Island biogeography

Key concepts

- Colonization-extinction balance

- Island-biogeography theory

Introduction

At the end of the last chapter, it was suggested that another mechanism for the maintenance of α-diversity is the phenomenon of *colonization-extinction balance*. Colonization-extinction balance refers to the fact that the number of species at a site changes only through colonization (or – much more rarely – local speciation), which results in an increase in the number of species, and extinction, which results in a decrease in the number of species. If the processes of colonization and extinction are "balanced" then the number of species will be at an equilibrium. Colonization-extinction balance is not a local mechanism *per se* because it reflects the combination of a local process (extinction) and a process that depends on the state of surrounding ecosystems as well (colonization). Thus, colonization-extinction balance is a process that links α- and γ-diversity.

Figure 1: *The Theory of Island Biogeography* by Robert MacArthur and E.O. Wilson.

Island biogeography theory

The process of colonization-extinction balance first received wide attention in association with the development of *island biogeography theory* by Robert MacArthur and E.O. Wilson. Island biogeography theory aims to explain why islands have the number of species that they do, both in relation to the mainland and in relation to other islands. This model made both quantitative and qualitative predictions about both the accumulation of species on an island over time and the equilibrium number of species. It therefore generated a tremendous amount of empirical work in the following decades to test and refine the theory for use in specific contexts.
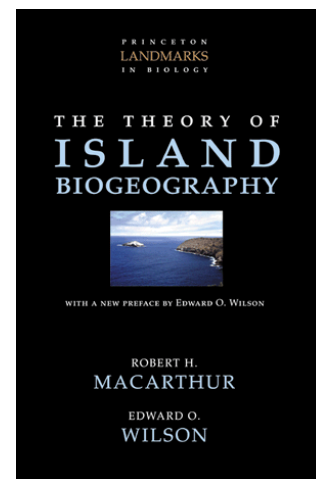
The basic theory aims to explain the number of species s, and depends on two rates:

- C: colonization rate per unit time

- E: extinction rate per unit time

The number of species is at equilibrium when these two rates are equal, i.e.,

$$C(s) = E(s). \tag{1}$$

These two rates, in turn, may be expressed in terms of other parameters:

- p: the total number of species in the species pool

- c: the mean rate of colonization averaged over species in the species pool; equivalently, the average time to colonization is $\tau_c = c^{-1}$.

- h: the mean rate of extinction averaged over species in the species pool; equivalently, the average persistence time of a species on the island $\tau_e = e^{-1}$.

The colonization rate C, for instance, depends on the number of species that might colonize. If the current number of species on the island is s out of a possible p species, then there remain $p - s$ potential colonists. These each colonize at an average rate c. Therefore the colonization rate is

$$C(s) = c(p - s) \tag{2}$$

We derive the extinction rate similarly. In this case there are s species which have average extinction rate h yielding

$$E(s) = hs. \tag{3}$$

Substituting equations 2 and 3 into equation 1 and solving for s we obtain the equilibrium number of species

$$s^* = \frac{cp}{c + h}. \tag{4}$$

This may be visualized by plotting C and E against s (Figure 2). The intersection corresponds to the equilibrum.

