed as families, genera and species, respectively. Vascular plants, including ferns, of all life forms were sampled for all sites except Canada, where only trees were sampled.

when heterogeneity in the data from different sites (Table 1) was corrected by weighting the regressions by sampling area ($F_{1,5} = 47.2$, $P = 0.001$, $R^2 = 0.90$), the reciprocal of sampling area ($F_{1,5} = 22.7$, $P = 0.005$, $R^2 = 0.82$) and years of sampling ($F_{1,5} = 29.4$, $P = 0.003$, $R^2 = 0.85$). Similarly, because the sampling effort per caterpillar species was variable, nonparametric techniques were used to estimate the total richness of host plants for each caterpillar species, which slightly strengthened the latitude–specialization relationship (using the Chao2 estimator, $F_{1,5} = 16.1$, $P = 0.01$, $R^2 = 0.76$).

Within a region (temperate or tropical), the ranges of many caterpillar species encompass multiple sites[14], enabling us to compile estimates of region-wide patterns of host plant use for these species. As a whole, temperate caterpillars fed on significantly higher numbers of plant species, genera, and families (multivariate analysis of variance (MANOVA), Wilks's lambda $F_{1,2637} = 311$; $P < 0.0001$; Fig. 2a). This pattern was significantly stronger for measures using host plant species versus genera and families (profile analysis, for both comparisons, $P < 0.0001$). The difference in diet breadth between tropical and temperate herbivores was not as marked when sampling was restricted to caterpillars feeding on eight randomly selected tree species (Fig. 2a), one of the sample sizes used by Novotny *et al.*[12]. These direct measures of diet breadth reveal that the host specificities of particular herbivore lineages (taxonomic families or superfamilies) were always significantly greater in tropical than in temperate sites, but varied by taxon (Fig. 2b). Larval Papilionoidea (all butterflies), for example, had relatively high host specificity in both temperate and tropical sites, whereas larval Geometridae, Noctuidae and Arctiidae (the most diverse families in the combined data set) had much higher host specificity at tropical sites than at temperate sites. In the most comprehensive tropical (Costa Rica) and temperate (Canada) data sets, the mean proportion of monophagous (that is, eating only one genus) herbivore species found on a given plant species was 0.64 (95% confidence interval (CI) 0.58–0.70) for Costa Rica ($n = 281$ plant species) and 0.11 (95% CI 0.08–0.18) for Canada ($n = 155$ plant species).

The analysis of β (beta diversity) as a proxy for specialization showed that turnover of herbivore species among host tree species was highest in tropical forests, intermediate in subtropical forests, and lowest in temperate forests (on the basis of non-overlapping 95% CIs; Fig. 3). This variable, computed with data from only eight host tree species per site, yielded the same site specialization rankings as the traditional taxonomic measures based on much more extensive sampling (Fig. 1). Similar results were obtained with 14 host tree species (Supplementary Information). Although thorough characterization of herbivore–plant affiliations for entire forests is ideal, many ecological studies focus on a subset of species for practical reasons. Using beta diversity as an indirect measure of herbivore specificity has the dual advantage of simplicity and robustness in the face of a limited sampling effort typical of most ecological studies, permitting more frequent tests of hypotheses about gradients in ecological specialization.

To circumvent problems arising from phylogenetic non-independence[12], we restricted our selection of host species to those from different genera in our analyses of herbivore β diversity. Additionally, in our analyses of herbivore diet breadth, we have included data from hundreds of host plant species representing a wide phylogenetic range of plant taxa in both tropical and temperate zones. By including a large proportion of the entire community we minimize potential bias in phylogenetic disparity (because both tropical and temperate data sets each contain many closely and distantly related taxa). Even if a bias in phylogenetic disparity among tropical and temperate plant

