

THE EVOLUTIONARY WORLD

How Adaptation Explains Everything
from Seashells to Civilization

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CHAPTER NINE

Dispatches from a Warmer World

There are three indisputable facts about the warming climate to which Earth is being subjected during our lifetime. First, warming is real, rapid, and global, with its greatest effects felt near the poles. Second, it results mainly from a sharp, accelerating, human-caused increase in the levels of greenhouse gases—especially carbon dioxide and methane—in the atmosphere, and is further fueled by runaway feedback processes allowing the planet to retain more of the sun's heat. Third, like many other changes, warming in the short term—on the timescale of human life, from decades to centuries—is on balance harmful, because neither we nor many other life-forms are well adapted to its immediate consequences; it threatens humanity and the rest of living nature with substantial disruption to the status quo. We must either adapt or suffer the consequences.

But there is also a fourth reality: in the long run, warmth coupled with productive ecosystems stimulates adaptive evolution. Ours is not the only time in Earth's history when temperatures worldwide have risen. The fossil record chronicles a fascinating history of climate, including many episodes of warming in times past. Not only does this record reveal how life on our planet was affected by previous

warming events, but more importantly it provides us with a long-term perspective on how life responded, a perspective that the brief history of warming over the last few centuries cannot offer. An interesting and largely unexpected finding emerging from studies of the prehuman past is that whereas the short-term consequences of change are nearly always harmful, the long-term effects, which incorporate evolutionary adaptation, are more favorable, enriching life's variety. This conclusion holds as long as other disruptions do not interfere with the temperature-related opportunities that warmth creates. For humanity, the big question is this: can the biosphere in which we live and of which we are a part benefit from this long-term silver lining, or are the convulsions we are visiting on Earth's economy of life—habitat fragmentation and elimination, appropriation of resources to the point of overexploitation, and pollution—so severe that they prevent surviving species from adapting?

If I had not immersed myself in the climate and life of the tropics and delved into the history of climate and life in the geological past, I might never have thought to ask such questions or to hazard such conclusions. Chemistry books told me that the pace of life quickens as temperatures rise from the freezing point of water to a temperature between 95 and 104 degrees Fahrenheit (35 and 40 degrees Celsius). Experiencing the luxuriance of tropical life firsthand, however, I began to grasp the reality that the effects of temperature on life in a forest or on a reef go far beyond the responses of individual creatures. Temperature affects every aspect of the environment, including the ways in which living things interact with one another. In a warmer world, competition intensifies, the range of adaptive options widens, diversity increases, and selection due to enemies strengthens.

Never was the contrast between tropical and high-latitude nature brought home to me more forcefully than during the summer of 1976, when over the course of less than a month I found myself first

in the midst of the luxuriant rain forest on Barro Colorado Island in Panama, and then in the equally enticing but much more staid coniferous forest on San Juan Island in Washington State. These back-to-back exposures taught me things that dozens of scientific articles and popular accounts could not convey. Reading about a place is by necessity a sequential act, filtered through someone else's sensibilities. On one page one might read about trees; on another there is a vivid description of the termites or the frogs or the birds. Being in the forest, one experiences everything at once, and one notices things that others overlooked or considered too trivial to mention. Shapes, sounds, smells, and weather come together to offer the prepared mind an emergent conception of the whole. The forest is like a city or the body of a single individual, whose living parts—each with its particular characteristics and relationships—interact with one another and with their inanimate surroundings to create an integrated structure with properties that none of the constituents possesses. The forest is a feast to all the senses, an accumulation of simultaneous, parallel perceptions. As I observe the whole, or stop to examine a leaf or listen to a cicada, comparisons race through my mind, not gradually or serially, but as multidimensional, disordered, yet memorable thoughts. My task as a scientific natural historian is to make sense of all this sensory and mental ferment.

Barro Colorado was once a hill in the midst of unbroken rain forest in central Panama, but when the Chagres River was dammed to form Gatun Lake as part of the Panama Canal in 1914, it became an island. Today it is a forest preserve operated as a research facility by the Smithsonian Tropical Research Institute (STRI), certainly the intellectually most furtive and productive scientific organization ever to have been created in the tropics. Before breakfast in the island's dining hall, one can wake up in the pleasant living quarters to hear the changing of the acoustic guard from crickets and frogs to a chorus of birds and howler monkeys, soon to be joined by a din of

cicadas. At STRI's headquarters just a few miles away in Panama City, there are weekly presentations by resident and visiting scientists, as well as the finest library on tropical biology anywhere in the world.