MacArthur and Wilson proceeded to ask how the basic rates might depend on other geographic properties of the islands. Particularly, they suggested that c should decline with distance (because colonists would be more likely to successfully find their way to close islands
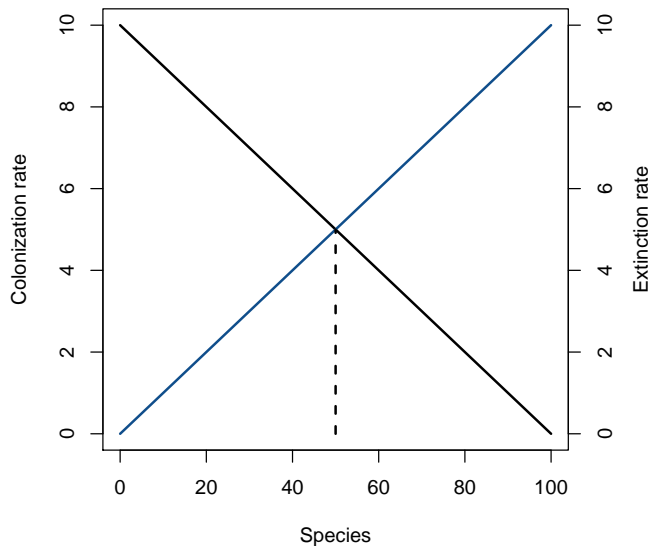
Figure 2: The basic model of island biogeography predicts that species number on islands is determined by the balance of colonization (black) and extinction (blue). The equilibrium ($s^* = 50$) is indicated by the vertical dashed line. Parameters of this model are $h = 0.1$, $c = 0.1$, and $p = 100$.

than distant islands) and that e should decline with island size (because larger islands would support larger populations less vulnerable to extinction). Including these factors requires introducing a few more parameters:

- d: the distance of the island from the mainland (the presumed source of colonists)

- a: the area of the island

- ϕ: a fit parameter governing the distance decay of colonization rate

- ϵ: a fit parameter governing the effect of area on extinction

For colonization, we suppose that the rate $c(p - s)$ is the maximum rate that applies in the extreme case where an island is directly adjacent to the mainland. For other islands, this must be discounted by a factor that depends on the distance, i.e. we multiple $c(p - s)$ by a quantity that is one when $d = 0$ but approaches zero as d gets large. Here, we assume this factor is an exponential decay, as if potential colonists are "falling off" at a constant rate ϕ the further the island is from the mainland. Accordingly, our new colonization rate is

$$C(s) = c(p - s)e^{-\phi d}. \tag{5}$$

For extinction, we derive a similar quantity. However, in this case rather than thinking of an attrition process we refer to theoretical results showing that demographic fluctuations cause density-dependent

populations near their carrying capacities to have logarithms of extinction time proportional to carrying capacity (k). Assuming carrying capacity is proportional to island area ($k \propto a$), we have

$$E(s) = se^{-\epsilon a}. \qquad (6)$$

In this case, the extinction rate goes to zero as the area gets large (ecologically plausible if fluctuations are due to demographic fluctuations, but not major disturbances like hurricanes). Additionally, the total extinction rate diverges (goes to ∞) as area goes to zero, which is also ecologically plausible: an island of area zero cannot support even one species! Thus, we no longer have need for the variable h. As before, we solve for the equilibium number of species:

$$s^* = \frac{cpe^{\epsilon a}}{ce^{\epsilon a} + e^{\phi d}}. \qquad (7)$$

One qualitative prediction of this model is that the number of species on islands will be directly proportional to p, the size of the species pool on the associated mainland. Other predictions are perhaps easier to see graphically (Figures 3 and 4). First, concerning distance to mainland, as the distance increases (different black lines in Figure 3), the equilibrium number of species declines. By contrast, the equilibrium number of species increases with area (different blue lines in Figure 4).
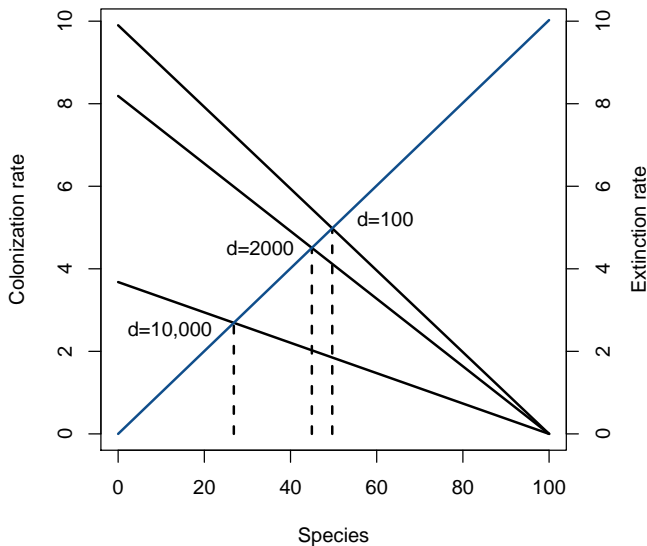

