CHAPTER 1

Welcome to the Monarchy

You who go through the day
like a wingèd tiger
burning as you fly
tell me what supernatural life
is painted on your wings
so that after this life
I may see you in my night

—Homero Aridjis, "To a Monarch Butterfly"

The monarch butterfly is a handsome and heroic migrator. It is a flamboyant transformer: an egg hatches into a white, yellow, and black-striped caterpillar; then a metamorphosis takes place inside its leafy-green chrysalis, which is endowed with gold spots; the adult butterfly that emerges flaunts orange and black (fig. 1.1). In the monarchs' annual migratory cycle—perhaps the most widely appreciated fact about them—individual butterflies travel up to five thousand kilometers (three thousand miles), from the United States and Canada to overwintering grounds in the highlands of Mexico. After four months of rest, the same butterflies migrate back to the United States in the spring. Come summer, their children, grandchildren, and great-grandchildren will populate the northern regions of America.

But there is much more to the monarch's story than bright coloration and a penchant for epic journeys. For millions of years, monarchs have engaged in an

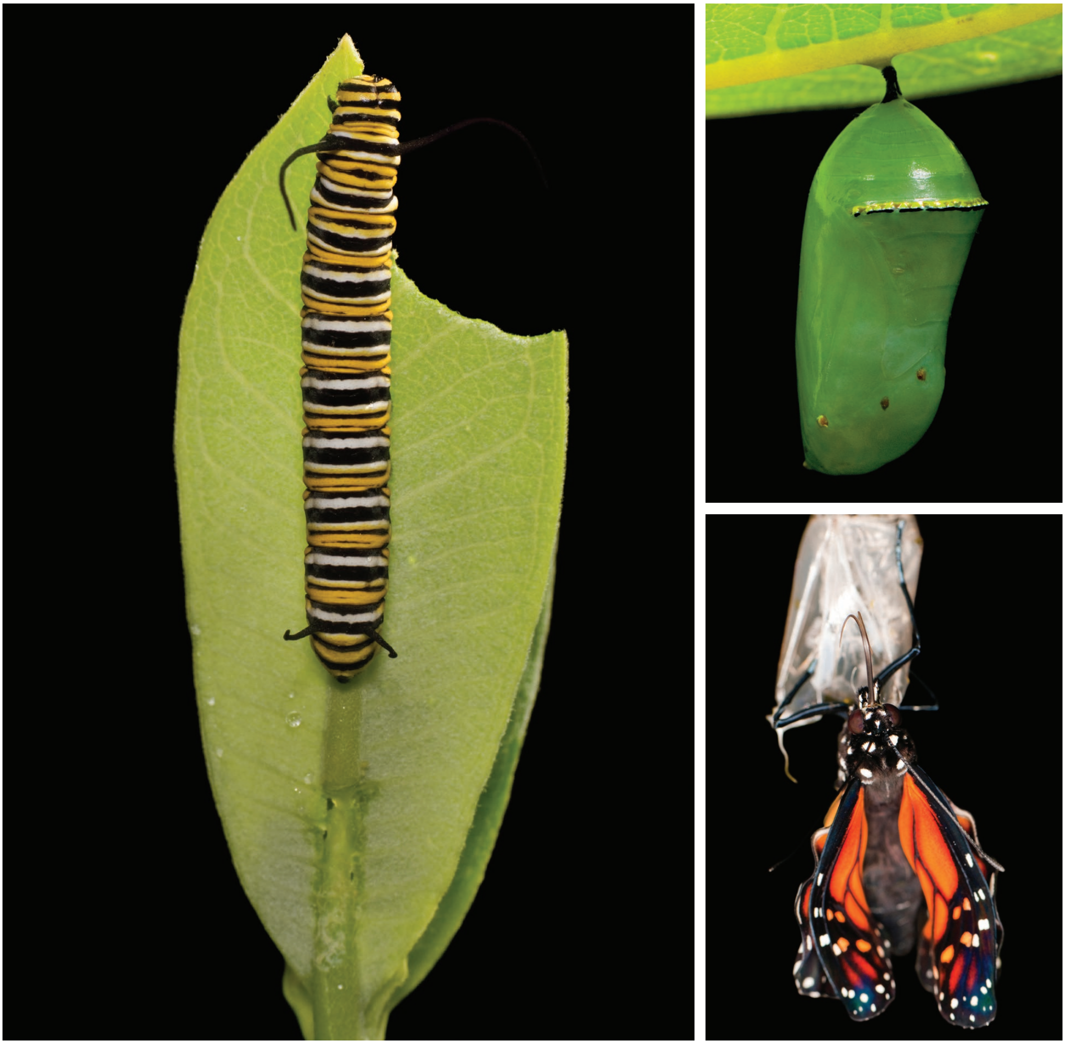

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FIGURE 1.1. The monarch butterfly in three stages: (a) a caterpillar eating a milkweed leaf, (b) a chrysalis undergoing metamorphosis, and (c) an emerging butterfly before it expands its wings.

evolutionary battle. The monarch's foe in this struggle is the milkweed plant, which takes its name from the sticky white emissions that exude from its leaves when they are damaged. The monarch-milkweed confrontation takes place on these leaves, which monarch caterpillars consume voraciously, as the plant is their exclusive food source. Milkweeds, in turn, have evolved increasingly elaborate and diversified defenses in response to herbivory. The plants produce toxic chemicals, bristly leaves, and gummy latex to defend themselves against being eaten. In what may be considered a coevolutionary arms race, biological enemies such as monarchs and milkweeds have escalated their tactics over the eons. The monarch exploits, and the milkweed defends. Such reciprocal evolution has been likened to the arms races of political entities that stockpile more and increasingly lethal weapons.