Egbert Leigh was our host and guide on the island. When I first met Bert at Princeton in 1966, he was a beginning assistant professor, a mathematician and theoretical biologist seemingly more interested in thermodynamics and in the equations of population genetics than in the messy world of living things. Ten years later, however, he was applying his mathematical acumen to tropical forests. Not only had he learned the names of most of the common shrubs and trees, but he soaked up everything he could about how these forest architects interacted with the birds and mammals that ate their fruits and dispersed their seeds. Bert was the rare scientist who combines the ability to construct a mathematical theory with a keen sense of natural history. And he did it in the rain forest, one of the most exciting and intellectually impenetrable habitats on Earth.

What, then, do forests reveal about warmth and life? I equate warmth with extravagance and variety in all sensory dimensions. Day and night, the Panamanian forest vibrates to the sounds of a multitude of calls, chirps, buzzes, and songs. Cicadas whine metallically in the canopy by day; frogs pulse at various pitches from the ground and low perches in the evening hours. Birds dueting high above are momentarily drowned out by the shrieks of spider monkeys, sounding too much like children fighting, and the uncouth bellowing and grunting of howler monkeys, all against a constant background of crickets. I am listening to an unrehearsed orchestra of many different instruments playing symphonies and concerti that are at once musically complex and pleasingly transparent. If only the twelve-tone composers of the twentieth century could have produced such lush textures.

Just as pleasing, but more spare and ethereal, are the sounds of the forest of Douglas fir and yellow cedar near the Friday Harbor Laboratories on San Juan Island. The long, low, gravelly croaks of ravens accompany the brilliant soprano singing of wrens, the most plaintive whistling of a white-sided flycatcher, and the owl-like, alto-voiced cooing of a distant fan-tailed pigeon. On rare sunny days, a subtle, delicate buzz of cicadas wafts from the conifers above. This is a soundscape of understated elegance and refinement, more *Eine Kleine Nachtmusik* than a Tchaikovsky symphony.

The architects of the forest—the trees—tell a similar story of contrasts. Hundreds of species vie for a place in the sun in the tropical rain forest, to the point where neighboring trees rarely belong to the same species. The coniferous forest of San Juan Island is no less dramatic. As in Panama, the trees create a moist, wind-still climate near the ground, but in contrast to the enormous diversity at Barro Colorado, there is a sameness to the conifers. Just two tree species—Douglas fir and yellow cedar—dominate the canopy, and many stands contain only one species.

The plants that fascinate me most in the rain forest are the lianes, or woody climbers. Some hang like ropes between trees; others wind so tightly around host trees that their flattened stems incise deep spiral welts on the trunks. Whether they climb with roots or with recurved hooks or by twining around their supports, these plants race toward the canopy to compete with their hosts for sunlight. During my first visit to a rain forest—in the La Selva preserve in Costa Rica—I had noticed that most of the lianes, at least in their understory portions, have heart-shaped leaves, whose broad base makes almost a right angle with the long leaf stalk. Canopy trees, by contrast, tend to have monotonously oblong leaves with a narrow base, with the short leaf stalk inserted in the same plane as the blade. The liane leaves can more easily change orientation to take advantage of the shifting

angles of the sun filtering through the canopy. Their broad shape enables the plants to cast maximum shade on the leaves of competitors below.

The tropical profusion of climbing plants makes the almost complete absence of vines in the coniferous forest all the more remarkable. The trunks of yellow cedar and redwood are conspicuously devoid of lichens and mosses, perhaps indicating a chemically hostile bark environment for climbers and epiphytes; but Douglas fir stems are thickly festooned with mosses, lichens, and even small ferns, and would therefore seem ideal for root-climbers; but one searches in vain for vines. Are such plants forbidden in this forest because they cannot grow fast enough to reach the canopy? Does the occasional frost compromise the wide water-conducting vessels in the stem needed to sustain rapid growth?

