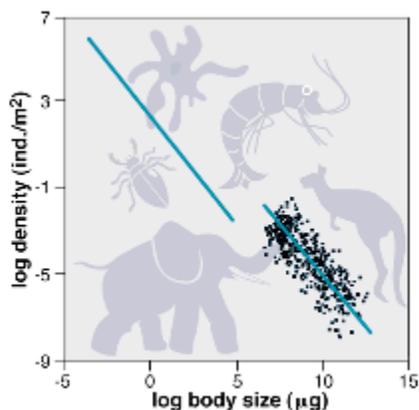


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Invariants, Scaling Laws, and Ecological Complexity

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Life on Earth has diversified to occupy every kind of environment. Within these environments, diffuse associations of organisms form ecological communities. To understand the structure and dynamics of these communities, ecologists have adopted two major approaches. The experimental, microscopic approach emphasizes the highly variable and idiosyncratic nature of communities (1). The alternative macroscopic, nonexperimental (macroecology) approach emphasizes the existence of statistical patterns in the structure of communities that seemingly reflect the operation of general principles or natural laws (2). The report by Schmid *et al.* (3) on page 1557 of this issue sheds new light on a well-known and much debated macroecological pattern: the relation between population density and body size. These investigators thoroughly analyzed the relation between population density and body size in more than 400 invertebrate species--from insects to tiny single-cell organisms (such as the testate amoeba, which weighs about 10^{-4} μg)--in two local stream communities, one in Austria and the other in Wales. Their study is among the first to take a statistically rigorous look at the density-body mass relation across a large number of invertebrate taxa that includes microorganisms. They demonstrate that the inverse scaling law (population density decreases as body size increases) holds across all the taxonomic groups and that it is not limited by energy requirements. (Given a fixed amount of available energy, species of small body size that require less energy to survive should be more abundant than larger species.)



Big is beautiful but lonely. The inverse scaling relation between population density and body size. Small organisms typically attain greater population densities than do larger species. The upper line describes the relation between population density and body size fitted to data collected from two totally separate local stream communities (3), where organisms ranged in size from insects to the testate amoeba. For comparison, the bottom line depicts the same relation for all mammals worldwide (8). Lines are fitted with the OLS-bisector method, and in both cases they have a slope or regression coefficient that is not different from -1.0.

As a colleague of mine likes to put it, the diversity of life is largely a matter of size. And he is right, for life spans more than 21 orders of magnitude. Macroecologists are well aware of this diversity and have commonly searched for empirical statistical patterns relating the size of organisms, usually expressed in mass units, with ecological and evolutionary traits (4). These relations take the form of a power law: $Y = Y_0 \times M^b$ where Y is the dependent variable (usually a physiological, ecological, or evolutionary attribute); Y_0 is a normalization constant; M is the independent variable, usually body mass; and b is the scaling exponent. These scaling relations have the valuable property of becoming linear after logarithmic transformation, and the scaling parameter b can be estimated as the slope of the regression between $\log Y$ and $\log M$. The scaling relation between population density and body mass has been the subject of intensive empirical research for more than 60 years, but, as yet, there is no consensus over its form, let alone the mechanisms that generate it (5).

The study by Schmid *et al.* (3) demonstrates that in local stream communities there is a strong negative scaling relation between population density and body size, in agreement with previous work in rocky intertidal habitats (6). Taken together, these findings make a strong case for the existence of a simple inverse relation between population density and body mass in local communities (see the figure). This is in contrast to the notion that polygonal relations--characterized by ample scatter restricted to a defined region of the population density-body mass plot--should be the common outcome at local scales (7). Furthermore, the thoroughness of Schmid *et al.*'s sampling methods makes the existence of sampling biases against small, rare species unlikely and also controls for artifacts that may arise from different census areas (5, 7).

The Schmid study also conveys the need for caution. To assess scaling relations in local ecological systems, the full diversity of the community must be represented together with carefully designed and standardized sampling schemes. The observed scatter in the relations reported by Schmid and co-workers suggests that if they had restricted their analysis to a smaller range of body sizes (by excluding the amoeba), they would have obtained a more polygonal and still negative but nonlinear scaling relation.

Compilation analyses of published data for closely related species worldwide (8) typically report that the slope of the relation between population density (D) and body mass (M) is about -0.75 using ordinary least squares (OLS) regression. Because metabolic rate (MR , an estimate of the energy required by an individual for the basic processes of living) increases with body mass raised to the 0.75 power, the scaling exponent of this relation has been taken as evidence that the abundance of species is limited by energetic requirements (8). Similarly, the total energy consumed by a species population per unit area (EU) can be assessed by multiplying the energy used by an average individual by the number of individuals per unit area. Thus, if both variables are related to body mass with similar exponents, but opposite sign, then the energy used by different species should be roughly equal and independent of body mass (that is, $EU = MR \times D \propto M^{0.75} \times M^{-0.75} \propto M^0$). This is the so-called "energy equivalence rule" (8). Hence,

depending on the estimated scaling exponents, larger, smaller, or none of the species use a disproportionate amount of the available energy within ecosystems. Although these kinds of algebraic operations have been questioned (9), the statistical issue of what is the best method to estimate scaling relations still remains contentious. Several studies have recommended alternatives to OLS regression, such as reduced major axis regression (RMA) (10), because both population density and body mass are subject to measurement error. Schmid and colleagues go one step further and apply a new method, the OLS-bisector: This method calculates the line that bisects the OLS (X versus Y) and OLS (Y versus X) best-fit lines. With this approach they demonstrate that the scaling exponent of population density is different from that of metabolic rate, and that the former varies across functional and taxonomic groups, implying that the pattern cannot be explained solely by the energy equivalence rule.

