Chapter 1
Ecological Thinking

"The Universe Is A Single Flower"

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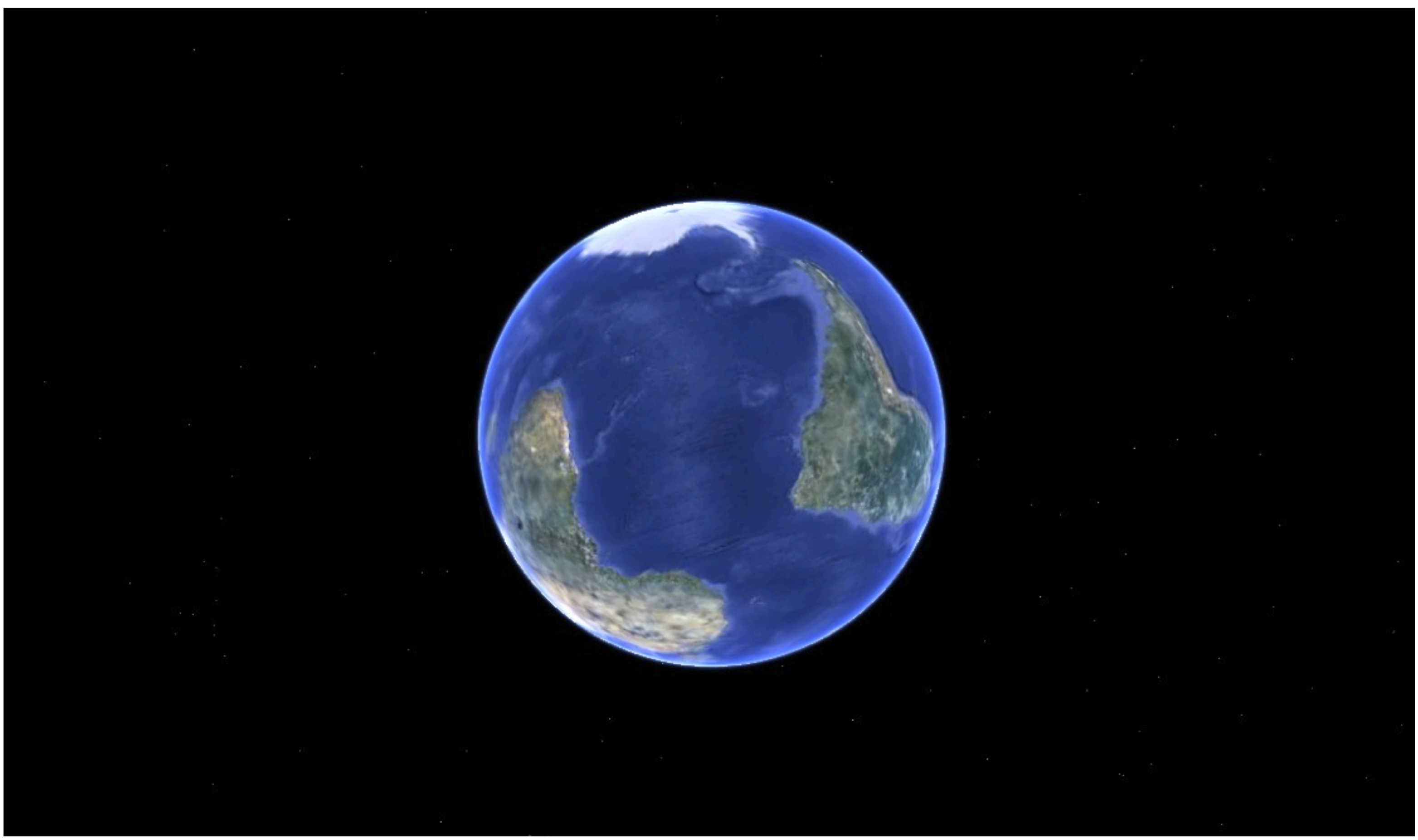


Why is Earth blue, green, brown and white? What are the consequences of this variation? What are the rules governing its inhabitants, their relationships with each other, and their relationships with the physical environment? How do these things change over time? All these questions are the subject of *ecology*, and this chapter describes the basic ways of how ecologists think about these questions.

DEFINING ECOLOGY

If you looked up “Ecology” on Wikipedia, as I did, one day in May of seasons past, you would have seen this introductory statement:

*“**Ecology** (from Greek: οἶκος, "house"; -λογία, "study of") is the scientific study of the relations that living organisms have with respect to each other and their natural environment.”* (Wikipedia, accessed 18 May 2012).

This parallels closely definitions proposed by several esteemed ecologists, and I think it is a great starting place. Almost every word in this definition has a rich panoply of layers and ideas connecting it to other ideas. Let us now explore several pieces of the definition.

Ecology Is The Study Of Relations

All life is connected to some other life and to the physical environment. If you take nothing else away from this book, I hope it is that ecology is the study of connections and relationships. There are many types of relations in ecological systems (Figure 1.1).

[Figure 1.1. *Ecology is the study of relations.* An entire multi-page fold-out of a beautiful montage of photographs and hand-drawn details, including smaller webs within, and influenced by state factors such as temperature. Solid arrows describe consumptive relations or fluxes between pools, and dotted arrows connect state factors to fluxes. The fluxes and pools represent carbon. Include death and decay as well as beauty and rebirth. It has to be visually stunning and intriguing--the best image in the book.]

One of the most profound types of connections is a *feeding* relation, between a *consumer and its resource*. All organisms consume resources, because each of us requires them--indeed, a wide variety of them--to build new constituent parts. You need calcium to build strong bones and a snail needs it to build a strong shell, but you both also need a wide variety of other nutrients. Sometimes, the consumed resources are inorganic molecules, as when a plant takes up carbon dioxide from the atmosphere (Fig. 1.1). Other times, the consumed resources are organic, as when a tropical leaf-cutter ant consumes fungus that it grew in its colony's garden (Fig. 1.1).

Exercise 1.x. Identify three other potential feeding relations in Fig. 1.1. Identify the resources (inorganic chemicals, hosts, or prey), and the consumers.

Ecology Is The Study Of Organisms And The Environment

Ecology the study of *organisms*, and in that sense, makes it a biological science. Ecology integrates all levels of biological organization (O'Neill *et al.* 1986), including the smallest molecules, cells, tissues, individuals, ecosystems, populations, communities, and landscapes, all the way up to the entire biosphere of Earth. To the extent that organisms are products of their genes, the environment and gene-by-environment interactions, genes play a central role in shaping the physical environment. A quick perusal of the online literature will reveal ecological topics in journals such as *Genetics* or *Heredity* and genetic topics in journals such as *Ecology* and *Journal of Ecology, and Ecology Letters*. Ecology also encompasses the study of dead organisms, because death and decay of organisms brings life and renewal to ecosystems.

Ecologists study the environment in which organisms live. The physical environment may be the focus of research --the response variable-- as when water clarity and transparency is the focus of in Lake Tahoe (CA, USA) (Fig. 1.2). Alternatively, the environment be a driver or cause of ecological change --an independent variable-- as when ecologists study how changes in climate (precipitation and temperature) influence the prevalence of a particular disease --a response variable-- such as malaria (Hay *et al.* 2002). On the other hand, the physical environment may be more in the background, if someone is trying to describe simply the variety of *Plasmodium* species transmitted by one of its mosquito vectors (Kim and Tsuda 2010). Regardless of whether the physical environment is studied explicitly, it is always present, and always provides context.

[Figure 1.2. Lake Tahoe water clarity has declined over time. Here the independent variable is depth, and the dependent, or response variable is visible light, as a fraction of light hitting the surface of the water. We typically refer to the causative factor as the *independent variable*, and the response as the *dependent variable*.]

The environment also includes the living, or *biotic*, environment (Fig. 1.1). The environment for *Culex pipens* (one of the mosquitoes that transmits malaria) includes the air temperature, the density of possible hosts from which females acquire their blood meal, bodies of water for laying eggs, the ratio of hosts infected and uninfected with *Plasmodium*, predators of adult flying mosquitoes, such as bats, birds and dragonflies, predators of the aquatic mosquito larva, *etc.* The environment is everything, both biological (biotic) and physical (abiotic) that is external to the organism of study.

Ecology Is Scientific

Of course you realize that ecology is a scientific discipline, but what does that mean? Ecology shares many features with the other natural sciences.

Science in general is the process whereby we create *more and more useful and predictive descriptions of the physical*[1] *universe*. Scientists take the position that there is a physical universe that is real. Thus, we assume that there is an external reality that includes you and me, the trees, and the stars. This is an important assumption. Science is the evidence-based endeavor to describe and explain this external reality. In this sense, no part of science is actually "the truth," but rather, different scientific disciplines strive toward more and more useful descriptions and explanations of a part of the external reality (Fig. 1.3).

[Figure 1.3. An schematic of an external and unknown reality, data (measured quantities of that reality), a scientist's head (inside of which resides a brain filled with descriptions and explanations), and a journal article which contains a small part of what is in the scientist's head and data]

Ecology uses methods common to many other sciences, and we discuss some of these in the next section in "The Logics Of Ecology." First, it uses set theory, formal logic, and probability theory as the basis of its underlying inductive and deductive logic (Jayne 2003). We also use every method imaginable to observe and describe the world. We use a wide variety of laboratory methods, such as those associated with genomics, proteomics, or physiology. We use field procedures and equipment that you might associate with agriculture or forestry, such as tractors and plows, chain saws or bulldozers. We use mathematics, borrowing from and occasionally contributing to other disciplines with a rich history of mathematics, such as physics (Cohen 2004).

Ecology is also scientific insofar as *science is a social process*. It is a social process because when people engage in it, they *compete and collaborate,* and this competition and collaboration is part of the power of modern science to progress rapidly and also be self-correcting. We discuss this social side of scientific collaboration and competition throughout the book, and focus on it especially in the next chapter.

[1] By 'physical' I mean the Universe that is possible to observe, in principle. Other people prefer the term 'natural' as in contrast to 'supernatural' which is beyond the physical, measurable, observable universe. In contrast to science, religious belief systems typically require a faith in a supernatural force or deity.

At one level, ecology is what ecologists do. What do we do? Here are just a few examples:

• we learn from the work of others, • synthesize information, • describe patterns, test hypotheses, • measure effects and rates of processes, • use mathematics to propose unambiguous hypotheses, combine information from direct observations and the work of others, • communicate our findings and ideas to our colleagues, • write papers, give presentations, talk with (other) students, • Go to parties and receptions,	• talk to politicians, • write grant proposals, • run gels, • watch grass grow, • program computer simulations, • do lab experiments, • do field experiments, • go hiking, fishing, and hunting, • drill holes in the ground, • build fences, • plow fields, • take pictures, • use our imaginations

The next time you meet an ecologist, ask "So,...what do *you* do?

Ecology Has Ancient Roots

I argue that Ecology is the oldest and most important discipline in the natural sciences (Egerton 2012), and yet many people consider ecology among the youngest sciences. A starting place for my argument is that *Homo sapiens sapiens* has always struggled to find food, mates and shelter, and in this struggle we learned about our world. Entire hominid hunter-gatherer groups and societies survived or died out depending on their ability to find, collect, and manage food resources and adjust to their environment. The understanding of the distribution and abundance of prey and other resources is what allowed what allowed populations of *Homo habilis* and other hominids to persist. Indeed, many have defined ecology as the "scientific study of the distribution and abundance of organisms and the interactions that determine distribution and abundance" (Begon et al. 2006). While we might quibble--nay, bicker!--about whether *H. habilis* studied the world in a scientific manner, one thing is clear: without the knowledge of where food was and the ability to predict where it would be, we would not be around today to quibble about the definition of "ecology." Certainly our prehistoric ancestors studied their environment in very careful and methodical manner, and developed increasingly useful and predictive ideas about the natural world. While some will argue that that practice it is not strictly science, it seems about as close as we can get to natural science, without a calculator.

As an example, agriculture is an ancient subdiscipline of ecology. It is the application of very specific knowledge about consumer-resource relations, natural history, climatology, plant-animal interactions, mutualisms, competition, herbivory, all focused on a very small number of species.

More recently, the academic discipline of ecology emerged out of a field called *natural history*. Natural history is the careful observation and description of specific details of the natural world. The core of modern biology, evolution, came into being via the patient and persistent study of organisms over several decades, by the greatest known natural historian, Charles Darwin. His focused attention to the details of both wild and domestic organisms, including both their structure and behavior, allowed him to gain insights that none others had (Fig. 1x.). In addition, his massive compilation of of details provided the *evidence* needed to support his ideas. Without this evidence, his idea would have been relegated to the dustbin of history, awaiting discovery by someone else. The natural history of organisms provided the evidence to support the ideas.

