



## Comment on "Why Are There So Many Species of Herbivorous Insects in Tropical Rainforests?"

David A. Norton, *et al.*  
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# Comment on “Why Are There So Many Species of Herbivorous Insects in Tropical Rainforests?”

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Novotny *et al.* (Reports, 25 August 2006, p. 1115) argued that higher herbivore diversity in tropical forests results from greater phylogenetic diversity of host plants, not from higher host specificity. However, if host specificity is related to host abundance, differences in relative host abundance between tropical and temperate regions may limit any general conclusion that herbivore diversity scales directly with host-plant diversity.

Novotny *et al.* (1) concluded that once the confounding effects of sampling intensity and the comparative phylogenetic diversity of host plants have been controlled for, there are no significant differences in either herbivore species density or host specificity of herbivores on tropical versus temperate tree species. Instead, they posited that higher herbivore species diversity in tropical forests must result from greater phylogenetic diversity of tropical vegetation—a classic “diversity begets diversity” argument (2). We suggest that differences in host-plant abundance between tropical and temperate regions may limit any general conclusion that herbivore diversity scales directly with host-plant diversity.

We agree that host plant diversity is a critically important determinant of tropical herbivore diversity. However, any strict interpretation by Novotny *et al.* that host specificity is constant

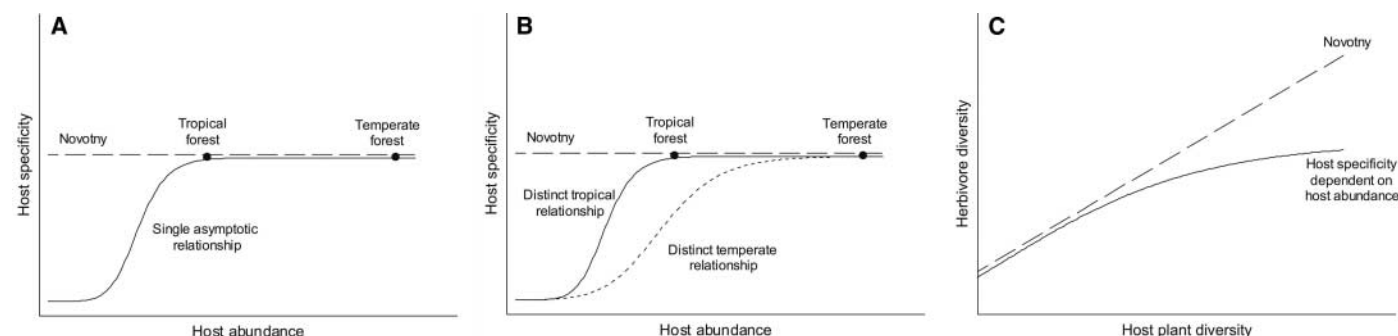
between tropical and temperate forests must first take into account host-plant abundance. Novotny *et al.* only sampled commonly occurring host tree species, which represented 85% of available host trees in their temperate forest but less than 20% of trees in their tropical forest. The majority of other host species in tropical forests are rare. Kelly and Southwood (3) clearly showed that herbivore diversity on trees scales as a power function of host tree abundance, even after controlling for host phylogeny. It is also widely conjectured that host specificity is inversely related to host abundance for both host-herbivore and host-parasite systems (4–10) because of the evolutionary trade-off between the potential increase in mean offspring fitness from specializing on one host species versus limitations on the rate of host detection when hosts become increasingly rare (11, 12)—frequently referred to as Janzen’s resource fragmentation hypothesis (4). In fact, Novotny *et al.* implicitly recognized this in their earlier work (13) when they suggested that herbivores may specialize more often on large plant genera than small ones because the former represent a larger resource base. Therefore, extrapolation of constant species

densities and constant host specificity rates to all host plant species, in general, may not be warranted without explicit consideration of relative host abundance.

The question is whether the theoretical rationale for expecting a positive relationship between host abundance and specificity has an important bearing on empirical host specificity relationships across regions. Unfortunately, there are no empirical data available on the form of the host abundance versus specificity relationship for herbivorous insects. However, there are at least two alternative interpretations of the equivalence in tropical and temperate host specificity data presented by Novotny *et al.* (1), and these have important implications for the apparent scaling of herbivore diversity with host plant diversity. First, the unresolved relationship between host abundance and specificity may have a strict lower limit arising from evolutionary constraints on host specialization, but approach essentially the same value in both temperate and tropical herbivore communities (Fig. 1A). Alternatively, the slope of the relationship between host abundance and specificity may differ substantially between biomes, such that the observed equivalence in host specificity in Novotny *et al.* may be coincidental (Fig. 1B). The latter would imply that host specificity may actually be higher in the tropics for an equivalent degree of host abundance, which would be an exciting proposition to test. In both of these hypothetical alternatives, there will be a net difference in host specificity between tropical and temperate forests, whether this is due simply to a quantitative difference in the diversity of rare host species in the tropics or to a qualitative difference in the abundance-specificity relationship. Therefore, although we agree that host plant diversity is indeed a critically important determinant of tropical herbivore diversity, it is unlikely that herbivore diversity will scale proportionately with increasing host diversity (Fig. 1C), but rather host plant abundance may

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**Fig. 1.** Host plant abundance may impose an upper limit on the diversity of host-dependent species. Novotny *et al.* found that host specificity of herbivore species is constant on commonly occurring tropical and temperate tree species (dashed line), but this does not take into account a possible relationship between host abundance and host specificity. Two hypothetical alternative possibilities for this relationship are (A) a single asymptotic abundance-

specificity relationship (solid line), or (B) distinct abundance-specificity relationships for tropical (solid line) versus temperate (dotted line) regions. (C) In contrast to Novotny *et al.* (dashed line), we argue that both of these hypothetical alternatives [(A) and (B)] imply that host abundance will impose an upper limit on the scaling relation between herbivore diversity and host diversity (solid line) because the majority of host tree species in the tropics are rare.

impose an upper limit on the diversity of host-dependent species.

#### References

1. V. Novotny *et al.*, *Science* **313**, 1115 (2006).
2. N. Janz, S. Nylin, N. Wahlberg, *BMC Evol. Biol.* **6**, 4 (2006).
3. C. K. Kelly, T. R. E. Southwood, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 8013 (1999).
4. R. A. Beaver, *Nature* **281**, 139 (1979).
5. D. H. Janzen, *Ecology* **62**, 532 (1981).
6. A. F. G. Dixon, P. Kindlmann, J. Leps, J. Holman, *Am. Nat.* **129**, 580 (1987).
7. B. A. Hawkins, M. R. Shaw, R. R. Askew, *Am. Nat.* **139**, 58 (1992).
8. D. A. Norton, P. J. de Lange, *Funct. Ecol.* **13**, 552 (1999).
9. D. A. Norton, M. A. Carpenter, *Trends Ecol. Evol.* **13**, 101 (1998).
10. D. P. Vazquez, R. Poulin, B. R. Krasnov, G. I. Shenbrot, *J. Anim. Ecol.* **74**, 946 (2005).
11. J. Jaenike, *Annu. Rev. Ecol. Syst.* **21**, 243 (1990).
12. J. N. Thompson, *The Coevolutionary Process* (University of Chicago Press, Chicago, 1994).
13. V. Novotny *et al.*, *Nature* **416**, 841 (2002).

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