This book tells the story of monarchs and milkweeds. Our journey parallels that of the monarch's biological life cycle, which starts each spring with a flight from Mexico to the United States. As we follow monarchs from eggs to caterpillars, we will see how and why they evolved a dependency on milkweed and what milkweed has done to fight back (fig. 1.2). We will discover the potency of a toxic plant and how a butterfly evolved to overcome and embrace this toxicity. As monarchs transition to adulthood at the end of the summer, their dependency on milkweed ceases, and they begin their southward journey. We will follow their migration, which eventually leads them to a remote overwintering site, hidden in the high mountains of central Mexico. Along the way, we will detour into the heart-stopping chemistry of milkweeds, the community of other insects that feed on milkweed, and the conservation efforts to protect monarchs and the environments they traverse.

To be sure, this story is about much more than monarchs and milkweeds; these creatures serve as royal representatives of all interacting species, revealing some of the most important issues in biology. As we will see, they have helped to advance our knowledge of seemingly far-flung topics, from navigation by the sun to cancer therapies. We will also meet the scientists, including myself, who study the mysteries of long-distance migration, toxic chemicals, the inner workings of animal guts, and, of course, coevolutionary arms races. We will witness the thrill of collaboration and competition among scientists seeking to understand these beautiful organisms and to conserve the species and the ecosystems they inhabit.

FIGURE 1.2. An unlucky monarch butterfly caterpillar that died after taking its first few bites of milkweed, the only plant it is capable of eating. In a violent and effective defense, toxic and sticky latex was exuded and drowned the caterpillar. A substantial fraction of all young monarchs die this way.

FROM SIMPLE BEGINNINGS

From a single common ancestor, milkweeds diversified in North America to more than one hundred species. And the monarch lineage is no slouch, with hundreds of relatives we call "milkweed butterflies" throughout the world. Although monarchs are perhaps best known in the northeastern and midwestern United States, they occur throughout North America, and self-sustaining populations have been introduced to Hawaii, Spain, Australia, New Zealand, and elsewhere (fig. 1.3). Interactions between butterflies and milkweeds now occur throughout the world, but this account focuses primarily on what happens in North America. The reason is quite simple: eastern North America is where the monarch (*Danaus plexippus*), considered by most to be the pinnacle of milkweed butterflies, coevolved with milkweeds.

The monarch's annual cycle in eastern North America involves at least four butterfly generations, with individuals crossing international borders several times. In spring, butterflies migrate from Mexico to the southern United States. Flight is fueled by nectaring on flowers and is punctuated by laying eggs on milkweeds. To grow and sustain each generation, milkweed is the only food needed. Three cycles—from egg to caterpillar, to chrysalis, to butterfly—occur as monarchs populate the northern United States and southern Canada each summer. And while nearly all mating, egg-laying, and milkweed eating occurs in the United States and Canada, each autumn monarchs travel to Mexico. At the end of summer, southward migrating monarchs fly thousands of kilometers and then rest for some four months before returning to the Gulf Coast states in the following spring. How and why they do it is a story that continues to unravel, and it no doubt will keep scientists busy for centuries.

The energy that builds a monarch butterfly's body ultimately comes from plants—as it does for all animals. For most butterflies and moths (collectively, the Lepidoptera), the caterpillar stage is essentially a leaf-eating machine. Perhaps it is not surprising then, that caterpillar feeding has led to the evolution of armament (or "defenses") in plants. The leaves of nearly all plant species are not only unappetizing to most would-be consumers; they are downright toxic. Milkweed's toxicity has long been known, and foraging on milkweed has surely killed countless sheep and horses. Most other animals avoid this milky, sticky, bitter weed, and yet monarchs came to specialize on it. While the toxic principles of milkweed keep most consumers at bay, monarchs and a few other insects have craftily adapted to the plant. Humans have used the chemical tonic of milkweeds as medicine for centuries, and so too have monarchs exploited their medicinal properties—at least at low doses. As the great Renaissance scientist Paracelsus noted five hundred years ago, "dose makes the poison"; there is often a fine line between poison and medicine. Much of this book is devoted to unraveling the evolution of poisonous and medicinal properties in plants that are habitual fodder for animals.