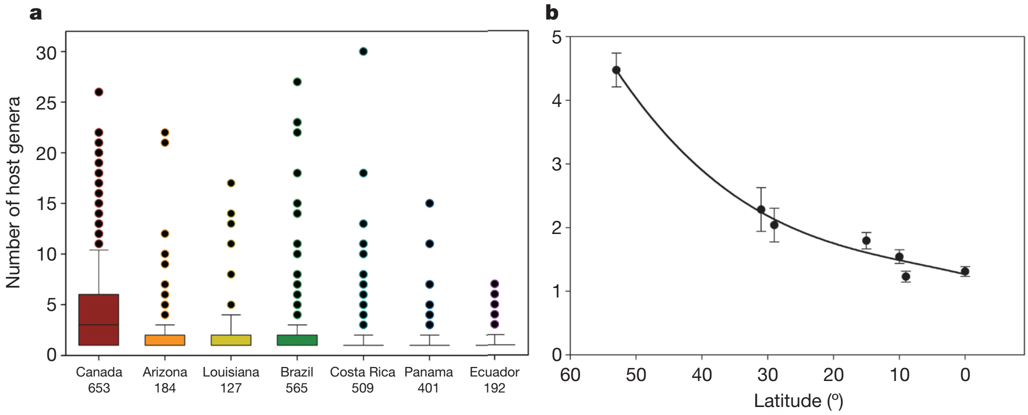

Figure 1 | Caterpillar diet breadth for one temperate site, two subtropical sites and four tropical sites. a, Box plots of number of host plant genera per caterpillar species at seven sites across a latitudinal gradient. Boxes are bounded by the first quartile, median, and third quartile; whiskers are 1.5 times the interquartile range; points outside the whiskers are outliers. Numbers of caterpillar species collected are listed beneath each site name. Measures based on number of species or families yielded similar distributions. All distributions are skewed towards specialists (feeding on one or two host genera), and outliers represent extreme generalist caterpillars. **b**, An illustrative quadratic regression (diet breadth = $1.4 - 0.007 \times (\text{latitude}) + 0.0012 \times (\text{latitude})^2$; $R^2 = 0.98$, $F_{2,4} = 103.1$, $P = 0.0004$); error bars indicate s.e.m.

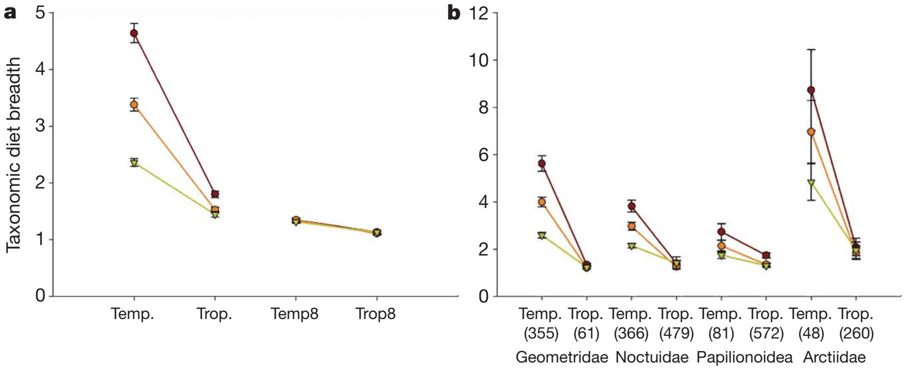

Figure 2 | Mean diet breadth of 1,585 tropical versus 1,052 temperate caterpillar species. **a**, Diet breadth was measured as the number of taxa of host plants per caterpillar species. Temp., temperate; trop., tropical. When eight focal host plant species were chosen randomly from each site, the difference between temperate (Temp8) and tropical (Trop8) diet breadths was greatly reduced (but was still significantly different; $F_{1,606} = 22.5$, $P < 0.0001$). **b**, Latitudinal differences in diet breadths were consistent for the best-sampled families of Lepidoptera (Geometridae, Noctuidae and Arctiidae), but the difference was modest for the butterflies (Papilionoidea). Numbers of species collected are shown in parentheses in **b**. Purple circles, host species; orange circles, host genera; yellow triangles, host families. Error bars indicate 95% CI.

taxa exists, our comparisons of host breadth at generic and family levels (where the relationship between phylogenetic distance and herbivore similarity breaks down[12]) confirm the higher specificity of tropical taxa. Although the most appropriate phylogenetic correction for analysing herbivore host specificity would be to correct for phylogeny of the herbivores themselves, no such phylogeny currently exists. Our temperate–tropical host range comparisons of the most diverse caterpillar families/superfamilies in our data set demonstrate that the greater specialization of tropical caterpillars is a common feature of all four clades (Fig. 2b).

It is clear that the approach outlined here should be accompanied by similar studies that correct for phylogeny, as argued by other authors[12,16,17]. Both approaches are necessary[16], because correcting for phylogeny limits the data to a subset of focal species, which can markedly alter ecologically relevant measures of diet breadth (Fig. 2a). Thus, the contrast between the results of our study and those of Novotny *et al.*[12] may be due to true biological differences between the Americas on the one hand and Europe and tropical Asia on the other, or it might just be a consequence of limiting the comparisons between Europe and Papua New Guinea to 8–14 focal host species.

