



A Global Experiment Under Way

HABITAT LOSS AND FRAGMENTATION ARE THE principal drivers of biodiversity loss, notably in the tropics (1). One of the most immediate results of fragmentation is the loss of top predators. As early as 12 years ago, evidence was provided for top-down effects of predator removal in tropical forest mammalian communities (2). Now, in their report “Ecological meltdown in predator-free forest fragments” (30 Nov., p. 1923), John Terborgh and colleagues have demonstrated that these effects percolate down to taxonomically diverse groups, affecting plant-herbivore dynamics in forest islands that resulted from dam construction in Venezuela. In the accompanying Perspective “Dammed experiments!” (30 Nov., p. 1847), Jared Diamond reminds us that these represent valuable “natural” experiments. Alternatives are more carefully controlled experiments, like the Biological Dynamics of Forest Fragments Project in the Brazilian Amazon, but they are also more costly and difficult to implement beyond a few areas.

Although these localized natural experiments are useful, a “natural” fragmentation experiment on a grand scale is possible because most biologically rich tropical forests retain less than 30% of their original extent (3). The Major Tropical Wilderness Areas of the Amazon, Congo, and New Guinea (4) could serve as controls. The impediment to the full use of the global experiment is deriving baseline biological and land use information over large areas, but we believe this limitation can now be overcome.

Over the last century, many now-fragmented landscapes were surveyed before fragmentation, and these data from museum collections are starting to become accessible in electronic format. With some incremental investment in transferring collection informa-

tion to databases, specimen accessibility could expand manifold (5). Species modeling efforts can complement such needs (6). Furthermore, emerging programs to undertake biological surveys and long-term ecological monitoring at unprecedented scales (7) are in the final stages of design or already producing needed biological information.

Other data that have become more acces-



Fragmented forest. This MODIS image, taken on 2 May 2001, shows various levels of forest fragmentation in Southern Amazon. The area is ~400 km across. Forest appears dark green, agriculture appears tan to light green, and clouds appear white. To the east (right) are isolated patches of remnant forest in an agricultural landscape. The large forest in the center of the image is the southern portion of the Kayapo Indigenous Area in Brazil.

sible, and more affordable, are remote sensing data sets necessary to identifying changes in land cover. We now have a 30-year archive of Landsat data to conduct wall-to-wall mapping of deforestation and precise patterns of fragmentation. Complementing these are near-real-time monitoring capabilities with daily observations from sensors such as MODIS (see the figure). Longer time series can be compiled with aerial photos that are distributed throughout many institutions and government agencies.

Applied at a pantropical scale, this framework can assist researchers in pinpointing appropriate areas to explore a wide range of questions. The grand-scale experiment is already under way, and answers to biodiversity challenges can

emerge before it’s too late for their application toward conservation. It’s now a question of resources, scientific wit, and a collaborative global research environment.

GUSTAVO A. B. DA FONSECA,^{1*} CLAUDE GASCON,²

MARC K. STEININGER,¹ THOMAS BROOKS,¹

RUSSELL A. MITTERMEIER,² THOMAS E. LACHER JR.^{1,3}

¹Center for Applied Biodiversity Science, ²Conservation International, 1919 M Street, NW, Suite 600, Washington, DC 20036, USA. ³Department of Wildlife and Fisheries Science, Texas A&M University, College Station, TX 77843, USA

*To whom correspondence should be addressed.

E-mail: g.fonseca@conservation.org

References and Notes

1. C. Gascon, B. Williamson, G. A. B. da Fonseca, *Science* **288**, 1356 (2000).
2. G. A. B. da Fonseca, J. G. Robinson, *Biol. Conserv.* **53**, 265 (1990).
3. N. Myers et al., *Nature* **403**, 853 (2000).
4. R. Mittermeier et al., *Conserv. Biol.* **12**, 516 (1998).
5. E. O. Wilson, *Science* **289**, 2279 (2000).
6. L. Boitani et al., *African Mammals Databank: A Database for the Conservation and Management of the African Mammals* (Istituto di Ecologia Applicata, Rome, 1999).
7. Examples of large-scale ecological monitoring projects include the Smithsonian Tropical Research Institute's field sites, the Costa Rican INBio inventories, the expanding International Long-Term Ecological Research Program, the All Species Foundation, and the recently announced Tropical Ecology, Assessment and Monitoring (TEAM) initiative to enable about 50 field stations in the tropics to monitor biodiversity (see <http://www.biodiversityscience.org>).