Figure 3: The modified model of island biogeography predicts that the colonization rate will go down as distance to the mainland (d) increases. Species number is determined by the balance of colonization (black) and extinction (blue). Thus, as distance to mainland increases, the equilibrium number of species decreases. Non-distance parameters of this model are $\phi = 0.0001$, $\epsilon = 0.001$, $p = 100$, and $a = 2300$.
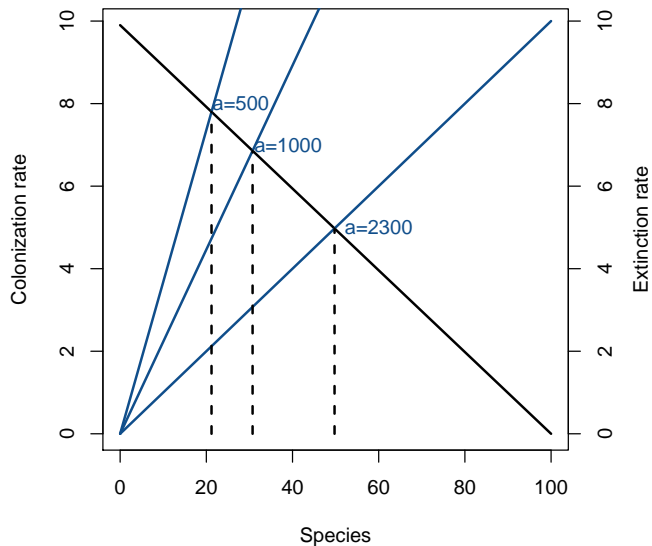
Figure 4: The modified model of island biogeography predicts that the extinction rate will go down as island area (a) increases. Species number is determined by the balance of colonization (black) and extinction (blue). Thus, as island area increases, the equilibrium number of species also increases. Non-area parameters of this model are $\phi = 0.001$, $\epsilon = 0.001$, $p = 100$, and $d = 100$.

Validation, extensions, and applications

Since its introduction, the theory of island biogeography has been tested in a variety of contexts and extended to new areas of application. A direct test of the theory is not possible because oceanic islands are clustered, resulting in both area and distances that are not uniformly distributed, and because the continental mainlands themselves differ in their species pools. Numerous indirect tests have been made, however. Perhaps most interesting are comparisons of island faunas with comparably sized regions on the mainland. Consistent with theory, these typically show that island faunas are depauperate (fewer species) compared with their mainland counterparts. A regional test of the distance part of the hypothesis was performed by Jared Diamond, who looked at the number of species on Pacific Islands as a distance from their common source in Papua New Guinea. The strong, nearly linear decline reported by Diamond is consistent with the theory of island biogeography.

Since the initial work of MacArthur and Wilson, island biogeography theory has also been applied to other "islands" such as mountaintops, forest fragments (for instance, songbirds in deciduous forests of the Eastern US), even the accumulation of microorganisms on suspended organic flocs in the ocean.

Homework

1. Derive equation 6 from the arguments in the paragraph preceding it in the text.

2. Sketch the equilibrium number of species given by the island biogeography theory (i.e., equation 7) as (i) a function of area, and (ii) a function of distance from the mainland.

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 is-
land biogeography as an explanation for the maintenance of α-diversity
as 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 pat-
tern 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 range 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 esti-
mated 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 6). 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 relation-
ships* 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.