The evolutionary war waged between monarchs and milkweed is a product

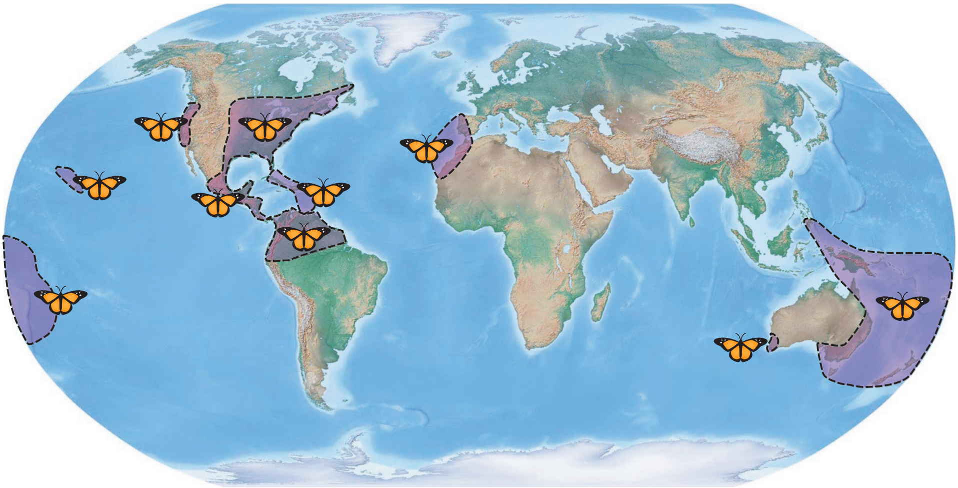


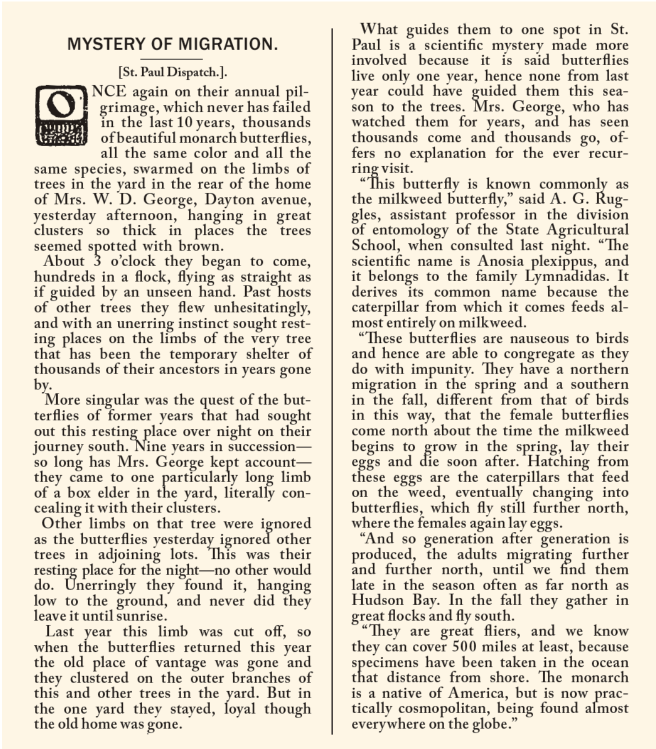
FIGURE 1.3. The worldwide distribution of monarch butterflies. Although native to the Americas, they have been introduced to the South Pacific, Australia, and Spain over the past few hundred years. The introduction of weedy milkweeds to these new regions, mostly the tropical milkweed *Asclepias curassavica*, preceded the establishment of monarchs. Monarchs are most abundant in North America.

of their intimate relationship. Monarchs not only tolerate milkweed's toxicity but have evolved to put it to work. For more than a century, insect enthusiasts have observed that most bird predators leave monarchs alone, presumably because their bright coloration signals a toxic body. Nonetheless, monarchs are not free of enemies. Flies and wasps consume them from the inside and eventually burst out. Tiny protozoan parasites infect their bodies, and monarchs medicate themselves with milkweed's toxins.

The milkweed plant is not a passive victim being devoured by monarchs. When the plant is attacked, its entire physiology, expression of genes, and toxicological apparatus kicks into high gear like an immune system. Milkweeds may lack an animal's central nervous system, but they possess all the other attributes common to the sessile sugar factories we call plants. They actively engage in strategies that defend against, tolerate, and when possible, manipulate insect enemies like the monarch butterfly.

While some mysteries of monarchs and milkweeds were only recently solved, much of what I present about the interaction between monarchs and milkweeds was reasonably well known (or at least hypothesized) more than a century ago (fig. 1.4). Searching through old newspapers, one can find beautiful accounts of their relationship. Although the classification of the monarch butterfly has changed over the past 150 years, the intimate interaction with milkweed was observed from the very beginning. Monarch "plagues" have been reported for at least as long, frightening entomophobes (people afraid of bugs). Nonetheless, because milkweed is sometimes considered an undesirable weed, an abundance of monarchs was also said to be beneficial by entomologists who knew the insect, as it might control the plant. There were newspaper reports of "Monarch Invasions from Canada" (as they migrated south past Rochester, New York) as early as the 1880s. Although there was some controversy about whether the butterflies migrated long distances, it was solidly hypothesized early in the twentieth century that this insect followed the seasons, south in the autumn, and with multiple generations moving northward each spring. How and why they migrate, and how and why they feed exclusively on milkweed, were discoveries made over the next hundred years. Honestly, they are not fully solved mysteries, but we have made great progress, and this book is about revealing the science behind these discoveries.

Monarchs have also been proposed as a sentinel, whose health as a species may be a "canary in a coal mine" for the sustainability of the North American continent. They travel through vast expanses, tasting their way as they go. Although they tolerate milkweed poisons, they are highly susceptible to others, especially pesticides. Summer and winter climates are likely the key drivers of the monarch's annual migration: feed on spring and summer milkweed foliage, follow the season north as it is progressively unveiled, rest in the chill mountain air in winter. Their time in Mexico is delicately balanced between being physiologically active, but cool, not burning precious energy before spring arrives. Our changing climate is certainly affecting monarch butterflies, although we are just beginning to understand the severity of these effects.



MYSTERY OF MIGRATION.

[St. Paul Dispatch.].

ONCE again on their annual pilgrimage, which never has failed in the last 10 years, thousands of beautiful monarch butterflies, all the same color and all the same species, swarmed on the limbs of trees in the yard in the rear of the home of Mrs. W. D. George, Dayton avenue, yesterday afternoon, hanging in great clusters so thick in places the trees seemed spotted with brown.

About 3 o'clock they began to come, hundreds in a flock, flying as straight as if guided by an unseen hand. Past hosts of other trees they flew unhesitatingly, and with an unerring instinct sought resting places on the limbs of the very tree that has been the temporary shelter of thousands of their ancestors in years gone by.

More singular was the quest of the butterflies of former years that had sought out this resting place over night on their journey south. Nine years in succession—so long has Mrs. George kept account—they came to one particularly long limb of a box elder in the yard, literally concealing it with their clusters.