Comparisons like these might be dismissed as special cases, especially because tropical forests are known to be the most diverse ecosystems on Earth, against which any other systems, including other tropical ones, would look simple. In fact, however, the differences between equatorial and cool-weather forests are replicated in all other ecosystems, notably in the sea. They reveal that, although the rate of production of available food is often highest in midlatitude waters, the range and specialization of adaptive types reach a maximum in the tropics and a minimum in polar oceans. The Guam reef flat, described in chapter 3, and Squirrel Island's rocky shore, mentioned in chapter 1, illustrate these contrasts nicely.

I come away from the geography of adaptation with the indelible impression that the warmth of the equatorial zone brings out an exuberance and flamboyance in its plants and animals that is muted in colder climates. It is as if tropical life operates without the constraints that at low temperatures limit the pace of life and keep extravagant colors, sounds, shapes, and behaviors within a smaller space

of possibilities. Warmth is more forgiving of extremes, more favorable to the exploration of new adaptive pathways, and altogether more conducive to the proliferation of species than is unrelenting cold.

At least on the surface, the explanation is simple. Everything an organism does—feed, make proteins and sugars, move, mate, reproduce, invest in offspring, and maintain the body—requires energy. As temperature rises, the chemical reactions underpinning all these activities speed up. Life processes that require copious free energy can take place under warm conditions, when more free energy is available. Many functions become energetically cheaper in the heat. Swimming is less costly in warm water than in cold, because warm water is less viscous, meaning that it offers less resistance to a moving body. Dynamic viscosity of seawater at 50 degrees Fahrenheit (10 degrees Celsius) is 1.27 times greater than at twenty degrees, and 1.48 times higher than at thirty degrees. The formation of mineral skeletons like shells and bones is faster and cheaper under warm conditions because the minerals are less soluble and are therefore more readily laid down in a framework of organic molecules than in the cold. The costs of maintenance increase as the surroundings warm, but these costs are more than offset by savings in most other functions. No thermal limitation prevents tropical plants and animals from leading sedentary lives, but life in the cold is more or less constrained to be slow. At low body temperatures, functions with very high energy demands can be performed only at great expense and with great sacrifice to other necessities, and are achievable only when food stores can be tapped in such structures as bulbs, tubers, or yolks. The higher the temperatures, the more adaptive options are available, and the greater is the realized range of adaptive possibilities.

The high cost of doing business at a low temperature may account for the limited adaptive options available to life in the cold, but the freedom from constraint that warmth offers does not guarantee that

the newly available possibilities will be realized. To explain tropical extravagance, we must understand how the permissiveness of warmth turns into evolutionary reality. The lifting of constraint is not enough; it must be accompanied by circumstances that compel exploration of new adaptive domains.

Paradoxically, as the physical restraints on adaptive options relax with increasing warmth, the rules that organisms impose on one another become more stringent. What impresses me most about the tropics, and about life in the hot summers of eastern North America, is that the extravagances of life under those conditions are the evolutionary result of intense competition for necessities that are not only locally scarce, but also under the control of other organisms. Each time individuals encounter each other over some resource like food, mates, or safe places, there is the potential for natural selection, because one party will succeed in acquiring the desired commodity (or retaining it), whereas the other party fails. Encounters among species whose body temperatures mirror those of the surroundings will be more frequent in warm conditions than in the cold, so that individuals in the tropics are tested—that is, subjected to selection—more often.

The signs of greater strife are everywhere. Leaf damage is greater in the tropics; so are nest predation in birds, predation of insects by spiders, shell destruction by fishes and other shell-breakers, seaweed consumption by fishes, and competition for light by plants. As we proceed toward the equator, we find both a higher frequency and greater expression of toxicity in plants and sponges, armor in snails and fish, and risk-minimizing methods of predation that reduce the time needed for a predator to kill and eat its victim. Selection is therefore not only more frequent in the tropics but it leads to greater expression of most traits thanks to the permissive energetics afforded by temperatures between 68 and 95 degrees Fahrenheit (20 and 35 degrees Celsius).