[1] Jl Martin. Impoverishment of
island bird communities in a Finnish
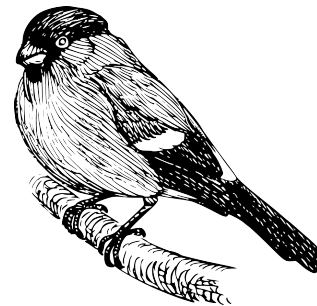archipelago. *Ornis Scandinavica*, 14
(1):66–77, 1983

Figure 5: Bullfinch (*Pyrrhula
Pyrrhula*) is found in the Sipoo
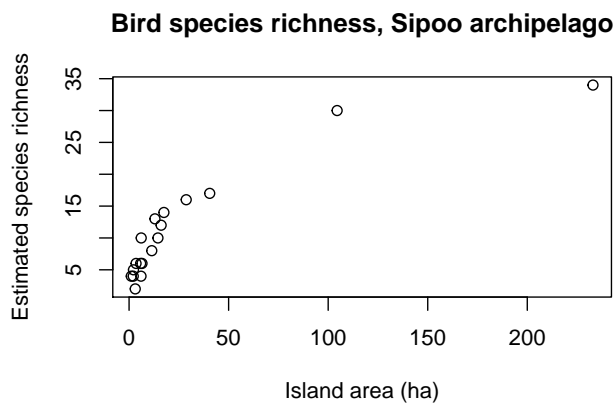archipelago, but only on the largest
islands.

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 by studying the *species area curve*. Species area curves were first constructed by Arrhenius in 1921[2] and continue to be of interest to ecologists both for their practical utility in quantifying biodiversity and as a regular pattern in nature that warrants ecological explanation.

[2] H a Gleason and No Jan. Species and Area. *Journal of Ecology*, 6(1): 66–74, 2008

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

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

$$s = ca^z, \tag{8}$$

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

Figure 6: 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,

$$\ln s = \ln c + z \ln a, \tag{9}$$

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 8 or equation 9. 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 model may be used. Figure 7 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.

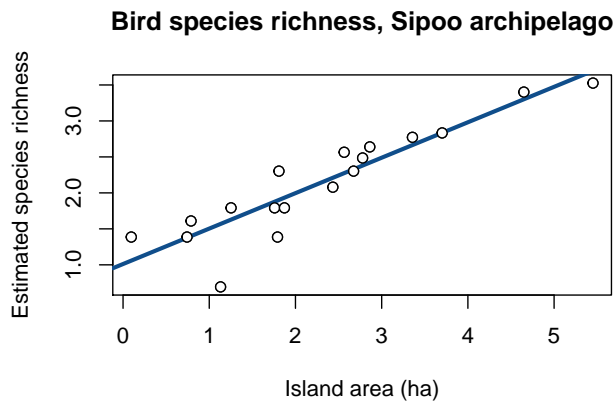**Bird species richness, Sipoo archipelago**

Figure 7: 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 8, the speed with which species richness increases with respect to area depends on both c and z. Thus, for instance, Figure 8 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.

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.

[4] Michael L. Rosenzweig. Reconciliation ecology and the future of species diversity, 2003
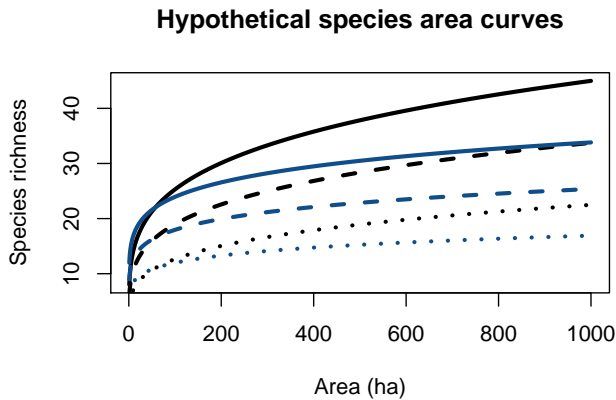
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Hypothetical species area curves

Figure 8: 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).

