

Bi/Ge 105: Evolution

Homework 2

Due Date: January 21, 2026

“I am losing precious days. I am degenerating into a machine for making money. I am learning nothing in this trivial world... I must break away and get out into the mountains to learn the news.”

John Muir

1. A feeling for the numbers in evolution, continued

Once again, we begin our discussion of evolution with a series of order-of-magnitude estimates. Whereas last time we explored some very “big” phenomena — like the movement and colonization of entire islands — today we will begin with the very small: cells, molecules, and atoms. As always, 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.

Viruses: Everything Everywhere All at Once

Viruses, by definition, are incapable of independent replication; they must infect a host in order to hijack its biomolecular machinery and propagate themselves. This leaves their classification in a no-man’s-land, somewhere between inert and living matter. That said, viruses are very much alike all other known life in that they possess nucleotide genomes — whether DNA- or RNA-based — that encode much of the information necessary for their existence. Moreover, some viruses are even capable of integrating into their host’s genomes; indeed, a nontrivial fraction of *your* genome consists of vestigial endogenous

retroviruses!¹ In the words of Lewis Thomas, “The viruses, instead of being single-minded agents of disease and death, now begin to look more like mobile genes.”² In the following problems, we will get a sense of the incredible abundance of viruses on Earth, as well as their crucial role in shaping genomes and evolution.

Question 1a. Viruses are found in almost every imaginable environment on Earth. In seawater alone, there are perhaps 10^6 virions/mL. (A virion is a viral particle, i.e. a single “individual”.) Given that the radius of the Earth $R_\oplus \approx 6 \times 10^3$ km, estimate the volume of the global ocean and hence the total number of virions it contains.

Most sources estimate that there are 10^{31} virions globally. This makes them the most abundant biological entities on planet Earth — beating prokaryotes, the next largest population, by a factor of 10 — and hence also the world’s largest reservoir of genomic information. This motivates another question: how thoroughly have Earth’s viruses explored the space of *possible* genomes?

Question 1b. How many unique viral genomes have existed in the history of life? State clearly and justify any assumptions you make to arrive at your answer. Assuming that viral genomes are 50,000 nucleotides in length, how does this compare to the total number of possible viral genomes?

Astronomical Proteins

Question 1c. How many different 300 amino acid proteins are possible? If you were to synthesize one copy of each, what volume would the resulting ball of proteins occupy? Look up the estimated size of the known universe and compare.

Mutations at the Large N Limit

Mutations are one of the main genomic ingredients of evolution. Even though the probability of a single mutation may be very rare, we will once again see that the picture can change once we consider large populations or long timescales.

¹For completeness, we note that while the word “virus” may conjure images of human disease in everyday speech, most viruses actually infect bacteria; such viruses are called *bacteriophage*.

²Thomas 1974.

Question 1d. Much like mice or fruit flies, the bacterium *Escherichia coli* is a model organism commonly grown in research labs. It is capable of rapid replication, with doubling times as fast as 20 minutes, and has a genome roughly 4 million base pairs in length. Consider a tube containing 5 mL of *E. coli* grown overnight in liquid culture. Starting from a single cell, how many cells are in the culture after 12 hours? Given that bacterial mutation rates are of order 10^{-9} mutations per base pair per replication, how many single base pair mutations do you expect to find here? Thus, how many times is each distinct possible point mutation represented?

Nanoscale Expeditions

The history of biology is filled with stories of great naturalist voyages: Humboldt, Darwin, Wallace, Huxley, Hooker, and others all traveled the world in search of biological discovery. But what about our exploration of the nanoscale?

Humanity's first forays into the microscopic world were made possible by optics invented in the 17th century by pioneers such as Robert Hooke and Antonie van Leeuwenhoek. Later, the development of electron microscopes — fantastically powerful tools with nanometer resolution — pushed the envelope of what we can see even further, past the optical limit imposed by light.

Question 1e. A typical electron micrograph corresponds to an area roughly $10^3 \mu\text{m}^2$. Estimate the total area humanity has viewed using electron microscopes in the entire history of science. What do you conclude about the extent to which we have “explored” our planet at the nanoscale?

Speciation

A great controversy in the history of evolutionary theory was the question of whether the Earth was old enough to accommodate evolution in the first place. Lord Kelvin argued that the Earth was only millions of years old, and that this was insufficient for the slow process of evolution to have occurred. Although we now know Kelvin's estimate was wrong, it is interesting to consider how long it might take for a new species to evolve from an existing one.

For example, we know that modern whales — such as the blue whale, the largest animal that has ever lived — evolved from a small terrestrial mammal that lived at the time of the extinction of the dinosaurs, some 65 million years ago. What would it take to achieve such stupendous size?

Question 1f. *Rodhocetus* and *Basilosaurus* are two extinct species of early

whale. By figuring out when they lived, how big they were, and their typical generation times, estimate the average change in body length per generation needed to evolve from *Rodhocetus* to *Basilosaurus*. Remark on the magnitude of your answer with reference to modern blue whales.

2. Evolution in the Anthropocene

Today, humans are arguably the world's greatest evolutionary force (Figure 1). Throughout the course, we will discuss the myriad ways in which this is the case — from the rise of antibiotic resistance, to the conversion of vast tracts of old-growth forest into agricultural land. We have also changed the face of the biosphere by altering the distribution and populations of animal species by selective breeding, habitat change, and even direct hunting. In the following problems, we will get a glimpse of the magnitude of those changes.

Question 2a. By reasoning about the modern human diet, estimate the total modern biomass of domesticated cattle. How does this compare to the total modern biomass of all wild terrestrial mammals (20 Mt)?³

Question 2b. Before the rise of fossil fuels in the mid-20th century, commercial hunting killed roughly 3 million whales. How much biomass does that represent?