The evolutionary dividends of a warmer world are attainable only if three conditions are met. First, populations must have ready access to a plentiful supply of necessary resources, so that when an imperfect innovation arises, it can linger in the population long enough to be improved by selection. If the population is allowed to grow under a permissive regime of predictable plenty, not every deviant individual is purged from the population, and selection has enough variation to work with. Second, competition for locally scarce resources—the main agency of enemy-related selection—must be intense enough and consistent enough to allow improvements to spread in the population. Third, there must be sufficient evolutionary time—thousands to millions of years—to allow selection to do its work. In order to adapt to greater warmth and to a biologically more demanding world, living things must do more than simply carry on at a higher temperature; they must adapt to, and compete effectively with, other organisms, which likewise are struggling for life under the new thermal regime.

In other words, success in warm surroundings requires adaptations that enable individuals to capitalize on the thermally more permissive environment by becoming better competitors. New, energy-intensive structures and new mechanisms that speed up predation and other risky activities should therefore arise predominantly in warm-adapted lineages that are already under intense selection by members of co-occurring species.

Here, then, is a prediction about history that can be evaluated with evidence from fossils. Shells, which have a prolific fossil record, and many of whose features are readily interpretable in functional terms, are ideally suited for putting this prediction to the test. I needed to identify a simple innovation—a new feature that arose independently in different lineages—that markedly speeds up some important activity in a mollusc's life and that therefore yields a competitive advantage.

I found a nearly ideal group of snails to carry out this test. Among the ways that predators evolved to attack victims that are encased in hard shells, two are particularly widespread in predatory snails. The first method involves drilling a small hole through the victim's shell, and then inserting the feeding organ (the proboscis) through the hole to ingest the soft tissues. Drilling is a time-consuming activity, taking hours or even days to complete. Moon snails tend to subdue their prey while buried in sand, and therefore reduce the risk of detection by their own enemies; but other drillers attack their prey on open surfaces, where potential competitors could easily encounter and interfere with them. The second method used by many predatory snails is to enter the victim's shell through an already existing opening, such as the mouth of a snail shell or the space between the two halves of a bivalve shell. When the victim closes its shell either by shutting the door or by clamping the valves together, access for the predator is difficult, and time-consuming prodding must be used to get inside. Even when access is gained, the proboscis might be severed as the victim tries to deny entry. Injecting a toxin to anaesthetize or disable the victim is one obvious solution to this problem; but wedging the shell, or creating an opening where skeletal elements meet, is another. Many lineages have adopted one or both of these labor-saving methods, which reduce the predator's vulnerability to danger.

It turns out that a small tooth or spine at the edge of the predator's shell lip is an effective tool to wedge open the valves of a clam, to enable the predator to drill or grind a hole at the shell margin, and to prevent the inserted proboscis from being severed. This so-called labral tooth thus cuts the time needed for killing and eating the prey by as much as two-thirds in cases that have been studied. The labral tooth is easily observed on fossil shells, and was therefore well suited as a minor, frequent innovation whose places and times of origin

could be inferred by carefully inspecting the fossil record of predatory snails.

Thus began a ten-year search for snails with a labral tooth. I started in my own large research collection, to which I continue to add. Important evidence also came from thousands of species descriptions that I read in eight languages in papers, monographs, and books published as early as 1758; but many of these descriptions were too cursory to be of much use. Had I relied exclusively on the scientific literature for the data I needed, I would have missed dozens of snail lineages that at some point in their history gave rise to species with a labral tooth. I needed to examine more specimens, which often revealed features that others had overlooked.

A particularly memorable instance of this occurred in New Zealand. Before my visit there in 1993, I had become reasonably familiar with its shore fauna, which according to the literature I consulted would contain no species with a labral tooth. I had even queried some colleagues, who assured me that the mudflats and rocky shores I would be visiting were free of such species. I was therefore more than a little astonished when the first shell I picked up on a mudflat on the South Island was a specimen of *Iosepha glandiformis*, an abundant species with a tiny but unmistakable tooth projecting from the middle of its shell lip. Evidently, no one had bothered to remark on the tooth's presence.

This incident reminded me that there is no substitute for carefully examining real specimens. I thus spent countless happy hours examining and measuring thousands of shells belonging to living and fossil species in a dozen European and American museums. Time and again, I uncovered species whose labral tooth had previously been overlooked. Everywhere I went, I compared the tooth-bearing species to related species lacking the tooth, so that I could determine when, where, and in which lineages this predation-enhancing feature

evolved. Just as gratifying were the collaborations that blossomed in the course of these investigations. I eventually worked with twelve other scientists on various aspects of the project. Science—even the scientific natural history I practice—is truly a global enterprise, one that, like nature itself, involves as much cooperation as friendly competition in a well-connected community.