- *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 9).

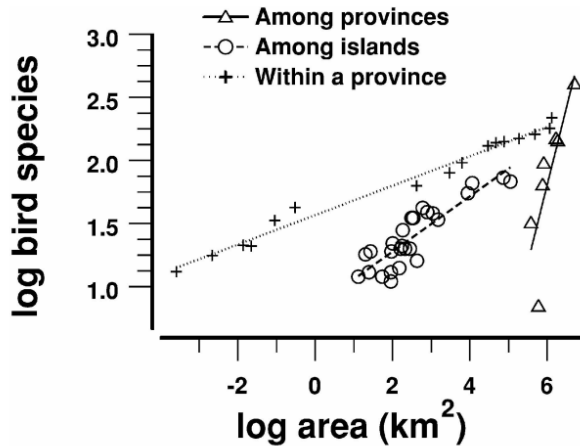
Figure 9: Species area curves for birds confirm Rosenzweig's three classes of species area curves. The slope of the species area curve (z value) is least within provinces, is slightly larger within islands, and is greatest among provinces.

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 10). 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?

Figure 10: Meta-analysis of Drakare et al. shows the effects of latitude and body size on the z values of species area curves.

Bibliography

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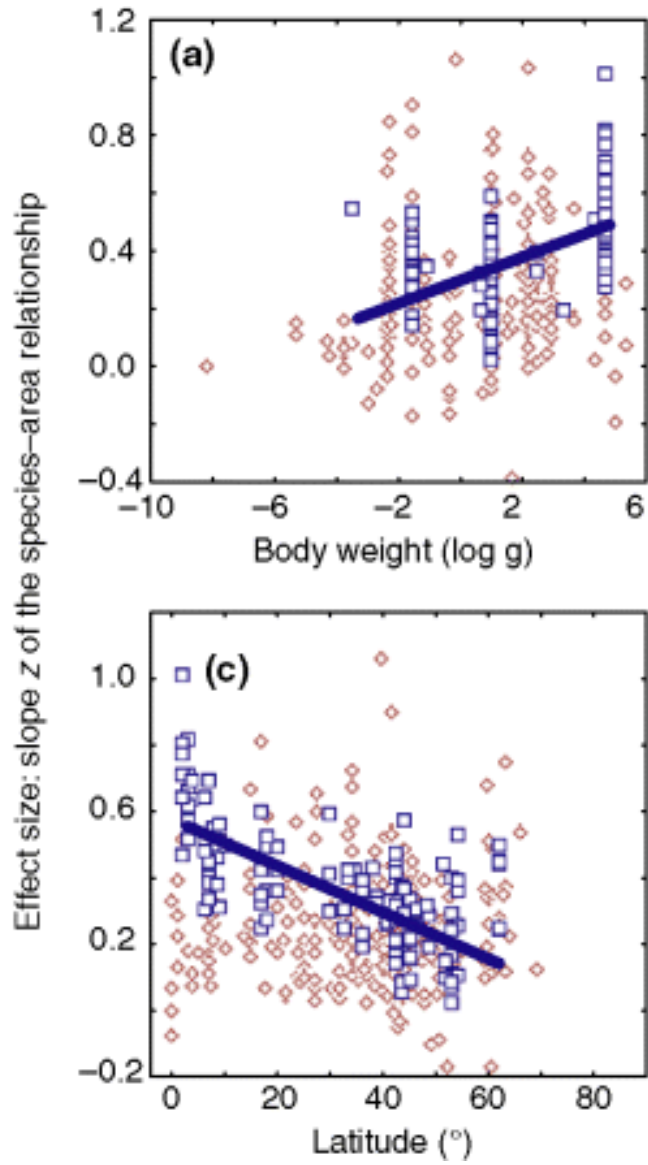
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