Refuges as a Predictor of Parasitoid Diversity

MICHAEL E. HOCHBERG* AND BRADFORD A. HAWKINS

A central problem in ecology is predicting the diversity of communities. Insect parasitoids may encompass 20 percent of all insect species; hence, establishing the mechanisms that drive parasitoid species richness represents a major step in understanding the diversity of terrestrial communities. An assemblage model, based on population dynamic constructs, shows how the presence of refuges from parasitoid attack can generate diversity patterns that are in good accord with global data on structural protection from parasitism resulting from host feeding biology. This theory offers a simple ecological explanation for the range of diversities observed in real parasitoid assemblages. Predicting parasitoid diversity may be a realistic goal, at least for those systems in which the basic demography is well understood.

PARASITOIDS ARE INSECTS THAT PARASITIZE, and eventually kill, other arthropods. They constitute some of the most diverse animal communities (*1*), with assemblages (*2*) commonly comprising 10 or more species per host species, and sometimes attaining more than 50 (*3*). Understanding why some parasitoid species assemblages are more diverse than others is thus an important step toward the comprehension of community-wide and global patterns of biodiversity (*4*) and has applications in areas such as species conservation and the biological control of insect pests. We present a quantitative theory, based on variation in the susceptibility of host individuals to parasitism, to explain observed patterns of variation in parasitoid species richness across species of host. This variability in the risk of being parasitized creates a sort of "refuge" for those hosts that are less vulnerable to the attack of adult female parasitoids.

Much of what is known about the effect of refuges on parasitoid persistence comes from models and experiments focusing on one, or a few, species of parasitoid. The models (*5–9*) consistently show that an important ingredient for parasitoid persistence is sufficient variation in the risk of parasitism from host to host. In particular, refuges resulting from a constant proportion of the host population being invulnerable to parasitoid attack have been suggested as important in stabilizing a number of host-parasitoid associations (*5, 7, 10*). Several cases (*7, 10–12*) indicative of such "proportional" refuges have been documented. For example, Murdoch and co-workers (*10*) have shown that individuals of the red scale, *Aonidiella aurantii*, which occur in limited areas toward the interior of citrus trees (about 75% of the population) are up to 27 times less vulnerable to attack by two species of parasitoid as compared to individuals feeding on the periphery. They attribute the relatively constant populations in the system to this physical refuge.

In our population model (*13*), we consider two sources of refuge from parasitoid attack. The first, spatial heterogeneity, has the effect of decreasing the mean parasitoid searching efficiency as parasitoid density increases (*6, 7*). The second, invulnerability to parasitism of a proportion of the host population, arises, for example, by complete protection from attack of those host individuals that feed and develop in physically inaccessible (or otherwise not searched) "structural" refuges, such as deep within plant stems or roots (*7, 10–12, 14*).

The model system is based on a spatially isolated population of an insect host, which exhibits discrete and non-overlapping generations (such as would be the case for many temperate species of Lepidoptera). During each generation, a proportion of the larval host population is vulnerable to parasitism by two types of solitary parasitoid species, *m* generalist species whose populations are assumed to be maintained at constant levels by other host species in addition to the single host species considered here, and *n* species of specialist whose populations are assumed to depend completely upon that of the host. The various species of parasitoid are assumed to exhibit a hierarchical ability to compete within host individuals that are attacked by individuals of more than one parasitoid species (*15*).

The difference equations for the general model, constituting the density of hosts (numbering N_{t+1} adults per unit area in generation $t + 1$), generalist parasitoids of species x produced by the host concerned here ($G_{x,t+1}$), and specialist parasitoids of species y ($S_{y,t+1}$), are given by

$$N_{t+1} = FN_t d\{N_t\}\left(\alpha + (1-\alpha)\prod_{i=1}^{m} g_i \prod_{j=1}^{n} s_j\right) \tag{1}$$

$$G_{x,t+1} = FN_t d\{N_t\}(1-\alpha)(1-g_x)\left(\prod_{i=1}^{x-1} g_i \prod_{j=1}^{q} s_j\right) \tag{2}$$