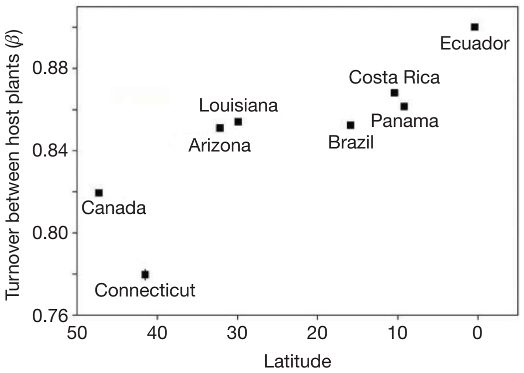

Figure 3 | Caterpillar species turnover among host plant species for eight forest and woodland sites across a latitudinal gradient. Modified Whittaker's β is shown for two temperate (Canada and Connecticut), two subtropical (Arizona and Louisiana) and four tropical (Brazil, Costa Rica, Panama and Ecuador) sites, ordered by an approximate modal latitude for each site. With this measure, insect species turnover across host plants is used as an index of host plant specialization, with higher values of β indicating higher levels of specialization. Symbol size was greater than the 95% CI for all sites except Connecticut (see the text for details on the computation of β).

The accuracy of delineating reproductively isolated units (that is, species) can markedly influence perceptions of the ecological specificity of organisms. Recent analyses of cytochrome *c* oxidase I (COI) haplotypes reveal that many tropical herbivore species with diets broadly distributed among available host plants may in fact be complexes of specialized cryptic species[18]. Although it has not been investigated whether such cryptic species complexes are more common in the tropics than in the temperate zone, temperate taxa are likely to be better resolved taxonomically, given the much greater attention they have received from systematists, forest managers and ecologists.

We conclude that host plant specificity of herbivorous insects is, on average, greater in the neotropics than at higher latitudes, and that a latitudinal gradient of dietary specialization is evident from our data. The evidence from this study is consistent with the hypothesis that ecological specialization is a factor in the origin and maintenance of high diversity of tropical herbivorous insects. Broad-scale empirical studies indicate that this increased specialization in tropical herbivore communities may be due to more intense trophic interactions with both host plants and enemies[19]. For example, comparisons of tropical and temperate forests indicate that tropical plants are chemically 'nastier'[20] and that selective pressures due to natural enemies are stronger in the tropics[12,21], both of which should select for narrower host ranges in herbivores. Additionally, there is some evidence that tropical tree species may be more chemically distinct than temperate tree species[21,22], selecting for narrower diet breadths. The underlying mechanisms for differences in specialization by latitude, and perhaps by longitude, should be the focus of future research. Although it is clear that a significant proportion of tropical insect diversity is a product of species richness in higher plants[12], our data also imply that greater ecological specialization contributes to the great α and β diversity of herbivores in low-latitude forests. Recent palaeontological studies of insect-feeding damage[23] and regional analyses of extant phytophagous insects[24] provide clear examples of decoupled plant and herbivore diversity. Such examples show that insect diversity cannot be assumed to result only from plant diversity, whatever the specific mechanism invoked. Moreover, these results provide support for ecological[25,26] and evolutionary theory[7,8], highlighting the key role of ecological specialization in the coexistence and diversification of species.

METHODS SUMMARY

Caterpillars were reared individually, at ambient temperature and humidity, on leaves of the plant species from which they were collected. To assess the degree of host specialization in each community we calculated the average number of host plant taxa per caterpillar species—the approach used in most other studies of diet breadth. We used linear regression to examine the relationship between median latitude and mean number of host plant families, genera and species (Fig. 1 shows a quadratic regression of genera on latitude for illustrative purposes). Regressions were then weighted by the size of the study areas and years of study to correct for variation between study sites. The reciprocal of area was also used in weighted regressions to decrease influence of very large collecting sites (namely Canada and Ecuador). To correct for unequal sampling per caterpillar species, we computed the Chao2 estimator[27] of the number of host plant species per caterpillar and examined its association with latitude by means of linear regression.

