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Why
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Matters

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CHAPTER 1

WHAT LIMITS THE GEOGRAPHIC DISTRIBUTION OF ORGANISMS?

KEY POINTS

- The distributions of many species are limited by geography and climate. In the past it was difficult for most species to move between continents. But humans are now moving species into new regions where some become serious pests.
- Climatic warming is also changing the distributions of many species, causing many ranges to expand toward the poles.
- On a very local level what limits the exact geographical ranges of species is not always clearly understood, and many ecological processes may be involved.

Penguins occur neither in Chicago nor in the Arctic. We are not particularly surprised about their absence in Chicago. Penguins hunt off the Antarctic ice pack and in the Southern Ocean for fish, and Chicago has neither pack ice nor an ocean. But penguins live happily in the Chicago zoo, so clearly the climate of Chicago is not the restricting factor. We should be surprised that penguins do not live in the Arctic, since it abounds with both ice packs and small fish, yet the reason is simple. Penguins have never reached the Arctic because the tropical oceans form a *barrier* that they have not been able to cross to enter the Arctic Ocean.

Barriers prevent dispersal movements, in particular the movement of an individual from its place of birth to a new place for breeding and reproduction. Movement is crucial in many ecological situations, but nowhere are the effects of movements more clearly shown than in the study of distribution. Isolation, or lack of dispersal, thus became a cornerstone of the early naturalists' view of how the animals and plants of the world came to be. This isolation is thus the reason we go to Africa to see giraffes and not to South America, and why we go to Australia to see kangaroos and not to North America. Our zoos are thus a popular monument to the role of dispersal in affecting the distribution of animal life on the globe just as our botanical gardens illustrate the same ideas about the distribution of plant life.

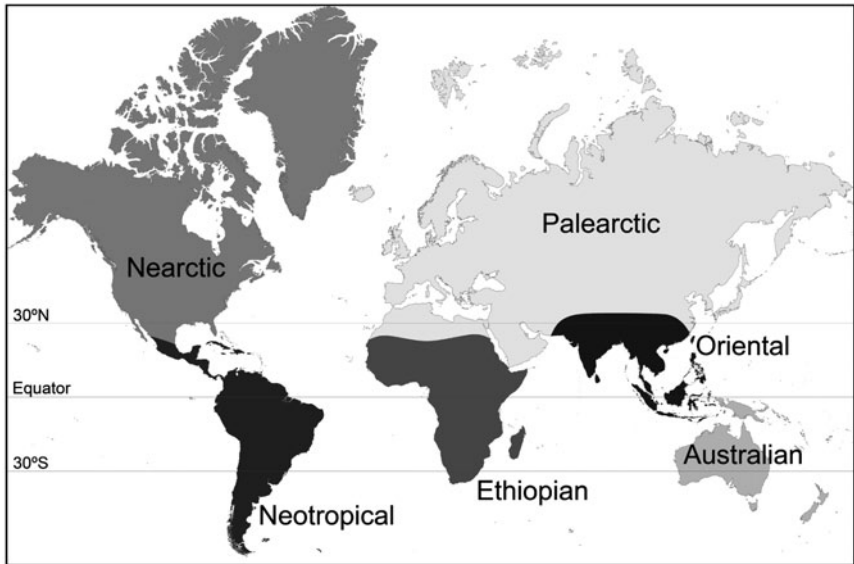


Figure 1.1 The Earth's biogeographic realms. These six broad regions are a product of continental drift over the last 200 million years and of barriers such as mountain ranges that have affected evolutionary processes. They were first recognized by Alfred Wallace (1876) and have been updated by Holt et al. (2013).