[Fig. 1.x. Figures from *On The Origin Of Species.*]

Throughout this book, we will be describing ecological studies wherein the natural history of organisms play pivotal roles. Be alert for these, and strive to see how they support and inform ecological ideas on relationships between organisms and their environment.

BIG IDEAS IN ECOLOGY

Ecology is a thrilling discipline that is expanding rapidly. What are some of the exciting things ecologists study? Here is my short list of highlights.

Life

Maybe the biggest idea in ecology is *life* itself. When you study ecology, everything you ever learned and will ever learn in biology can be important. Different kinds of ecologists study life in different ways, peering at it through different lens. A physiological ecologist may study the growth or metabolic rate of an individual whereas an ecosystem ecologist may study productivity of an entire forest. In either case, the ecologists might be measuring similar things, such as carbon gain per unit time, or CO_2 and O_2 exchange. A population ecologist might measure fecundity as the number of eggs laid, seeds produced, or doubling time of bacteria. All of these ecologists are measuring life and its renewal. Death is intrinsic to life, so ecologists spend a tremendous amount of time and energy studying the causes and consequences of mortality. The death of one organism brings life to others, and thus is all of life interconnected.

[Figure 1.4. Graphs of pulled from the literature, with corresponding images showing gas fluxes, productivity, and mortality.]

As ecology is the science of life, writ large, we ask questions about its maintenance and spread:

- How deep into Earth's mineral crust does life extend, and how does it persist *far* below Earth's surface *(*Kallmeyer *et al.* 2012)?
- Why do species that evolved in one part of the world sometimes become wildly successful and invasive in different parts of the world (Petitpierre *et al.* 2012)?
- What is the minimum set of components required for a self-sustaining life support system for interstellar travel?[2]

These and an infinite number of other questions will continue to drive ecologists in their pursuit in

[2] http://www.b2science.org/

understanding the causes and consequences of life.

Consumption

All of nature is an enormous economy (Vermeij 2012, Ricklefs 2012), in which agents seek resources, and share goods. All of life can be perceived through this lens of consumption. Organisms possess an infinite variety of adaptations that enable them to search for and capture these resources, to cope with shortages, and to sequester surplus. Consumerism was not invented by people, but rather is the stuff of life itself. This constant search for resources has consequences: consumers compete for shared resources, and victims succumb to predators, pathogens, and parasites. Lord Tennyson referred famously to "...Nature, red in tooth and claw" for good reason: it's a rough world out there. Nature is an economy where organisms seem to compete endlessly, and where mortal enemies come in all shapes and sizes. The Red Queen Hypothesis (Van Valen 1973) states that life is so difficult, populations are in a constant arms race against their enemies and competitors, constanting evolving *just to avoid extinction*.[3]

[Figure 1.5. Graphs of pulled *from the literature* with corresponding pictures of organisms showing trait variation and differential resource acquisition, predator-prey cycles, and disease outbreak.]

What do organisms consume, and how do they avoid becoming someone else's lunch? Ecologists are asking these and other questions:

- To what extent are populations limited by multiple resources at once, or are they just limited by one resource at any point in time (Barantal *et al.* 2012)?
- How important are top predators for entire ecosystems (Estes *et al.* 2011)?
- How successful are an organism's defenses, and how much do they cost to maintain (Parker *et al.* 2011)?
- What can we learn from successful defenses that can be applied to the national security of nations (Sagarin *et al.* 2010)?

Consumption, in all its guises, plays a central role in most subdisciplines of ecology.

Exercise 1.x. Identify in Fig. 1.1 three pairs of interactions between consumers and their resources or prey.

Exercise 1.x. Identify in your own diet five different species of organisms that you consume. ("Vegetable" is not a species; "spinach" is a species.) Of these five, are there any that are essential?

Cooperation

In the face of the ruthless economy, life thrives and diversifies, but how? It turns out that cooperation is a big part of the answer (Nowak 2006, 2012, Leigh 2010). Consider for a moment that life itself relies on

[3] The name of this hypothesis comes from Lewis Carroll's *Through The Looking Glass.* Alice and a chess piece, the Red Queen, had been running very hard, but not moving from underneath a tree. Alice expressed surprise about running hard but staying in place, and the Red Queen responded "Now, *here*, you see, it takes all the running *you* can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!"

the cooperation of atoms, molecules (including genes), and organelles to form functional cells, and, for multicellular organisms, those cells and constituent tissues cooperate to create functional individuals. Individuals often cooperate for the purpose of sexual reproduction or bacterial conjugation.

[Figure 1.6. Pictures of coral mutualists and coral habitat, and mycorrhizal associates and forests.]

Mutually beneficial interactions between species --mutualisms-- abound in nature, and give us major habitats of the world. Corals, which create diverse and beautiful shallow marine habitats, are based upon a symbiotic cooperation between photosynthetic protozoans (*Symbiodidinium* dinoflagellates) and animals (cnidarians). The dinoflagellates are able to share their excess photosynthate (sugar) with the cnidarians, which in turn share typical animal waste (e.g., ammonium and carbon dioxide) with the dinoflagellates. The vast majority of plant species around the world rely on mycorrhizal fungi to expand their root networks, and provide much needed nutrients and water from the soil. Those fungi receive sugar (photosynthate) in return. In some cases, these fungi provide protection from pathogens and herbivores. Thus are supported major forests, shrublands and grasslands of the world, enabling their existence and enhancing their productivity. Ants and humans, two of the most dominant animal groups the planet has ever seen, both rely profoundly on cooperative, altruistic behavior.

What are we to make of all this? How is it that life involves both cooperation and competition? Ecologists are asking questions such as these:

- How do fungus-plant mutualisms aid a plant's resistance to pathogens (Jani *et al.* 2009)?
- What are the emergent properties of a wolf pack (Muro *et al.* 2011)?
- How many species, aside from humans, rely on reputation (indirect information regarding fitness) to structure mating and other social interactions (Nowak 2006)?
- What lessons from Nature can we use to help human societies avoid the Tragedy Of The Commons (Barker *et al.* 2012)?

The tension, between cooperation and competition, mutualism and consumption, or friends and enemies, provides an important backdrop in the theater of life.

Exercise 1.x. In Figure 1.1, identify three examples of cooperation, either between species or within a single species.

Exercise 1.x. Identify four behaviors in your own life that are cooperative.[4] For each behavior, list costs and benefits of the cooperation.

Biodiversity

One of the most amazing aspects of the natural world is its seemingly endless variety of life forms. There are 2 million nonmicrobial species on the planet...or maybe 50 million. Sadly, we don't know, although

[4] Note that holding a door open for someone is cooperation: it costs you energy to change the forward direction of your momentum, hold the door, and apply force to initiate forward momentum. It also costs time lost toward doing other activities.

we are trying to figure it out (Scheffers et al. 2012, Naeem et al. 2012). At least as troubling is that we don't even know *how* to count the millions of different species of bacteria.

[Figure 1.7. Figures from the literature showing variation in diversity and pictures showing a variety of organisms from different habitats, including something from the human microbiome project.]

Each separate species is unique and, by definition, are sufficiently different from other species to prevent successful reproduction. In addition to the variety of species, individuals within each species are genetically distinct. The biological variety on this planet is beyond our comprehension, though we try our best. Many ecologists are seeking to understand the causes and consequences of biodiversity, and to answer questions such as these:

- How many species inhabit Earth (Scheffers et al. 2012)?
- Why do the tropics have so many more species than the temperate and polar regions (Mittelbach *et al.* 2007)?
- How much of Earth's ecosystem services depend on the variety of species and their functional traits (Cardinale *et al.* 2012, Naeem *et al.* 2012)?

The variety of life --biodiversity-- is a fundamental characteristic of life, and ecologists are trying to understand its causes and consequences.

Exercise 1.x. In Figure 1.1, count the number of different species that you can see.

Exercise 1.x. (a) In your own daily life, identify the most biologically diverse habitats you *see directly* on most days. For instance, if you drive past a nature preserve on your way to work or school, or walk past a patch of woods or a stream, that may be the most diverse habitat you *see* that day. (b) Identify the least diverse area in your live (perhaps you study or work in a room with no windows and no plants). (c) What fraction of your waking hours is spent out of sight of non-human species?

Our Lonely Little Biosphere

Humans have recently entered a new era that some are calling a new geological epoch, the *anthropocene* (Steffen *et al.* 2004, Biermann *et al*. 2012). Humans now occupy more than half of Earth's land surface (Ellis and Ramankutty 2008), and shape global climate (Steffen *et al.* 2004). Our little blue planet is floating out in our solar system, containing the only life we know. That life is smeared as thin film on only the moist outer surface. The diameter of Earth is almost 6400 km and the thickness of the biosphere is about 15 km, from subsurface sediments in the ocean to the atmosphere and alpine tundra. That means our biosphere is about 0.23% as thick as Earth. In contrast, the peanut butter on my sandwich in front of me right now is about 20% as thick as the piece of bread I spread it on. This means that the biosphere is 100 times thinner than my peanut butter, and, unlike my peanut butter, our biosphere is floating around alone in a galaxy otherwise devoid of life (as far as we know). Humans are now the dominant species on this lonely thin biofilm.

[Figure 1.x. Figures of great white shark, tropical rain forest, the Gulf Stream]

Ecologists are studying this global biofilm at large scales, like never before. We collaborate to collect data with people and from sensors deployed all around the planet. We use these data in more and more comprehensive computer simulation models to try to understand climate, biodiversity, and ecosystem services from the scale of a single bacterium to the entire globe. We try to predict future scenarios and try to predict the uncertainty itself. Global ecologists are asking many of the same questions listed above, but now we are starting to do it across the entire planet. In addition, global scientists are asking questions specific to the global scale:

- Can we begin to learn how sharks and fish connect the world's oceans (Block 2005)?
- Will a warming planet cause the Gulf Stream to release vast amounts of methane into the atmosphere (Phrampus and Hornbach 2012)?
- How do rainforests help regulate Earth's hydrological cycles (Spracklen *et al.* 2012)?
- Which of the planet's coral reefs will disappear due the acidification of Earth's oceans (Cooper *et al.* 2012)?
- Along with earthworms and ants, humans are one of the great animal ecosystem enginneers - how can we use this capacity to protect our lonely biosphere (Foley *et al.* 2011)?
- Does Gaia exist (Moody 2012)?

It is an exciting time to be an ecologist, as more and more of the sciences are focusing on planet-level questions with clear application to both human and nonhuman life.

Exercise 1.x. Use Google Scholar™ to search for articles on global change. Look through at least three pages of results, and write down the titles of three peer-reviewed (scholarly) papers (not books). Choose one of the papers, and print or copy by hand the abstract of the paper. Write a two sentence summary of the abstract.

Laws Of Mass And Energy

Of course life obeys the physical laws of the universe. However, ecologists are still discovering just what that means. An ecologist is an unusual type of physical scientist because we study how physical laws shape organisms and their relationships with their environments. The laws of physics and chemistry apply as much to life as they do to wave-particles, atoms, and molecules. The laws of thermodynamics, the conservation of mass and energy, and the physical and spatial structure of organisms and the systems they live in govern life at least as much the emergent properties of self-replication, consumption, and cooperation.

[Figure 1.8. probability clouds of electrons in atoms, metabolic scaling law (O_2 *vs.* mass), greenhouse effect]

Physical laws are important in two ways. First, they are important because they provide inviolate rules, such as

- Metabolism uses up energy, and an organism must consume calories in order to live and grow (Brown *et al.* 2004).
- The ratio of chemical elements in an organism must be a function of the elemental ratios of inflows and losses (Sterner and Elser 2002).
- radiant energy trapped by atmospheric gases is a function of the energy inflows and the chemical

composition of the atmosphere (Steffen *et al.* 2004).

Inviolate rules such as these may either provide an answer to an ecological question, or provide a solid foundation upon which to investigate the consequences of life's causes and consequences. For instance, ecologists are asking,

- How do pathogens and the diseases they cause influence energy expenditure and overwintering survival of hibernating animals (Reeder *et al.* 2012)?
- How does body mass of predator and prey determine the behavior of populations and food webs (Brose 2010)?
- How important to arctic warming is the positive feedback loop between vegetation growth and carbon dioxide concentration in the atmosphere (Chapin *et al.* 2005)?

Nearly all questions in ecology rely on assumptions made about the physical world. Ecology is the science that studies the relationship of life to the physical world.

[Figure 1.x. Photos and data graphs related to the above three topics.]

Another more subtle reason that physical laws are important is that the mathematical and conceptual methods we use to study atoms and energy can often be applied to organisms and ecological processes. The mathematics of describing these physical laws have made important contributions to the understanding of life, not only because life is constrained by the physical universe, but because modes of conceptual and abstract thinking inherent in mathematics are fertile ground for ecologists (Cohen 2004). Mathematics provides a mode of formal logic that allows us to understand and predict the consequences of biological assumptions.

