Regional species diversity

Key concepts

- Two principles of species-area relationships
- Species area curve

Introduction

The previous chapter introduced MacArthur and Wilson's theory of island biogeography as an explanation for the maintenance of α-diversity is a result of the interplay between a local process (extinction) and a regional process (colonization). One feature of that theory was that the equilibrium number of species on an oceanic island would increase with the area of that island. Martin[1] investigated this pattern in greater detail for the bird communities of the Sipoo islands, an archipelago of forested islands in the Baltic Sea off the coast of Helsinki, Finland. These islands ranged in size from 1.1 to 233 hectares. Bird species richness was estimated by counting the number of species vocalizing in 20 minute intervals at sampling sites distributed so that each island would be uniformly sampled. Bird species richness estimated in this way ranged from 2 to 34. A plot of bird species richness against island size illustrates the pattern predicted by MacArthur and Wilson (Figure 2). In fact, this figure illustrates another principle: the rate at which species richness increases with island area declines as the area gets large. Equivalently, species richness decelerates with island area. In fact these two fundamental principle of *species-area relationships* have been found to hold for almost all ecological communities, not just oceanic islands.

- *Principle 1.* Species richness increases with area.
- *Principle 2.* Species richness decelerates with area.

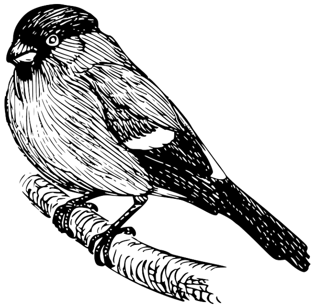

Figure 1: Bullfinch (*Pyrrhula Pyrrhula*) is found in the Sipoo archipelago, but only on the largest islands.

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[1] Jean-Louis Martin. Impoverishment of Island Bird Communities in a Finnish Archipelago. *Ornis Scandinavica*, 14(1):66–77, 1983

Species area curves

How are these two principles quantified? Do these principles provide a way to compare the diversities of two regions? This section answers these questions using a technique called the *species area curve*. Species area curves were first constructed by Arrhenius in 1921.[2]

The basic idea is to find a nonlinear equation the captures the relationship between species richness and the area surveyed and which contains terms that characterize the speed at which species richness increases with respect to area and the deceleration. Literally dozens of models are available to choose from.[3] However, one model, a power function introduced by Arrhenius, has been found almost always to fit empirical data very well and is almost universally used for this purpose. This equation is

$$s = ca^z, \tag{1}$$

where s is the number of species, a is the area, and c and z are fit constants.

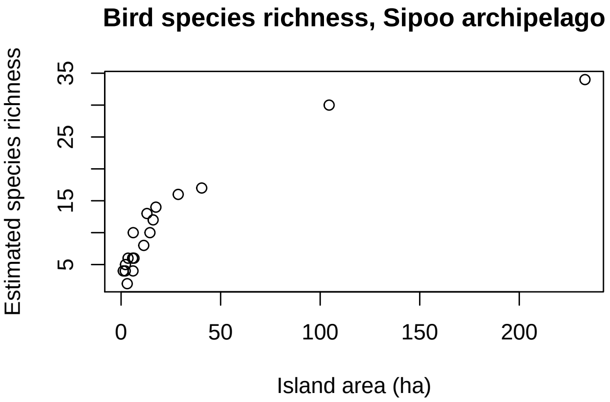

Figure 2: The dependence of bird species richness on island area in the Sipoo archipelago, Finland.

By taking logarithms of both sides, this model may be transformed to a linear equation,

$$\ln s = \ln c + z \ln a, \tag{2}$$

with intercept $\ln c$ and slope z. For this reason, z is often called the *slope parameter* regardless of whether the model is considered in the form of equation 1 or equation 2. This linear equation suggests a simple two-step diagnostic check to determine if Arrhenius's power function is indeed an acceptable model for a particular data set. (1) Take log-transformations of both species number and area and plot them. (2) If the data are close to falling on a straight line then the

[2] O Arrhenius. Species and area. *Journal of Ecology*, 9(1):95–99, 1921

[3] J Dengler. Which function describes the species-area relationship best? A review and empirical evaluation. *Journal of Biogeography*, 36(4):728–744, 2009

model may be used. Figure 3 shows the bird species richness of the Sipoo archipelago transformed in this way. It is then straightforward to estimate $\ln c$ and z by fitting a linear regression to the transformed data.