Alfred Wallace in 1876 outlined the broad pattern of the distribution of species on Earth with a classic view of the globe, divided into regions based mainly on the mammal fauna. Wallace distinguished North America (Nearctic) from Eurasia (Palearctic), and defined four other regions that divided the mammal fauna of the globe—South America (Neotropical), Africa (Ethiopian), Australia, and the Indian Subcontinent (Oriental) (Figure 1.1). Wallace recognized the patterns we see today when we go to Africa to see giraffes and to Australia to see kangaroos. This global view of the distribution of life has been the basis of the analysis of geographical distributions of animals, plants, and microbes, and provides a good starting point for understanding species ranges. It is a pattern written by the isolation of continents and regions by geographic barriers, leading to different evolutionary paths and thus different assemblages of species. It is the starting point for trying to understand why a particular species lives in a specific region, and also for understanding what the consequences might be of moving species across these boundaries.

But a problem arises here. Evolution has certainly produced different plants and animals in different geographical realms, but what assurance

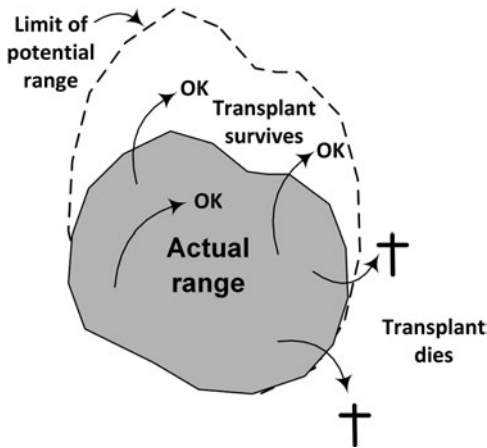


Figure 1.2 Hypothetical sets of transplant experiments. The grey area represents the actual current geographical range of a particular species. Each arrow indicates a transplant experiment. Arrows indicate successful transplants (OK) or unsuccessful transplants (+). In this example the species can potentially occupy a larger range (enclosed within the dashed line) than it currently does. In practice, many separate transplant experiments may be needed to define the limits of a species' potential geographic range.

do we have that any one of these organisms could in fact live in a quite different area? This question can be answered very simply by a transplant experiment—move the organism to a new area. If it survives there and reproduces, you have good evidence that the former distribution was restricted by a lack of dispersal. Figure 1.2 illustrates the logic of the simple transplant experiment.

People have carried out transplant experiments, often inadvertently, since the earliest times, but in the last two centuries this trickle of transfers has turned into a flood. Most of the crops we grow are introduced species of plants, and so transplant experiments can benefit humans. But many of our serious pests are also introduced species, and the ecology of invasive species has a strong economic impact on our lives. Many of the pest species transplanted are accidentals—seeds caught in bales of wool, or mice transported in bales of hay. An elaborate series of inspection and quarantine procedures in different nations illustrates how people strive to prevent the accidental or deliberate introduction of organisms harmful to humans and their domestic animals from one region to another.

Paradoxically, some of the worst pest species have been introduced deliberately. Consider just two examples. The European starling (*Sturnus vulgaris*) has spread over the entire United States and much of Canada within a period of sixty years. The starling is considered a pest because it is bold and aggressive, attacks some fruit crops, and has displaced several native bird species. Originally it occurred in Eurasia, from the Mediterranean to Norway and east to Siberia. Many early attempts were made to introduce the starling into the United States. One attempt was made at

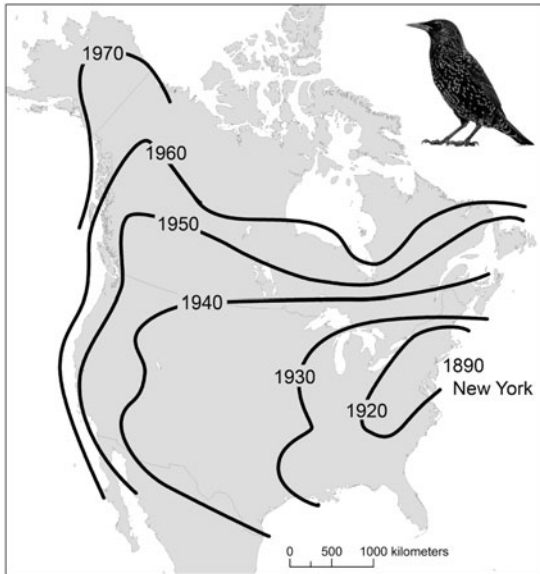


Figure 1.3 Westward expansion of the geographic range of the European starling (*Sturnus vulgaris*) in North America. The starling was introduced into New York City in 1890 and spread rapidly westward and northward. (Modified from Johnson and Cowan 1974.)