Exercise 1.x. Of Mice And Humans.
a. Before looking back at the above figures, guess how many more calories you burn per unit time than a mouse - 10 times? 100 times? 1000 times?
b. Use Fig. 1.x to estimate more accurately how many more calories you burn.
c. Use this expression, Kcal = $a\,M^{0.75}$, to estimate the calories burned by you and a mouse: Let a = 75; assume a mouse weighs 0.030 Kg. Figure out your mass in Kg, and find the ratio of your Kcal burned to the mouse's Kcal burned.[5] The answer to this is the ratio is how much more food you need to consume than a mouse (assuming that the mouse is sitting on a couch studying ecology).

Exercise 1.x. Estimate energy consumption of three different species in Fig. 1.1. To do this, first select three species. Use a reputable source such as Wikipedia to identify approximate masses. Last use the above formula to estimate energy consumption.

THE LOGICS OF ECOLOGY

Ecologists are used to thinking very logically, using ideas about systems, formal logic, and probability. In this section, we work through some core ideas in all of these areas. In addition, they all have a firm

[5] For me, the ratio is about 360 Kcal/Kcal

grasp of basic biology and evolution. We introduce evolution here, but take it up at greater length in later chapters.

Evolutionary Biology

An ecologist is a type of biologist because we the products of evolution. "Nothing in biology makes sense except in the light of evolution," so wrote Theodosius Dobzhansky[6] (Dobzhansky 1973). These are words one often hears among scholars and students of biology.

The processes of evolution provide the means by which all of life has come to be, and as such, provides ecologists with a sort of biological logic. First, evolution gives rise to an organism's *natural history*, the unique details of which provide the biological basis of ecology. Second, evolution gives rise to *shared similarities* among different types organisms, in processes such as convergent evolution and adaptive radiation, wherein a single population can give rise, relatively quickly, to a variety of new species that fill once vacant niches. Adaptation radiation has been shown to occur in a wide variety of organisms, from bacteria to birds. Third and finally, evolution gives us a *constantly shifting foundation* upon which to study organisms. This is *constantly shifting* because evolutionary processes are resulting in organisms whose traits are constantly changing in both subtle and not so subtle ways. It is a *foundation* because the processes and mechanisms of evolution, including genetic drift, natural selection, and speciation, are permanent features of life on Earth, and probably elsewhere in the universe.

[Figure 1.x. Convergent evolution of cacti and euphorbs, and fur and feathers. Adaptive radiation in Darwin's finches, and Rainey's *Psuedomonas*.]

The famous ecologist G.E. Hutchinson used the metaphor of "the ecological theater and the evolutionary play" to convey how ecology and evolution complement each other. Evolution is both simple and profound, and we devote many pages to some of its simpler ideas as they apply to ecology.

A Very Brief Introduction To Systems Thinking

Ecologists think about ecological systems, and we sometimes refer to this as "systems thinking" because we have to study how all the parts interact with each other (Meadows 2008, O'Neill et al. 1986, Bertalanffy 1980). This type of thinking, about connections and relationships among many different elements appears to be relatively unusual among biologists, whereas it is central for ecologists.

[Figure 1.9. depicting images of organisms, including a human,
and with a stock and flow diagram, labelling elements and surroundings.]

A *system* can be defined as one or more *elements* within *surroundings*. By definition, *open systems* exchange energy, matter, or information with their surroundings and *isolated systems* exchange nothing with their surroundings. Ecologists always study open systems and often study multiple, connected systems. All ecological systems have internal complexity and interact with their surroundings. Ecologists

[6] The title of a famous essay (http://en.wikipedia.org/wiki/Nothing_in_Biology_Makes_Sense_Except_in_the_Light_of_Evolution)

refer to these surroundings as "the environment." Your body (Fig. 1.9) is one big complex system composed of many smaller complex systems, such as your gastrointestinal and circulatory systems. Food enters you via one source (your mouth) and enters at a rate that is controlled by the external environment and your behavior. The food that you do not retain exits directly or indirectly via your lungs, skin, anus and urethra. Food that you retain adds to your mass. *You* have internal complexity and are composed of many smaller systems. You are also a part of larger systems, including the entire Earth system. To an ecologist, anything that she studies, such as Earth as a whole, or an individual human, a population of oak trees, or a bacterial biofilm are all open systems.

Ecologists understand implicitly that the entire world is a great big messy, very, very complicated system, composed of many, many, many smaller systems (Figure 1.1). In Appendix A, I introduce systems thinking in a bit more detail, but here we get started. Here are a few ideas about systems that you will probably find useful:

- Systems have structure and behavior.
- Models of systems are useful simplifications of real systems.
- Ecological systems are hierarchical: they are composed of nested subsystems.

While not every ecologist uses *systems theory* in an abstract sense, we all understand some basic ideas about systems.

[Figure 1.10. Structures of systems: Earth and its carbon, a lake and its phosphorus, a food web and its energy, and a person and her nitrogen.]

System structure and behavior

All systems have structure and behavior; structure is what it *is* and behavior is what it *does*. The *structure* of a system is the set of elements and the connections between particular elements. When we imagine a real system, or create of model of that system, we typically keep keep track of just one narrow view. For instance, we may keep track of carbon in Earth's atmosphere, phosphorous in a lake, or energy in a food web (Fig. 1.10). You may keep track of calories (a unit of energy) in your own diet.

The *behavior* of a system is what the system does: Earth traps and and re-radiates particular forms of energy. Precisely how the atmosphere, the oceans, the land and organisms trap and reradiate energy is also part of the behavior of the system. The intake of food and all outflows are important parts of an individual's behavior, as are all the associated metabolic processes. A population of oak trees --as a group-- takes in collectively resources and energy, and gives off materials and energy it does not incorporate. Interactions *among* individual (e.g., pollination, pheromone signalling) as well as interactions among cells *within* individuals are all part of the behavior of this system. The flow of phosphorus through a biofilm is regulated by the physical and chemical environment created by the bacteria, as well and the uptake and release of phosphorus by individual cells.

A system's behavior can be described as its *dynamics*, that is, how its parts change over time. The physical world is always changing, and different aspects of it change at different rates. Weather changes minute to minute, but temperature and precipitation (i.e., climates) change on longer timescales as well.

On top of this template of a constantly shifting physical world, life is evolving in new ways, in sometimes stochastic new directions, and different species are even coevolving, that is, evolving in response to each other. For instance, while Earth is changing, a population of oaks is evolving under the influence of both random forces of mutation and genetic drift, and also the nonrandom forces of natural selection in response to both its physical and biological environments. Change itself varies, and is inescapable.

[Figure 1.11. Behaviors of systems. (Two examples of of systems and time series showing dynamics)]

Models of systems

A *model* is our conception of a real system. A model is a useful simplification of a real system. Reality is reality, and our conception of it is incomplete and simplified. We call that conception a *model* of the real system. As we stated above, Science is the process of creating useful simplifications of reality and is thus a process of making increasingly useful models. For instance, a road map of Buenos Aires, Argentina, is not Buenos Aires itself. Rather, it is a simplified abstraction of Buenos Aires that is extremely useful for a particular purpose. All scientific ideas share these characteristics -- they are simplified abstractions that are useful and valid for a particular purpose. For instance, variation among individual humans precludes us from having an exact size, length or structure of “the” gastrointestinal tract. However, we have a concept of a gastrointestinal tract that facilitates a general understanding of its form and function. We call our concept of a real system a model.

While ecology is the study of relations, this does not imply that everything is connected equally to everything else. Perhaps the most important goal of ecology is to understand what connections exist and to estimate their relative importances.

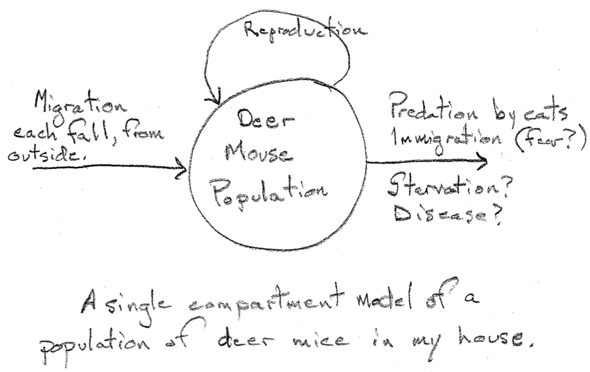
Box 1.x. A recipe for making a one-compartment model of a real system.

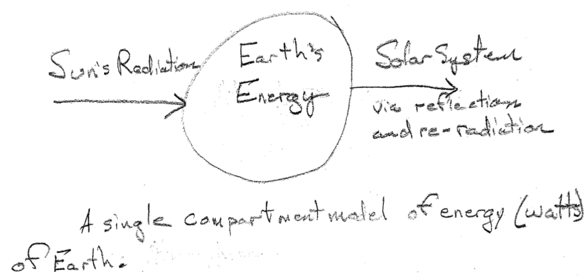
Here is how to create a single compartment model of a real open system:

1. Pick a real system. Examples: you, a blade of grass, a population of acacia trees in the Serengeti, a pond.
2. Pick a *variable* to keep track of, and decide on units. Examples of variables (with units): numbers of individuals (individuals), carbon (g), energy (Joules or calories), dry biomass (g), number of infected hosts (individuals), information (bits).
3. Draw (by hand, with a pencil, on scrap paper) a circle and put the name of your real system inside. The circle you drew is your single compartment. This circle represents the *compartment* for this model, and the amount of stuff in it is the *pool*, also known as the *stock*.
4. At the bottom or top of the page, write “A single compartment model of [variable (units)] in [real system name]. ”
5. Add arrows for inflows, outflows, and maybe reproduction.
    a. Inflow: On the left side, draw an arrow from open space toward the compartment, with the point touching the edge of the compartment. Above the arrow add a list of all the sources of your variable that could enter your system compartment.
    b. Outflow: On the right side, draw an arrow from the edge of the compartment pointing into open space. Above the arrow add a list of all the ways that your variable could leave your

system compartment.

c. Reproduction: If and only if you are tracking *number of individuals in a population*, then you should include reproduction. In that case, draw a loop that starts out at the edge of the compartment going away (like an outflow) and circles back to the compartment, so that the arrow points inwards (like an inflow). Because it is reproduction, this loop counts as *inflow*, but not outflow.





We refer to the amount inside the circle or compartment as a *stock* or a *pool*. Thus, each of these is a single-compartment model with fluxes and a single pool.

Exercise 1.x. Draw a single compartment model of a real system, keeping track of just carbon (carbon is easy-it is typically strongly correlated with the mass of an individual). Remember that organisms (plants, animals, fungi, and most bacteria and archaea) respire carbon dioxide, CO_2. Include and label all the inflows and outflows of which you can conceive. Describe in 1-2 sentences some of the complexity inside the system.

Exercise 1.x. When you are finished your sketch, share it with a colleague, and see if they understand it. Ask them to give you one or two ways to improve it.

Exercise 1.x. Return to the system you drew above, and suggest what might happen to the pool if you do the each of the following without changing anything else (a) increase inflow rates. (b) increase outflow rates. (c) decrease outflow rates. (d) decrease outflow rates.

Ecological systems are built of subsystems

All ecological systems have internal complexity. Typically, we view that complexity as a set of subsystems. So, all ecological systems we can imagine are built up of simpler subsystems.

- An individual organism is built of interconnected organ systems, which are built up of interconnected tissues, …, all the way down to the biochemistry of molecules, and atoms, and the particles that comprise them.
- Food webs are built from populations, and populations are built of individuals, … and you already know how complex an individual is.
- Earth's carbon cycle is composed of the atmosphere, the biosphere, and the geosphere. The

biosphere is, as we described briefly above, very complex and composed of many subsystems. Even the atmosphere and geosphere, which are relatively simple compared to the biosphere, have different components that hang onto carbon for different lengths of time.

The complexity goes all the way down, with systems inside of systems inside of systems. Once we realize that all systems have internal complexity, we can relax and not let the complexity befuddle us.

When we do research, some of us tend to start with a favorite study system, such as a single population Song Sparrows, or a salt marsh food web, and then ask the kinds of questions that are appropriate for that system. Other scientists start with a question, such as, *what determines the number of species on an oceanic island?* and we then we find a real system that allows us to answer the question. Regardless of whether we start with a favorite system, or start with a question, the system perspective always plays a role in our thinking.

[Figure 1.x. Nested subsystems, with photographs and corresponding nested compartment models, including a multispecies biome film ("How do biofilm species interactions facilitate resistance to antibiotics?"), a food web ("What controls the lengths of food chains?"), and a two compartment model of Arctic energy flux between land and atmosphere ("Does atmospheric warming initiate a positive feedback loop between atmospheric warming land surface warming?").]

