CC/NUMBER 1
JANUARY 1, 1990

This Week's Citation Classic®

Connor E F & McCoy E D. The statistics and biology of the species-area relationship. *Amer. Naturalist* 113:791-833, 1979.
[Department of Biological Science, Florida State University, Tallahassee, FL]

The number of species found on an island, in a woodlot, on an individual plant, on a harbor piling, in a county, or in virtually any circumscribed region increases as a function of the area or size of that region. Three biological mechanisms operating simultaneously underlie this pattern. The statistical description of this pattern yields parameters that are of biological significance only when comparing the species richness of regions of different areas or sizes. [The *SCI*® indicates that this paper has been cited in over 235 publications.]

Species-Area Relationships—10 Years After

Edward F. Connor
Department of Environmental Sciences
University of Virginia
Charlottesville, VA 22903
and
Earl D. McCoy
Department of Biology
University of South Florida
Tampa, FL 33620

May 8, 1989

Our curiosity about the statistics and biology of species-area relationships grew out of our interest in another geographical pattern, latitudinal gradients in species richness. We were both young graduate students searching for ideas that our professors thought worth pursuing for thesis projects. We were puzzled by a report by J.W. Wilson III[1] that the mammals of North America did not exhibit the ubiquitously observed decline in species richness at higher latitudes. After reanalyzing Wilson's data, we were surprised to observe that the species richness of mammals was inversely correlated with the decline in land area that occurs in the low latitude regions of North America. In essence it was due to a species-area relationship. This initial observation led us to collect and reanalyze a large sample of published studies reporting species-area relationships and to collect more data to test for species-area relationships.

When we outlined the idea for this review to one of our professors who edited a journal but was noted to disdain anyone's ideas but his own, he offered to publish our review within six months of receipt. We were amused and set about a project that we completed and submitted two years later. G.C. Williams, then editor of the *American Naturalist*, warned us that if our paper was accepted for publication we would be required to pay at least half of the page charges, about $1,000, because it was so long—a comforting note to graduate students supported on generous $2,500 teaching assistantships. Fortunately, when our paper was accepted, our department chairman, A. Gib deBusk, volunteered to pay the page charges. Neither of us used this project for our thesis, and we returned later to the problem of latitudinal gradients in the species richness of the mammals of North America.[2]

The observation of species-area relationships dates from 1835 and the statistical description of them from 1921. However, it was the proposition of the "equilibrium theory of island biogeography" by F.W. Preston[3] and R.H. MacArthur and E.O. Wilson[4] in the 1960s that led to an explosion of interest in the species-area relationship. Much of our review on the species-area relationship focused on its underlying biological causes and on the biological interpretation of the parameters of its statistical description. We implicated three mechanisms, habitat diversity, area *per se*, and passive sampling, as possibly causing any given species-area relationship, and we suggested that the three were not mutually exclusive. We also challenged the biological interpretation of the statistical slope and intercept parameters, suggesting they were merely fitted constants of use only when comparing species richness from regions with different area.[5,6]

In one respect our review became the "last word" on species-area relationships because it coincided with a dramatic reduction in the publication of individual species-area studies. Most authors now appear to think of factoring out the effect of area as a routine first step in analyzing species richness patterns, and few assign much biological significance to the particular shape of a species-area curve. Research continues on the mechanisms underlying species-area relationships, and the use of species-area curves as guides in designing nature reserves is still hotly debated.[7] The species-area relationship remains a useful generalization, not a puzzle.

1. **Wilson J W.** Analytical zoogeography of North American mammals. *Evolution* 28:124-40, 1974. (Cited 20 times.)
2. **McCoy E D & Connor E F.** Latitudinal gradients in the species diversity of North American mammals. *Evolution* 34:193-203, 1980. (Cited 10 times.)
3. **Preston F W.** Time and space and variation of species. *Ecology* 41:611-27, 1960. (Cited 50 times.)
4. **MacArthur R H & Wilson E O.** *The theory of island biogeography*. Princeton, NJ: Princeton University Press, 1967. 203 p. (Cited 1,940 times.) [See also: **Wilson E O.** Citation Classic. *Current Contents/Agriculture, Biology & Environmental Sciences* 19(36):14, 5 September 1988.]
5. **Sugihara G.** S=CA^z, z=¼: a reply to Connor and McCoy. *Amer. Naturalist* 117:790-3, 1981. (Cited 30 times.)
6. **Connor E F, McCoy E D & Cosby B J.** Model discrimination and expected slope values in species-area studies. *Amer. Naturalist* 122:789-96, 1983. (Cited 10 times.)
7. **Zimmerman B L & Bierregaard R O.** Relevance of the equilibrium theory of island biogeography and species-area relations to conservation with a case from Amazonia. *J. Biogeography* 13:133-43, 1986. (Cited 10 times.)

IA-16