Modeling Macroscopic Patterns in Ecology

THE GOAL OF COMMUNITY ECOLOGY AND macroecology has long been to focus on the general processes that generate macroscopic patterns associated with abundance, diversity, and distribution within and across ecological systems (1–3). In the review “Neutral macroecology” (*Science's Compass*, 28 Sept., p. 2413), we disagree with Graham Bell that neutral models provide a general theory of biodiversity capable of “predicting the fundamental processes and patterns in community ecology,” and “that functional interpretations of [diversity] patterns must be reevaluated” (p. 2413). A priori “statistical fits” of a neutral model to empirical patterns are qualitative and are not based on quantitative predictions from first principles. As Bell notes, by choosing “the normal configuration” for values of each parameter of a neutral model, one can create patterns asso-

ciated with range size, abundance, and distribution—including patterns that imitate the real world. We urge caution in interpreting neutral model claims, as it is tempting to fiddle with parameter values to fit observed data and assert causation from pattern similarity. Ecology is rife with examples of disparate models claiming to describe similar distributions (3, 4) based on different mechanisms.

Bell's proposition to restructure community ecology and conservation biology around a neutral model excludes many important attributes of biological diversity. The fundamental assumption of a neutral model (co-occurring species have identical demographic characteristics) is violated in most ecological assemblages. Co-occurring species often differ in their ability to grow, reproduce, and disperse. Such variation reflects important phylogenetic differences and life history trade-offs (5). Even within diverse tropical forests, functional variation in fundamental demographic and life history attributes leads to structuring of local communities (6). Contrary to Bell's comment that there is little support for "local adaptation over moderate distances within a single habitat" (p. 2418), several studies have shown strong evidence for local adaptation, even within species with wide dispersal (7). Furthermore, the ability to grow, reproduce, and disperse varies across biotic and abiotic gradients (8). Species respond to environmental change in an individualistic fashion—their distribution and dynamics are not neutral, but instead are linked to physiological and ecological requirements (2, 9).

We also disagree with Bell that "null hypotheses based on randomization are not appropriate for evaluating ecological patterns that stem from species distribution, because local dispersal readily gives rise to spatial patterns" (p. 2418). Neutral models only enable testing of the difference between the observed pattern arising from unknown mechanisms and that produced by a random model. Null models, as Bell notes, do not specify demographic processes and therefore offer no mechanism of community structure—an observation that we be-

lieve applies to neutral models as well. With null models, it is assumed that demographic parameters and processes (or the results of these processes) are distributed randomly among taxa, unless otherwise constrained. Neutral models are special cases of null models, ones where the demographic processes are equal but constrained to fit observed data or assigned parameter values.

Despite these misgivings, the development of neutral models could yield important insights into ecological patterns and

3. S. P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton Univ. Press, Princeton, NJ, 2001).
4. J. Harte, in *Scaling in Biology*, J. H. Brown, G. B. West, Eds. (Cambridge Univ. Press, Cambridge, 2000), pp. 325–342.
5. E. L. Charnov, *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology* (Oxford Univ. Press, Oxford, 1993).
6. P. C. Jackson et al., *Oecologia* **101**, 197 (1995); J. Terborgh, R. B. Foster, P. Nunez, *Ecology* **77**, 561 (1996); B. J. Enquist, G. B. West, E. L. Charnov, J. H. Brown, *Nature* **401**, 907 (1999); M. N. Holbrook, J. L. Whitbeck, H. A. Mooney, in *Seasonally Dry Tropical Forests*, S. H. Bullock et al., Eds. (Cambridge Univ. Press, New York, 1995), pp. 243–270; R. Condit et al., *Science* **295**, 666 (2002).
7. J. B. Mitton, *Selection in Natural Populations* (Oxford Univ. Press, Oxford, 1997).
8. D. S. Wilson, *Ecology* **78**, 2018 (1997).
9. T. L. Root, *Ecology* **69**, 330 (1998).

Response

THE NEUTRAL THEORY OF COMMUNITY ecology does not have much in common with Hardy-Weinberg equilibrium, perhaps, but it does have a great deal in common with the neutral theory of population genetics. The two theories have a common goal, to explain the great diversity of ecologically similar organisms to be found in most natural populations and communities. The general principle they invoke is that the bulk of natural diversity arises from the existence of a large class of types, whether genotypes or species, that have very similar demographic properties. The core of the rebuttal by Enquist and co-authors is a comprehensive denial of the existence of this class, and therefore of the general applicability of the neutral theory. They give three chief reasons for this position.

First, species obviously differ in demography. Thus, some will have many offspring and others few, and so forth. The neutral model does not deal with these details, only with their consequence: essentially, the probability that one reproductive adult individual has given rise to another reproductive adult individual during a given period of time.

Second, there is strong evidence for local adaptation. So there is, but the issue does not hinge on the occurrence of local adaptation, but rather on its pervasive influence in determining local species composition and diversity. The functionalist point of view is that most species are specifically adapted to a particular subset of conditions within any given site, and that the balancing selection created in this way is primarily responsible for the maintenance of diversity. This is plausible on large geographical or ecological scales, but whether it is equally plausible at the smaller scales that we are usually concerned with is not as clear. The conditions for the maintenance of diversity in heterogeneous landscapes are strict (1).