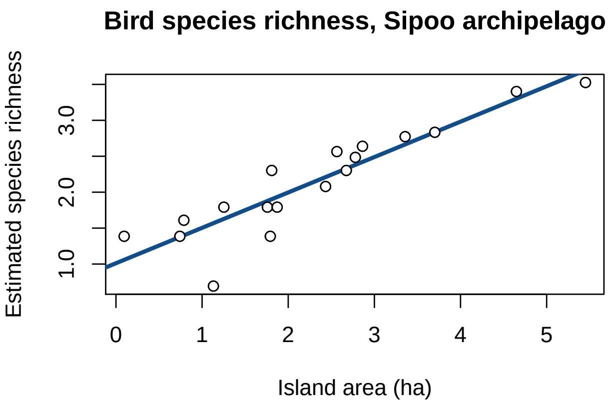

Figure 3: The species area curve of the Sipoo archipelago, Finland, plotted on logarithmic axes. A linear regression is shown in blue with fit intercept $\ln \hat{c} = 1.011$ and $\hat{z} = 0.493$.

Because of the power law expressed in equation 1, the speed with which species richness increases with respect to area depends on both c and z. Thus, for instance, Figure 4 shows a range of possible species area curves at different combinations of c and z. Clearly, as c increases (holding z constant), the number of species to be found within a given area will increase as well. However, the overall shape of the curve depends more strongly on z. Thus, a relatively small value of z (e.g. $z = 0.15$) causes species richness to increase rapidly at first before leveling off quickly. By contrast, a regional species pool with a relatively large z continues to climb substantially no matter how large the area becomes.

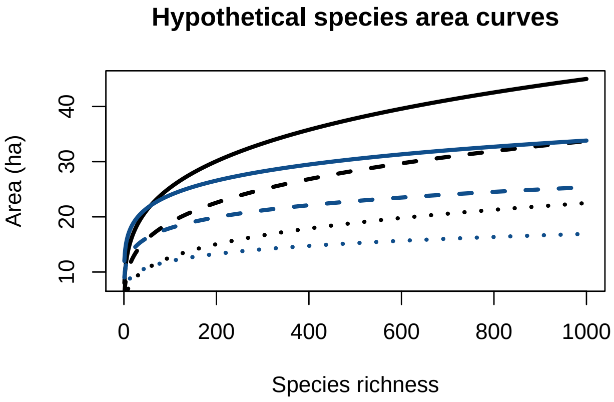

Figure 4: Effects of c and z on the species area curve. Black lines are $z = 0.25$. Blue lines are $z = 0.15$. Solid lines are $c = 8$ (black) or $c = 12$ (blue). Dashed lines are $c = 6$ (black) or $c = 9$ (blue). Dotted lines are $c = 4$ (black) or $c = 6$ (blue).

Comparing z values

A feature of this property is that the value of z may be used to characterize the shape of the species area curve of a regional species pool. For instance, it has been documented that z values are lower for taxonomic groups that disperse well compared with those that do not. Rosenzweig[4] proposed that the differences among z values may be amenable to theoretical explanation. For instance, he identified three different kinds of species area relationships that differ with respect to the areas under consideration.

- *Within-province species area curves.* Rosenzweig defined a biogeographic province as an area whose species originate from within it by speciation. Within a province, an increase in the area typically will correspond to an increase in the number of habitats represented. Thus, the two principles of species area relationships will hold. However, because habitats are connected, and vary slowly, within-province species area curves will exhibit the lowest x values.
- *Between island species area curves.* Within-province species area curves are contrasted with species area curves calculated for groups of islands or archipelagoes. These species area curves combine the habitat sampling process of within-province species area curves with the colonization-extinction balance of MacArthur and Wilson. The net effect is to depress the number of species on small islands compared with an area of equal size on the mainland (due to the remoteness of the island, reducing recolonization). But, as the islands become large, they behave like a mainland. At very large sizes, islands should have a species richness similar to that of an equivalent area of the mainland. Of course, the species area curve must connect these small and large islands. As a result, the z value must be larger in islands than among similarly chosen areas of a mainland.
- *Between-province species area curves.* Finally, Rosenzweg asks what must the slope of the species area curve look like when calculated over different provinces. Since (by definition) the species in biogeographical provinces have predominately originated there, they must be nearly additive. Strictly additive species area relationships would give rise to z values of one. Strict additivity is unlikely (there is some migration and colonization even among provinces) but this extreme cases suggests that inter-province species area curves should have the largest z values.

Censuses of bird species richness confirm these thoeretical predictions (Figure 5).

[4] Michael L. Rosenzweig. Reconciliation ecology and the future of species diversity, 2003. ISSN 0030-6053

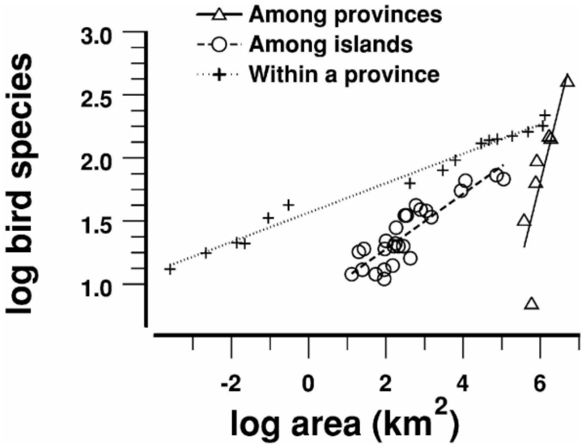

Figure 5: Species area curves for birds confirm Rosenzweig's three classes of species area curves. The slope of the species area curve (z value) is least within provinces, is slightly larger within islands, and is greatest among provinces.