Exercise 1.x. Create your own two compartment model of phosphorus (P) fluxes and pools with plants and herbivores, with one compartment for living plants, and one compartment for living herbivores. Phosphorus "enters" the plant compartment from the outside the system, as plants and their fungal partners extract P from the environment. Phosphorus exits the plant compartment in two ways: via death going back into the environment, and via consumption moving into the herbivore compartment. Phosphorus exits the herbivore compartment, going back out into the environment via egestion, excretion of waste, and death.

Exercise 1.x. Sketch a three compartment model of phosphorus, with plants, herbivores, and predators.

A Very Brief Introduction To Logic

Science is nothing if not reasoning. Because science --and clear thinking generally-- is based on formal reasoning, it helps to remind ourselves of a few of its terms and principles. Probability is a description of uncertainty, and it flows from formal reasoning (Jaynes 2003).

First a word on sets and notation. A set is just a collection of elements grouped for a purpose, such as 'the set of all vascular plant species native to the Amazon basin' or 'the set of all aquatic invertebrates in the Yangtze River.' A set can even be empty, as in 'the set of all living passenger pigeons.' We refer to such sets as 'empty' or 'null.' By convention, we usually refer to sets with uppercase letters, as in

$$A = \{\text{all vascular plant species native to the Amazon Basin}\}.$$

We can make pictures of sets using Venn diagrams, called set spaces. In Fig. 1.12??, the set space, S, is the set of all vascular plant species. A is the subset of S that includes all those that are native to the Amazon Basin. B is the subset of all species that are native to Brazil. The region of overlap represents the *intersection* of sets. The intersection is itself a subset, including all species that are native to the part of the Amazon Basin that is in Brazil. The *union* of A and B is the part of S inside the two circles A and

B. The union therefore includes all species native to anywhere in the Amazon Basin plus those native to other parts of Brazil. It is also very common to use *negation*, for example, not-*A*. In Fig. 1.12, not-*A* is everything outside the set *A* and within *S.* Therefore we can say that not-*A* is the set of all vascular plant species that are not native to the Amazon Basin or are native to someplace other than the Amazon Basin.

All scientific arguments, including ecological hypotheses and corresponding experiments, can be illustrated using Venn diagrams.

[Figure 1.12. Venn diagram or set space of vascular plants, *S*, plants with sufficient resources, *A*, and plants that are growing, *B*. *B* is nested inside *A*.]

Let's move on to *deductive* and *inductive reasoning.* We all use these each day, almost continuously. Clear thinking, via deduction and induction, about very complex topics requires methodical, stepwise thinking. Here we explain deduction and induction using examples of *syllogisms.* A syllogism is a very simple *argument*, distilled to its essence, and consists of one or more premises, and a conclusion. All syllogisms can be illustrated using Venn diagrams.

Deduction

Deduction or deductive reasoning is the process of arguing from a general rule to a specific conclusion. A *valid* deduction is a conclusion which follows logically from those premises. If those premises are true, then the conclusion must also be true. For instance, consider the following *valid* argument (Fig. 1.13):

Premise 1: *If a vascular plant is growing, then it has sufficient resources at that moment.*
Premise 2: *Shrub A is growing.*
Conclusion: *Shrub A has sufficient resources at that moment.*

[Figure 1.13. Venn diagram of all vascular plants, *S*, plants with sufficient resources, *A*, and plants that are growing, *B*. *B* is nested inside *A*.]

If both of these premises are true, then the conclusion must also be true. Deduction, or deductive reasoning, begins with general principles and follows them to a more specific conclusion. Note that if a deductive argument is constructed correctly, it is *valid*, that is, the conclusion must be true if the premises are true. Note also that if one or more premise is false, the argument is still valid but the conclusion may or not not be true. The term "valid" refers to the structure of the argument, not the truth of the premises or conclusion.

Exercise 1.x. Change the above conclusion to create (a) an invalid argument with a false conclusion. (b) an invalid argument in which the conclusion is true.

Exercise 1.x. Change premise 2 to be "*Shrub A is not growing.*" Can we conclude that Shrub A does not have sufficient resources? Why or why not?

Now let's consider a different premise 2 for the situation in Fig. 1.13.

Premise 1: *If a vascular plant is growing, then it has sufficient resources at that moment.*

Premise 2: *Shrub A does not have sufficient resources at that moment.*
Conclusion: *Shrub A is not growing.*

This argument, known by its latin name as *modus tollens*, is another valid deductive argument (Box 1.1). In its abstract form *modus tollens* argument is "If A, then B; not B. Therefore, not A."

Some would argue the *modus tollens* is the most important type of syllogism in Science. It is the foundation of what we refer to as the *hypothetico-deductive argument* (Popper 1979). In this type of argument, premise 1 constitutes our hypothesis, and premise 2 is a test of that hypothesis. When we get a negative result (not B), then we have *falsified* our hypothesis. Karl Popper, a reknowned philosopher of science and chief advocate of the hypothetico-deductive approach, has argued that the strongest hypotheses are those that have withstood the most challenging attempts at falsification. Popper would argue that Science only advances through falsification, because we can never use logic to prove that a scientific hypothesis is true.

Deductive arguments and data can only prove that a hypothesis (premise 1) is false. That is, we can only falsify hypotheses. We can never demonstrate unequivocally that a hypothesis is true. Consider these premises:

Premise 1: *If a vascular plant is growing, then it has sufficient resources at that moment.*
Premise 2: *Shrub A has sufficient resources at that moment.*

What can we conclude from these premises? Karl Popper (1979) would say "nothing!" Premise 1 does not guarantee that sufficient resources are always accompanied by growth; it states only that *if* it is growing, then it must have enough resources. Therefore, the conclusion is,

Conclusion: *Shrub A is growing or Shrub A is not growing.*

That is, we have learned nothing definitive. However, note that we have learned something. Premise 1 & 2 tell us that a lack of resources is not the reason that

Let's look at some examples of real, albeit simplified, ecological hypotheses. We'll start with one from Arditi and Ginzburg (2012):

Premise 1: *If predators interfere with each other, then predator and prey populations will tend to maintain steady population sizes.*
Premise 2: *Experiments show that predator and prey populations maintain steady population sizes.*
Conclusion: *Predators interfere with each other, OR, predators do not interfere with each other.*

[Figure 1.x. Evidence corroborating ratio dependent predation.]

As you can see, this is a very wishy-washy conclusion. For this reason, Karl Popper would say that such experiments *corroborate* the hypothesis, or that the experimental data are *consistent with* the hypothesis. All we can say is that experiments either falsify, or do not falsify hypotheses. If they do not falsify the hypothesis, then they corroborate the hypothesis.

Another example, from Ripple *et al.* (2001):

Premise 1: *If wolves limit herbivory on tree seedlings and saplings by elk, then reintroduction of wolves to Yellowstone National Park (Wyoming, USA) will cause increases in growth and recruitment by tree seedlings and saplings.*
Premise 2: *Reintroduction of wolves to Yellowstone National Park (Wyoming, USA) caused increases in growth and recruitment by tree seedlings and saplings.*
Conclusion: *Wolves limit herbivory on tree seedlings and saplings by elk, OR, wolves did not limit herbivory..*

[Figure 1.x. Evidence corroborating the effects of wolves on aspen growth.]

Isn't this annoying? When scientists perform an experiment, and the experiment generates results that are predicted, we can't conclude anything! Instead, our results continue to corroborate or be consistent with our hypothesis. Let's see an example of falsification.

One more example, from Clark and McLachlan (2003):

Premise 1: *All abundances of forest trees are caused only by chance, through random fluctuations in population sizes.*
Premise 2: *Eastern hemlock trees in several locations in southern Ontario, Canada, showed non-random changes in abundance over the past 5000 y.*
Conclusion: *Not all differences in the abundances of forest trees are caused only by chance.*

[Figure 1.x. Evidence showing non-random fluctuations in hemlock abundance.]

At last, we are getting somewhere. Clark and McLachlan (2003) falsified the hypothesis that chance determines tree abundance, for at least one population. The scientific hypotheses that do not get rejected remain behind, and form a tentative basis of knowledge.

Mathematical deduction

I mentioned above that, in Science, we cannot prove anything to be true -- only in mathematics (including formal logic) can we prove something to be true.[7] We can turn this around to our advantage when we realize that mathematics gives us a tool -- a tool to prove something to be true, given particular assumptions. Mathematical proof is a form of deduction, in part because mathematics is full of general rules.

How does mathematics help us? It helps by allowing us to see the consequences of our assumptions. Humans have terrible quantitative intuition. This is probably part of the reason why some of us get into financial difficulty. We do not understand the power of compounded interest, whether it works in our favor as, in the stock market, or against us, as with credit card debt. Mathematics allows us to make simple assumptions about how the world works, and then *we can let mathematics prove the consequences of these assumptions*. Thus, ecologists can focus on simple and important ideas about

[7] Some would argue that this is only because we make the rules, but others disagree (Colyvan 2012).

organisms and their environments, and then let mathematics show us the consequences of our assumptions.

Mathematics allows ecologists to make deductions, or predictions, about the future:

- In October 2012, a global average estimate for CO_2 concentrations was about 391ppm.[8] We are adding about 2 ppm CO_2 into Earth's atmosphere annually (net increase). Given this annual net increase when will we reach 450 ppm CO_2? What about if the annual net increase is itself increasing by about 25% each decade?
- In 2000, populations of amphibians around the world were probably declining by about 50% annually (Houlahan *et al*. 2000). At that rate, how many years would it take for a population of 1000 adult frogs to fall to below 100 individuals? below 10 individuals?
- There are about 21,000 trees belonging to about 250 species in a 50 ha plot in a Panamanian tropical forest (Hubbell 2001). Let's assume that each tree has have a 0.1 percent chance of dying each year. If each dead tree is eventually replaced by a single offspring from any one of the remaining 20,790 individuals, what are the consequences of this random death and replacement process?

Humans have poor quantitative intuition. Fortunately, mathematics allows us to turn simple assumptions into the predictions in our scientific hypotheses.

What if we find out that our math-based predictions are wrong? Has the math led us astray? No. Rather, because math doesn't lie, we go back to our assumptions. When the math gives goofy predictions, it is because we made goofy assumptions. That is, when the predictions do not correspond to our (eventual) observations, it means our understanding was flawed, and we must reconsider our assumptions. This self corrective process of using data to check our understanding is perhaps the core of science (Platt 1964, Suroweicki 2005). Mathematics simply helps us see the complicated or non-intuitive consequences of our assumptions.

While deduction and falsification are essential in science, they are not the only kind of argument that scientists make. Next we discuss the other type, induction.

Box 1.1. Simple set notation and rules. Of all the rules below, perhaps the two most important in ecology are *modus tollens*, and the fallacy of affirming the consequent. *Modus tollens* is fundamental to good science. It is the form of an argument by which we falsify our hypotheses. It is through attempting to falsify our hypotheses that we strengthen our ideas (Platt 1964). In contrast, the *fallacy of affirming the consequent* is a common mistake we all make from time to time. It is a trap that requires active practice to avoid. In the example below, it is possible that you can be alive and not be eating at any particular moment.

[This will require typesetting that is easily mangled in word processors]. Defining a set The empty set	Intersections of sets Unions of sets Negation

[8] http://www.esrl.noaa.gov/gmd/ccgg/trends/ accessed November 2012.

Modus ponens If A, then B A Therefore B	If you are eating, then you are alive. You are eating. Therefore you are alive.
Modus tollens If A, then B Not B Therefore not A	If you are eating, then you are alive. You are not alive. Therefore you are not eating.
Fallacy of affirming the consequent If A, then B B Therefore A	If you are eating, then you are alive. You are alive. Therefore you are eating.
Fallacy of denying the antecedent If A, then B Not A Therefore not B	If you are eating, then you are alive. You are not eating. Therefore you are not alive.

Induction

Induction or inductive reasoning is the process of making an educated guess on the basis of current knowledge. Consider the following inductive argument:

Premise: *Every species of vascular plant that I have ever seen is green.*
Conclusion: *Therefore, all species of vascular plants are green.*

Induction of this type is a *generalization*. A generalization starts with evidence and seeks to extend the evidence into a new general principle. This is a very important class of arguments by which we try to make sense of the world. When we are toddlers, we learn about gravity when we shove bowls of food off the table and they land on the floor with a big, exciting splash. We also learn the permanence of objects, that "out of sight" does not mean "gone forever." Induction as generalization is a critically important means by which we build scientific theories.

Another common form of inductive argument is *prediction*, that is, the prediction of a single future event, based on past similar events. Here are two examples:

Premise: *All the plants I have ever seen are green.*
Conclusion: *The next plant I see will be green.*

Premise: *I have never hit a deer with my car.*
Conclusion: *The next time I go for a drive, I will not hit a deer.*

In inductive prediction, we reason from past experience to a future event.

