Bi/Ge 105: Evolution
Homework 1
Due Date: Wednesday, January 14, 2026

> "The real voyage of discovery consists not in seeking new landscapes but in having new eyes."
>
> Marcel Proust

1. A feeling for the numbers in evolution

Evolution takes place across many different scales in both space and time — from the mutations arising during a single round of genomic replication to the movement of continents over millennia. The goal of this first problem is nothing more than to explore some of these characteristic scales in order to start building quantitative intuition. These estimates are intended to be done using simple arithmetic of the "one-few-ten" variety (i.e. few times few is ten), and to give an order-of-magnitude picture of the phenomenon of interest. Take pride in your results: state and justify (with citations) any assumptions you make, and give a simple, intuitive description of how you came to your answer. Please don't report "significant" digits that you have not earned!

Also: although we are regular users of "chatbots" — and may even employ them during the term — for this homework, we request that you please do not appeal to them in any way.

The Theory of Island Biogeography

Darwin's voyage to the Galápagos did more than inspire the development of the theory of evolution; it also firmly established the importance of islands in the study of biology. In the words of Peter Grant:

> "One of many approaches to a problem as broad as [evolution] is to seek an understanding of a small and simplified part of it... This is the essence of experimentation. Islands provide that simplicity, naturally, because they are discrete pieces of the environment and often very small.

> As well as being convenient models of larger realms and larger-scale processes, islands and their inhabitants have special features that command attention from evolutionary biologists. An outstanding feature is their strangeness; many of them are downright weird. Naturalists of the last three centuries, Darwin and Wallace among them, brought back to centres of civilization accounts of strange and unimagined creatures found only on remote islands. Dodos. *Sphenodon*. The Komodo dragon. Daisies as tall as trees. What is it about islands that promotes such strangeness?"[1]

Central to the discipline now known as island biogeography is a deceptively simple question: if islands are separated from the world by water, then how did the flora and fauna which populate them get there in the first place? Therefore, how did the "strangeness" of speciation on islands arise? The answers have been fiercely debated for centuries, but two of the leading hypotheses are *vicariance* and *dispersal*.

Vicariance refers to the geographical separation of species, and their subsequent speciation as a result of relative isolation. For example, both New Zealand and Madagascar were once attached to larger landmasses; the vicariance hypothesis holds that their current flora and fauna reflects these initial origins.[2]

However, not all islands were once continentally connected. Oceanic islands are those which have never been in contact with the mainland, such as those arising from volcanism, coral atolls, or the deposition of sediment. This total geographical isolation led the great botanist Joseph Hooker to remark in an 1866 lecture that "Oceanic islands are in fact, to the naturalist, what comets and meteorites are to the astronomer." It also means that an alternative mechanism is required to explain their colonization. Enter dispersal: the idea that rare and often random events, like the arrival of a species carried across the ocean by currents, can explain the biology on islands. This reliance on seemingly improbable occurrences is at the heart of the critique of the dispersal hypothesis; it has been pejoratively called "a science of the improbable, the rare, the mysterious, and the miraculous."[3]

Is this criticism warranted? Below, we'll embark on a series of estimates aimed at building quantitative intuition for the probabilities and timescales involved in dispersal.

[1] **grant_evolution_1998**.

[2] This has led some to denote, with tongue in cheek, New Zealand as "Moa's Ark".

[3] **nelson_candolle_1978**.

To begin, we return to the Galápagos (Figure 1). Like the islands of Hawaii, this archipelago is produced by a volcanic “hotspot” which in this case is located near present-day Isabella and Fernandina islands. As they are created, plate tectonics cause the islands to move in a southeasterly direction towards the coast of South America. How fast or slow are these processes?

