SCIENCE'S COMPASS

ments that deal with multiple incident carrier streams are also of interest. Such experiments would permit the investigation of exchange effects on the noise, which represent an explicit demonstration that we deal with indistinguishable particles. If carriers were incident from both contacts 1 and 3, the conductor in panel B of the figure would be noiseless in the zero-temperature limit. All current correlations would then vanish. A first experiment in this direction has recently been performed by Liu et al. (8), who demonstrated that in the presence of currents incident from two contacts the noise is reduced below the value that is measured if current is incident from one contact only.

In contrast to conductance, which can be specified in terms of transmission probabilities for one carrier to traverse the conductor from one contact to another, exchange effects in noise correlations are specified by scattering amplitudes with an amplitude and a phase (4). The conductor in panel C of the figure is one possible experimental setup that would permit demonstration of the phase sensitivity of exchange effects. This conductor is an electrical equivalent of an optical interferometer. The contacts connect to a central orbit that circles the outer wall of the conductor. In the presence of two incident currents, the exchange effect in one of the current-current correlations is a function of the phase of the periodic orbit; depending on this phase, the exchange effect either vanishes or is as large as the noise of the two currents added classically.

Current-current correlations are a sensitive probe of the statistical properties of a system. In systems that are composed of superconductors and normal conductors (such as metals or semiconductors), it has been predicted that the correlation functions can change sign because of strong electron-hole correlations resulting from reflections at the interface between the superconductor and the other material (9). Measurements of current-current correlations in the fractional quantum Hall regime should be even more interesting. Current theoretical understanding attributes such states to quasi-particles that are very unconventional in that they are neither fermions nor bosons. In contrast to the integer quantum Hall effect, which can be explained by using the edge states described above, our understanding of the fractional quantum Hall effect is rather limited. Presently, it is not even clear whether noise should be generated at the interface of a normal contact and a two-dimensional electron gas (10) in a fractional quantized

Optical experiments have reached a particularly high level of sophistication since sources producing twin pairs of photons have become available. Sources that produce such entangled states (coherent superpositions of multiparticle states) of electrons are not yet available but are clearly desirable for noise experiments and also in the emerging field of quantum computing. The Pauli principle works to suppress noise. But its effectiveness can be overcome in systems far from equilibrium if collective electron motion becomes important. This was demonstrated in recent experiments on resonant tunneling structures (11) and has been investigated theoretically (12). Yet another interesting avenue is the connection of shot noise and the dephasing of quantum coherent electron transport (13). These considerations promise interesting future experiments on electron coherence and statistical effects in a wide variety of systems.

PERSPECTIVES: ECOLOGY

References and Notes

- 1. R. Hanbury Brown and R. Q. Twiss, Philos. Mag., Ser. 7 45, 663 (1954); R. Loudon, in Disorder in Condensed Matter Physics, J. A. Blackman and J. Taguena, Eds. (Clarendon, Oxford, 1991), pp. 441-455
- M. Henny et al., Science 284, 296 (1999).
- 3. W. D. Oliver, J. Kim, R. C. Liu, Y. Yamamoto, ibid., p. 299
- 4. M. Büttiker, Phys. Rev. Lett. 65, 2901 (1990); Phys. Rev. B 46, 12485 (1992).
- 5. T. Martin and R. Landauer, Phys. Rev. B 45, 1742 (1992).
- 6. For a perspective on the early noise measurements in mesoscopic conductors, we refer the reader to L. Kouwenhoven [Science 271, 1689 (1996)]
- 7. B. J. van Wees et al., Phys. Rev. Lett. 62, 1181 (1989); Komiyama and H. Hirai, Phys. Rev. B 54, 2067 . (1996).
- R. Liu et al., Nature **391**, 263 (1998).
 M. P. Anantram and S. Datta, *Phys. Rev. B* **53**, 16390 (1996).
- 10. C. L. Kane and M. P. A. Fisher, ibid. 52, 17393 (1995). 11. G. lannaccone et al., Phys. Rev. Lett. 80, 1054 (1998);
- V.V. Kuznetsov et al., Phys. Rev. B 58, R10159 (1998). 12. Y. M. Blanter and M. Büttiker, ibid., in press (available
- at http://xxx.lanl.gov/abs/cond-mat/9807254) 13. E. Buks et al., Nature 391, 871 (1998); M. Büttiker and A. M. Martin, http://xxx.lanl.gov/abs/condmat/9902320

Heeding the Warning in **Biodiversity's Basic Law**

Michael L. Rosenzweig

■he great 19th-century scientist Alexander von Humboldt gave ecology its oldest law: Larger areas harbor more species than smaller ones (1). Even back then, naturalists were quick to perceive the mathematical regularity of this

Enhanced online at www.sciencemag.org/cgi/ content/full/284/5412/276

species-area relationship (2). For most of the 20th century ecologists have keenly stud-

ied this relationship convinced that, in finding the explanation for it, they would uncover the key to understanding and predicting Earth's biodiversity (3). The report by Harte et al. on page 334 of this issue (4) is an elegant contribution to the onslaught of recent advances leading toward an explanation. The puzzle of the species-area relationship is now in full retreat. Admittedly, we have not yet achieved its unconditional surrender. But, given the mass extinction of plant and animal species that human culture and population growth have set in motion, our progress toward that surrender comes just in the nick of time.