Although this kind of work never ends—more and more lineages with a tooth turn up all the time—I currently estimate that some sixty snail lineages evolved a labral tooth. In agreement with the prediction, all lineages with a tooth arose in warm, productive waters, and never in the cold-temperate or polar zones or in the cold deep sea. The tooth would presumably still benefit snails under these frigid conditions—in fact, several tooth-bearing lineages invaded these habitats—but the slow pace of life there might make the advantages too inconsequential for selection to favor the evolution of a time-saving device.

The most interesting result, however, came from the fossils. Times of origin of the tooth were heavily concentrated during four brief time intervals: the Late Cretaceous (80 to 75 million years ago), the Late Oligocene to Early Miocene (25 to 19 million years ago), the Late Miocene (11 to 8 million years ago), and the Early Pliocene (5 to 3 million years ago). Particularly the last three of these intervals correspond to times of conspicuous global warming coupled with widespread productive conditions. The one interval of global warming without the evolution of lineages with a labral tooth is the Late Paleocene to Early Eocene (55 to 52 million years ago). This episode differs from the three later ones in that many marine molluscs remained small, perhaps meaning that seas at that time were relatively unproductive.

Why were there no snails with a labral tooth before about 80 million years ago? It certainly wasn't because seas were cool. One of the warmest episodes in Earth history occurred around 90 million years

ago, when tropical seawater temperatures might have been as high as 95 degrees Fahrenheit (35 degrees Celsius)—a full 5 degrees warmer than the maximum average we see in the tropics today—and even polar seas might have been as warm as 68 degrees Fahrenheit (20 degrees Celsius). Despite these truly hot conditions, the main groups of drilling snails had not yet evolved, and the traits of predators and victims alike indicate that predation had not yet escalated to the levels it reached later. Warmth, in other words, may be favorable to energy-demanding innovations to arise, but it is not enough. It is organisms who must take advantage of the enabling conditions to transform potential into reality.

If organisms could maintain high body temperatures even in the cold, they could reap many of the evolutionary benefits enjoyed by tropical species whose body temperatures vary according to their surroundings. This is, of course, exactly what many animals and even some flowering plants can do. Evolutionarily advanced mammals and birds maintain body temperatures of 93 degrees Fahrenheit (34 degrees Celsius) or higher, with some songbirds operating at a regulated temperature as high as 108 degrees Fahrenheit (42 degrees Celsius). Species belonging to groups that diverged early from the mammal and bird branches in the evolutionary tree generally maintain somewhat lower temperatures but are still warm-blooded. Many adult insects—dragonflies, bees, wasps, moths, and large beetles and flies—can raise the temperature of their flight muscles by as much as 30 degrees Celsius above that of the surrounding air, and maintain it during flight. The ability to raise core temperatures to high constant levels has evolved in at least one group of sharks and in various lineages of tuna and their relatives, which are actively swimming hunters. Although their maintenance costs are high, these warm-blooded animals are highly effective competitors. Warm-blooded vertebrates are the competitive dominants on all continents, most islands, and even in most marine habitats, from the shore to the open ocean and the

tropics to the poles. At least eight separate groups of flowering plants have evolved the ability to heat their flowers, apparently as an effective means of broadcasting the scent that attracts (and sometimes enforces a night's stay of) pollinating insects.

All these warm-blooded creatures thus evolutionarily tamed, and in some measure have become independent of, the thermal regime of their environment. They have, quite literally, incorporated the opportunities implicit in a high-temperature world into their own bodies, capitalizing on those benefits even where external conditions are thermally hostile. The costs of maintaining these temperatures are, of course, very high, and the use of energy is extremely inefficient compared to that in low-energy life-forms with unregulated body temperatures. As in the case of high-energy humans, whose efficiency of energy use is likewise extremely low, the benefits of warm-bloodedness far outweigh the costs as long as the quantity of available resources is sufficient to sustain such a profligate physiology.