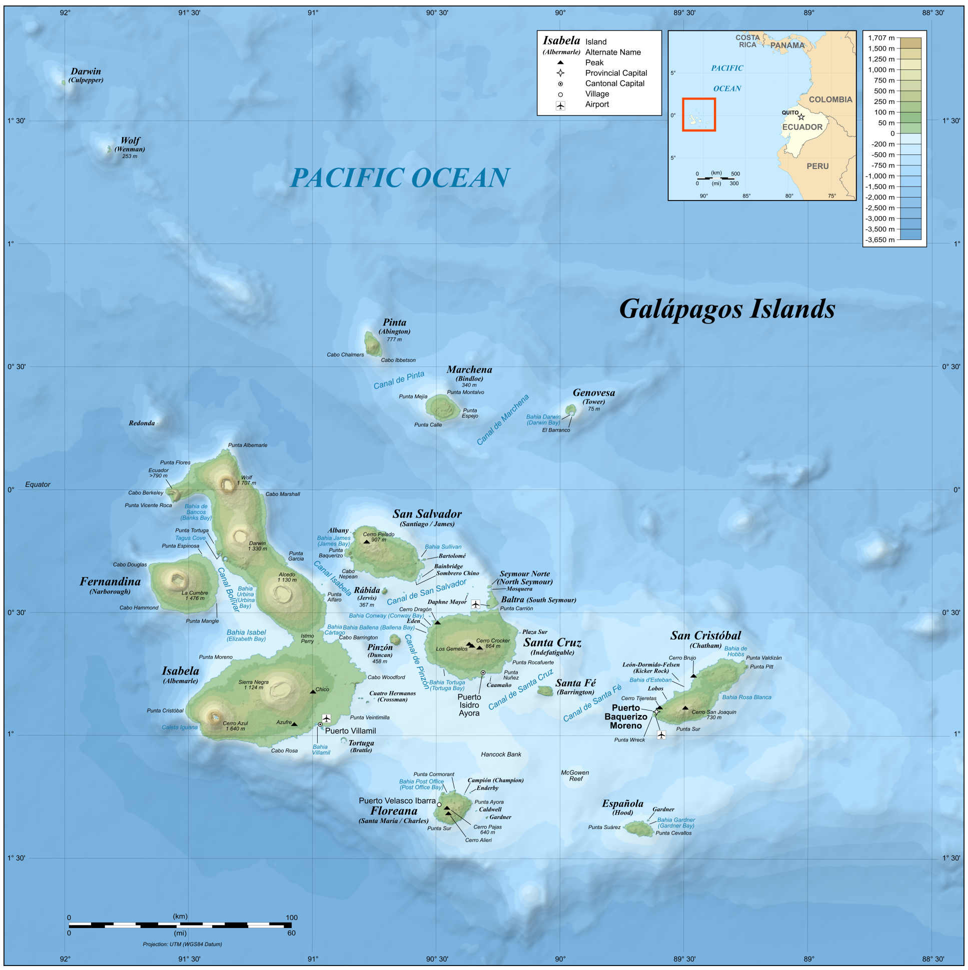

Figure 1: Map of the Galápagos Islands with scale bar.

Question 1a. Given that the island of Española is roughly 3.5 million years old, estimate the rate at which the islands are moving every year. Give your answer in units of cm/year.

Question 1b. Assuming that the speed you found above is typical for volcanic island chains, estimate the age of Kauai (a Hawaiian island) using similar logic. Explain your reasoning. What factors might complicate this comparison, and how would they affect your conclusions?

Earlier, we mentioned a generic example of dispersal via ocean currents, akin to the archetypal image of a coconut floating away from shore and landing on a desert island. We now consider two specific, parallel cases:

1. In December of 2004, an earthquake in Indonesia triggered a devastating tsunami. Many people were swept out to sea in the chaos; some, like Rizal Shahputra, were fortunate enough to later be found alive (Figure 2).

2. In that same month and on the opposite end of the Indian Ocean, a giant tortoise from the island of Aldabra was found washed up — alive! — on the coast of Tanzania (Figures 3 and 4). Barnacles attached to its body suggested it had indeed made an inadvertent ocean crossing, perhaps after being washed to sea in a storm.[4]

Question 1c. Estimate the speed of ocean currents experienced by Shahputra. Thus, estimate how long the Aldabra tortoise was adrift at sea during its journey.