West Chester, Pennsylvania, before 1850 and the next at Cincinnati, Ohio, in 1872–1873, but nothing came of these or several other importations. In 1889 twenty pairs were released in Portland, Oregon, but these gradually disappeared. No one knows why these early introductions failed—perhaps too few individuals were released.

The permanent establishment of the starling in the United States dates from April 1890, when eighty birds were released in Central Park, New York City, by the president of the American Acclimatization Society, which tried to introduce every bird species mentioned in the works of William Shakespeare into North America. In March of the following year eighty more were released. About ten years were required for the starling to become established in the New York City area. It has since expanded its range across North America (Figure 1.3). This rapid expansion of the breeding range has been due to the irregular migrations and wanderings of non-breeding juvenile birds, one and two years of age. Adult starlings typically use the same breeding area from year to year and thus do not colonize new areas. About three million square miles were colonized by the starling during the first fifty years after its successful introduction, and a bird unknown to our forefathers has now become one of the more common birds in North America.

The cane toad (*Rhinella marina*) is native to Central and South America

from Mexico to Brazil. It was widely introduced during the 1930s to islands in the Caribbean and the Pacific because it was believed to control scarab beetles, an insect pest of sugarcane. It was brought into northeast Queensland, Australia, in 1935, where it failed to control any insect pests and instead became a pest itself. Cane toads have parotid glands that contain a poison that causes cardiac arrest. All forms of the toad are poisonous, and humans eating cane toad eggs have died from the toxin. Cane toads eat almost anything but mainly insects, often those insects that do more good than harm. What they do not do is control the insect pests of sugarcane, the original justification for their introduction. They breed prolifically, females laying 8,000–35,000 eggs at least twice a year

Cane toads are toxic to many of their potential predators, but some species learn to avoid eating them or evolve resistance to the toxin. Because of their toxicity and high reproductive rate, cane toads have been moving across northern Australia since their introduction in 1935 (Figure 1.4). Cane toads have been moving west at about 40 kilometers per year and in 2009 crossed into Western Australia. Individual marked toads have moved up to 1.8 kilometers per night, primarily along roads that have served as convenient habitat corridors for rapid spread.

Cane toads must breed in small ponds, and one way to halt their spread into much of western Australia is to eliminate water holes in critical areas. Tingley et al. (2013) identified three points along the coastline of northwestern Western Australia that could be critical barriers to the spread of cane toads further south. Eliminating artificial water bodies in these areas would be highly effective in stopping the continued expansion of the range of the cane toad in Australia. The problem is that most of the water bodies that would have to be drained are on pastoral lands and are thus unlikely to be implemented because of economic losses to the immediate landholder.

Since cane toads are toxic in all their life history stages from eggs to tadpoles to toads, there was considerable worry during the 1990s and 2000s that their invasion shown in Figure 1.4 would cause massive mortality to predatory birds, reptiles, and mammals. Fortunately the impact of this toxic pest has not been as severe as was anticipated (Shine 2010). Populations of large predators such as lizards, elapid snakes, and freshwater crocodiles have been reduced temporarily by the cane toad invasion, but poisoning impacts are highly variable. Some of the predators severely reduced by toad invasion (like freshwater crocodiles) have recovered within a few decades, via learning to avoid eating cane toads. No native predators have gone extinct as a result of toad invasion, and many native taxa widely