We used MANOVA followed by profile analysis to compare the number of plant species, genera and families fed on by each of the caterpillar species in tropical and in temperate latitudes. To compare diet breadths on the basis of focal plant taxa, eight plant species in different families were randomly selected from each site, and the diet breadth of the subset of caterpillars feeding on these hosts was calculated using only those focal plants. We also used modifications[28] of Whittaker's[29] index of beta (β) diversity as an alternative measure of specialization. For each site, eight host plants from different genera were used to calculate β. This process was repeated for 1,000 random combinations of host plant species per site, generating an estimate of β for each site, along with 95% confidence intervals. Sites for which 95% CIs did not overlap were considered to be statistically different.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

Received 14 March; accepted 27 April 2007.

1. Hillebrand, H. On the generality of the latitudinal diversity gradient. *Am. Nat.* **163,** 192–211 (2004).
2. Hutchinson, G. E. Homage to Santa Rosalia, or Why are there so many kinds of animals? *Am. Nat.* **93,** 145–159 (1959).
3. MacArthur, R. H. & Levins, R. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101,** 377–385 (1967).
4. Connell, J. H. Diversity in tropical rain forests and coral reefs. *Science* **199,** 1302–1310 (1978).
5. Grant, P. R. & Grant, B. R. Evolution of character displacement in Darwin's finches. *Science* **313,** 224–226 (2006).
6. Farrell, B. D. 'Inordinate fondness' explained: why are there so many beetles? *Science* **281,** 555–559 (1998).
7. Schluter, D. *The Ecology of Adaptive Radiation* (Oxford Univ. Press, Oxford, 2000).
8. Thompson, J. N. *The Geographic Mosaic of Coevolution* (Univ. of Chicago Press, Chicago, 2005).
9. Darwin, C. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (John Murray, London, 1859).
10. Wallace, A. *Tropical Nature and Other Essays* (MacMillan, London, 1878).
11. Armbruster, S. W. in *Plant–Pollinator Interactions* (eds Wasser, N. M. & Ollerton, J.) 260–282 (Chicago Univ. Press, Chicago, 2006).
12. Novotny, V. *et al.* Why are there so many species of herbivorous insects in tropical rainforests? *Science* **313,** 1115–1118 (2006).
13. Price, P. W. in *Plant–Animal Interactions* (eds Herrera, C. M. & Pellmyr, O.) 3–26 (Blackwell, Oxford, 2002).
14. Thomas, C. D. Fewer species. *Nature* **347,** 237 (1990).
15. Lewinsohn, T. M., Novotny, V. & Basset, Y. Insects on plants: Diversity of herbivore assemblages revisited. *Annu. Rev. Ecol. Syst.* **36,** 597–620 (2005).
16. Irschick, D., Dyer, L. A. & Sherry, T. Phylogenetic methods for studying specialization. *Oikos* **110,** 404–408 (2005).
17. Ødegaard, F., Diserud, O. H. & Østbye, K. The importance of plant relatedness for host utilization among phytophagous insects. *Ecol. Lett.* **8,** 612–617 (2005).
18. Hajibabaei, M., Janzen, D. H., Burns, J. M., Hallwachs, W. & Hebert, P. D. N. DNA barcodes distinguish species of tropical Lepidoptera. *Proc. Natl Acad. Sci. USA* **103,** 968–971 (2006).
19. Janzen, D. H. Coevolution of mutualism between ants and acacias in Central America. *Evolution Int. J. Org. Evolution* **20,** 249–275 (1966).
20. Coley, P. D. & Barone, J. A. Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* **27,** 305–335 (1996).
21. Dyer, L. A. & Coley, P. D. in *Multitrophic Level Interactions* (eds Tscharntke, T. & Hawkins, B.) 67–88 (Cambridge Univ. Press, Cambridge, 2002).
22. Marquis, R. J. & Braker, H. E. in *La Selva; Ecology and Natural History of a Tropical Rain Forest* (eds McDade, L., Bawa K. L., Hespenheide, H. A. & Hartshorn, G. S.) 261–281 (Univ. of Chicago Press, Chicago, 1994).
23. Wilf, P., Labandeira, C. C., Johnson, K. R. & Ellis, B. Decoupled plant and insect diversity after the end-Cretaceous extinction. *Science* **313,** 1112–1115 (2006).
24. Hawkins, B. A. & Porter, E. E. Does herbivore diversity depend on plant diversity? The case of California butterflies. *Am. Nat.* **161,** 40–49 (2003).
25. Tilman, D. *Resource Competition and Community Structure* (Princeton Univ. Press, Princeton, 1982).
26. Chase, J. M. & Leibold, M. A. *Ecological Niches: Linking Classical and Contemporary Approaches* (Univ. of Chicago Press, Chicago, 2003).
27. Colwell, R. K. & Coddington, J. A. Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond. B* **345,** 101–118 (1994).
28. Kiflawi, M. & Spencer, M. Confidence intervals and hypothesis testing for beta diversity. *Ecology* **85,** 2895–2900 (2004).
29. Whittaker, R. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* **30,** 279–338 (1960).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank D. Janzen, D. Gruner, G. Rodriguez, J. Landosky and R. Forkner for helpful suggestions for improving the manuscript; G. Howse for making available the CFIS data; E. Selig, A. Frevert, J. McGrath and M. Walker for their efforts in constructing the Canadian database; and a large number of taxonomists, field assistants and students for their help in generating all data. Funding came from the US National Science Foundation, Earthwatch Institute, National Geographic, Tulane University, University of Missouri Research Award, Wesleyan University's Hughes Summer Research Program, and the National Institute for Climate Change Research.