Although these examples don't "prove" anything, they help begin to give us a sense for the speeds and timescales involved in dispersal via ocean currents. But dispersal need not proceed by strictly abiotic means; animals can also serve as vectors for material such as plant seeds, e.g. by brushing up against plant matter that becomes attached to their exteriors (*epizoochory*), or ingesting seeds in one location and egesting them in another (*endozoochory*). In this last example, we will investigate the possible role of endozoochory by seabirds in colonizing a new oceanic island.

Surtsey: Isle of the Fire Giant

In 1963, fishermen some 30 km off the coast of Iceland encountered an undersea volcanic eruption. Over the next several years, it birthed the virgin island of Surtsey, named for the fire-bearing giant of Norse mythology. Recognizing its immense value as a blank slate for the study of island ecology, researchers designated it as a scientific preserve, and began a decades-long series of careful

[4] **gerlach_first_2006**.

Tsunami man survives week at sea

An Indonesian man has been found floating on tree branches in the Indian Ocean, eight days after a devastating tsunami struck the region.

Rizal waved to a passing cargo ship

Rizal Shahputra, 23, said he was initially swept out to sea with other survivors and family members, but that one by one they drowned.

He was rescued on Monday by a passing container vessel.

He was taken to Malaysia where officials said he was in good condition - he survived eating floating coconuts.

Rizal said he was cleaning a mosque in Banda Aceh on the northern tip of Sumatra on 26 December when the tsunami struck. Children ran in to warn him, but he was swept out to sea, along with several other people.

"At first, there were some friends with me," Rizal told reporters. "After a few days, they were gone... I saw bodies left and right."

He drank rainwater, and ate coconuts, which he reportedly cracked open with a doorknob.

Rizal said at least one ship sailed by without noticing him before the MV Durban Bridge spotted him, 160km (100 miles) from Banda Aceh.

Figure 2: Article about a tsunami survivor from the 2004 Boxing Day earthquake in Indonesia.

Figure 3: In 2004, this giant tortoise from Aldabra was found on the coast of Tanzania. Note the barnacles encrusting its body.

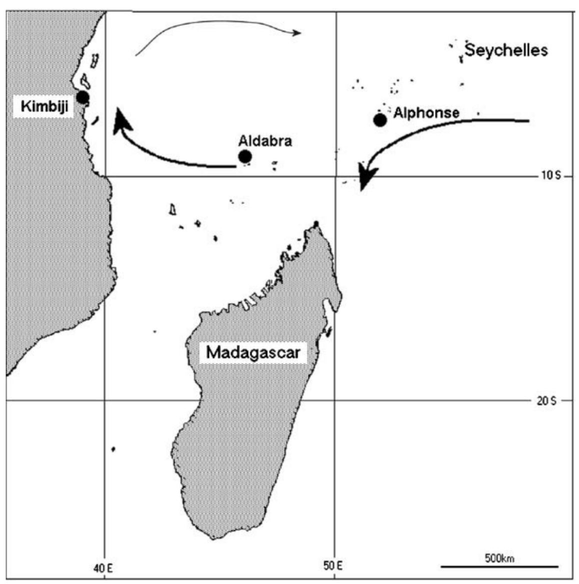

Figure 4: Map of the Seychelles and the African coast with scale bar.

experiments aimed at observing changes to the flora and fauna of the initially barren rock. The result is an incredible dataset cataloging the history of Surtsey's colonization by plants, seabirds, seals, and even insects and fungi. Figure 5 shows a glimpse of this data by plotting the total number of vascular plant species observed on the island since its birth.