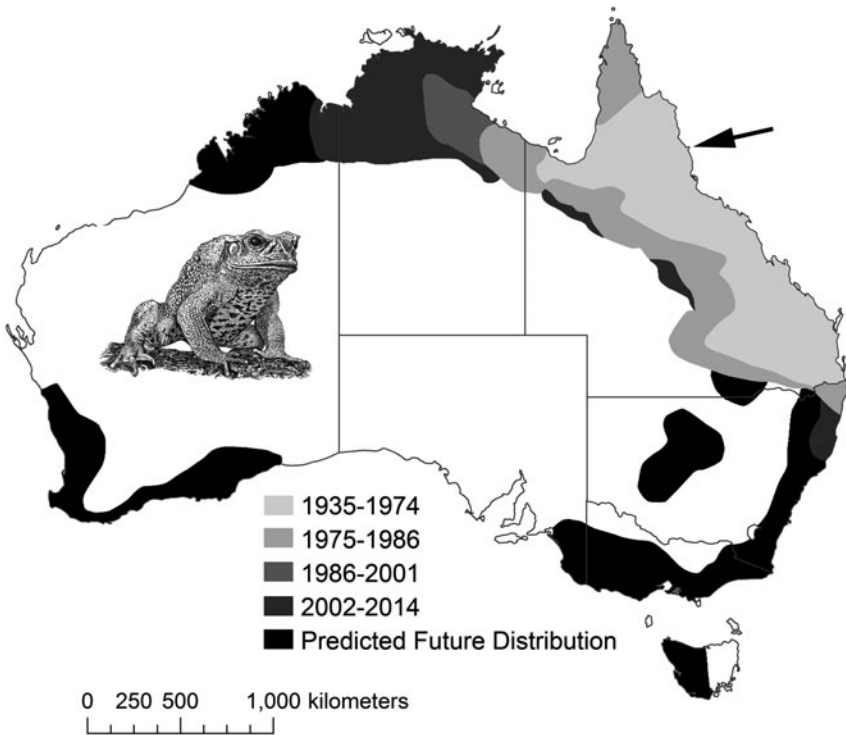


Figure 1.4 The spread of the introduced cane toad (*Rhinella marina*) from its introduction in 1935 in Queensland (arrow) to 2014 and its predicted future spread to suitable areas in Southern and Western Australia. (After Urban et al. 2007 and data from Western Australia Parks and Wildlife Department 2014.)

imagined to be at risk are not affected, largely as a result of their physiological ability to tolerate toad toxins, as well as the reluctance of many native amphibian-eating predators to consume cane toads, either innately or as a learned response. The general conclusion of a modest impact by this introduced pest has to be tempered by the fact that detailed data on the populations of its predators and competitors, as well as the insects eaten by cane toads, was largely lacking. Ideally ecologists need before-and-after data to evaluate the impact of any introduced species, and little of this has been available for most pest species.

The other message left by the cane toad has been the warning that we should not introduce species in the belief that they are beneficial without very extensive study. Too many “desirable” introductions over the last two centuries have turned out to be ecological disasters.

Not all introduction experiments have harmful results, and one of the challenges of ecology is to sort out the positive and the negative before the transplant is done. We benefit from many introduced species—most of our agricultural crops qualify as successful transplant experiments. Many fishes have been introduced into new areas successfully, with a resulting improvement in fishing. The rainbow trout (*Oncorhynchus mykiss*) is a native of cool rivers and streams of western North America, and a prize game fish among fishermen. Rainbow trout have been introduced all over the globe during the last hundred years, and are now firmly established on all continents except Antarctica. Although originally the rainbow trout did not occur east of the Continental Divide in North America, it now occupies streams in all the Canadian provinces and most of the United States, as well as some of the river systems in Mexico and Central America. Trout fishing has expanded greatly because of these introductions. But even these apparently desirable introductions may have undesirable side effects in some regions. For example, rainbow trout can displace native brook trout, another prized game fish, in the southern Appalachians.

Not all transplant experiments are successful, and the dramatic effects of the successful transplants, such as the starling in North America, tend to overshadow the humdrum failures of many other introductions. Considerable historical research has been done on introductions of birds and mammals into Australia and New Zealand by acclimatization societies whose major purpose was to make New Zealand and Australia more like Europe and North America.