There remains the vexing problem of why so many species live together and evolve in the tropics. It has long been recognized that the number of coexisting species in the tropics exceeds that in comparably large cool-temperate areas by a factor of three or more, and that far more species and lineages originate in regions of warm climate than elsewhere. Curiously, the same geographic pattern applies to human cultures and languages. The greater range of adaptive possibilities at high temperatures implies that there is ample opportunity for organisms to explore avenues of adaptation that are otherwise inaccessible, but it does not explain why adaptive space is filled by so many different kinds of species or cultures instead of by one or just a few entities.

Isolation is the key to species formation as well as to the origins of human cultures. A population of sexually reproducing individuals achieves isolation when a mating barrier separates it from its parent

and sister populations. Often this barrier is geographic, a zone of unfavorable habitat across which individuals cannot disperse; but selection can amplify and even create isolating barriers as well. For example, if an ancestral population occupies several habitats, reproduction may take place at different times in each, so that mating is largely between individuals living in the same local environment. This can happen in a parasitic species infecting several host species, or to a population of snails living in vertically separated levels on a rocky seashore. Selection may transform an initially uniform habitat into a patchwork of environments in which the conditions of life differ to the point that descendants become specialized to, and further accentuate, the new regimes. This kind of location selection-driven differentiation has been experimentally demonstrated in laboratory cultures of bacteria. In an initially homogeneous bacterial clone, mutations arise that enable affected cells to form a dense mat, a physically very different environment from the fluid medium in which the original, unmutated cells live. Selection in the two habitats differs, and therefore promotes specialization. Other mutations affect whether certain foodstuffs can be used, and add further dimensions of environmental variation and occupational specialization. Still more subdivision is possible when mutations resisting resident microbial predators or viral parasites arise. Although these bacteria reproduce asexually, lineages under novel regimes of selection create a new environment that is anything but uniform.

In the case of flowering plants, isolation is promoted less by resources than by consumers. Pollinators and seed dispersers faithful to a particular plant species or to a particular type of flower or fruit can quickly help make local mutations into the new norm and promote genetic isolation in their hosts. The same effect applies to specialized herbivorous insects or fungal pathogens. Selection from these sources creates new dimensions of environmental variation and

multiplies opportunities for isolation and adaptive divergence. Evidence from both marine and land-based life indicates that selection due to consumers is more intense in the permissive tropics than at the more spartan higher latitudes. The environment of pests, potential helpers, and resources is thus subdivided more finely in the tropics not because of some intrinsic property of the equatorial zone, but because of the selective regimes that organisms are able to impose on each other there.

A similar mechanism seems to be at work among human groups. A common language serves both to unite a group and to distinguish it from others. Groups concentrated near each of several scattered favorable sites may at first speak dialects of the same language, but the dialects quickly diverge to become mutually unintelligible languages. Cultural isolation through language therefore contributes to group differentiation. There is evidence that human groups practicing agriculture or living as hunter-gatherers in forested or mountainous tropical environments are more sedentary than the more nomadic groups on open grasslands at higher latitudes. As a result, cultural and linguistic diversity is markedly higher in the tropics.

Isolation of populations is further promoted by intense sexual selection. As Darwin already knew, the most distinctive attributes of species in which the union between egg and sperm takes place within the body or in an external space controlled by one partner (usually the male) reside in the elaborate reproductive organs and in mating-related displays. There is often intense competition among males for females, as well as discrimination by the female among potential suitors based on the males' weapons, brightness of color, song, or visual antics. Mutations in any aspect of these traits can result in selective mating, and create or amplify mating barriers. There is also abundant evidence for antagonistic coevolution between the male and female organs involved in copulation, where potential injury inflicted by one partner is counteracted by adaptations in the other.

Extremely bizarre reproductive rituals and structures have evolved as a result, especially in insects and in hermaphroditic snails in which mating between partners remains obligatory. Again, mutations involving reproductive structures make isolation of populations easier, and thus contribute to the formation of new species. It is not known whether these isolation enhancements are more common in the tropics than elsewhere.