Other limbs on that tree were ignored as the butterflies yesterday ignored other trees in adjoining lots. This was their resting place for the night—no other would do. Unerringly they found it, hanging low to the ground, and never did they leave it until sunrise.

Last year this limb was cut off, so when the butterflies returned this year the old place of vantage was gone and they clustered on the outer branches of this and other trees in the yard. But in the one yard they stayed, loyal though the old home was gone.

What guides them to one spot in St. Paul is a scientific mystery made more involved because it is said butterflies live only one year, hence none from last year could have guided them this season to the trees. Mrs. George, who has watched them for years, and has seen thousands come and thousands go, offers no explanation for the ever recurring visit.

"This butterfly is known commonly as the milkweed butterfly," said A. G. Ruggles, assistant professor in the division of entomology of the State Agricultural School, when consulted last night. "The scientific name is Anosia plexippus, and it belongs to the family Lymnadidas. It derives its common name because the caterpillar from which it comes feeds almost entirely on milkweed.

"These butterflies are nauseous to birds and hence are able to congregate as they do with impunity. They have a northern migration in the spring and a southern in the fall, different from that of birds in this way, that the female butterflies come north about the time the milkweed begins to grow in the spring, lay their eggs and die soon after. Hatching from these eggs are the caterpillars that feed on the weed, eventually changing into butterflies, which fly still further north, where the females again lay eggs.

"And so generation after generation is produced, the adults migrating further and further north, until we find them late in the season often as far north as Hudson Bay. In the fall they gather in great flocks and fly south.

"They are great fliers, and we know they can cover 500 miles at least, because specimens have been taken in the ocean that distance from shore. The monarch is a native of America, but is now practically cosmopolitan, being found almost everywhere on the globe."

FIGURE 1.4. A newspaper article about the monarchs' migration from the *Washington Post*, September 17, 1911.

In some respects, human activities have enhanced habitat for milkweeds and monarchs north of the overwintering grounds. Logging and agriculture have been good for monarch populations in some regions, like the eastern United States, where these pursuits likely made milkweed and its associated butterflies much more abundant. However, farming surely destroyed much of the midwestern prairie, where milkweed had previously been prolific. Now the same processes, combined with the indirect influences of other human activities, have been suggested as drivers in the decline of monarch butterfly populations. I evaluate what is known about the causes of monarch and milkweed ups and downs toward the end of this book. If they are truly sentinels, then much more than the sustainability of monarchs is at stake, and careful study of their biology—past, present, and future—is in order.

GETTING INFECTED

How ecological interactions—plants and insects, monarchs and milkweeds—caught my attention is a story in and of itself. I grew up in a fairly rural area of suburban Pennsylvania, where fields of red clover and foxtail grasses were common, and my brother and I were encouraged to spend much of our time outside. Vacations were spent camping; my mother was, and continues to be, an insatiable gardener; and the corn fields growing behind my home prompted me to want to be a farmer. As a college student at the University of Pennsylvania, I felt the bliss of self-discovery, yet also the pressures of being a child of immigrant parents who were unfamiliar with most academic endeavors outside of medicine and engineering. My parents' proviso concerning my college education was that, in addition to exploring my interests in social science and the humanities, I take introductory science and math classes, so as not to close too many doors. Fair enough.

As a sophomore, I decided to take introductory biology. But, because the lecture halls were limited in their seating, and because many colleges feel pressure to have smaller classes (after all, small classes enhance students' learning, as well as college rankings), there were two offerings of the course that semester—similar classes, covering much the same material, but taught by different professors. To choose, I did what many students did, and still do: I consulted what was known as a "skew guide," a "for the students, by the students," survey of courses that outlined the degree of difficulty, what was liked and disliked by students who had taken the course previously, and unashamed caricatures of the esteemed faculty—the clothes they wore, comments about their hygiene, and notes about their traits, usually having little to do with their ability to impart scholarly information. Sad but true, what sealed the deal for me was the characterization of one of the professors: "typically comes late to class and leaves early." I actually don't remember if that ended up being true, but the course, and his approach to biology, caused a profound shift in my own development as a student. Dr. Daniel Janzen presented biology as a set of stories, far

FIGURE 1.5. In a memorable lecture on butterflies and poisonous plants, Dr. Janzen showed this slide depicting the unpalatability of milkweed. The toxic plant flourished under grazing pressure because it was avoided by horses (*right side of the fence*). But where horses were absent (*left*), milkweed was less abundant and suffered from competition with grasses.

stranger than any science fiction I had read. Biology was a series of mysteries that could be solved by careful observation and clever manipulation. Biodiversity was presented as a bottomless mine of species and interactions that had been shaped by both millions of years of evolution and the now dominant species on the planet, *Homo sapiens* (fig. 1.5).

A recurring theme of the course and the professor's favorite organisms for study were plants that were damaged by insects. Insects eating plants? What about the charismatic megafauna: lions, tigers, and sharks? Or at least buffalos and birds? Now that I am a professor, I annually teach a course called "Chemical Ecology" with several faculty colleagues at Cornell University. In this course we analyze how chemicals in the natural world mediate interactions between species. Why are chilies and horseradish spicy? How do monarch butterflies gain their toxicity? And, are there really human pheromones? Yet, our lectures often focus on insects eating plants. Comments from students in our course evaluations occasionally plead, "Enough with the caterpillars already!" Yet it is the abundance, diversity, and general importance of insect-plant interactions that motivate our course, as well as my own fascination and research focus on monarchs and milkweeds.