$$S_{y,t+1} = FN_t d\{N_t\}(1-\alpha)(1-s_y)\left(\prod_{i=1}^{p} g_i \prod_{j=1}^{y-1} s_j\right) \tag{3}$$

where generalist species x follows generalist $x - 1$ and specialist q in the competitive hierarchy, and specialist species y follows specialist $y - 1$ and generalist p in the competitive hierarchy. Further, F is the finite rate of increase of the host population (the average number of offspring produced per host), α is the proportion of the host population that is protected from parasitism, and $d\{N_t\}$ is the proportion of all hosts surviving from intraspecific competition [assumed to be compensatory, with $d\{N_t\} = 1/[1 + N_t(F - 1)/Q]$, where Q is the environmental carrying capacity of the host population (*7, 16*)]. Obviously, $F > 1$ is a minimum condition for the host population to persist in the face of a parasitoid assemblage.

Further, g_i and s_j are the functional responses (relating parasitoid and host densities to the average probability of a host escaping parasitism) of generalist and specialist parasitoids, respectively, and are given by

$$g_i = \left[1 + \frac{a_i\hat{G}_i\{N_t\}}{k_i(1 + a_iFN_t(1-\alpha)/\eta_i)}\right]^{-k_i} \tag{4}$$

$$s_j = \left[1 + \frac{a_jS_{j,t}}{k_j(1 + a_jFN_t(1-\alpha)/\eta_j)}\right]^{-k_j} \tag{5}$$

Here, a (that is, a_i and a_j) is the per capita searching efficiency of the parasitoids, η is the maximum number of hosts that a single parasitoid individual may attack in a given generation, $\hat{G}_i\{N_t\} = h_i(1 - \exp\{-FN_t(1 - \alpha)/b_i\})$ [with h_i the maximum number of parasitoids attacking and b_i a constant (*7, 17*)] is the actual number of generalist parasitoids of species i that launch attacks on the host concerned here, and k is the clumping parameter of the negative binomial distribution of parasitoid search (with small values of k signaling increased heterogeneity).

We were not able to derive easily understandable analytical expressions for the diversity pattern produced by the general model. Therefore, we conducted extensive numerical simulations of the system (all simulations were run for at least 1000 generations), both for a range of realistic pa-

M. E. Hochberg, Ecole Normale Supérieure, CNRS-URA 258, Laboratoire d'Ecologie, 46 rue d'Ulm, 75230 Paris Cedex 05 France.
B. A. Hawkins, NERC Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY England.

---

*To whom correspondence should be addressed.

rameter values (*18*) and initial densities of specialist parasitoid and host populations. To standardize the measure of diversity (*19*), a particular parasitoid species was considered to contribute to species richness if at least a single individual adult was produced per unit host sample (unless otherwise stated, 1000 host individuals) in the final generation of the simulation and the populations were constant by the end of the simulation. In cases where less than the requisite density of hosts was present for sampling, diversity was counted as zero, since the number of parasitoid species present could not be standardized with other host systems on a density basis (*19, 20*). In addition, we excluded from consideration those cases where, by the final generation of the simulation, the population of the host had not settled to an equilibrium (*20*).

When sufficient numbers of parasitoid species are present in a given assemblage, the basic pattern generated by the model is an increase in the number of parasitoid species sampled as the proportional refuge increases, until a maximum diversity is achieved, after which diversity again falls (Fig. 1). Highly diverse generalist assemblages were readily generated (Fig. 1A), whereas although purely specialist assemblages could be quite diverse (Fig. 1B), this necessitated that the other refuge-generating mechanism, spatial heterogeneity, be pronounced. Changes in the values of the model parameters and in the sample size of the host population could readily affect the magnitude of the diversity relationship but, as long as the parasitoids accounted for sufficient levels of mortality, did not alter the general domed shape (*21*) (Fig. 1, C through F).