Author Contributions All authors designed and performed data collection protocols and contributed substantially to writing the paper; M.S.S. proposed the original idea for the paper; M.S.S. and L.A.D. designed the analyses and wrote the first full draft of the paper; J.O.S., R. J. Marquis, J. T. Lill and R. E. Ricklefs contributed extensive revisions; L.A.D. performed statistical analyses and created figures.

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METHODS

Methods of rearing the caterpillars used in this study are described in detail in refs 30–35. The Connecticut data included only 13 host plant genera; diet breadth is therefore underestimated for this site; these data were only used in the β diversity measure of diet breadth. Voucher specimens of adults were deposited at appropriate museums (Supplementary Information). Tropical plant species were identified by knowledgeable taxonomists (Supplementary Information).

We used MANOVA to compare the number of plant species, genera, and families fed on by each of the caterpillar species in tropical versus temperate latitudes. Profile analysis was used to compare the response of these different taxonomic measures of diet breadth between the two latitude classes. To compare diet breadths on the basis of focal plant taxa, eight plant species in different families were randomly selected from each site, and the diet breadth of the subset of caterpillars feeding on these hosts was calculated using only those focal plants. We also examined herbivore species turnover across focal host plant species as an alternative measure of specialization. We used modifications[28] of Whittaker's[29] index of beta (β) diversity across eight host plants as an index of specialization. Mathematically, β represents the probability that a lepidopteran species with an average diet breadth on the eight plant species will be missing from a host plant randomly picked from the eight species. Thus, $\beta = 0$ when all lepidopteran species occur on all host plants, and β approaches 1 when all Lepidoptera are restricted to a single host plant. Higher values of β indicate greater host specialization. For each site, eight host plants, each from a different genus, were selected from the plant species sampled at each site to calculate β. This process was repeated for 1,000 random combinations of host plant species per site. The number of focal plant species (8) in each combination was chosen to mimic one approach used by Novotny *et al.*[12]; subsets of randomly selected plant species of other sizes (6, 14) yielded similar results (Supplementary Information). The number of host plants from which the subsets were randomly drawn varied between sites (see Supplementary Information), but only host plants with at least 50 rearing records are included in the general pool. This process generated an estimate of β for each site, along with 95% CIs. Sites for which 95% CIs did not overlap were considered to be statistically different.

30. McGugan, B. M. (ed) *Forest Lepidoptera of Canada Recorded by the Forest Insect Survey* Vol. 1, *Papilionidae to Arctiidae* (Department of Forestry of Canada, Ottawa, 1958).
31. Gentry, G. & Dyer, L. A. On the conditional nature of neotropical caterpillar defenses against their natural enemies. *Ecology* **83,** 3108–3119 (2002).
32. Stireman, J. O. & Singer, M. S. Determinants of parasitoid–host associations: insights from a natural tachinid–lepidopteran community. *Ecology* **84,** 296–310 (2003).
33. Stireman, J. O. *et al.* Climatic unpredictability and caterpillar parasitism: implications of global warming. *Proc. Natl Acad. Sci. USA* **102,** 17384–17387 (2005).
34. Coley, P. D., Bateman, M. L. & Kursar, T. A. The effects of plant quality on caterpillar growth and defense against natural enemies. *Oikos* **115,** 219–228 (2006).
35. Diniz, I. R. & Morais, H. C. Lepidopteran caterpillar fauna of cerrado host plants. *Biodiv. Conserv.* **6,** 817–836 (1997).