As important as induction is, this form of reasoning can, and frequently does, make mistakes. Using the inductive argument above, a plant biologist could easily tell us that not all vascular plants actually contain enough chlorophyll to be green. Similarly, I can tell you that I hit a deer with my car for the first time, just the other day. Unlike deductive arguments, inductive arguments are not generally considered valid or invalid, but simply correct or incorrect depending on the truth of the conclusion.

Although induction is not typically evaluated on its validity, we may refer to inductive arguments as *strong* or *weak*, or *plausible* or *implausible*, depending on the likelihood of the conclusion, given the premise. For instance, if we do not even know what a plant is and know nothing about them, then we have no idea what color a plant might be: is it purple? clear? black? However, if we have seen a lot of plants, this knowledge constitutes our premise, and makes the conclusion more plausible. An induction is therefore evaluated on the basis of whether the degree of knowledge in the premise provides strong or weak evidence for the conclusion.

[Figure 1.12. Probability space example of vascular plants, *S*, plants that I have seen, *A*, and plants that are green, *B*. *A* and *B* overlap. With induction, the question becomes one of evidence for non-empty sets]

Exercise 1.x. Change the premise above to "*I have seen several species of plants, and they were all green.*" What does that do to the strength of the inductive argument?

Exercise 1.x. Change the premise above to "*I have seen hundreds of plant species in a wide variety of habitats and regions of the world, and all of them have been green.*" What does that do to the strength of the inductive argument?

We can see clearly how probability creeps into inductive reasoning. Consider this example:

Premise: *Every species of vascular plant that I have ever seen is green.*
Conclusion: *Therefore, all vascular plants are probably green.*

Now the conclusion has been hedged--we say "probably." This moves us toward a *statistical syllogism*, which we discuss next.

If we understand the premise well and can quantify the knowledge in it, then we may be able to ascribe a probability to the conclusion, beyond saying simply "probably green." If we do this, we can call this kind of argument a *statistical syllogism*. For instance,

Premise: *I have seen a random sample 1000 out of approximately 280,000 species of vascular plants, and all of them have been green.*
Conclusion: *Therefore, I can be between 99.7-100% sure that all plants are green.*[9]

When we do this, we call this kind of argument a statistical induction or statistical syllogism. It is given this name because statistics is the science of induction, of starting with data (some knowledge of plants) and generalizing to a larger population (generalization about all plants).

This inductive argument is extremely important in science (Jaynes 2003), because Science proceeds

[9] Based on uninformed Bayesian inference. See appendix A.

stepwise toward increasingly useful generalizations about nature. We use both induction (especially generalization) and deduction, along with falsification, to help us formulate tentative conclusions about nature (Platt 1964).

Exercise 1.x. Change the premise above to "*I read somewhere on the internet that all plants are green.*" What does that do to the strength of the inductive argument? Does it matter *where* on the internet I read this?

A Very Brief Introduction To Probability

"*In this world nothing can be said to be certain, except death and taxes.*" (Benjamin Franklin).

I would also say that nothing in ecology is certain except death and the physical laws of nature. Therefore, we need to understand uncertainty. Probability is the science of uncertainty, and is considered by some to be the logic of science (Jaynes 2003). Probability is especially important in ecology and evolutionary biology because the world we study is so complicated that we have to be explicit about chance events.

We use probability to describe either the long-term average of repeated events (e.g., coin flips) or the degree of belief in a certain outcome:

- "It is very unlikely for a particular seed to survive and grow to maturity."
- "There is about a 50% chance that this seedling will get browsed by an herbivore."
- "Our generalized linear model estimated that these seeds have a 0.03% chance (95% confidence region: 0.001-0.007%) of colonizing a suitable microsite on this forest floor."

The above descriptions are increasingly precise and quantitative ways of expressing the probability of events. However, we can interpret each one of them in either of two ways. We could interpret each statement as expressing a degree of belief about the chance of something happening in the future. Alternatively, we could interpret each statement as our estimate of the long-term average of the repeating the hypothetical experiment in exactly the same way an infinite number of times. Statisticians sometimes debate the merits of thinking about probability as either a degree of belief, or as the long-term average of identical, repeated trials of an event (Jaynes 2003, Christensen et al. 2011). We can withhold our opinion on the precise meaning of probability, and for now, work with what makes sense to us.

The probability of an event is always stated with respect to a particular probability distribution. That is, the probability of event *A* is always stated, either implicitly or explicitly, relative to the the probability of other events such as events *B,* and *C,* or even event not-*A.* For instance, the probability of rolling a 1 on an unbiased die is ⅙, in part because the probability of rolling something that is not 1 is ⅚.

Probability distributions

A *probability distribution* is merely the probabilities associated with a set of different events. For instance, the probability distribution for getting heads with a single flip of an unbiased coin is

y	0 Heads (i.e. Tails)	1 Head
f(*y*)	0.5	0.5

We could present this in a graph as well, which we call a *histogram* (Fig. 1.13). The *x*-axis contains the categories, and the *y*-axis describes the *probability density,*[10] which happens to be equal to the probability of getting a head or a tail.

Exercise 1.x. Write down a probability distribution for a heavily biased coin, in which the chance of heads is three times as great as for tails. Remember that the probabilities have to add up to 1.0.

Now imagine that, instead of flipping a coin once, we flipped a twice. what are the possibilies of heads and tails (H & T)? We could get TT, HT, TH, or HH. There are two ways to get one head.Therefore, the probability distribution for the number of heads with two flips of an unbiased coin is

y	0 heads	1 head	2 heads
f(*y*)	0.25	0.5	0.25

We could present this in a graph as well, which we call a *histogram* (Fig. 1.13). The *x*-axis contains the categories, and the *y*-axis describes the *probability density,*[11] which happens to be equal to the probability of getting a head or a tail.

Exercise 1.x. Write down a probability distribution for a heavily biased coin, in which the chance of heads is three times as great as for tails. Remember that the probabilities have to add up to 1.0.

The probability distribution of final grades in my nonmajors ecology class in 2011 (*Ecology of North America*), was approximately

y	A	B	C	D	F
f(*y*)	0.15	0.40	0.35	0.08	0.02

As you can see, I am pushover when it comes to grading. A student would have had a 55% chance of

[10] Note for the statistically-minded: Here I follow the relaxed convention of referring to both discrete and continuous probability functions as ‘density’ rather than the more formal ‘mass functions’ for discrete variables, and ‘density functions’ for continuous variables.

[11] Note for the statistically-minded: Here I follow the relaxed convention of referring to both discrete and continuous probability functions as ‘density’ rather than the more formal ‘mass functions’ for discrete variables, and ‘density functions’ for continuous variables.

getting an A or B, and only a 2% chance of getting an F.

Exercise 1.x. What is the probability of getting a C or better in my class? Show your work.

Exercise 1.x. Write down a probability distribution for a strange six-sided die, that has 1's on three surfaces, 2's on two surfaces, and 3 on one surface.

We could present the above distributions in graphs as well (Fig. 1.13). The *x*-axis contains the ordered grade categories, and the *y*-axis describes the *probability density*, which happens to be equal to the probability of getting a particular grade. In the case of the grades, the density distribution is the direct result of data from my students. There is no underlying theory I am trying to communicate. Therefore, we refer to the distribution as an *empirical probability distribution.* In contrast, the coin flip was described as a hypothetical distribution, in which we defined the coin as 'fair' or unbiased, by assuming that there is exactly a 50-50 chance of heads or tails.

[Figure 1.13. Four different probability distributions. A. Discrete probability density function for two flips of an unbiased coin flips. B. Empirical discrete probability density function for grades in my nonmajors ecology class C. Estimated continuous probability density function for western hemlock tree growth on Mt. Rainier. D. Estimated continuous probability density function for chlorophyll concentration in Acton Lake, Ohio, USA.]

Exercise 1.x. A sample of 11 black bears in Yellowstone National Park (USA) shows that about 70% of the diet is plant-based (e.g., nuts, berries), 20% human food (e.g., taken from campsites, trash cans), and the rest is animal-based (e.g., arthropods, fish) (Hopkins and Ferguson 2012). Construct an empirical probability distribution for this diet.

Continuous probability density functions are very common, but they add a quirky wrinkle to their interpretation. The probability density for a particular event in a discrete variables is typically the probability of that event. For instance, the probability density for receiving an A in my class is 0.15. The height of the "A" bar in Fig. 1.13B is 0.15. Students had a 15% chance of getting an A. In contrast, the probability density function for continuous variables has no such straightforward interpretation. That is because for continuous variables, one observation occupies a hypothetical point of zero length along a real number line. Recall your elementary school geometry: how many points lie in a line? Answer: an infinite number of points lie in any line segment. Therefore the probability of observing one *particular* value is infinitely small, or zero. This is why --for a continuous variable-- we cannot interpret the probability density (the *y*-axis of its density distribution) as a probability.

In spite of the differences between discrete and continuous probability distributions, they do share some features. For instance, we can say that any probability distribution must include all possibilities. That is, the sum of the bars in a discrete distribution, or the integral[12] of a continuous probability density must equal 1. Appendix A takes up systems, syllogisms and probability at greater length, in a bit more gory detail.

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[12] An *integral* is a form of summation that is part of *calculus*. It is the area under a curve.

WHERE DO ECOLOGICAL IDEAS COME FROM?

Scientific ideas come from people --real people-- like you and like me. I am confident that you will think of many of your own scientific ideas as a result of reading this book.

I like to imagine the development of a scientific idea as a helix (Fig. 1.x), because I although feel like I am going around in circles, I actually make steady progress. For me, going around in circles is really just the process in which I

1. have a vague idea or question (e.g., why is my world mostly green?),
2. find and read previous research related to my idea,
3. ponder the data and ideas in what I am reading and simultaneously blend these ideas with my own idea,
4. use this new (slightly less vague) idea to go back to number 1, and look for more previous research.

By continuing to go around in circles, I actually make slow progress in a direction that is largely orthogonal or perpendicular to the plane of the circle (Fig. helix).

[Fig. 1.x. Scientific thinking is a bit like a helix and a bit like a spiral, in which we keep going through the process of asking questions, framing arguments, collecting data, asking more penetrating questions, framing more precise and relevant arguments, and collecting more relevant data, *ad infinitum*.]

A Hypothetical Example

Imagine for the moment that among the interests in your life, you are an English Literature major, love vacationing at the beach, and you like whales. Given these interests, it is not a great stretch to imagine yourself at the beach. As you stroll down the beach, gazing out past the surf, you might wonder whether there are whales out there, just out of sight. Perhaps you wonder what kind of whales might be out there, and if they are there, you might wonder what they are doing. Are they eating, or mating? You might even wonder whether whales get sick. “Surely, they must get sick!” you think, but the question lingers in your mind.

How would an ecologist think about these issues? An ecologist could have the exact same questions that you do, but then a couple other things would start to percolate. The ecologist might start to ask additional questions that are more specific, which concern the details of particular species in particular environments (Table 1.x). Ecologists refer to these details of species as *natural history*. In addition, the ecologist would also start to ask questions that are more abstract and general (Table 1.x).

Table 1.x. Questions that you and other ecologists might ask while on vacation at the beach.

First questions	**Additional questions**
Are there whales out there?	What species are present? If they are present, what is their density? How does density vary over time?

What are the whales doing?	What do these whales prey on, how do they forage, and do whales influence prey populations? What social structure do whales have? How do they select mates?
Do whales get sick?	What species of pathogens and parasites use whale hosts? What controls their immune responses? Do pathogens influence population density or alter behavior?

Ecologists ask many of the same questions you might ask. In addition, we ask *lots* of questions. A few of those questions turn out to be useful.

Beginner's Mind

As you develop your scientific skills, it is useful to remain naive, open and inquisitive. In that way, scientists often seem childlike, because they are often very curious about their world. Infants and toddlers are born scientists. The willingness to ask seemingly simple questions and the openness to explore new ideas is sometimes referred to as the beginner's mind (Suzuki 1970). A quote that is often attributed to Albert Einstein keeps us humble, open and inquisitive: "If we knew what it was we were doing, it would not be called research, would it?"

Perhaps you are picking up on it, but in case you are not, *I believe that just about everyone can be an ecologist.* Because humans have been ecologists for so long, we are surprisingly adept at thinking about ecological questions. Stepping back even further, we can be surprisingly adept at asking and understanding scientific questions (Firestein 2012). Many of the particular methods we use can be a little difficult to learn, but generating vague but interesting ideas may be easier than you think. Throughout this book, I will encourage you to ask questions, and write those questions in the margins of this book or of the scientific articles you read.