The domed pattern results because the proportional refuge first generates increasing parasitoid diversity by preventing the depression of the host population to levels too low for the detection of parasitoids (or levels too low for some specialist parasitoid species to persist, or both), but eventually constrains diversity by reducing the probability of hosts being exploited by individuals of a given parasitoid species (Figs. 1 and 2, A and B). If the parasitoid assemblage does not limit the host population to densities too low to permit cross-species comparisons (*21*), then the diversity pattern can take the form of a plateau of maximum richness followed by a monotonic decrease to zero diversity at $\alpha = 1$, or just a simple monotonic decrease for all α (with maximum diversity occurring at $\alpha = 0$). The commonalities among all patterns we observed are (i) a monotonic decrease in diversity beyond a certain level of refuge, (ii) a monotonic increase in host density for all α (Fig. 2C), and (iii) a monotonic decrease in parasitoid-induced mortality of the host population over all α (Fig. 2D).

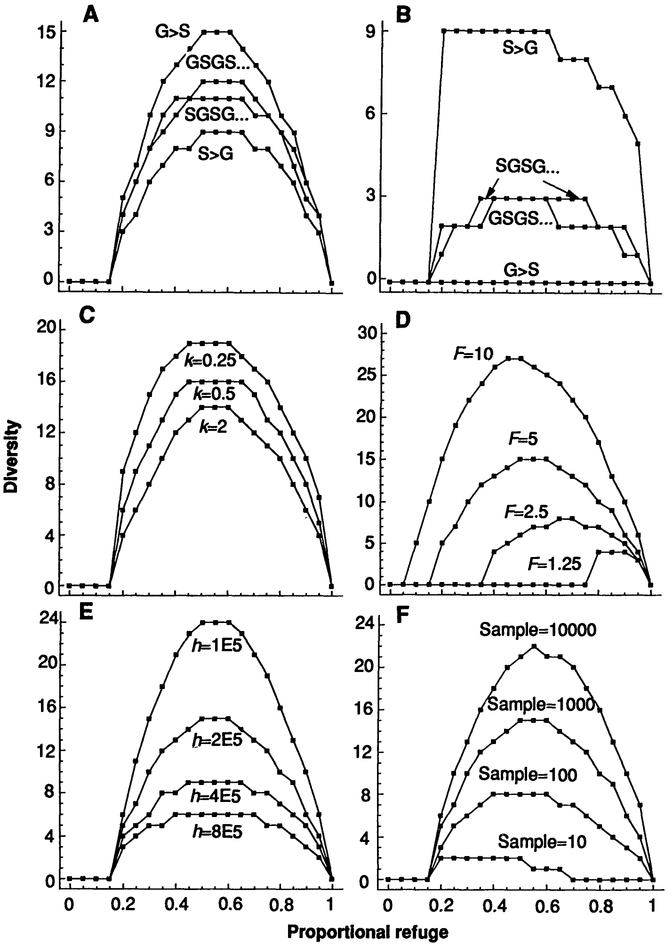

Fig. 1. Examples of the domed relation between the proportion of hosts in the refuge (α) and parasitoid diversity for different values of some of the model parameters. (**A** and **B**) The effect of the competitive hierarchy between generalist and specialist parasitoids on the diversity of (A) generalists (G) and (B) specialists (S). Changing the within-host competitive ability in favor of one type of parasitoid resulted in the same or more of that type and the same or fewer of the other coexisting over a range of proportional refuge levels [G > S = all 15 species of generalist (m = 15) superior to 15 specialists (n = 15); S > G = vice versa, GSGS . . . = alternating superiority with a generalist as the dominant competitor, and SGSG . . . = vice versa]. (**C**) Higher levels of spatial heterogeneity (that is, low k_i) result in more diverse assemblages. (**D**) Increasing the finite rate of increase of the host (F) results in greater diversity and shifts the maximum diversity to smaller levels of refuge. (**E**) Higher per species potential numerical responses (h_i) result in decreases in diversity. The same effects can be shown for decreases in Q and increases in η_i. (**F**) Increasing the sample size used to detect parasitoids results in higher observed diversity. (C) through (F) involve purely generalist assemblages. Parameters unless otherwise noted: $F = 5$, $Q = 10^7$, $h = 0.02$ Q, $b = 0.1$ Q, $a = 0.1$, $\eta = 20$, $k_i = 1$, $k_j = 0.25$, $m = 50$, and $n = 0$.

