For over a century, ecologists have been captivated by the tendency for number of species within a taxonomic group to increase with island area. This “species–area relationship” has been found for a broad range of organisms in numerous archipelagoes around the world. A partial list of studies demonstrating the relationship includes land plants on the Galápagos (Fig. 1) and Aleutian Islands; insects on the Tuscan Islands and on subantarctic islands; reptiles on islands in the Gulf of California and in the West Indies; birds on the Canary, Solomon, and Aegian Islands; and mammals on islands in the Philippines and North American Great Lakes. Although most studies are of higher organisms, even protozoans and diatoms have shown the relationship. To explain the occurrence of the species–area relationship, ecologists have proposed several hypotheses.
on causal mechanisms, which shed light on the processes that structure biological communities. Conservation biologists have applied the relationship to the design of nature reserves.

**STATISTICAL MODELS**

The species–area relationship can be estimated statistically using the power equation

\[ S = k A^z \] (1)

where \( S \) = number of species, \( A \) = area of island, and \( k \) and \( z \) are fitted parameters. Logarithmic transformation of both sides of the power equation yields the linear equation

\[ \log S = \log k + z \log A \] (2)

in which \( z \) is the slope of the estimated species–area relationship (i.e., the rate of increase of \( \log S \) with \( \log A \)). Because the scales are logarithmic, the \( z \)-value is independent of scale, allowing comparisons between different studies even when the units for area are different. A second equation, with \( S \) instead of \( \log S \) in Equation 2, is often used instead.

Log-transformed data on number of land plant species and area for the Galápagos Islands (Fig. 1, bottom) show a positive linear relationship with a slope (\( z \)-value) of 0.33. Similarly, many other studies have found that the data fit the log-log model with \( z \)-values usually ranging from 0.20 to 0.40. Preston developed a mathematical explanation for the prevalence of the linear log-log relationship, with specific assumptions about the distribution of species abundances and other biological processes, in which the \( z \)-value is expected to be approximately 0.27. However, a detailed analysis of 100 studies by Connor and McCoy showed that the data often fit other statistical models just as well or better, suggesting that biological interpretation of parameters in statistical models should be made cautiously.

**WHY DOES THE NUMBER OF SPECIES INCREASE WITH ISLAND AREA?**

Although the species–area relationship is one of the surest generalizations in ecology, there has been much debate on the causal factors and processes. There are six major hypotheses, as follows.

**Random Sampling**

Assuming that the individuals on a given island are a random sample from a nearby mainland or other source containing all species, and larger islands contain more individuals, then the number of species should increase with island area. An analogy would be a bowl of colored marbles with ten marbles of each of ten different colors. The larger the handful of marbles you take, the more different colors you will get on average. This simple explanation may serve as a null model to compare with the other five hypotheses, all of which incorporate biological processes.

**Larger Populations and Less Extinction on Larger Islands**

The hypothesis that populations are larger on larger islands, implying lower extinction rates, is an integral part of the equilibrium theory of island biogeography developed by MacArthur and Wilson in 1964. According to this theory, the number of species present on an island is determined by the dynamic equilibrium between the rate of immigration of species not already on the island from a source pool and the rate of extinction of species already on the island (Fig. 2A). Because larger islands...
contain more individuals (larger population size) in each species, and extinction rate is inversely proportional to population size, extinction rate of species on small islands is higher than on large islands, so the equilibrium number of species is positively related to island area. In 1976 Simberloff provided experimental evidence for this hypothesis by showing that the number of species on mangrove islets decreased when he reduced the area of islets. In addition to the area effect, the equilibrium theory contains a distance effect; immigration rates are higher for islands near the source pool than for those farther away (Fig. 2B).

Larger Interception Area and More Immigration on Larger Islands
In addition to the lower extinction rate in the equilibrium model, a larger island may also be a bigger “target” for colonists; this causes the immigration curve of a large island to be higher than that of a small island, thereby increasing the equilibrium for the large island.

Higher Habitat Diversity on Larger Islands
Because the number of different types of habitats may increase with island area and different species often occur in different habitats, more species occur on larger islands. Hence, the species-area relationship may be indirect via the positive effect of area on habitat diversity. This hypothesis is most popular among ecologists familiar with the natural histories of the species in their studies. Early on, Watson found that habitat diversity was a better predictor of Aegean bird species number than by area. Very recently, Morrison found that the number of ant species on islets in the Bahamas was predicted by number of land plants species better than area; in this case, different plant species may serve as different types of habitats or provide different types of food resources for ants. Returning to Galápagos land plants, Hamilton and collaborators showed in 1964 that elevation (a proxy for habitat diversity) was a better predictor of number of species than was area.

Lower Abiotic Disturbance on Larger Islands
The impact of abiotic disturbances, such as hurricanes and tsunamis, may be more devastating on small islands than on large islands, exterminating species mostly on the former and thereby causing the positive species-area relationship. Such an effect could go well beyond the effect of population size on extinction, as equivalently sized populations could be more vulnerable on smaller islands. Whittaker pointed out that such disturbances can affect island communities for decades or even centuries, during which time species would not be at a dynamic equilibrium as in the MacArthur–Wilson model. In addition to the effect of episodic major disturbances, chronic non-catastrophic disturbances, such as wind and salt spray, may affect small islands more than large ones because of the greater perimeter-area ratio on small islands. Only species that can tolerate these harsh conditions could persist on small islands.

Greater Speciation on Larger Islands
The larger the island, the more likely that geographic barriers exist that cause isolation between viable subpopulations of a species; this can lead to allopatric speciation. The effect may be geometric, as the opportunity for speciation is itself proportional to species number, causing an especially high species–area slope.