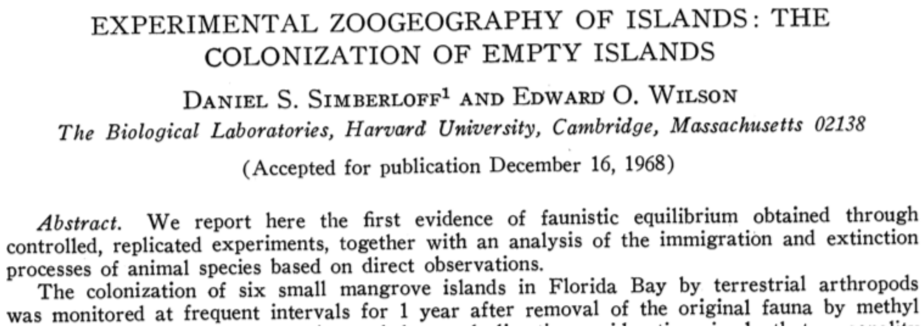
Exercise 1.x. Write down three ecological questions on a piece of paper. Share them with someone else, and together describe what you think is interesting about all the questions. If you have trouble remembering that you were a born ecologist, remember that you experience weather every day; you have a couple of decades experiencing seasons, and climate; you are a rich and fascinating ecosystem unto yourself -- you are home to more microbes than you have human cells in your body; you interact with many others of your own species and exhibit behaviors that in most cases have been studied in other species.

Exercise 1.x. Identify one ecological question that is particularly interesting to you (perhaps one from the previous exercise), and use it to create more specific questions, and more abstract questions. Come up with at least three of each type. Share these with another person or group, and discuss them with each other. Ask questions about each other's questions and help each other clarify your intents.

Examples Of Syllogisms In Action

Scientific theories and hypotheses can always be phrased in terms of inductive and deductive arguments. Let's consider a couple of real examples from the literature. In each case, I'll introduce a paper from the literature, including its title from the journal page, and some of the ecological thinking underlying the work. For each example, identify the *system*, the *inductive* and *deductive* reasoning underlying the hypotheses, and how *probability* helps us draw conclusions about our hypotheses.

Example 1, Island biogeography


EXPERIMENTAL ZOOGEOGRAPHY OF ISLANDS: THE COLONIZATION OF EMPTY ISLANDS

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Abstract. We report here the first evidence of faunistic equilibrium obtained through controlled, replicated experiments, together with an analysis of the immigration and extinction processes of animal species based on direct observations.

The colonization of six small mangrove islands in Florida Bay by terrestrial arthropods was monitored at frequent intervals for 1 year after removal of the original fauna by methyl

Figure 1.x. The title, authors, and beginning of the abstract of Simberloff and Wilson (1969).

A graduate student, Dan Simberloff, and his faculty advisor,[13] Ed Wilson, tested a model that had recently been proposed to explain the biodiversity observed on oceanic islands: the *equilibrium theory of island biogeography* (MacArthur and Wilson 1963). Robert MacArthur and Ed Wilson had developed this theory in part to help explain two observed patterns:

- oceanic islands farther from mainlands tended to contain fewer species than islands close to mainlands.
- small oceanic islands contained fewer species than large islands.

MacArthur and Wilson collaborated to combine

1. Wilson's interest and experience with biological diversity on islands, especially ants,
2. MacArthur's interest and experience natural history of birds, and especially his understanding mathematics, and
3. the collective experience of biologists and ecologists concerning island plant and animal diversity which was already shared in the primary literature.

Using inductive reasoning and their own experience, they proposed that the number of species on an island was a dynamic balance between the rate at which new species arrived on the island (colonization rate), and the rate at which species became extinct (extinction rate). Let's represent these ideas as a system and with the more formal shape of inductive and deductive syllogisms.

An island as a system

We can represent an island as a system (Fig. 1.x): the island is the single element or compartment, the

[13] Graduate students work closely with an "advisor" in an expert-apprentice relationship. The "advisor" is member of a university faculty who does research and advises, or mentors, graduate students. This faculty member is often referred to as the student's major professor, or graduate supervisor. The advisor-student relationship can occasionally be a very challenging one, in which case the advisor is sometimes referred to by other names.

variable we are tracking is the number of species and the pool or stock is the number of species present. The inflow is immigration by new species, not already present on the island, and the outflow is local extinction. The size of the pool is the balance between the inflow and the outflow.

Induction 1

Premise: We know that species move around the planet, and in particular cases, we have seen the recolonization of newly formed volcanic islands.
Conclusion: Species will colonize islands in the future, and such behavior is common.

Induction 2

Premise: We have seen many instances in which species population sizes fluctuate, and sometimes species become extinct, either globally, or just in a particular location.
Conclusion: Fluctuations in population size are generally common, and most species have some chance of extinction.

Both of these inductive arguments were based on MacArthur and Wilson's personal experience and also on their reading the scientific works of others. As inductions, they prove nothing, but if they are strong inductive arguments, they provide *plausible* conclusions that become part of our hypotheses. They used a little mathematics to describe the rates of colonization and extinction, and the mathematics allowed them to deduce several characteristics of the number of species on islands, and the turnover rate, that is, the rate at which new species arrived and old species became extinct. Perhaps the simplest of these deductions looked a bit like this:

Deduction

Premise 1: If islands function as open systems with the inflows (immigration) and outflows (local extinction) of species, then the number of species observed at any one time results from the balance of inflows and outflows.
Premise 2: Islands function as open systems with the inflows and outflows of species.
Conclusion: The number of species observed at any one time results from the balance of inflows and outflows.

MacArthur and Wilson posited that a major determinant of colonization rate was how far an island was from the mainland: islands near to large continents would get more accidental colonists that islands far from large continents. They also posited that small islands would have higher extinction rates than large islands, due to the small population sizes supported on small islands.

[*Figure 1.x. Cartoon of islands and predictions. Islands are dynamic systems, constantly gaining and losing species at rates that depend - in part - on their sizes and their distances from likely sources of immigrant species. The long-term average number of species on an island is thought to be the dynamic equilibrium of immigration and extinction. A. Small and large islands, near and far from a mainland. B. Fig. 5 from MacArthur and Wilson 1963.*]

Test of the idea

Dan Simberloff and Ed Wilson wanted to test this new theory of island biodiversity (Simberloff and Wilson 1969). In particular, they wanted to test whether, as predicted, the number of arthropod species on islands resulted from the balance of two dynamic processes: continual colonization and continual extinction. To test this idea, they used a *field experiment* (Box 1.2).

This field experiment was conducted on *very* small mangrove islands (264--1263 m^2) in the Gulf of Mexico, off coast of Florida (Figure 1.x A). Mangroves are trees that belong to one of a variety of species that inhabit coastal saltwater sediments. They provide an extensive and unique habitat on the coasts of many of the world's oceans. Mangroves create a stable physical environment that helps other species, including *Homo sapiens*, establish in the marine and terrestrial habitats associated with this mangrove forests. The mangrove islands studied by Dan and Ed existed in very shallow water of the coast of Florida, and the trees themselves provided the primary physical structure of the islands.

The arthropods that Dan and Ed studied often had traits that we might associate with long distance dispersal (Fig. 1.x). Many of the insects wings and could fly. Many of the spiders could balloon; that is, they are could make silk in long threads that would catch the wind and send them sailing away to another location. Other species of arthropods had no such obvious means of long distance dispersal, and may have drifted in with flotsam and jetsam. The mangrove islands were small enough that they could identify all of the arthropods on each island they studied, cover them with a tarp and fog them with insecticide to kill and remove all the individuals, and, in later experiments, could even reduce their sizes (using saws and hard work).

[Figure 1.x. Pictures of mangrove trees and habitat from Wilson and Simberloff (1969), and images of selected arthropods sampled in Simberloff and Wilson (1969).]

Simberloff and Wilson (1969) found that, as predicted by the theory of island biogeography, islands quickly recovered to contain approximately the same number of invertebrate species as they had before they fumigated the islands with insecticide (Figure 1x B). In particular, they showed that there was continual ongoing local extinction of species, but that they were replaced by different species. They argued that this provided support for the theory of island biogeography. Let's examine their argument a little more closely.

Box 1.2 Ecologists use different approaches to tackle questions from different angles.

One distinction that is often made is between *theoretical* and *empirical* research. Theoretical research uses mathematics and/or computer programming to explore the logical consequences of ideas of how populations or ecosystems change over time. Empirical research is research that measures stuff and results in data. Sometimes theoretical research leads to hypotheses that empirical research can test, and sometimes empirical research provides inspiration for new theories.

The two main types of theoretical research are analytical and simulation. *Analytical theory* uses mathematics including set theory, dynamical systems theory, network theory, statistical thermodynamics, and probability to explore the complexities of how ecological systems may work. *Simulation-based theory* uses computer programming to simulate ideas numerically, using the brute force of a computer, rather than the sophistication of higher mathematics. The choice of the approach depends on the particular expertise of the investigators, and also on the particular questions they are tackling.

Empirical research includes all the approaches that use or result in data. These approaches include techniques for both the laboratory ("the lab") and in the field ("the field" refers to outdoors). Often samples are collected in the field, but require laboratory methods to extract the information. For instance, an ecologist may collect soil samples that must be analyzed in the lab for chemical nutrient composition. Other times, the data are collected right outside - in the field.

When data are collected, the research may be *observational* or *experimental*. *Experiments* are studies in which investigators assign treatments randomly to multiple replicate experimental units. A *field experiment* is is what it sounds like: an experiment conducted outdoors, in a natural or semi-natural setting, with all of the important elements of a good experiment (Hairston 1991), including i. knowledge of initial conditions (e.g., initial number of insect species), ii. replication of experimental units (e.g., multiple islands), and iii. randomization in assigning treatments to replicates (e.g., islands assigned randomly as controls, insect removal, or size reduction).

Observational studies collect data on a system that has not undergone experimental manipulation. Ettinger *et al.* (2011) is a good example where they used observations collected on temperature and precipitation, and tree growth in the absence of any intentional manipulation. Some studies take advantage of abrupt changes in the environment, such as a fire or unusual weather event. These sometimes referred to as natural experiments.

These approaches are reflected in the types of research papers that ecologists write. We refer to these as empirical or theoretical (or modeling) studies, and experimental or observational. Another type of paper we find in the primary literature is the review paper. A review is a thorough coverage of a specific topic. All empirical and theoretical papers include a very brief review of literature that is most relevant. However, a review paper includes all of the past primary literature. We will discuss more about different types of papers in the next chapter.

The theory of island biogeography make a variety of assumptions and predictions. Here is one that Simberloff and Wilson tested; their hypothesis and prediction comprise the first premise of a deductive argument.

Premise 1

- Hypothesis: If the theory of island biogeography (***TIB***) describes accurately the processes controlling the number of species on an island, then an island that loses all it species should recover the same equilibrium number of species (***E***) relatively quickly.
- Abstraction: **If *TIB*, then *E*.**

A good experiment creates conditions that could falsify the hypothesis. That means that it needs to (1) create conditions wherein the hypothesis can operate if it is true, and (2) has a reasonable possibility of succeeding or failing. Simberloff and Wilson created empty islands that could be recolonized, if colonization is an ongoing process. Given this experimental system, two results are plausible, and these lead to two different, alternative conclusions:

Alternative *a*	Alternative *b*
Premise 2a	*Premise 2b*

● Result: The number of species on an island *does not return to* its original number over a short time period. ● Abstraction: ***not-E*** *Conclusion a* ● The processes of colonization and extinction assumed by the theory of island biogeography does not operate on these islands. ● Abstraction: ***not TIB***	● Result: The number of species on an island *returns to* its original number over a short time period. ● Abstraction: ***E*** *Conclusion b* ● The processes of colonization and extinction, *or some other process,* caused the number of species on these islands to return to their pre-defaunation levels. ● Abstraction: ***TIB or not TIB***

Both of the above sets of premises and conclusions constitute valid arguments. Premise 1 is the scientific hypothesis and is proposed as a general principle, just like the deductive syllogisms above. Premise 2 is the result from an experiment in which the hypothesis can operate. It introduces a specific element just like in the deductive syllogisms above. The conclusions are the logical deductions we can make if our premises are true. Note the difference between Conclusion *a vs.* Conclusion *b*. If the theory is correct,[14] then the experiment should result in observations that match the Conclusion *b*. If the theory is incorrect, then the experiment should result in observations that match the Conclusion *a*. If that is the case, then the theory has been falsified.

[Figure 1.x. A. Picture of a mangrove island in the Bay of Florida, from Wilson and Simberloff 1969, B. Results from 1969 paper, showing increased diversity over time for all islands.]

Simberloff and Wilson found that the islands recovered their arthropod communities quickly (Fig. 1.x).