For realistic parameter values (*18*), diversity patterns can be generated that are consistent in both form and magnitude to that found in real parasitoid assemblages, when hosts are classified according to their feeding biology and ranked in terms of the extent to which they occupy structural refuges to parasitoid attack (*22*) (Fig. 3). The single obvious exception to the congruence between the theoretical and empirical patterns is externally feeding hosts, which support an average of six to seven parasitoid species, whereas the examples we provide from the model would predict that hosts with no structural refuge either could not be sampled (corresponding to unrealistically high levels of host depression) or should have the highest levels of diversity. However, it should be borne in mind that exophytic hosts may have nonstructural refuges (*12, 14, 23*); for instance, mobile external feeders may benefit from a probabilistic refuge by being able to move away from leaf damage to which parasitoids orient, or may use behavioral or chemical defenses against parasitoid attack (*14*). The model can be modified to include a second proportional refuge axis (that is, constitutive escape from parasitism), and in so doing enables predictions of parasitoid diversity for external host species that are in accord with the patterns presented in Fig. 3. That such a modification is reasonable is borne out by data on patterns of parasitoid-induced mortality in hosts. Mortality data (Fig. 4) do not show the monotonic decreasing relationship between diversity and proportional refuge predicted by the model (Fig. 2D) because of the lower than expected mortality of exophytic hosts. We propose that two types of proportional refuge, structural and constitutive, contribute to determining patterns of host mortality and parasitoid diversity.

There is additional empirical evidence (*24*) that refuges from mortality can promote species diversity. For example, Shorrocks and Rosewell have shown how guild

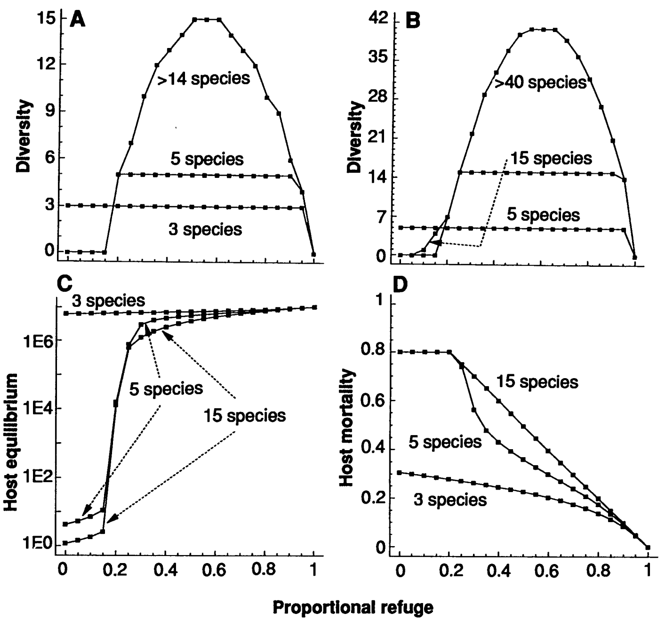

Fig. 2. Examples of the effect of level of proportional refuge and the number of parasitoid species in the system on diversity, the host equilibrium and host mortality. (**A**) The relation between diversity [evaluated per 1000 hosts sampled (*19*)] and proportional refuge is always domed as long as there are more than three species in the parasitoid pool. (**B**) When diversity is evaluated on a per unit area basis (a parasitoid species contributes to diversity if at least one adult is produced per unit area), the diversity measure is higher and positive diversities more readily occur for $\alpha < 1/F$ (as long as the threshold for parasitoid species detection is sufficiently low). (**C**) At a level of refuge $\alpha \approx 1/F$, the host population goes from being parasitoid limited to competition limited. With three or fewer species it is limited by competition no matter the level of α (as long as the initial density of hosts is large enough). (**D**) Host mortality decreases monotonically. It can never take on a value larger than $1 - 1/F$. Other parameters as for Fig. 1.

size in *Drosophila* exploiting patchy resources is positively associated with probabilistic refuges from competition, created by aggregated distributions of the various species. We also find that refuge from mortality can be important to species richness, but at the third trophic level.