This and other theoretical work suggested that the slopes of species area curves might therefore differ in predictable ways. Drakare et al.[5] performed a *meta-analysis* (an analyis-of-analyses) to look at the distribution of z values in 794 published species area curves. Interestingly, their only major findings were that larger z values were found at lower latitudes (i.e. in the tropics) and by larger organisms. They found some differences among major ecosystem types, but did not generally find differences between terrestrial and aquatic ecosystems (Figure 6). Because high z values means that small changes in area may correspond to large changes in species number, Drakare et al. concluded that the differences in slope between two groups of species are an indicator of their relative sensitivity to habitat loss and climate change. This is a topic we will explore in a reading next week.

Test yourself

1. What are the two principles of species area relations?

2. What is a species area curve?

3. How does one obtain an estimate of z for a species area curve from data on the number of species in different plots?

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[5] Stina Drakare, Jack J Lennon, and Helmut Hillebrand. The imprint of the geographical, evolutionary and ecological context on species-area relationships. *Ecology letters*, 9(2): 215–27, February 2006

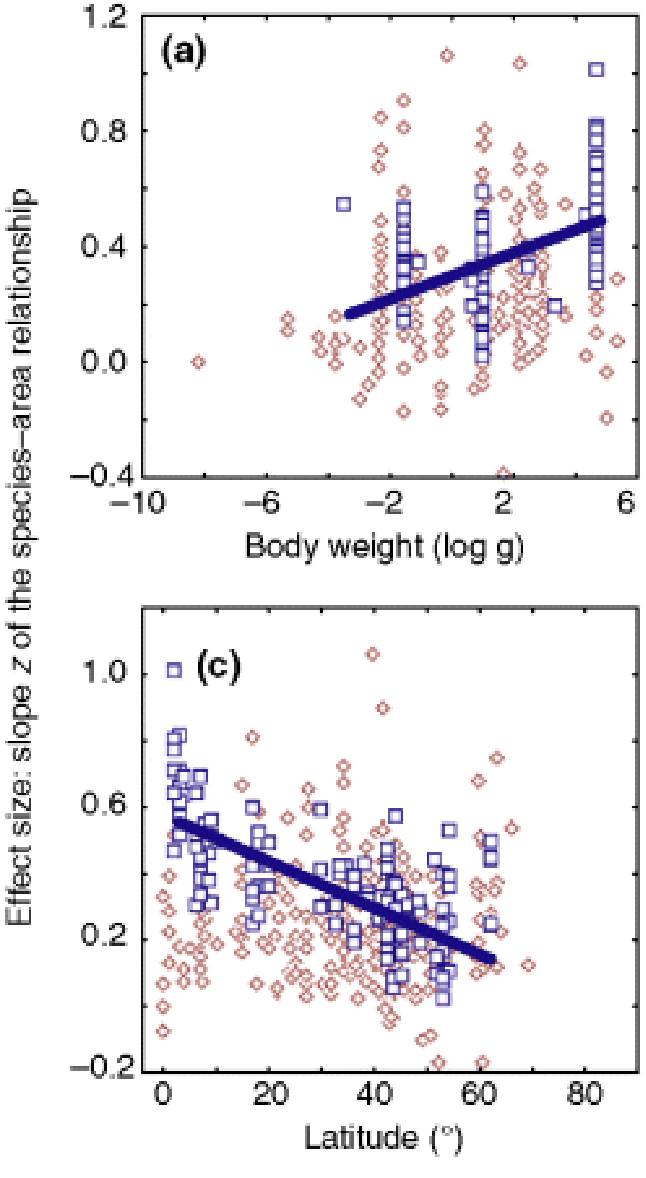

Figure 6: Meta-analysis of Drakare et al. shows the effects of latitude and body size on the z values of species area curves.

Bibliography

[1] O Arrhenius. Species and area. *Journal of Ecology*, 9(1):95–99, 1921.

[2] J Dengler. Which function describes the species-area relationship best? A review and empirical evaluation. *Journal of Biogeography*, 36(4):728–744, 2009.

[3] Stina Drakare, Jack J Lennon, and Helmut Hillebrand. The imprint of the geographical, evolutionary and ecological context on species-area relationships. *Ecology letters*, 9(2):215–27, February 2006.

[4] Jean-Louis Martin. Impoverishment of Island Bird Communities in a Finnish Archipelago. *Ornis Scandinavica*, 14(1):66–77, 1983.

[5] Michael L. Rosenzweig. Reconciliation ecology and the future of species diversity, 2003. ISSN 0030-6053.