ARTHROPOD-PLANT INTERACTIONS

What can little creatures like monarch butterflies and their vegetarian habits teach us about nature? First, the source of essentially all of the energy that powers an animal—really, any food chain—comes from plants. They constitute an exclusive group of organisms that can process nonliving matter and turn it into the energy that is needed for life. That process is photosynthesis, and that energy is sugar. Plants take sunlight, carbon dioxide from the air, and water, and through a chemical reaction produce oxygen and sugar. That sugar powers life on earth. Sure, we don't typically think of lions, tigers, and sharks as relying on plants. But they do. They eat other animals that survive by eating plants. Meanwhile, plants "eat" earth, wind, and sun. As such, plants make up the largest fraction of living matter (what biologists call "biomass") on the planet. Milkweed is but one of hundreds of thousands of plants species, yet it is an excellent representative to teach us about biology.

$$6CO_2 + 6H_2O + \text{photons} \longrightarrow C_6H_{12}O_6 + 6O_2$$
$$\text{carbon dioxide} + \text{water} + \text{light energy} \longrightarrow \text{sugar} + \text{oxygen}$$

Second, there are two pathways by which plant energy enters a food chain: as compost and as salad. Most of it, probably 80 percent or so, enters the food chain as rotting compost. As leaves fall off plants, microbes, worms, and microarthropods shred it, transform it, and make it available as broken-down food and nutrients for others. The rest, about 20 percent of plant material,

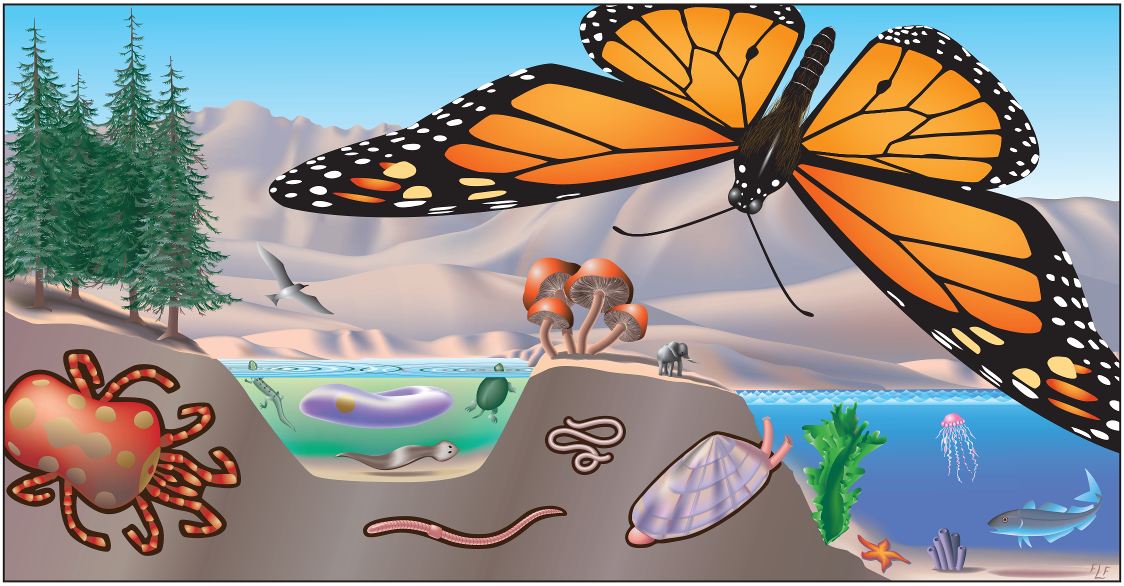


FIGURE 1.6. *The Bioscape*, where taxonomic groups are drawn proportional to the number of currently known species. In this diagram, the monarch represents all insects. Among the 2 million described macroscopic species (visible to the naked eye), about one quarter are herbivorous insects. Yet, our best guesstimates of the actual number of herbivorous insects on the planet range from 2 million to 5 million species. As we discover the rest of the species, plants are likely to constitute about 10 percent of the total number of species. Even by the most generous estimates, all vertebrates combined (including mammals, birds, fish, reptiles, and amphibians) would hover around 2 percent of species, and 70 percent of species are likely insects (about half of which are herbivorous). Accordingly, in terms of the source of the planet's overall energy, biomass, and biodiversity, plants and herbivorous insects play a dominant role.

enters the food chain fresh, as a "salad." Monarchs are but one of the millions of leaf-eating species that can teach us about the consumption of living plant tissues by animals. And, yes, although it is true that zebras and porcupines are charismatic megafaunal herbivores (big mammals that eat plants), in other ways, insects like monarchs dominate the scene (fig. 1.6).

The third reason for a focus on insects and plants is quite practical. These organisms are typically easy to cultivate in large numbers, in relatively small spaces, and with relatively little interference from animal rights activists. The consequence for scientists is that we can work toward strong inference in our studies. "Strong inference," a term introduced by a biophysicist and philosopher of science, J. R. Platt, in 1964, refers to going beyond single factors as explanations of natural phenomena, and going beyond correlations as explanations for the causes of patterns. Many correlations are statistical associations that have no "causal" basis. The variable on the *x* axis of a graph, although correlated with a variable on the *y* axis, is not the cause of variation in the variable on the *y* axis. Take, for example, the strong positive correlation between the per capita consumption of chocolate in a country and the number of Nobel laureates from that country. To quote from a tongue-in-cheek article published in the *New England Journal of Medicine*: "[We] estimate that it would take about 0.4 kg of chocolate per capita per year to increase the number of Nobel laureates in a given country by 1." To evaluate correlations rigorously, and hence to promote strong inference, one typically needs large numbers of study subjects, the testing of alternative explanatory factors, and a critical experiment. The abundance of insects on plants, along with the ability to raise them in both the laboratory and field, makes them ideal scientific subjects. Distinguishing between correlation and causation is critical to our understanding of the biology and conservation of monarchs and milkweeds. Turing back to our study of chocolate: countrywide spending on science also correlates with per capita income, the latter of which correlates with chocolate consumption (at least in the Western world). Even so, I would happily participate in a controlled study to determine the influence of chocolate consumption on scientific discoveries.