Our approach has been to start with a simple model of a parasitoid assemblage so as to be able to identify some of the more general influences on patterns of diversity. Although changes in the values of the model parameters and ordering of processes can change the magnitude of the relationship, they do not alter the basic finding that, when sufficient numbers of parasitoid species are present in the assemblage, maximal parasitoid diversity occurs for some intermediate level of proportional refuge. Clearly, the similarities in shape and magnitudes of some of the theoretical curves with the empirical patterns do not constitute a definitive test of our theory; nevertheless, it is encouraging that the patterns generated by our theory are broadly consistent with empirical data. The model should be viewed as a hypothesis; it remains to be seen if alternative hypotheses can contribute to explaining parasitoid species diversity patterns.

Although we have yet to explore more detailed models of parasitoid assemblages, the theory developed here provides a fairly robust framework from which predictions can be made pertaining to, for instance, the effect of introducing a parasitoid species into a system for the biological control of an insect pest, the conservation of rare species of parasitoid, or the intensity of competitive interactions within or between species of parasitoid. For example, our analysis suggests that percentage mortality and host abundance are not necessarily good indicators of the intensity of competition between parasitoids. This is particularly the case when $\alpha > 1/F$ and density-dependent mortalities other than parasitism dominate the host's population dynamics. We argue that the quantification of refuges from parasitism is a necessary step toward the better understanding of parasitoid community ecology.

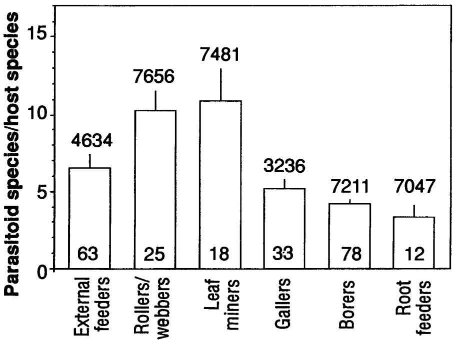

Fig. 3. Patterns of diversity for the parasitoid complexes of 229 well-studied holometabolous host species (each with more than 1000 host individuals sampled) extracted from the primary global literature. Bars represent the geometric mean number of primary larval and pupal parasitoid species per host species for the number of host species given at the base of each bar. Vertical lines represent one standard error of the mean. Numbers above bars represent geometric mean sample sizes for hosts in each feeding classification. See (*25, 26*) and references in (*22*) for details of methods and ranking.

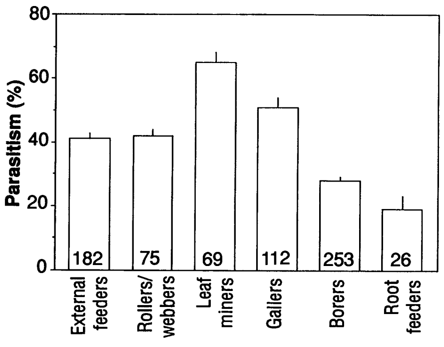

Fig. 4. Patterns of parasitoid-induced larval or pupal mortality or both for the populations of 717 holometabolous host species. Mortality is expressed as the mean percentage of parasitism for the number of host species in each feeding classification given at the base of the bars. For each host species, the maximum parasitism rate of a single host population and generation was recorded from studies extracted from the global literature. Vertical lines represent on standard error of the mean. See (*27*) for details of methods.