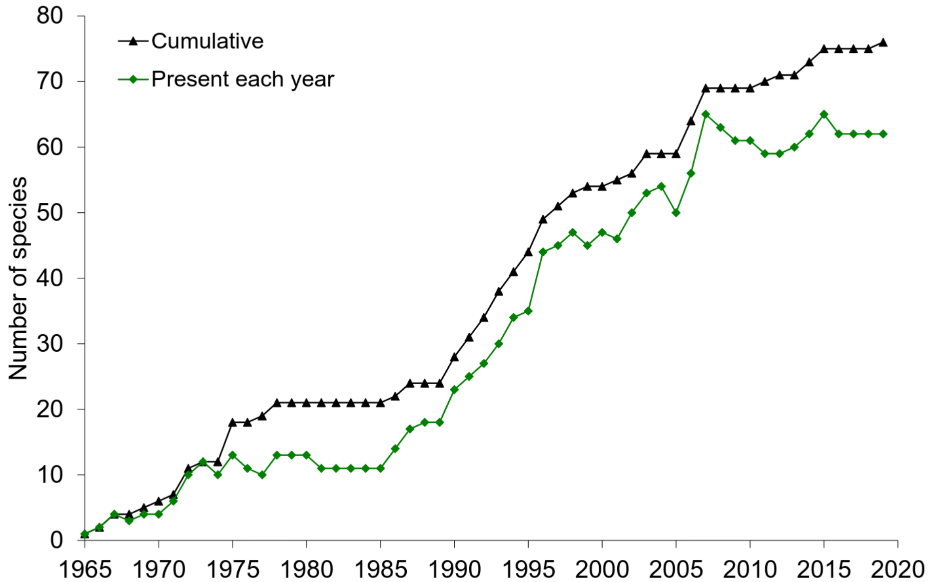

Figure 5: Number of vascular plant species found on Surtsey during 1965-2019.[6]

One striking observation made by the researchers on Surtsey was of the transformative effect of seabirds on the island's ecology. Beginning around 1986, a small colony of gulls established itself at the southern tip of the island; in the years since, their presence has correlated — in both time (Figure 5) and space (Figure 6) — with a relative explosion in plant colonization rates!

Why might this be so? We will return to the question of nutrient subsidies by seabirds (i.e. the fertilizing effect of their manure on the environment in which they nest) later in the course. For now, let's use these observations to build a careful estimate of the potential role of seabird endozoochory for plant dispersal on Surtsey. In other words, how often do we expect seabirds to bring plant seeds to the island from elsewhere? We can phrase this as a calculation of the expected number of yearly seed dispersal events X such that

$$E[X] \approx n_{\text{birds}} * \frac{n_{\text{trips}}}{\text{bird yr}} * P_{\text{ingest}} * P_{\text{egest}} * P_{\text{success}}, \tag{1}$$

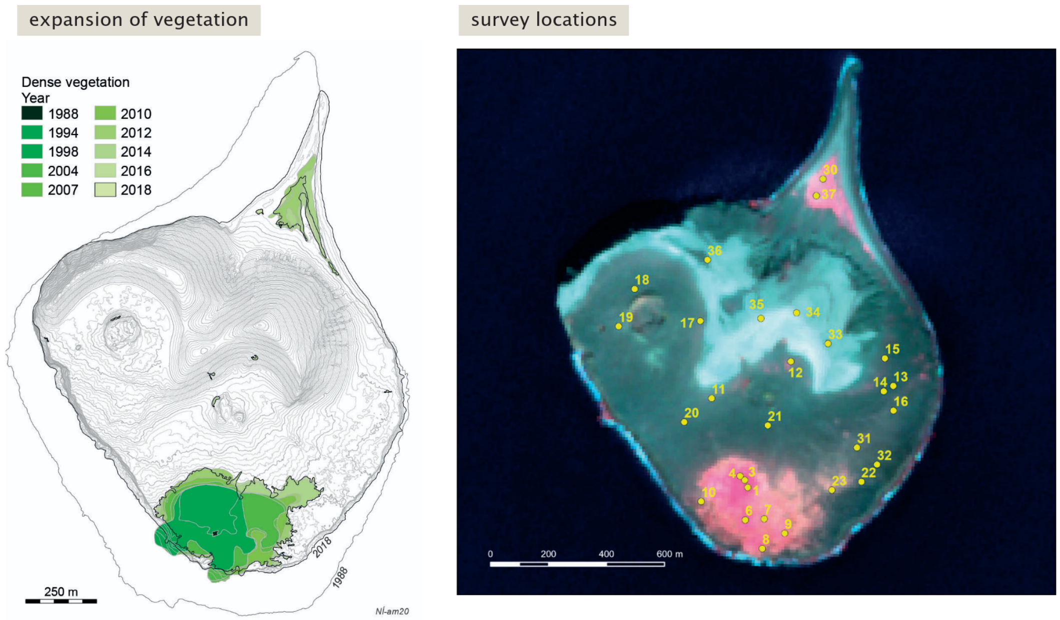

Figure 6: Map of Surtsey depicting expansion of vegetation (left panel, green), and areas inhabited by seabirds (right panel, red).[8]