The OLS-bisector method is commonly used by astrophysicists and has been shown to outperform other approaches if both variables are subject to measurement error and it is not clear which variable should be treated as the independent and which as the dependent (11). The usual convention in allometric studies is to use body size as the independent variable (12). However, there is no way to logically prove the independent nature or causal role of body size (13) because body size and physiological or ecological traits do not evolve in isolation, but affect each other. In fact, plant ecologists have traditionally treated the sizes of individual plants as though they were determined by population density (the Thinning Law) (14).

The study of whole communities containing a wide array of taxonomic groups is a daunting task. Such an approach is badly needed, however, if we are to glean insights into the structure of ecological systems. The identification of invariant scaling relations as reported by Schmid *et al.* (3, 6) and, more generally, the existence of simple scaling laws (15) suggest that general principles underlie the complex organization of ecological systems.

References and Notes

1. J. M. Diamond and T. Case, *Community Ecology* (Harper and Row, New York, 1986); R. M. May, *Ecology* **67**, 1115 (1986); J. H. Lawton, *Oikos* **84**, 177 (1999).
2. J. H. Brown, *Macroecology* (Univ. of Chicago Press, Chicago, IL, 1995)[[publisher's information](#)]; B. A. Maurer, *Untangling Ecological Complexity* (Univ. of Chicago Press, Chicago, IL, 1998)[[publisher's information](#)]; J. H. Brown, *Oikos* **87**, 3 (1999).
3. P. E. Schmid, M. Tokeshi, J. M. Schmid-Araya, *Science* **289**, [1557](#) (2000).
4. J. T. Bonner, *The Evolution of Complexity* (Princeton Univ. Press, Princeton, NJ, 1988); P. Yodzis and S. Innes, *Am. Nat.* **139**, 1151 (1992); J. H. Brown, P. A. Marquet, M. L. Taper, *Am. Nat.* **142**, 573 (1993); T. M. Blackburn and K. J. Gaston, *Trends Ecol. Evol.* **9**, 471 (1994); E. Siemann, D. Tilman, J. Haarstad, *Nature* **380**, 704 (1996); B. J. Enquist *et al.*, *Nature* **401**, 907 (1999).
5. T. M. Blackburn and K. J. Gaston, *J. Anim. Ecol.* **66**, 233 (1997).
6. P. A. Marquet, S. A. Navarrete, J. C. Castilla, *Science* **250**, 1125 (1990).

7. J. H. Lawton, *Oikos* **55**, 429 (1989); J. H. Lawton, *Philos. Trans. R. Soc. London Ser. B* **330**, 283 (1990).
8. J. Damuth, *Nature* **290**, 699 (1981); J. Damuth, *Biol. J. Linn. Soc.* **31**, 193 (1987); J. Damuth, *Nature* **351**, 268 (1991).
9. P. A. Marquet, S. A. Navarrete, J. C. Castilla, *J. Anim. Ecol.* **64**, 325 (1995); R. G. Medel, F. Bozinovic, F. F. Novoa, *Am. Nat.* **145**, 154.
10. M. LaBarbera, *Annu. Rev. Ecol. Syst.* **20**, 97 (1989); D. Griffiths, *J. Anim. Ecol.* **61**, 307 (1992).
11. G. J. Babu and E. D. Feigelson, *Commun. Stat. Simulation* **21**, 533 (1992).
12. R. H. Peters, *The Ecological Implications of Body Size* (Cambridge Univ. Press, Cambridge, 1983); W. A. Calder III, *Size, Function and Life History* (Harvard Univ. Press, Cambridge, MA, 1984); K. Schmidt-Neilsen, *Scaling, Why Is Animal Size So Important?* (Cambridge Univ. Press, Cambridge, 1984).
13. M. L. Taper and P. A. Marquet, *Am. Nat.* **147**, 1072 (1996).
14. B. J. Enquist, J. H. Brown, G. B. West, *Nature* **395**, 163 (1998).
15. T. H. Keitt and P. A. Marquet, *J. Theor. Biol.* **182**, 161 (1996); T. H. Keitt and H. E. Stanley, *Nature* **393**, 257 (1998); J. Harte, A. Kinzig, J. Green, *Science* **284**, 334 (1999)[[334](#)]; M. A. Ritchie and H. Olf, *Nature* **400**, 557 (1999)[[Medline](#)]; G. B. West, J. H. Brown, B. J. Enquist, *Science* **284**, 1677 (1999)[[1677](#)]; J. H. Brown and G. B. West, *Scaling in Biology* (Oxford Univ. Press, Oxford, UK 2000)[[publisher's information](#)].
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