Debate about the mathematical form taken by the species-area relationship began about 1920 and still continues (5). The

form $S = CA^{z}$ (the number of species found in a sampled patch of area A is a constant power of A) proved a convenient mathematical equation for reporting, organizing, and analyzing this relationship. No one claimed to understand why. Then Fisher connected the problem of species diversity to that of species abundance (6). Preston soon introduced and championed the lognormal form of species-abundance distribution (7). He also supplied a flawed, although enchanting, proof that a certain type of log-normal distribution implied a species-area relationship that came quite close to $S = CA^z$ with z about 0.26 (a number close to values derived from data sets of island plant and animal diversity) (8). May's flourishes and extensions (9) to Preston's work were so impressive that they made us believe, for a while, that we could finally tuck this chapter of ecology into its bed for good.

But the data would not cooperate (10). Species-area relationships with z-values strikingly different from 0.26 kept popping up (11). Worse still, these z-values had a definite pattern: Larger scales of space and time generated species-area relationships with larger z-values.

The theoretical bubble burst too (12). It had relied on a tacit assumption of self-similarity among species (the abundance distribution of complete sets of species is the same regardless of the spatial scale at which

The author is editor-in-chief of Evolutionary Ecology Research and is in the Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721–0088. USA. E-mail: scarab@u.arizona.edu

it is measured). But log-normal abundance distributions at one scale of space turn out not to be log-normal at any other! May's proof also tacitly required that there be no relationship between the size of a species' geographical range and its population density. But species that are abundant where they are found, tend to occur in more places than those with sparse populations (13).

Harte et al. turn the problem on its head. They do not rely on the lognormal (or any other) distribution. They assume only self-similarity. From that they deduce $S = CA^{z}$. They also deduce an abundance distribution more realistically heavy-tailed than the sacrosanct log-normal. (Heavy-tailed distributions imply that many improbable events will occur. In this case, these events are the appearance of scarce species.) The many scarce species in those heavy tails are precisely what make the tropics and other rich biotas so diverse. The log-normal abundance distribution simply does not fit.

I am less sanguine than Harte et al. about the chance that self-similarity will hold true over the entire range of spatial scales. As they admit. some data do not fit, the diversities of tropical freshwater fishes in different biogeographical provinces, for example. The cumulative diversities of these fishes have a zof 1.36, and future discoveries of new species will change that value very little (14). Yet, the mathematical maximum allowed by the Harte model is 1.

The difficulty may arise because diversity is determined by different processes at different scales (3, 15). The largest scale is the biological province, defined as an area in which most of the species originated internally (by the relatively slow process of speciation). The diversity of provinces depends on their rates of speciation. The diversity of islands depends on the rates at which species colonize the islands from a nearby province and then become extinct on the island. And the diversity of provincial patches depends on the number of habitats they contain and the rate at which individuals move in to shore up the ever-declining local sink populations. (Sink populations are those that cannot reproduce fast enough to replace themselves.)

If diversity is controlled by such different processes at different scales, is it fair to expect a single model to predict diversity at all scales? I suspect that Harte et al. have cracked the problem just for traditional species-area relationships, the areas of which are cumulative patches within a sin-

SCIENCE'S COMPASS



Losing biodiversity. The relationship between the area of land and the number of species it supports (larger areas support more species than smaller areas) is called the species-area relationship (SPAR). Because humans have expropriated 95% of Earth's surface from other species, life faces a mass extinction in three phases. After a decline in species diversity in a provincial area, a biota first loses all of its endemic species, that is, those populations whose habitat has been entirely expropriated (phase 1). Then a provincial area loses all of those species that become sink species (those unable to reproduce fast enough to replace themselves) as a result of the area's decline (phase 2). Finally, the provincial area descends to a new lower steady state because its accidental losses fail to be replaced fast enough to maintain the old diversity. In each case, we can predict the loss of diversity by using the species-area relationship of the appropriate scale.

> gle province. That is a major achievement, but it leaves open the question of possible explanations for other kinds of species-area relationships (such as interprovincial and inter-island) as well as the question of why diversity is a self-similar property of area within biogeographical provinces.

> We can use our increased understanding of species-area relationships to help conserve species. Most conservation efforts concentrate on saving habitats rather than area. But if, in the long run, area is the true prime mover on which diversity depends, we should reevaluate how little emphasis we place on it.