Given the attributes of insects and plants, it is perhaps not surprising that their study has become a bit of cottage industry among biologists. We even have a specific journal dedicated to publishing scientific studies on insect-plant interactions. Well, to be honest, it is called *Arthropod-Plant Interactions*, so as to include studies of related creatures with more than six legs, such as spiders, mites, millipedes, and centipedes. The main point, however, is that in addition to their general abundance, diversity, fascinating biology, and tractability of study, these insect-plant systems have become a general model for understanding biology. Given the millions of species on the planet, biologists make progress through the in-depth study of several "model systems" that intensely examine a few selected organisms, with the hope of generalizing to other systems. Sometimes these "models" are specific species (like the lab rat). In other cases, however, the models may be habitats or groups of species that have their own ecologies.

Monarchs and milkweeds have proven to be an excellent model system through which we can understand the coevolution and conservation of species. Like all plants, milkweeds have an arsenal of toxins, evolved by natural selection, to ward off pesky herbivores. Like all herbivores, monarchs have a diverse portfolio of tolerances and strategies that leave them undeterred from feeding on their food. And all animals have their own enemies, predators, parasites, and microbial infections. Monarchs are no exception, and yet the detailed study of their relationships has revealed a role for milkweed's toxic properties in the interaction between monarchs and their enemies. The monarchs' spectacular form and flight, although extravagant, demonstrates the lengths to which natural selection can go. And because of the food and habitat needs of the monarch along its annual migratory cycle, monarchs have now become important in understanding general principles of species conservation. Monarchs and milkweeds have served as an important icon for debates and concerns about genetically modified organisms, climate change, and environmental issues more broadly.

FINDING MONARCHS AND MILKWEEDS

Inspired by Professor Janzen's introductory biology class, fueled by a newly found passion for studying insects on plants, and advised to find one of the big state universities ("the land grant colleges," as they are called), I ended up pursing a PhD at the University of California, on the Davis campus. I landed at UC Davis probably because of the confluence of several factors: it was far enough from home that it sparked some sense of exotic mystery; it provided the opportunity to study with a talented and beloved mentor, Dr. Richard Karban, who remains a friend and inspiration; and it had one of the top programs in ecology and evolutionary biology. My parents were slightly befuddled, if not worried, by this choice. The university was not a big name school, it was far from home, and, after all, I was leaving the traditional lines of inquiry to become some sort of bug doctor.

It was not until near the end of my time at Davis, however, when my wife, Jennifer Thaler, and I had both secured faculty jobs in the Botany Department at the University of Toronto, that a path first led me to the world of monarchs and milkweeds. As I looked forward to starting new research projects at a new job, I found it both an exciting and daunting challenge. How to pick a fruitful set of organisms to work on, one that would provide scientific insights, prove amenable to discovery, and perhaps above all, promote inspiration? My friend, collaborator, and graduate student colleague, James Fordyce, known to most as Jimmy, and to some as Uncle Jimmy, suggested that I consider working on monarchs and milkweeds (fig. 1.7). Now a professor at the University of Tennessee, he had worked on milkweed insects for his master's degree. The reasoning behind Jimmy's proposal is worth explaining, because it directly relates to what makes monarchs and milkweeds ideal study subjects.

The first attribute of monarchs and milkweed is that they have long been the recipients of love and affection from all kinds of people. And this love is expressed is various ways: by observations in nature, hands-on husbandry, the buying and selling of butterflies and seeds, digital information, symbols in the logos of organizations, and scientific study. Hundreds of thousands of monarchs are reared each year in classrooms and homes in the United States alone. At least as many are reared by butterfly breeders for sale and releases at weddings and other special occasions. Any search of "monarch butterfly" on the Internet yields hundreds of thousands of websites. Over the past twenty years, the *New York Times* alone has published more than one hundred articles about monarchs, averaging one every two to three months. Monarchs have become logos and symbols for organizations far and wide, including the Union of Con-

FIGURE 1.7. A typical summer sight in eastern North America—a monarch caterpillar getting ready to feast on the common milkweed, *Asclepias syriaca*.

cerned Scientists, many K–12 schools, the non-GMO project, and numerous corporations whose businesses range from manufacturing to banking. And, finally, a recent survey of thousands of Americans revealed that, collectively as a nation, households are willing to donate nearly $5 billion to aid in the conservation of monarch butterflies. The study revealed a willingness to donate on par with many endangered vertebrate species (although not as much as for bald eagles, elephants, and gray whales).

As a result of public interest and much scientific study, we know a tremendous amount, not only about these two organisms' natural history, but also about their coevolutionary basics. Common milkweed was transplanted and established in Europe as a possible (failed) source of rubber for tires and fluffy fill for pillows. Milkweeds are toxic plants that most animals do not eat. Monarchs cannot live without the milkweeds; it is the only food they eat. But milkweeds and monarchs are both toxic. The plant poisons, which have been used medicinally for hundreds of years, are taken up by monarchs and ward off bird predators. The monarch migration is legendary, mind-boggling, and indefatigable. The list goes on. This plant-insect interaction brings together a renowned butterfly, attractive plants, and a rich vein of history, biology, and ecology.