Still another factor contributing to high tropical diversity is the ability—and often the necessity—for species to maintain themselves as small populations of widely scattered individuals. Following early experimental work by Daniel Janzen in tropical America and Joseph Connell in Australia, Egbert Leigh and his colleagues have emphasized that intense pressure from specialized tropical pests prevents seedlings of trees germinating near their parents from surviving, because the chance that the enemy finds and consumes the seedling is very high near the vicinity of the parent. Low population density of tropical trees can be maintained only because of wide-ranging seed-dispersers and pollinators, which defecate seeds or fertilize flowers of a given species far and wide. Strong selection by friends and enemies in the tropics thus places a premium on distinctive, isolation-promoting reproductive traits. This is yet another indication of how important evolved interdependencies—in this case among plants, pests, and pollinators—is for the evolution of complex ecosystems. If we wiped away the herbivores and the fungal pests, there would be less imperative to maintain a large distance between neighbors of the same species. And if the pollinators and dispersers were eliminated, plants faced with intense pest pressure could no longer maintain viable populations, for they could not afford to be rare.

A warming world, with its poleward expansion of equatorial and temperate climates, enables a large number of species that have already adapted to warm conditions to expand. More intense competition,

together with relaxation of the constraints on life's activities, leads over evolutionary time to a greater variety of species. By expanding the opportunities for adaptation, warmth coupled with a dependable and prolific supply of raw materials allows life to flourish and diversify in vigorous profusion.

This long-term enrichment is amply demonstrated in the fossil record. All periods of warming are associated with increases in the local and regional number of species, implying that many new species arise during such times. Tropical lineages, which are usually unable to penetrate higher latitudes because of conservative limits on tolerance of the cold, can break through the thermal barrier and extend into temperate zones during episodes of warming. Cold-adapted species apparently never penetrate the tropics and subtropics no matter what the state of the climate. Warming thus invites evolutionary innovation and diversification.

Inevitably, not every species or lineage can take advantage of these opportunities. Cold-adapted species will be geographically compressed by the expanding warm belt to a narrow band. Their number, however, is relatively small, because there are few cold-adapted species compared to the vast profusion in warm regions. Moreover, the fossil record indicates that few polar species succumbed to extinction during geologically recent warm intervals. The reasons for this are not clear, but one possibility is that, unlike the situation in the tropics where many species are rare, species from polar latitudes tend to be regionally abundant. Barring other disruptions separate from the effects of warming, the loss of temperate and polar species through geographic compression of their comfort zones should be relatively small.

Another potential problem is that many species cannot extend poleward because of unbridgeable barriers unrelated to temperature. Terrestrial species in southern Australia or South Africa would be forced into the sea if their thermal environment is eliminated by

global warming. In the human-dominated world of fragmented habitats, many species have become restricted to islandlike patches from which escape is all but impossible without assistance. Rising sea levels, changing patterns of precipitation, and other changes accompanying warming may further erect or broaden barriers to the poleward spread of land-dwelling and freshwater species.

Why should the short-term effects of warming often be harmful when the long-term consequences are on the whole beneficial? The answer comes down to adaptation. If an organism, population, or ecosystem is well suited to its situation, almost any change will make it less so. This is why most genetic mutations are harmful, why many ecosystems are disrupted when species are introduced to them, and why many workers suffer when new labor-saving methods are put in place. If, however, the system is able to adapt, or to accommodate to the changes, the short-term deficits can give way to long-term benefits. For example, mutations are an important source of variation, which is a necessary raw ingredient on which selective processes can work to fashion a better-adapted whole. The spread of species into communities they did not originally occupy can add resources and regulation to those communities, and becomes essential for reconstituting ecosystems that have been devastated by catastrophe. Change is universal. Those organisms, lineages, ecosystems, and societies that can accommodate it flourish while those that cannot will either wither away or become marginalized. Evolution, in other words, can transform adversity into opportunity.

Whether warming is a curse or a blessing thus depends entirely on whether living systems subjected to it can adapt or move. If they can, warming presents an opportunity, especially if the surroundings are healthy and productive. If they cannot, warming becomes a hardship, an insuperable challenge. Humanity should do what it can to limit the rate at which the world is heating up, but above all we must adapt to a warming world. If we want to maintain some

semblance of wild nature in the face of warming and habitat fragmentation, we must preserve—or, better yet, enhance—opportunities for species to adapt. We must give them wiggle room, not box them in. We must allow evolution and adaptation to do their work.