> Species-area relationships suggest that because we have wrested away some 95% of Earth's surface from the world of nature (16), life faces a mass extinction in three phases (see the figure). Phase 1 (predicted by equation 7 of the Harte study) is the loss of endemic species, that is, all species whose entire range of habitat disappears into human hands. This loss is modest but instantaneous. Phase 2 is relaxation to an island state owing to the loss of the sink species, that is, those species whose remaining populations are all sink populations. Together, these two phases will cost Earth about half of its plant and animal species (3). Modeling the rates of loss is a significant challenge, but data suggest that the loss will take centuries (17). No wonder some complain that we have not seen enough extinction to confirm the importance

of area for the maintenance of diversity. But they should rejoice at the gift of all that time---time to ameliorate the damage.

Loss of the sink species will not end the story. There will be a third phase of extinction. Diversity will relax to a new sustainable steady state. If we continue to exclude nature from 95% of Earth's terrestrial surface, species-area relationships teach us that the new steady state will only be about 5% of current diversity (3).

Phase 3 depends upon rare accidents that happen within the same time scale as speciation. So phase 3 may take tens of thousands of years to complete. But such accidents include the introduction or evolution of new diseases, or the total disappearance of habitat owing to climate change. Thus, we may not have as much time as one would have predicted from considering only the science of species-area relationships.

The problem suggests its own solution. The land remains. Share it more generously with other species (18). Do the research to discover gentler ways to occupy the land, ways to reconcile our uses with those of the many species that also need it to sustain life.

References and Notes

- 1. F. H. A. von Humboldt, Essai sur la geographie des plantes [Sherborn Fund facsimile, no. 1, Society for the Bibliography of Natural History, London, 1959 (1807)].
- J. G. Dony, Watsonia 5, 377 (1963).
- 3. M. L. Rosenzweig, Species Diversity in Space and Time (Cambridge Univ. Press, Cambridge, 1995)
- J. Harte, A. Kinzig, J. L. Green, Science 284, 334 (1999). O. Arrhenius, J. Ecol. 9, 95 (1921); H. A. Gleason, Ecology 3, 158 (1922); C. B. Williams, Patterns in the Balance of Nature (Academic Press, London, 1964); G. Sugihara, Am. Nat. 117, 790 (1981); B. D. Coleman, M. A. Mares, M. R. Willig, Y. Hsieh, *Écology* **63**, 1121 (1982); K. A. McGuinness, *Biol. Rev.* **59**, 423 (1984); M. R. Williams, Ecology 76, 2607 (1995) and many others
- 6. R. A. Fisher, A. S. Corbet, C. B. Williams, J. Anim. Ecol. 12, 42 (1943).
- F. W. Preston, *Ecology* 29, 254 (1948).
 _____, *ibid.* 43, 185 (1962); *ibid.*, p. 410.
- 9. R. M. May, in Ecology and Evolution of Communities, M. L. Cody and J. M. Diamond, Eds. (Belknap of Harvard Univ. Press, Cambridge, MA, 1975), pp. 81-120. 10. R. G. Hughes, Am. Nat. 128, 879 (1986).
- 11. E. F. Connor and E. D. McCoy, ibid. 113, 791 (1979).
- 12. W. A. Leitner and M. L. Rosenzweig, Oikos 79, 503
- (1997) I Hanski, J. Kouki, A. Halkka, in Species Diversity in Ecological Communities, R. E. Ricklefs and D. Schluter, Eds. (Univ. of Chicago Press, Chicago IL, 1993), pp. 108–116; K. J. Gaston, Oikos 76, 211 (1996).
- 14. Data from tropical Southeast Asia, Amazon basin, Congo basin, and Madagascar in [M. L. Rosenzweig and E. A. Sandlin, *Oikos* **80**, 172 (1997)]. Different tropical continents are scarce, so there are only four points. Nevertheless, the fit is quite close: $R^2 = 0.999$ for the regression through the four points.
- R. D. Holt, in Species Diversity in Ecological Commu-nities, R. E. Ricklefs and D. Schluter, Eds. (Univ. of Chicago Press, Chicago IL, 1993), pp. 77–88; M. W. Palmer and P. S. White, *Am. Nat.* **144**, 717 (1994). 16. M. Huston, Science 262, 1676 (1993).
- B. A. Wilcox, in M. E. Soulé and B. A. Wilcox, Eds., Con-17. servation Biology (Sinauer, Sunderland, MA, 1980), pp. 95–117; S. L. Pimm and T. M. Brooks, in *The Sixth* Extinction: How Large, How Soon, and Where?, P. H. Raven and E. O. Wilson, Eds. (National Academy Press, Washington, DC, in press).
- 18. M. L. Rosenzweig, Eco-Health: News and Views 2 (no. 1), 4 (1996).