REFERENCES AND NOTES

1. N. E. Stork, *Ecol. Entomol.* **12**, 69 (1987); I. D. Gauld, *Biol. J. Linn. Soc.* **35**, 351 (1988); J. LaSalle and I. D. Gauld, *Redia*, in press.
2. The term "assemblage" as used here refers to those species of parasitoid, present in a given geographical area, which are capable of completing their life-cycle as parasites of individuals of a given species of host.
3. J. Fahringer, *Z. Angew. Entomol.* **28**, 335 (1941); W. Baltensweiler, *Mitt. Schweiz. Anst. Forstl. Versuchswes.* **34**, 399 (1958); V. Delucchi, *Entomophaga* **27**, 77 (1982); D. M. Harman and H. M. Kulman, Eds., *Univ. Md. Nat. Resour. Inst. Contrib. 527* (1973), p. 79.
4. For example, see R. M. May, *Science* **241**, 1441 (1988).
5. M. P. Hassell and R. M. May, *J. Anim. Ecol.* **42**, 693 (1973).
6. R. M. May, *ibid.* **47**, 833 (1978).
7. M. P. Hassell, *The Dynamics of Arthropod Predator-Prey Systems.* (Princeton Univ. Press, Princeton, NJ, 1978).
8. For example, see V. A. Bailey, A. J. Nicholson, E. J. Williams, *J. Theor. Biol.* **3**, 1 (1962); M. P. Hassell and R. M. May, *J. Anim. Ecol.* **43**, 567 (1974); W. W. Murdoch and A. A. Oaten, *Adv. Ecol. Res.* **9**, 2 (1975); P. L. Chesson and W. W. Murdoch, *Am. Nat.* **127**, 696 (1986); M. P. Hassell and R. M. May, *J. Anim. Ecol.* **55**, 923 (1986).
9. R. M. May and M. P. Hassell, *Am. Nat.* **117**, 234 (1981).
10. W. W. Murdoch, R. F. Luck, S. J. Walde, J. D. Reeve, D. S. Yu, *Ecology* **70**, 1707 (1989). The possibility that the observed stability in the red scale system is due to a physical refuge was first suggested by J. D. Reeve and W. W. Murdoch [*J. Anim. Ecol.* **55**, 1069 (1986)].
11. Examples of types of proportional refuge include structural or physical protection [*7, 10*; B. A. Hawkins, H. W. Browning, J. W. Smith, *Entomophaga* **32**, 483 (1987)], spatial or temporal incoincidence [M. P. Hassell, *J. Anim. Ecol.* **38**, 329 (1969); M. Münster-Swendsen and G. Nachman, *ibid.* **47**, 159 (1978)], and constitutive escape (the evolution of specific mechanisms to escape parasitoid attack or, if attack succeeds, to prevent the subsequent development of parasitoid larvae (*12, 14, 23*; S. B. Vinson and G. F. Iwantsch, *Annu. Rev. Entomol.* **25**, 397 (1980)]. It should be borne in mind that these categories need not be mutually exclusive.
12. P. W. Price *et al.*, *Annu. Rev. Ecol. Syst.* **11**, 41 (1980).