Lomolino’s Combined Model
Lomolino proposed in 2000 a general model for the species-area relationship that integrates disturbance and equilibrium dynamics along with speciation on islands. In this model the species-area relationship has three regions (Fig. 3): (1) On small islands, the stochastic effects of disturbances are predominant, making the relationship between number of species and island area variable and unpredictable (an example is given in the later discussion of spiders in the Bahamas). (2) On medium to large islands, the deterministic effects of area on extinction/immigration and habitat diversity dominate, and number of species increases at a decreasing rate as the number of species in the source pool is approached. (3) The largest islands contain barriers isolating species populations, leading to allopatric speciation. Losos and Schluter assessed the speciation component for Anolis lizards of the West Indies. For these relatively poor dispersers, the sharp increase in the species–area slope due to speciation obliterates the flattening portion (region 2) of Lomolino’s model.
ECOLOGICAL CORRELATES OF VARIATION IN THE SPECIES–AREA SLOPE

Comparisons among different kinds of organisms have revealed substantial variation in the slope of the species–area relationship. Wright showed that on islands in the West Indies, the slope was greater for non-flying mammals than for bats or birds, suggesting that dispersal ability influences the relationship. A plausible explanation is that islands are more isolated for species with low dispersal ability, so most of them do not occur on small islands, whereas species with high dispersal ability are frequently found on small islands because their immigration rates are high even though they may not persist for long. Schoener suggested that $z$-values should be greater for species occurring at low density (e.g., territorial carnivores) than for those occurring at high density because the low-density species can only persist on larger islands. Holt and collaborators developed a mathematical model predicting that the $z$-value for species at the top of the food chain is higher than for species in lower trophic levels.

SPIDERS ON BAHAMIAN ISLANDS

Studies of web spiders occurring on islands in the Bahamas by Schoener and Spiller illustrate the species–area relationship and address several of the issues discussed above (Fig. 4). Complete censuses of all web spiders occurring over the entire areas of 64 islands were conducted annually over a ten-year period. Number of species (mean over time) was positively correlated with island area for four reasons. First, larger islands tended to have larger populations, which in turn had lower extinction rates than did small populations, increasing their number of species. Second, larger islands have a higher immigration rate: the “target effect.” Third, some species are habitat generalists (e.g., Argiope argentata), occurring in areas with high or low vegetation, whereas others are more specialized (e.g., Gasteracantha cancriformis), living in only high vegetation (Fig. 5). Small islands tend to have only low vegetation, whereas large islands contain areas with both low and high vegetation. Therefore, only generalists occur on small islands, whereas both generalists and specialists occur on large islands with more types of habitats. Fourth, tropical storms can affect smaller islands more drastically: During several recent hurricanes, smaller Bahamian islands, which are lower, were completely inundated by high water, apparently killing all spiders. Note that variation in the numbers of spider species on small islands is relatively high as in Lomolino’s model. Another factor that can affect number of species is the presence of lizards, which are major predators of spiders and which occurred on about half of the study islands: Islands with lizards tended to have fewer spider species (Fig. 6). This “lizard effect” is more apparent for larger islands than for smaller islands, and the slope of the species–area relationship is greater for islands without lizards (Fig. 7). Hence, the $z$-value is greater for islands without lizards, on which spiders occupy a higher level in the food web, as in Holt’s model.
THE DESIGN OF NATURE RESERVES

In addition to “true islands” (bodies of land surrounded by water), the species–area relationship has been well documented for many types of “island analogues” (patches of suitable habitat for species isolated by unsuitable habitat) on mainlands. Knowledge of the factors that shape the species–area relationship can be used to evaluate different strategies for designing nature reserves that maintain the highest number of species. Of course, the ideal strategy would be to have many huge preserves, but this may not be feasible. Hence, the problem that conservation biologists have pondered is whether one large reserve or several small reserves with the same total area is better. The answer to this question, sometimes referred to as the SLOSS (single large or several small) debate, is not obvious: A single large reserve will have a lower per-species extinction rate than will any smaller reserve, but the more reserves there are, the less chance there will be for a species to disappear simultaneously from all of them. In a review of land plants, insects, and vertebrates on islands, Quinn and Harrison showed that total numbers of species on groups of several small islands were higher than on a comparable area consisting of only one or a few large islands. Among other explanations, they suggest that the several small islands were distributed over a larger region and contained more types of habitats, enabling more species to exist on the entire set of islands. Similarly, genetic diversity within a species, which reduces extinction likelihood, may be increased with a certain amount of reserve-area fragmentation. In conclusion, several small preserves distributed over a large or varied region may sometimes be the better conservation strategy.

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SPIDERS

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The ability to produce silk is a distinctive feature of spiders. Silk-mediated airborne dispersal has allowed spiders to colonize even the most remote archipelagoes. Spiders on islands have served as models for the study of the evolutionary and ecological underpinnings of biodiversity. Because of their generalist predatory habits, introduced spiders may pose a serious threat to islands’ native fauna.

DEFINING A SPIDER

Spiders (order Araneae) comprise a megadiverse group of arthropods that includes close to 40,000 species distributed in 109 families. The origin of spiders can be traced back to the Devonian, about 400 million years ago, representing some of the earliest evidence of terrestrial life on Earth. As the dominant non-vertebrate predators in most terrestrial ecosystems, spiders have enormous ecological importance.

ACCESSING ISLANDS

Dispersal capabilities and generalist predatory habits make spiders formidable pioneers. Spiders have a unique