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processes (3). In many ways, Bell's use of neutral models in macroecology is akin to the use of the Hardy-Weinberg model in population genetics (which assumes random mating, infinitely large population size, nonoverlapping generations, no natural selection, no mutation, no immigration or emigration, and so on). Although these assumptions rarely hold, the model nevertheless provides a heuristic framework to assess these often-unrealistic assumptions.

B. J. ENQUIST,^{1,2*} J. SANDERSON,² M. D. WEISER¹

¹Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA.

²Center for Applied Biodiversity Science, Conservation International, 1919 M Street, NW, Suite 600, Washington, DC 20036, USA

*To whom correspondence should be addressed.
E-mail: benquist@u.arizona.edu

References and Notes

1. R. H. MacArthur, *Geographical Ecology* (Princeton Univ. Press, Princeton, NJ, 1972).
2. J. H. Brown, *Macroecology* (Univ. of Chicago Press, Chicago, IL, 1995).

Letters to the Editor

Letters (~300 words) discuss material published in *Science* in the previous 6 months or issues of general interest. They can be submitted by e-mail (science_letters@aaas.org), the Web (www.letter2science.org), or regular mail (1200 New York Ave., NW, Washington, DC 20005, USA). Letters are not acknowledged upon receipt, nor are authors generally consulted before publication. Whether published in full or in part, letters are subject to editing for clarity and space.

Situations that meet these conditions can readily be contrived in laboratory microcosms (2), but whether they also hold—as a general explanation for the bulk of diversity—in natural communities at modest spatial scales remains to be proven. Well-documented instances of precise local adaptation are of great interest from many points of view, but they are not a refutation of the neutral model.

Third, growth, reproduction, and dispersal vary among sites. Although true, this is beside the point. Neutral theories of diversity assert the equivalence of species, not of sites.

Regarding the comments by Enquist *et al.* on null models, explanations of distribution and diversity fall into three categories. Random models attribute the patterns to the effect of chance alone; neutral models to chance and history; and functional models to chance, history, and selection. Either a random or a neutral model might supply the appropriate null hypothesis for a particular functional interpretation, but it is important to distinguish between them. Neutral models readily lead to highly nonrandom outcomes, such as the distribution of abundance among species (3) or the correlation of species distributions with environmental

factors (4). Random models are not based on dynamic processes such as local dispersal, do not give rise to realistic ecological patterns, and are of limited utility in evaluating functional interpretations.

The neutral theory is one of diversity; it is not a theory of processes such as ecological succession, just as the neutral theory of population genetics is not a theory of adaptation. Within its restricted realm, however, it is very successful, and its impressive ability to explain patterns that have puzzled ecologists for a century has not yet been challenged. This ability might merely reflect some unexpected statistical anomaly, as Enquist *et al.* suggest, but it also raises the exciting possibility of a conceptual unification of community ecology with population genetics, to form a general theory of variation and diversity extending from single-nucleotide polymorphism to plant community structure. This goal seems well worth striving toward.

GRAHAM BELL

Redpath Museum, McGill University, Montreal, Quebec, Canada H3A 2K6. E-mail: gbell2@po-box.mcgill.ca

References and Notes

1. J. Maynard Smith, R. Hoekstra, *Genet. Res.* **35**, 45 (1980).
2. R. Kassen, A. Buckling, G. Bell, P. Rainey, *Nature* **406**, 508 (2000).
3. S. P. Hubbell, in *Preparing for Global Change: a Mid-western Perspective*, G. R. Carmichael *et al.*, Eds. (Academic Publishing bv, Amsterdam, 1995), pp. 171–199; G. Bell, *Am. Nat.* **155**, 606 (2000); S. P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton Univ. Press, Princeton, NJ, 2001).
4. G. Bell, M. J. Lechowicz, M. J. Waterway, in *Integrating Ecology and Evolution in a Spatial Context*, J. Silvertown, J. Antonovics, Eds. (Blackwell Science, Oxford, 2001), pp. 117–135.

CORRECTIONS AND CLARIFICATIONS

NEWS OF THE WEEK: “Leukemia protein spurs gene silencing,” by J. Marx (8 Feb., p. 943). The name of researcher Jean-Pierre Issa, mentioned on p. 945, second column, was misspelled. Furthermore, his correct affiliation is with the University of Texas at MD Anderson Cancer Center in Houston.

NEWS OF THE WEEK: “Pulsars solve mystery of missing gas” by G. Schilling (19 Oct., p. 497). The paper by P. C. Freire *et al.* discussed in this article was erroneously stated to have been published in the 10 October 2001 issue of *Astrophysical Journal Letters*. The paper was published in the 20 August 2001 issue of the journal (vol. 557, pp. L105–108).