Large baleen whales (like humpbacks, fin whales, and blue whales) predate mostly upon krill, a tiny crustacean found in great abundance in Earth's polar oceans. Recent measurements and models suggest that an individual whale can consume about 10 t of krill every day when feeding in the summer months.⁴

Question 2c. By reasoning about the relationship between your diet and defecation, and using the information above, estimate the mass of feces produced by a whale each year. Thus, how much whale feces was “removed” from the global ocean due to whaling? Comment on your findings, considering that feces (i.e. manure) are rich in nutrients.

³Greenspoon et al. 2025.

⁴Savoca et al. 2021.



Humans as the World's Greatest Evolutionary Force

Stephen R. Palumbi

In addition to altering global ecology, technology and human population growth also affect evolutionary trajectories, dramatically accelerating evolutionary change in other species, especially in commercially important, pest, and disease organisms. Such changes are apparent in antibiotic and human immunodeficiency virus (HIV) resistance to drugs, plant and insect resistance to pesticides, rapid changes in invasive species, life-history change in commercial fisheries, and pest adaptation to biological engineering products. This accelerated evolution costs at least \$33 billion to \$50 billion a year in the United States. Slowing and controlling arms races in disease and pest management have been successful in diverse ecological and economic systems, illustrating how applied evolutionary principles can help reduce the impact of humankind on evolution.

Human impact on the global biosphere now controls many major facets of ecosystem function. Currently, a large fraction of the world's available fresh water, arable land, fisheries production, nitrogen budget, CO_2 balance, and biotic turnover are dominated by human effects (1). Human ecological impact has enormous evolutionary consequences as well and can greatly accelerate evolutionary change in the species around us, especially disease organisms, agricultural pests, commensals, and species hunted commercially. For example, some forms of bacterial infection are insensitive to all but the most powerful antibiotics, yet these infections are increasingly common in hospitals (2). Some insects are tolerant of so many different insecticides that chemical control is useless (3). Such examples illustrate the pervasive intersection of biological evolution with human life, effects that generate substantial daily impacts and produce increasing economic burden.

Accelerated evolutionary changes are easy to understand—they derive from strong natural selection exerted by human technology. However, technological impact has increased so markedly over the past few decades that humans may be the world's dominant evolutionary force. The importance of human-induced evolutionary change can be measured economically, in some cases, and is frequently seen in the exposure of societies to uncontrollable disease or pest outbreaks. Attempts to slow these evolutionary changes are widespread but uncoordinated. How well do they work to slow evolution? Can successes from one field be generalized to others?

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The Pace of Human-Induced Evolution

Paul Müller's 1939 discovery that DDT killed insects won him the 1948 Nobel Prize, but before the Nobel ceremony occurred, evolution of resistance had already been reported in house flies (3, 4). By the 1960s, mosquitoes resistant to DDT effectively prevented the worldwide eradication of malaria (5), and by 1990, over 500 species had evolved resistance to at least one insecticide (6). Insects often evolve resistance within about a decade after introduction of a new pesticide (7), and many species are resistant to so many pesticides that they are difficult or impossible to control (3). Similar trajectories are known for resistant weeds (8), which typically evolve resistance within 10 to 25 years of deployment of an herbicide (Table 1).

Bacterial diseases have evolved strong and devastating resistance to many antibiotics. This occurs at low levels in natural populations (9) but can become common within a few years of the commercial adoption of a new drug (Table 1). For example, virtually all Gram-positive infections were susceptible to penicillin in the 1940s (2, 10) but in hospitals today, the vast majority of infections caused by important bacterial

agents like *Staphylococcus aureus* are penicillin-resistant, and up to 50% are resistant to stronger drugs like methicillin (11). Treatments that used to require small antibiotic doses now require huge concentrations or demand powerful new drugs (10). But such solutions are short-lived. For example, vancomycin, one of the only treatments for methicillin-resistant infections, has been overcome by some of the most frequent infectious agents in hospitals (2, 12). Antibiotics also generate evolution outside hospitals. Resistant strains are common on farms that use antibiotics in livestock production (13) and have been found in soils and groundwater affected by farm effluents (14).

Retroviruses with RNA genomes evolve even more quickly than bacteria (15). Every year, vaccinations against influenza must be reformulated, making prediction of next year's viral fashion one of preventative medicine's chief challenges (16). The virus that causes AIDS, human immunodeficiency virus-1, evolves so quickly that the infection within a single person becomes a quasi-species consisting of thousands of evolutionary variants (15). Over the course of months or years after HIV infection, the virus continually evolves away from immune system sup-

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Table 1. Dates of deployment of representative antibiotics and herbicides, and the evolution of resistance. [Source (75)].

EVOLUTION OF RESISTANCE TO ANTIBIOTICS AND HERBICIDES

Antibiotic or herbicide	Year deployed	Resistance observed
Antibiotics		
Sulfonamides	1930s	1940s
Penicillin	1943	1946
Streptomycin	1943	1959
Chloramphenicol	1947	1959
Tetracycline	1948	1953
Erythromycin	1952	1988
Vancomycin	1956	1988
Methicillin	1960	1961
Ampicillin	1961	1973
Cephalosporins	1960s	late 1960s
Herbicides		
2,4-D	1945	1954
Dalapon	1953	1962
Atrazine	1958	1968
Picloram	1963	1988
Trifluralin	1963	1988
Triallate	1964	1987
Diclofop	1980	1987

Figure 1: The first page of Palumbi 2001.