

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.

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.

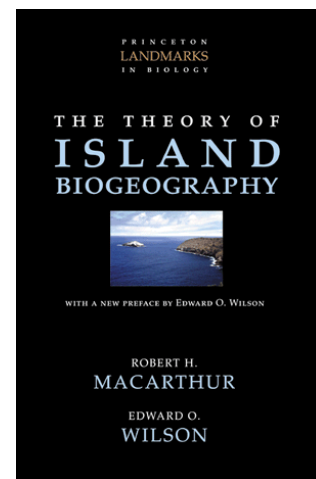


Figure 1: *The Theory of Island Biogeography* by Robert MacArthur and E.O. Wilson.

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.,

$$C(s) = E(s). \quad (1)$$

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 $\tau_e = h^{-1}$.

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

$$C(s) = c(p - s) \quad (2)$$

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

$$E(s) = hs. \quad (3)$$

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

$$s^* = \frac{cp}{c + h}. \quad (4)$$

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

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

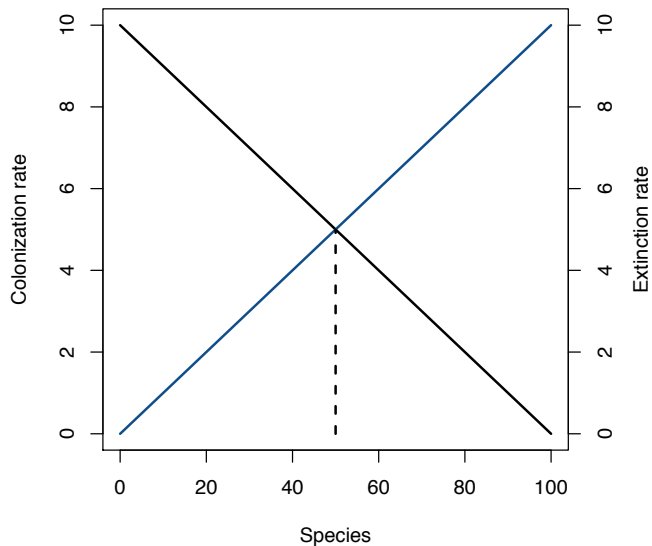


Figure 2: The basic model of island biogeography predicts that species number on islands is determined by the balance of colonization (black) and extinction (blue). The equilibrium ($s^* = 50$) is indicated by the vertical dashed line. Parameters of this model are $h = 0.1$, $c = 0.1$, and $p = 100$.

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 multiply $c(p - s)$ 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

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

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

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

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 equilibrium number of species:

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

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).

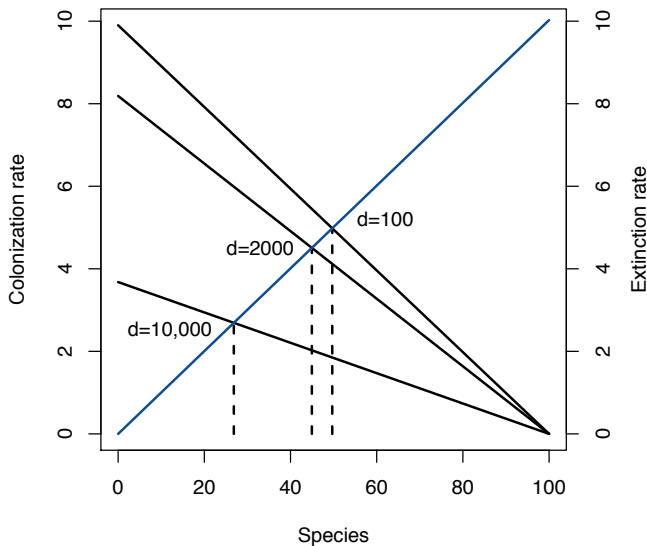


Figure 3: The modified model of island biogeography predicts that the colonization rate will go down as distance to the mainland (d) increases. Species number is determined by the balance of colonization (black) and extinction (blue). Thus, as distance to mainland increases, the equilibrium number of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

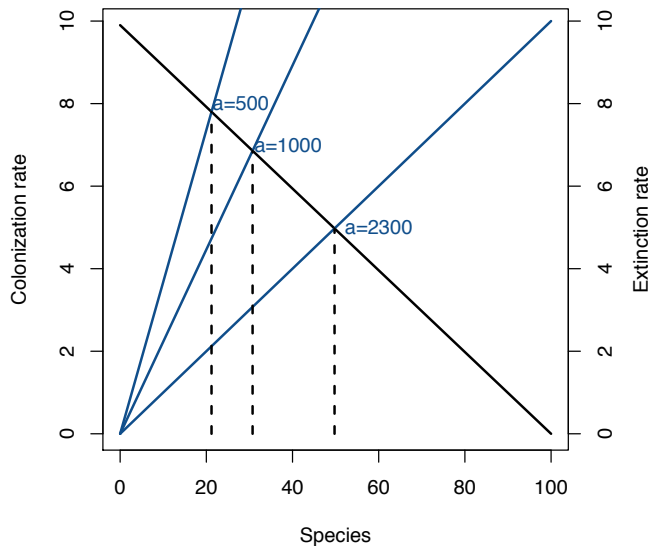


Figure 4: The modified model of island biogeography predicts that the extinction rate will go down as island area (a) increases. Species number is determined by the balance of colonization (black) and extinction (blue). Thus, as island area increases, the equilibrium number of species also increases. 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.