- Following fumigation, arthropods began to recolonize quickly and the number of species increased for about a year (Fig. 1.xA.). The number of species seemed to reach a peak, and then bounce around a bit, eventually coming back down.
- Species often colonized and then later became locally extinct (Fig. 1.xB).
- Among other conclusions, Dan and Ed wrote that their data "indicate strongly that a dynamic equilibrium number of species exists for any island" stating that by day 250, the number of species on all islands except the most distant from the mainland had returned to pre-fumigation levels.

What does it mean to "return to pre-fumigation levels"? Science is about eliminating ambiguity, so we will get a little more specific, and relate their findings to our introduction to probability above. Let's be

[14] "True" and "false" have specific meanings in logic; in Science we know that the best we can do is to create theories that are approximately true. Therefore, I will always hedge my wording and avoid saying that an ecological theory is "true" unless I refer to a mathematical formalism that, for instance, proves the equality of 2x + 2x and 4x. Only mathematics and logic can prove something to be true by deduction.

pessimists or contrarians and say "I don't think they did return to pre-fumigation levels!" The burden of evidence falls on Simberloff and Wilson to provide unambiguous evidence for their conclusions. Examining their data, we can see that none of the islands had exactly the same number, and, indeed, the theory predicts that the number will bounce up and down as species colonize, become extinct, and recolonize due in part to chance. How could we pose a question in a way that would allow us to be completely unambiguous, and "put the numbers to the test?"

We can rigorously evaluate the statement "returned to pre-fumigation levels" by making it less ambiguous. Below I list three examples of conditions that seem less ambiguous.

1. *The average number of species on an island does not differ significantly between the first and last census.*
2. *At some time during the censuses, the number of species on all islands after fumigation equalled or exceed the number before fumigation.*
3. *By the end of the censuses, islands were just as likely to have more species than they started with as fewer species than they started with.*

There are other ways of rephrasing their statement, but it is simple enough to address our statements numbers 2 & 3. A quick look at the data would show us that condition 2 was met. What about condition 3? What do we mean by "just as likely"? Does it mean there must be exactly three islands with more species, and three islands with fewer, or does it mean something else? Are we guilty of excessive ambiguity?

To assess condition 3, let's use a favorite model of probability, the coin flip. We will use a coin flip as a model of an island: heads means an island ended up with more species than it started with, and tails means fewer. If we flip six coins, how many heads do we get? The number of heads depends on chance or luck. We use probability to describe the uncertainty about the number of heads we can expect to see (Fig. 1.xD).

Here is how we might apply those ideas of probability and coin flips:

1. Let heads = an island ends up with more species than it started with, and tails = fewer.
2. Flip six coins, one for each island. Count the number of heads.
3. Repeat #2 a gazillion times, each time recording the number of heads, so that we wind up with a gazillion records of the number of heads.
4. Count the fraction of times (out of one gazillion) that two heads (out of six coins) were counted. This fraction is a measure of how likely their results are *if* the islands recovered, but fluctuated randomly up and down around their "equilibrium."

These one gazillion repeated "trials" of six flipped coins resulted in this distribution of probabilities[15]:

y = heads	0	1	2	3	4	5	6

[15] In this case, rounding error prevents the frequencies from adding up to 1.0.

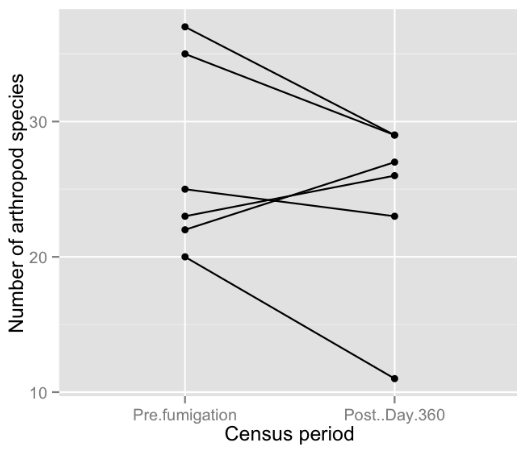
frequency	0.016	0.094	0.236	0.311	0.234	0.093	0.016

Thus, if coin flips provide a useful standard against which to compare Dan and Ed's data, then we can say that those data had about a 23.6% chance of happening by chance alone, assuming that the coin flip and our condition 3 are reasonable models of reality.

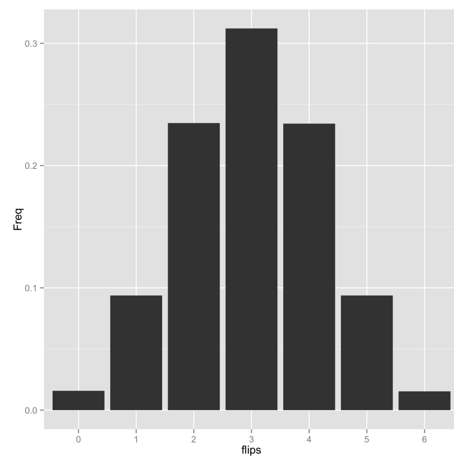
Exercise 1.x. What is the chance of getting 2 *or fewer* heads? Getting 3 or more heads?

A. …

B. …



C.



D.

[Figure 1.x. Results from Simberloff & Wilson (1969). A. Results from 1969 paper, showing increased diversity over time for all islands. B. Island E1 data from Appendix of S & W (1969). C. New graph of data. D. Histogram of a gazillion sets of six coin flips (here a gazillion = 10^6)]

With just the line of evidence discussed above -- that islands returned to their original numbers of species -- Simberloff and Wilson found that their data were consistent with the theory of island biogeography. Unfortunately, *other explanations may be possible*. This is a critical point. When observations match our predictions, scientists like to say something like "Ah, ha! Our data are *consistent with* our hypothesis!" or perhaps "Awesome! Our data *support* our ideas!" Karl Popper would say that our data *corroborate* our hypothesis. We can say this because we have constructed hypotheses, an experimental system, and predictions that constitute a valid deductive argument.

When observations match our predictions, as above, scientists do *not* say "Great! We proved that our hypothesis is true!" Quite the contrary. First, only mathematicians and logicians prove anything is true. More importantly, we need to always remind ourselves that other theories, perhaps unbeknownst to us, might have made the same predictions. There may be other explanations for our observations, explanations that we do not yet know about. *To get a result that is consistent with our hypothesis makes us vulnerable to the trap of the fallacy of affirming the consequent* (Box 1.x). Unfortunately, that is how deduction works. There could be an infinite number of possible explanations for our observations that we have not yet ruled out. That is why, when our results match our predictions, we say with great humility that our data are *consistent with* our hypothesis. Logical deduction can never prove that our hypothesis is true. It can only rule out hypotheses.

Based on other results of Simberloff and Wilson (1969) and the work many, many other scientists, we now recognize that the theory of island biogeography is a very useful model of how the number of species is regulated on islands of all types. Let's move on to another example of ecological thinking.

Example 2, Conifer range limits

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Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers

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Abstract. Does climate determine species' ranges? Rapid rates of anthropogenic warming make this classic ecological question especially relevant. We ask whether climate controls range limits by quantifying relationships between climatic variables (precipitation, temper-

Figure 1.x. The title, authors, and beginning of the abstract of Ettinger *et al.* (2011).

Like a lot of people, Ailene Ettinger (a graduate student at the time) and her colleagues were drawn to the beauty of the mountains of western North America. More importantly, they were also pondering how Earth and its inhabitants are going to respond to climate change. Ailene's graduate advisor, Dr. Janneke Hille Ris Lambers, is interested generally in what factors control species range limits. (A species distribution or range is the geographic area where that species is found; a range limit is the boundary of that geographic area.) When Ailene joined the lab group, Janneke was just beginning to establish a research program on Mt. Rainier in western Washington (Fig. 1.x). Ailene jumped at the chance to do her research there.

In an email, Dr. Hille Ris Lambers said "I was strongly influenced in my interest in the effects of climate change *vs*. other factors on range limits by work by Craig Loehle (Loehle 1998) as well as Connell's seminal work on barnacles (1961). That, in combination with our interests in using tree cores to document climate sensitivity of the species we were working on, led to Ailene and I having a lot of discussions of what we would expect climate sensitivity to look like along an altitudinal range."

Janneke (Dr. Hille Ris Lambers) decided to establish a research program on Mt. Rainier because she realized that it provided several key features of an excellent *model system*. In this context, a "model system" is a real natural system which shares important features of other natural systems in which you are interested. For example, the white rat (an albino lineage of *Rattus norvegicus*) is an excellent model system for humans and other mammals because it (i) shares many features of its physiology and genetics with humans (and other mammal species), (ii) is easy to raise and maintain in a lab, and (iii) has already been studied a lot, making lots of previous information available. For Janneke, the forests on Mt. Rainier provide an excellent model system for studying species range limits because the tree species are similar to those elsewhere in the mountain regions of western North America. In addition, the size of the mountain insured that they would be able to study range limits across a very wide range of temperatures and other climate variables. Mt. Rainier not remote, allowing researchers regular access to their study areas. Last, and critical to Janneke's and Ailene's research, it has a very thoroughly documented history of weather and climate.

[Figure 1.x What limits montane tree distributions - species interactions, or the physical environment? Populations in landscapes are dynamic systems. The number of trees in a population and their spatial distribution is a constant and slowly shifting balance between inflows (births/seed production, dispersal, establishment and growth) and losses (death). Ettinger et al. studied how climate and species interactions influence this balance. Pictures of Mt. Rainier, tree cores, and people.]

A species range as a system

We can use systems thinking in a variety of ways to help us understand research on range limits. Perhaps the simplest is to imagine an individual tree that is near the boundary of a species range (Fig. 1.x). We examine growth at the boundary because it is at the boundary where climate is thought to show its effects the most strongly. At the boundary, an individual grows rapidly when conditions are highly conducive to growth, and it does not grow when conditions are sufficiently bad. The more years it does not grow, the more likely it is to die.

[Fig. 1.x. A tree, or three, as a system.]

We know that climate, resources, mutualists, and enemies determine whether an individual lives or dies. For instance, if climate is a very important determinant of growth, then growth should increase in good years and decrease in bad years. That is, growth of an individual tree should be correlated with climate.

Induction 1

Ecologists, including Janekke and Ailene, have reasoned that climate controls plants. Here we use inductive reasoning as we *generalize* from *many species* to *all species*.

Premise: The distributions of plant species around the world appears correlated with climate.
Conclusion 1: The distribution of all plant species are correlated with climate.

Note the leap of faith in this inductive generalization. We are assuming that because the distributions of plant species around the world (i.e. tropical rainforests, grasslands, deserts, tundra) are associated with different climates, then that will be the case for the next species we examine.

Induction 2

In this premise, we *predict* from *two or more spatial and temporal scales* to another particular spatial and temporal scale.

Premise: Climate determines plant growth at global scales (e.g., tropics vs. desert) and at small scales, as when we observe plants wither and die from extremely hot, cold, wet or dry conditions.
Conclusion 2: The boundaries or range limits of montane conifer tree species are determined directly by

climate (Fig. 1.x).

In this inductive argument, we applying ideas formed from observations at completely different spatial and temporal scales --the existence of biomes *vs*. the growth and death of individual plants-- and applying them to another situation.

Induction 3

In addition to the above arguments, Janekke and Ailene realized that trees can respond strongly to resources, mutualists and enemies. If trees are responding to these factors, this might tend to hide any response to climate. Therefore, they reasoned that

Premise: Fossils and other evidence have shown that species have not always responded to climate, and mutualists and enemies may regulate species distributions (Fig. 1.x).
Conclusion 3: Species range limits do not correlate with climate.

[Figure 1.x. Climate appears to control upper limits but not lower limits of species distributions. Images from Ettinger et al. 2011, Fig. 1, and scatterplots of growth vs. temp. for two trees, showing strong, and no correlation.]

Deductive arguments

Given that we know so much about plants, it is to use the conclusions generated by the inductive arguments as premises in deductive arguments.

In addition, to the above arguments, Ettinger and her colleagues also recognized that if climate is important, most individuals of a particular species that are exposed to the same climate should respond in a similar way. At a particular elevation, climate is relatively uniform over a broad area. Therefore, the growth of individuals of the same species at the same elevation should be *correlated with each other*. Using the above reasons, Ailene and her colleagues formed a predictive hypothesis for range limits of different conifer species on Mt. Rainier in Washington, USA. They collected pencil-sized cores cut out of over 600 individual living trees of six conifers species (Fig. 1.x), and from these cores were able to use the growth rings to measure growth rates of each tree of the last 90+ years (Fig. 1.x). They also used weather data that was collected at park ranger stations at different elevations on Mt. Rainier over the same 90+ year interval.

Ettinger and her colleagues used the following syllogism to address their questions. Their above hypothesis was based on a careful reading of the primary literature.