Second, what makes monarchs and milkweeds good scientific subjects is advertised by the plant's common name. How I have lamented the "weed" in the name "milkweed." As Ralph Waldo Emerson once quipped, a weed is simply "a plant whose virtues have not yet been discovered." Other previously used names for this beautiful plant include swan plant and silky swallow-wort, but none other than milkweed stuck. Nonetheless, the weediness, at least of common milkweed (*Asclepias syriaca*), and the weediness of monarchs themselves, is an attribute that makes them great biological subjects because they are abundant. The insects and plants alike are easy to spot. The butterflies are colorful, typically not elusive, and active during the daylight hours. These species make the process of doing science—rearing lots of them, screening them for their traits and behaviors, finding them in the field, and grinding them up in the laboratory, an easier process. Although working on rare species is certainly an important task for ecologists, rarity presents a set of challenges before scientific investigation even begins.

Third, both monarchs and milkweeds are native to North America. Biologists are often obsessed with this notion of "native," because it is thought to reflect some primordial state untouched by humans. Of course, nothing could be further from the truth. Even in the depths of the Amazon or Siberia, humans have had an impact on most organisms and the habitats they occupy. Nonetheless, the native state of both partners in an ecological and evolutionary relationship makes it such that their behaviors and their biology were potentially shaped by their long-term interactions with one another. And monarchs and milkweeds do share a deep evolutionary history; they have existed together for a very long time, likely millions of years. Thus, we can interpret the ecology of this system through the lens of natural selection and coevolution.

And finally, monarchs and milkweeds are a natural system with some balance between complexity and simplicity. Complexity can mean many things, but here I am thinking about diversity—of species, habitats, and interactions between species. Monarchs come from a group of some 6,000 brush-footed butterflies (in the family Nymphalidae), and many of the smaller grouping of 170 "milkweed butterflies" (in the tribe Danaini) interact with milkweeds (fig. 1.8). As I will discuss later, monarchs have an intimate association not only with milkweeds but also with microbial parasites, some of the other insects that eat milkweed, and a whole community of predators, from birds to spiders, and from stinkbugs to wasps. Not only does this diversity of potential interactions set the stage for endless scientific study, but the monarchs' yearly travels expose them to substantial variation in when and with what they interact. It is this diversity of species, interactions, and environments that they live in that is food for scientists: mysteries to be solved. Yet, for groups that are much more diverse, or associated with wildly different plants and parasites, the complexity can be overwhelming and make scientific progress quite slow.

The complexity-simplicity balance also applies to the plants. Milkweeds come from a genus with about 130 species (given the genus name *Asclepias* by Carolus Linnaeus after the Greek god of medicine and son of Apollo, Asklepios). All *Asclepias* live in the Americas, with most living in Mexico and northward. It is not a tropical group of plants. The evolutionary sister group to *Asclepias* are more than 250 species in an African genus called *Gomphocarpus* (fig. 1.9). Of the American milkweeds, most are rare, and only a few species, like common milkweed, *Asclepias syriaca*, are highly abundant and noticeable in many environments. Species of milkweed do, however, inhabit some of the most diverse habitats available, from standing water to the driest of the dry deserts. And although most *Asclepias* live in open habitats, preferring full sun,

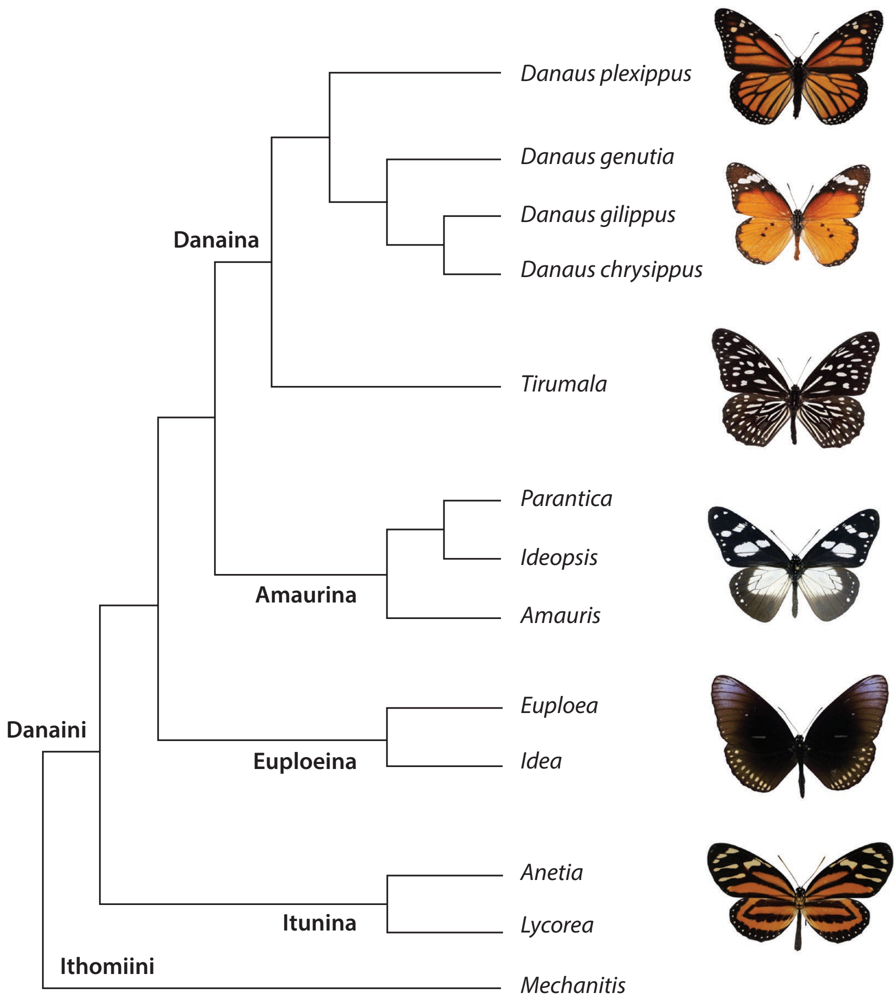


FIGURE 1.8. The monarch arose from a group of about 170 physically similar, yet evolutionarily distinct species known as the milkweed butterflies (tribe Danaini). Shown is a phylogeny, or visual representation of the evolutionary relationships in this tribe. Note that most milkweed butterflies are not shown here (for example, there are twelve recognized species in the genus *Danaus*). Instead, representatives of each of the major groups are shown. The Ithomiini is the sister tribe to the Danaini and contains several hundred tropical species.