where n_{birds} is the number of birds resident on Surtsey; $\frac{n_{\text{trips}}}{\text{bird yr}}$ is the mean number of foraging trips undertaken to the mainland by a given bird each year; P_{ingest} is the probability that it ingests a plant seed while foraging there; P_{egest} is the probability that it egests (i.e. regurgitates or defecates) it upon returning to Surtsey; and P_{success} is the probability that an egested seed remained viable and successfully takes root on the island.

In the following problems, we will work through each term in Equation 1. Again, the goal is not to "prove" anything, but rather to use order-of-magnitude reasoning to assess whether this mechanism is plausible in the first place.

Question 1d. Today, there are about 300 breeding pairs of seagulls in the Surtsey colony. During the breeding season (approximately 100 days of the year), these gulls establish nests, lay eggs, hatch chicks, and forage in order to feed themselves and their young. Birds from Surtsey have been observed foraging near the Icelandic coast, which is 30 km away and the nearest major source of plant diversity. By reasoning about seabird flight speeds, estimate the frequency and duration of foraging trips. Hence on average, how many times does each bird visit the mainland every year? How many is this in total? Assume that parents take turns foraging, i.e. one travels while the other remains at the nest.

Question 1e. We next consider P_{ingest}. Estimate its value and share a brief explanation of your reasoning. Thus, how many foraging trips do you calculate involve seed ingestion? You may find it helpful to use the trick we discussed in lecture: try to set upper and lower bounds on the value, and then take the geometric mean.

Question 1f. By reasoning about seabird egestion rates, estimate P_{egest}. Remember that this value describes events where (1) the egesting bird may have ingested a seed, and (2) the egestion occurs on or over Surtsey, not the ocean or the mainland.

Question 1g. Finally, estimate P_{success} (again, briefly explain your reasoning), and hence compile your ultimate estimate of the expected yearly number of seed dispersal events in accordance with Equation 1. Discuss your findings with reference to the data in Figure 5. Do you think seabird endozoochory is a plausible mechanism for plant colonization on Surtsey? Why or why not?

Question 1h. In one paragraph, identify at least two shortcomings of your estimate, and discuss how they might affect your conclusions. Propose an experiment that would generate data that could improve your estimate.

We will return to the topic of island biogeography, and especially the problem of colonization of oceanic islands, many more times in this course. For now, we leave you with a few thoughts as you reflect on the problems above. The first is that no matter how unlikely dispersal might seem as a mechanism, we have observed real, verified examples of it in our lifetimes. As for the second — well, we will simply defer to G. G. Simpson:

> "Probability of dispersal is affected... by the size of the population subject to dispersal. If the chance that any given individual will cross a geographic barrier is, say, one in a million, p =.000001, then in a population of a million individuals the chance that at least one will cross the barrier is almost two in three, p =.63. An event so extremely improbable for a single individual that most of us would think of it as impossible becomes more likely than not for the population as a whole. The passage of time has the same effect: it multiplies the opportunities for occurrence, whether one considers this as giving the same individuals (or their successors)

more opportunities for dispersal or as increasing the number of successive individuals that have such opportunities. If the probability that some member of a population will cross a barrier is .000001 in any one year, in a large population this means that the probability for any one designated individual is almost infinitesimally small, so much so that it would seem absolutely impossible to even the best qualified observer in the field. Yet during the course of a million years the event would be probable, p =.63, again. In the course of 10 million years the event would become so extremely probable as to be, for most practical purposes, certain, p=.99995. In other words, there would be only about one chance in 20,000 that it would not occur. One million or 10 million years is not a particularly long time, as time goes in dealing with many problems of historical biogeography. This example, in itself, should give pause to those who speak of the "improbability" of transoceanic dispersal on the basis of their observations of a few individuals for a few years."[9]

2. Deep time and Earth history

On a related note, one of the most fascinating stories in science is how we have learned to probe "deep time": the vast timescales of geology, planetary science, and the evolution of life which stretch far beyond human experience. It is a concept we will return to again and again in this course. For example, dating the age of a fossil often relies on dating the rock stratum in which it was found — but how is that actually done?