13. Among the models assumptions are (i) nonparasitoid-induced density-dependent mortalities act after all parasitism is accounted for, and healthy and parasitized hosts suffer equally [for theoretical exceptions to the latter, see C. Bernstein, *Oikos* **47**, 176 (1986)]; (ii) there is a 1:1 sex ratio for both host and parasitoid species [for theoretical exceptions, see M. P. Hassell, J. K. Waage, R. M. May, *J. Anim. Ecol.* **52**, 889 (1983)]; (iii) in any given generation of the host, a constant proportion of the host population is not encountered by searching parasitoids (*5, 7, 10*); (iv) the parasitoids do not search for hosts in the proportional (for example, structural) refuge [S. B. Vinson, in *Semiochemicals: Their Role in Pest Control*, D. A. Nordlund, R. L. Jones, W. J. Lewis, Eds. (Wiley, New York, 1981), pp. 51–77; J. H. Lawton, in *Insect Parasitoids*, J. K. Waage and D. Greathead, Eds. (Academic Press, London, 1986), pp. 265–287]; (v) attacks on hosts outside of the proportional refuge are distributed negative binomially (*6, 7*); and (vi) outside of the proportional refuge, the distributions of parasitism among parasitoid species are independent of one another [for theoretical exceptions, see N. Kakehashi, Y. Suzuki, Y. Iwasa, *J. Appl. Ecol.* **21**, 115 (1984)]. Certainly for some real systems, one or more of these assumptions will be oversimplifications.
14. B. A. Hawkins and P. Gross, *Am. Nat.*, in press.
15. R. R. Askew, *Parasitic Insects* (Heinemann, London, 1971); for theoretical model and other examples, see W. L. Hogarth and P. Diamond, *Am. Nat.* **124**, 552 (1984).
16. M. P. Hassell, J. H. Lawton, R. M. May, *J. Anim. Ecol.* **45**, 471 (1976).
17. T. R. E. Southwood and H. N. Comins, *ibid.*, p. 949.
18. Justification for the ranges and relationships of parameter values employed in this study can be found, for example, in (*7, 17*) and, for spatial heterogeneity, in M. P. Hassell and S. W. Pacala [*Philos. Trans. R. Soc. London Ser. B* **330**, 203 (1990)]. The ranges of parameter values explored in our study are (parameter [minimum, maximum]): $F[1, 10]$, $h[1, Q]$, $b[1, Q]$, $a[0.01, 1]$, $\eta[0, 40]$, $k[0.1, 10]$, $m[0, 50]$, $n[0, 50]$, $N_0[1, Q]$, $S_{j,0}[1, Q]$ (for all j), and sample size of host population [10, 10,000] (parameter Q acts as a scaling factor relative to other parameters).
19. The measure of diversity is standardized based on the propensity to sample parasitoid species in a fixed unit area of habitat, rather than on the sole basis of percentage parasitism. One of the shortcomings of this index is that it omits the quantification of those assemblages in which the host is too rare to meet the minimum size requirements of the sample (see Fig. 2B for an alternative measure of diversity, based on the number of parasitoid individuals per unit area). Even if the host is common enough to permit a standardized sample, then the diversity measure may still omit the rarest parasitoid species (in terms of relative frequency on the host species considered here). The full complement of parasitoid species can be assessed only if the host population is exhaustively sampled.
20. Only for $\alpha < 1/F$ did we observe cases in which there were either too few hosts to provide a standardized sample or cyclic populations; for $\alpha > 1/F$, changing the initial densities of specialist parasitoids and/or the host had no effect on the final diversity estimate. Cyclic systems generally occurred when specialist parasitoids were prominent in the competitive hierarchy.
21. The details of the shape of the diversity curve, especially for $\alpha < 1/F$, depend on the diversity index employed (see Fig. 2, A and B) and the ability of the parasitoid assemblage to exploit hosts that are not in the proportional refuge. Exploitation potential increases with the number of parasitoid species in the assemblage, their respective abilities to parasitize the host, for example, $\hat{G}_i\{N_t\}$, and smaller host carrying capacities, Q. For example, when the total parasitoid species pool is not sufficiently numerous, the diversity curve flattens (Fig. 2, A and B) such that maximal numbers of parasitoid species are found over a range of intermediate α. As the species pool decreases to still lower levels, eventually variation in diversity will all but disappear except for extremely high levels of refuge ($\alpha \rightarrow 1$). In assemblages dominated by generalist species, a sufficiently low exploitation potential can sometimes lead to alternatively stable equilibria for $\alpha < 1/F$, one yielding low diversity and the other high diversity.
22. The general argument that host concealment translates into a refuge from parasitism has been made recently in (*14*). For comparison with the diversity patterns generated by our model, hosts are classified by feeding-biology and ranked by increasing structural refuge [(*23, 26*; B. A. Hawkins and J. H. Lawton, *Nature* **326**, 788 (1987)]. For example, externally feeding folivores, being fully exposed, occupy no structural refuge, whereas rollers have a slight refuge within their shelters but remain susceptible to parasitoids searching for exophytic hosts and often leave their shelters for varying lengths of time to feed or construct new ones. Among endophytically feeding hosts, leaf miners receive some protection by being within plant tissues, but otherwise receive little physical protection from mines; gallers are better protected but provide visual cues to their presence (that is, their galls); and borers are both physically protected and well concealed. Root feeders occupy the most extensive refuge by being underground. It should be emphasized, therefore, that this ranking is a qualitative one and that variation in actual levels of proportional refuge between species within any single feeding class will tend to blur the ranking of the categories represented in Figs. 3 and 4.
23. S. B. Vinson and G. F. Iwantsch, *Annu. Rev. Entomol.* **21**, 109 (1980).
24. B. Shorrocks and J. Rosewell, *J. Anim. Ecol.* **55**, 527 (1986); in *The Organization of Communities: Past and Present*, J. H. R. Gee and P. S. Giller, Eds. (Blackwells, Oxford, 1987), pp. 29–51. A. R. Ives [*Ecol. Monogr.* **61**, 75 (1991)] has demonstrated a similar result for carrion flies.
25. B. A. Hawkins, *J. Anim. Ecol.* **57**, 137 (1988).
26. ______, *ibid.* **59**, 57 (1990).
27. ______, in *Hymenoptera and Biodiversity*, J. LaSalle and I. D. Gauld, Eds. (C. A. B. International Press, London, in press).
28. We thank T. M. Lewinsohn, H. C. J. Godfray, and M. P. Hassell for comments on the manuscript. We are especially grateful to J. H. Lawton and R. M. May for their encouragement and discussions during the course of the study. This work forms part of the program of the Natural Environmental Research Council's Centre for Population Biology at Silwood Park.