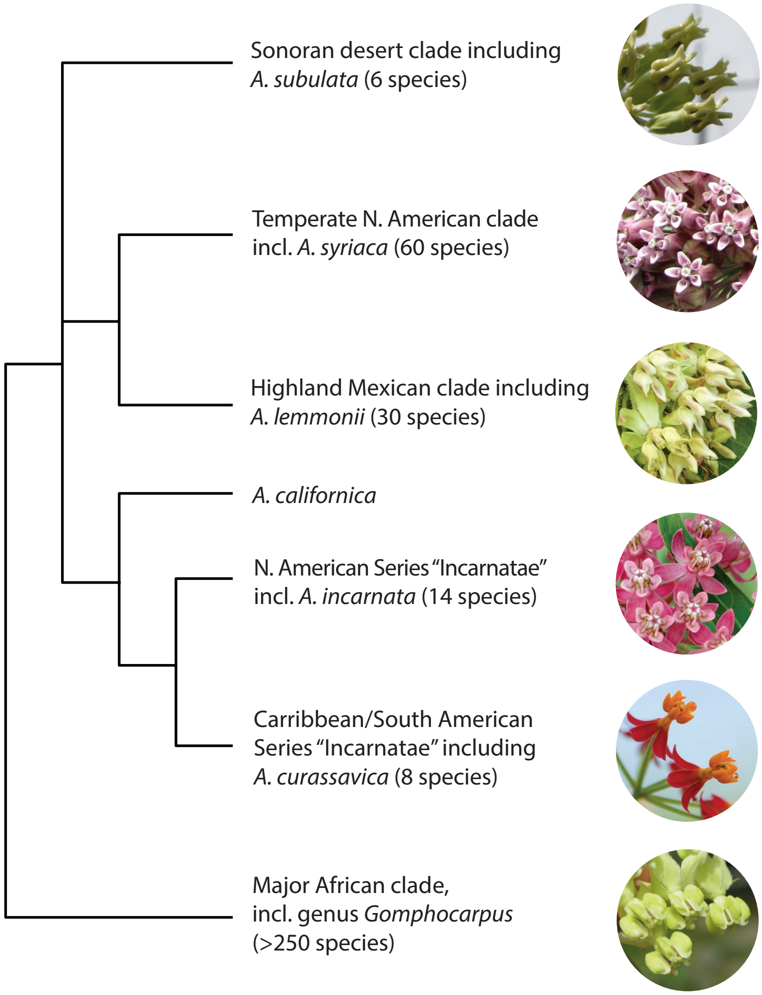


FIGURE 1.9. A summary phylogeny showing the evolutionary relationships of the milkweeds in plant genus *Asclepias* (with about 130 recognized species in North America), here trimmed to show representatives of the major groups. No image of *Asclepias californica* is shown, and the representative of *Gomphocarpus* is *G. fruticosus*.

a few species inhabit the forest shade. All are herbaceous (not woody) and perennial. Together these attributes point to a level of manageable complexity. That is, the plants have evolved from a single ancestor into many species, into many habitats, and with some variation in their ecology.

Like all plants, these evolutionarily related species of milkweeds have their own special community of herbivores, giving the plants a predictable and well-defined group of insect enemies. And this too is an attractive attribute of the milkweeds for scientific study. Take the common milkweed, which is fed upon by eleven insects: three aphid species suck the phloem sap, two lygaeid bugs eat seeds, three different beetle species bore through the roots, tunnel in the stems, or eat the leaves, and a small flattish fly mines between leaf layers (see figures in chapter 7)—not to mention a moth and a butterfly species whose caterpillars chew the leaves. The insect community is complex yet simple. The complex part is that these insect herbivores have divvied up the plant, with different species eating different plant parts. Also, these insects span a tremendous taxonomic breadth, covering some 350 million years of evolutionary history. What I mean by this is that the diverse species of insects that now eat milkweed shared a common ancestor about 350 million years ago—the proto-insect. Over the past hundreds of millions of years, the insects' ancestors rampantly diversified, giving rise to honeybees, mosquitos, beetles, and butterflies, and many times independently distinct groups of these insects would colonize and adapt to eating milkweeds. Interestingly, these insect species are essentially all specialists. They are not omnivorous. They are not even adventurous. All they eat is milkweed. And therein lies the simplicity of monarchs and milkweed. The insects are confined to feeding on milkweed, and therefore we know where to find them; their dietary habits are well-defined; and they are decidedly pests on the plant.

Our journey will now start in earnest by placing monarchs and milkweeds in the context of their stockpiling arms race. The nature of the monarch-milkweed interaction is simplified by the fact that monarchs are unquestionably pests and are not also pollinators or beneficial in any other way. Milkweeds must defend themselves. Early studies of this interaction led to the birth of a new scientific discipline called chemical ecology, which among other topics, tries to decipher the mechanisms and consequences of such arms races. Now that the field is maturing, it has created new scientific questions. What is most fascinating about monarchs is that they have cracked the milkweed's code of defense, forever changing the course of their coevolutionary interaction.