Here we consider a simple model of radioactive decay as relevant to one common method of radioisotope dating, while recognizing that there exist many other dating methods — each with their own uses — which we will not have time to cover here.

Potassium-Argon Dating

Many minerals contain potassium, which has a radioactive isotope (^{40}K) that slowly decays into argon gas (^{40}Ar). When rocks are molten, as in lava, this argon can freely escape; but once the rocks cool and crystallize, any subsequent gas becomes trapped within them. Thus, we can estimate the age of a rock by

[9] **bhl166126**.

measuring how much argon it contains. This natural stopwatch enables the technique known as potassium-argon (K-Ar) dating.

More formally, let $t = 0$ denote the time at which a rock first crystallizes. We presume that the amount (in terms of number of nuclei, N) of ^{40}Ar here is zero:

$$N_{Ar}(0) = 0. \tag{2}$$

As for potassium, denote the decay rate of ^{40}K into ^{40}Ar as λ. Thus at each small time increment Δt, every potassium nucleus has a probability $\lambda\Delta t$ of decaying. We can now write an equation for the number of potassium nuclei at $t + \Delta t$ as

$$N_K(t + \Delta t) = N_K(t) - (\lambda\Delta t)N_K(t). \tag{3}$$

We also employ the important constraint that the total number of nuclei in the system must remain constant:

$$N_K(0) = N_K(t) + N_{Ar}(t). \tag{4}$$

We are now ready to construct differential equations to find the relationship between $N_K(t)$, $N_{Ar}(t)$, and t.

Question 2a. Using the equations above as a guide, write differential equations for $N_K(t)$ and $N_{Ar}(t)$. How do these two expressions relate to one another?

Question 2b. Next, we note that the solution for a linear differential equation of the form $\frac{dx}{dt} = kx$ is given by $x(t) = x(0)e^{kt}$. Use this result to solve for $N_K(t)$.

Question 2c. Finally, use the constraint in Equation 4 to write an equation for the lifetime of the rock, t, in terms of the ratio $\frac{N_{Ar}}{N_K}$.

The Age of the Galápagos

Potassium-argon dating has been used in several real-world contexts central to the themes of this course. When we are in the Galápagos, our guides will tell us about the ages of islands we visit. But how are these numbers known, and what evidence substantiates these claims when naturalist guides make them? The ages of the islands were first reported in a 1976 paper by Kimberly Bailey, where she used potassium-argon dating on samples from Santa Cruz, San Cristobal, and Española.[10] In this section, we'll take a closer look at her original data.

Question 2d. Read Bailey's paper and give a brief, 1 paragraph synopsis of her approach and findings.

Unfortunately for us, real-world K-Ar data is generally not neatly presented in the form of N_{Ar} and N_K. Instead, geologists often measure a concentration of ^{40}Ar in mol/g and a weight percent of K_2O. From there, the data must be converted appropriately in order to identify the number of ^{40}Ar and ^{40}K nuclei in the sample. For ^{40}K, this involves (1) using the weight percentage and the total mass of the sample to find how much K is present, and (2) accounting for the isotopic abundance of ^{40}K, because most K is found in the stable ^{39}K and ^{41}K isotopes. You may let $\frac{^{40}\mathrm{K}}{\mathrm{K_{total}}} \approx 1.2 \times 10^{-4}$ and $\lambda \approx 5.8e - 11yr^{-1}$.

Question 2e. Using the results from Table 1 of Bailey's paper for samples H70-130 and JD1088 (from the first row for each), determine the ages of Santa Cruz and Santa Fe Island. You will need to navigate some of the subtleties noted above.

[10]**bailey_potassium-argon_1976**.