11 September 1991; accepted 8 January 1992

Neotropical Mammals and the Myth of Amazonian Biodiversity

MICHAEL A. MARES

Data were compiled on the distribution of mammal taxa (883 species, 242 genera, 45 families, and 10 orders) among South America's six major macrohabitats: lowland Amazon forest, western montane forests, Atlantic rain forest, upland semideciduous forest, southern mesophytic forest, and drylands. The drylands are the richest area in numbers of species supported and are more diverse than the other habitats, including the lowland Amazon rain forest, when endemics are considered. An analysis of number of endemic and nonendemic taxa versus size of area found a simple positive linear relationship: the drylands, almost twice as extensive as the Amazon lowlands, support more endemic taxa. Conservation plans that emphasize the wet tropics and fail to consider the drylands as special repositories of mammal diversity will be unable to preserve a significant number of novel taxa.

A GREAT DEAL OF CONTROVERSY HAS been focused on the suggestion that the biosphere is approaching a massive, human-induced extinction episode rivaling or surpassing the megaextinctions chronicled in the fossil record (*1*). There is evidence that Neotropical ecosystems, especially the lowland Amazon rain forest, contain an unusually rich array of species, whether vertebrates, invertebrates, or plants are considered (*2, 3*). Because tropical countries are primarily developing nations, efforts to preserve species have assumed importance in the international political arena (*4*); issues of environmental integrity have influenced government policies concerning economic development throughout the world.

Biologists have used the biodiversity issue to rally support for increased funding for research in the wet tropics (*5*), yet there are problems associated with arousing public concern with visions of doomed species. For one thing, data on which such negative scenarios are based may be incorrect (*6, 7*). Additionally, if species are disappearing at a rate below what has been suggested, the public could perceive biologists as alarmists, unnecessarily predicting a mass extinction—one that neither seems demonstrable with hard data nor ever seems to arrive.

In the literature dealing with the potential loss of diversity, at least one important question has yet to be posed: Is the tropical rain forest uncommonly diverse? Few investigators have examined organismal diversity in South America's deserts, grasslands, or scrublands (*8*). I report that when numbers of species and higher taxa of mammals are compared between the Amazon lowlands

---

Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma, Norman, OK 73019.