Premise 1

- Hypothesis: If climate controls range limits of tree species through direct effects on growth and survival (***CRL***), then growth rates *of most individuals* of a single species at a particular elevation will correlate strongly with climate variables(***I***) (Fig. 1.x).
- Abstraction: *If* ***CRL****, then* ***I****.*

Remember that a good experiment creates conditions that could falsify the hypothesis. That means that a good experiment needs to (1) create conditions wherein the hypothesis could operate if it is true, and (2) has a reasonable possibility of either succeeding or failing. Ettinger and her colleagues collected data that would show whether individual growth rates correlated with climate on not. Given these data, two results are plausible, and these lead to two different conclusions:

Premise 2a ● Result: Growth rate of most individual trees does not correlate with climate. ● Abstraction: *not **I*** *Conclusion a* ● Climate does not control species range limits. ● Abstraction: ***not CRL***	*Premise 2b* ● Result: Growth rate of most individual trees correlates with climate. ● Abstraction: ***I*** *Conclusion b* ● Climate, or some factor correlated with climate, controls species range limits. ● Abstraction: ***CRL or not CRL***

As in the previous example (island biogeography, Simberloff and Wilson 1969), we see the structure of a deductive syllogism. Premise 1 provides the mechanistic and general hypothesis. Premise 2 provides possible specific results, and the conclusions of the syllogisms must follow logically from the premises.

[Fig. 1.x. Bar graph or dot plot showing proportion of trees that respond to climate variables, grouped by high and low elevation species, and upper and lower range limits]

Ettinger and her colleagues found that at the upper elevation range limits of the high altitude species, individual tree growth almost always correlated strongly with climate. However, at lower elevations, these correlations tended to disappear. That is, only in the harshest climate -- at the high elevation treeline -- were tree species were limited by climate. Thus their data were *consistent with* their hypothesis for some limits for some species and falsified the simple effect of climate for lower elevation range limits. This is leading them to new questions about the range limits of organisms.

CONJECTANEUM

Ecology is messy. Ecology is messy, and I can think of three ways in which it is messy. First, it can be messy when it takes us outdoors, in direct contact with nature. An ecological study might have us scaling 300 ft tall trees to study insects in the forest canopy, or snorkeling down in streams or along coral reefs. We might be crawling along the forest floor looking for seeds, spelunking through deep caverns, or digging ditches in a reclaimed strip mine. This part of ecology is sometimes referred to as *field ecology* or *field biology*, but for most ecologists it is just “ecology.”

[Figure 1.x.Images of messy ecologists and their noisy data]

Ecology is also messy in the sense that our data are full of *noise* because the world seems infinitely complex. That is, we seem to be trying to tune in a radio that is not getting good reception, and most of what we hear is static noise; sometimes we can tune into a radio station if we are really really careful, but we never get completely free of the static. Usually, most of the variation in our data is unexplained.

Ecology is also messy in that it is very complicated. Even if we could understand all the "noise" in our data, it would still be wildly complicated. If you think that the vertebrate brain is complicated, consider that it is housed in a complicated physiological system which we call an organism, and that organism is home to billions of microbes, and that vertebrate host is swimming in a sea of other organisms beyond count in a physical environment that is constantly changing. In a way, it is amazing that we understand as much as we do.

In spite of the messiness, ecology reveals order in at least two ways. First, there are regularities or patterns in the structure of ecological systems (Dodds 2009), and we will discuss these throughout the book. Most of this seems to comes directly from the physical laws of nature, and from evolution tending to maximize fitness in under physical constraints. Order also appears when ecologists focus on processes that are shared across systems. For instance, we find that predation seems to follow some fairly similar rules, regardless of the particular species that we might be studying at a particular point in time. We find simplicity in the processes, even if evolution has created an infinite variety of organisms that consume other organisms.

Thus is ecology an ordered mess. Ecology is science of understanding the order so that we can predict the mess.

SUMMARY AND REVIEW

1. Ecology is the scientific study of the relations between organisms and their environments. Sometimes ecologists focus more on the organisms, and sometimes less, but we are always interested in the interplay between organisms of different types, how the physical world interacts with life, and the consequences these have for the physical environment.
2. Life, consumption, cooperation, biodiversity, the biosphere, and physical laws constitute a sample of the important ideas in ecology. Earth contains infinitely complex life, and ecology is the science of how it persists on this tiny blue planet.
3. Ecologists develop habits of mind that allow them to utilize disciplinary thinking, that is, ways of thinking shared among members of a discipline. Unlike purely physical scientists, ecologists are accustomed to thinking about biology, natural history, and biological evolution. Evolution is the central discipline in biology, and ecologists often rely upon their understanding of evolutionary processes to help them understand the ecology of their system of interest.
4. Like all scientists, ecologists use explicit inductive and deductive reasoning to create and test scientific ideas. Inductive reasoning allows scientists to use specific data about the natural world to propose more general rules. Inductive arguments may use a lot of good evidence (strong inductive arguments), or instead may rest upon little or no evidence (weak inductive arguments) Deductive reasoning uses general rules in the form of "if-then" statements, along with specific cases to make predictions. Deductive arguments are essential for falsification. Falsification may be the keystone of modern science. If an idea cannot, in principle, be falsified, or be subject to falsification, then it is not a scientific idea. Probability is an extension of formal reasoning, and facilitates both inductive reasoning, and the falsification of deductive predictions.

5. Like some physical scientists, ecologists are good systems thinkers because they are used to thinking about interconnections and relationships. Systems, in general, have structure and behavior, and ecologists both. All ecological systems are open systems, exchanging energy and materials with the environment outside the system of interest. All systems are nested within other systems, and all systems have internal complexity. Unlike most biologists, ecologists are accustomed to thinking about systems, and about relationships between organisms and their physical environment, organisms and their enemies and prey, and organisms and their social groups.
6. All scientific research can be broken down into its elemental inductive and deductive structure. It takes hard work and persistent practice to develop the habits of mind to understand scientific research. Scientific thinking also relies imagination, and requires the asking of lots of questions. Anyone can learn to be a better ecologist.
7. Although ecology is messy in both the literal and conceptual meaning of the word, we can make sense of this infinitely complex, ever changing natural world. Making sense of it requires both knowledge of natural history (biological details of organisms), and the ability to think abstractly about similarities of form and function of both organisms and more complex systems.

Problems

1. For Fig. 1.1, identify the source pool and sink pool for every arrow.
2. Write the answers. Let $x = 2$.

a. x^3	b. $x^{0.5}$	c. $\sqrt{x}$
d. ln(x)	e. ln(x+1)	f. $\log_{10}(x)$
g. $\log_{10}(10x)$	h. $\log_{10}(100x)$	i. $\ln(e^x)$
j. $\log_{10}(10) + \log_{10}(x)$	k. $\log_{10}(x/10)$	l. $\log_{10}(x)-\log_{10}(10x)$

3. On one graph, sketch the three lines for $y = a M^z$, where z = 0.5, 1, and 2. Assume $a = 1$, and *M* is the set of real numbers from zero to 3. Indicate on the *x*-axis tick marks for 0, 1, 2, 3.
4. On one graph, sketch the three lines for $\log_{10}(y) = \log_{10}(aM^z)$, where z = 0.5, 1, and 2. Assume $a = 1$, and *M* is the set of real numbers from 0.1 to 100. Indicate on the *x*-axis tick marks for 0, 1, 2.
5. Identify inflows, outflows and reproduction in Figs. 1.x.
   a. Fig. 1.x.a.
   b. Fig. 1.x.b.
   c. Fig. 1.x.c.
   d. Fig. 1.x.d.
6. Create model system diagrams with one element or pool for the following natural systems. Include only those fluxes listed, in addition to reproduction and death where appropriate.
   a. Individuals in a human population of a city, that gains individuals through migration.
   b. Individuals in a population of *Chorella* (a single celled alga), that gains and loses individuals through migration.
   c. Individuals in a population of *Mycoplasma pneumoniae*, in a human body.
   d. Carbon in the atmosphere, that gains through cellular respiration of organisms, diffusion out of water, and burning of fossil fuels, and loses carbon through uptake by plants and algae, and diffusion into water.
   e. Water in a reservoir, with inflows from an inlet river and groundwater, and outflows through evaporation, and on outlet river below the dam.
7. Create model system diagrams with two elements or pools for the following natural systems. Make sure to include reproduction and death where you think it is appropriate.
   a. Individuals in populations of Snowshoe hare (prey) and lynx (predator).
   b. Water in the atmosphere, and in oceans and lakes.
   c. Carbon in the atmosphere and on land in plants.
   d. Individuals in human populations that are either susceptible to a pathogen (pool 1), or infected (pool 2). Flux from pool 1 to pool 2 occurs when a susceptible individuals becomes infected.
8. Identify whether the following deductive syllogisms are valid

a. All men are mortal. Pat is a man. Therefore Pat is mortal.	b. All men are mortal. Pat is not a man. Therefore Pat is not mortal.	c. All men are mortal. Pat is mortal. Therefore Pat is a man.
d. All men are mortal. Pat is not mortal. Therefore Pat is not a man.	e. If A then B A Therefore B	f. If A then B not A Therefore not B
g. If A then B B Therefore A	h. If A then B not B Therefore not A	i. All kittens like to play. This animal is a kitten. Therefore this animal likes to play.
j. All kids like food. Sarah likes food. Therefore Sarah is a kid.	k. All humans have six legs. Hank is human. Therefore Hank has six legs.	l. All insects have exoskeletons. This ant has an exoskeleton. Therefore this ant is an insect.
m. All people like food. Sarah likes food. Therefore Sarah is a person.	n. Money does not grow on trees. The item in my pocket did not grow on a tree. Therefore the item in my pocket is money.	o. All plants require water. A daisy requires water. Therefore a daisy is a plant.

9. For all of the deductive syllogisms above, try to determine the conclusion is true. For valid syllogisms with false conclusions, identify the false premise. For invalid syllogisms with true conclusions, create a valid deductive argument that would support the conclusion.
10. Identify whether the following inductive arguments are strong or weak, and in one sentence explain your answer.

a. During my lifetime, sun has always risen in the east. The sun always rises in the east.	b. When I yawn, I notice that other people start to yawn also. Yawning is contagious.	c. Every coin that I have ever flipped landed either heads up or tails up. All coins always land either heads or tails.
d. I flipped this coin ten times, and got ten heads. This coins always lands heads up.	e. I have fallen in love and gotten hurt. I will always get hurt when I fall in love.	f. In my experience, clouds come before rain. Clouds cause rain.
g. I have never seen a fire that didn’t produce smoke.	h. When I have told a lie, I often find it complicates my	i. In the past, the editorial pages of this newspaper

Where there's smoke, there's sure to be a fire.	life. "Oh, what a tangled web we weave/When first we practice to deceive![16]	have dismissed factual and verified scientific evidence for major environmental problems as overstated or weak. Therefore, the editorial pages of this newspaper are not a reliable factual source of information on environmental science.

11. You roll a 20-sided die. What is your chance of rolling
    a. a 20?
    b. a 10?
    c. 10 or less?
    d. 16 or greater?
12. On your twenty sided die, you roll two consecutive 3's.
    a. What is the probability of that consecutive roll?
    b. You are about to roll again. What is the probability of rolling a 3 on this single roll?
13. You sample 100 shrubs in Princeton, New Jersey, USA, and you find evidence for browsing by deer on 92 of them. Sketch a histogram of the empirical probability density distribution of these data.
14. You sample 50 oak trees in Linesville, Pennsylvania, USA, and you find that 35 contain silk "tents" of gypsy moths. Of these 35, 20 of them are completely defoliated (no leaves) and the others have some visible damage. (a.) Sketch a histogram of the empirical probability density distribution of the presence and absence of gypsy moth caterpillars. (b.) Sketch a histogram of the empirical probability density distribution of damage including no damage, some damage, and complete defoliation.

Discussion Questions

1. What about the natural world interests you? Explain.
2. Of the six "big ideas" listed above, which is most interesting to you? What intrigues you about that topic? Is there a second idea from the list that you imagine fitting in with, or complementing your first idea? If so, how do the two ideas fit together?
3. Do you think consumption or cooperation dominates the interactions in Figure 1.1? Support your answer with a short paragraph.
4. What do you think you like about systems thinking? What do you think you might not like about systems thinking? Can you imagine representing any small part of your daily life as a system? Why or why not?
5. You hear that a defendant in a legal case tested positive for anabolic steroids. Consider whether the following conditions influence your belief that the person was actually taking steroids.

[16] Sir Walter Scott, 1808, *Marmion*.

    a. The defendant was a professional athlete.
    b. The defendant was not an athlete.
    c. The defendant had a history of illegal drug use.
    d. The plaintiff had a history of false accusations.
6. Represent the above legal case examples in the form of a syllogism.

References Cited And Suggested Reading