Many exotic species of birds and mammals were introduced into New Zealand during the 19th century. Acclimatization societies in some areas kept meticulous records of how many birds of each species were brought in and released in each year. One of the many findings from these careful records has been the observation that if more individuals of a species were introduced, the species was more likely to survive and colonize the island (Figure 1.5). This finding has become a cornerstone of a set of generalizations about invasive species introductions—more releases increase the likelihood of success. Small populations face a variety of chance events that can lead to extinction—bad weather or predator attacks that kill only a few individuals but tip the balance toward failure. Of 133 exotic bird species brought to New Zealand only about 45% survived to become permanent residents.

But as with many generalizations in ecology, there are exceptions. Sambar deer (*Cervus unicolor*) were introduced into New Zealand successfully

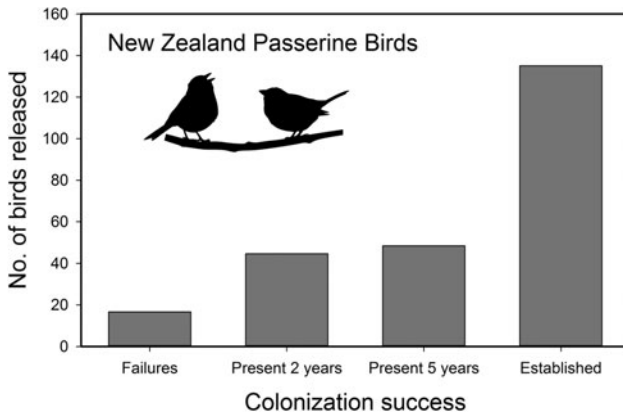


Figure 1.5 Average number of passerine birds released in New Zealand during the 19th century in relation to colonization success. The greater the numbers of individuals released, the more likely the success for any particular species. (Data from Blackburn et al. 2013.)

with only 2 individuals, and Himalayan tahr (*Hemitragus jemlahicus*) was successful with an introduction of 5 individuals in 1904. But in general for ungulates with adequate data, 11 of 14 species established and as we have just seen for birds, the more individuals released in general the higher the success rate of colonization.

The problems of invasive species have highlighted the general processes by which species can move into new areas. These processes are complicated and this is the reason why we have at present few general explanations about success or failure of introduced species. There are four major steps of the invasion process—transport, establishment, spread, and impact—and the invasion process can fail at any of these four steps. The final impact of the invasive species may be large or small, and the impact depends in part on human perception.

Transplants or movements of plants and animals into a new area may fail for two general reasons: either the biological environment may eliminate the newcomer or the physical-chemical environment may be lethal to the organism or prevent it from reproducing. Predators may prevent the establishment of some species. A good illustration of the role of predators can be seen in the common mussel (*Mytilus edulis*), which lives attached to rocks along sea coasts throughout the world. On the exposed southern coast of Ireland small mussels are abundant, but in protected waters mussels are often absent. The reason for this can be seen very easily if one moves pieces of rock with mussels attached from exposed coast to pro-

tected waters. Mussels disappear rapidly from protected waters because they are eaten by three species of crabs and a starfish. If you transplant the mussels to protected waters and put them inside a wire mesh cage, they will live happily as long as the predators cannot get into the cage. The crabs and the starfish are uncommon on the open coast because of heavy wave action in the intertidal zone, and the mussels thus have a refuge where they are relatively safe.

The expansion or contraction of geographical ranges is an important topic now because of climate change. Increases in carbon dioxide and other greenhouse gases in the atmosphere have triggered a gradual warming of the climate and changes in the distribution of rainfall. Global warming has left a strong imprint on the geographical ranges of many species (Burrows et al. 2014, Cahill et al. 2014). A combined analysis of 1,367 species responses around the world produced an average movement away from the equator of 18 kilometers per decade. This analysis covered plants, mammals, birds, beetles, grasshoppers, butterflies, intertidal algae and invertebrates, and spiders, and the average length of observations was 25 years (Chen et al. 2011). Similar data for movements higher up mountains averaged 12 m elevation per decade, and the average length of observations was 35 years. Detailed data on range boundary changes in spiders and butterflies from Britain are shown in Figure 1.6.

If climatic factors are the only explanation for changes in geographic distributions, we would expect all species to shift as climate warms. This is not the case because a whole range of factors can affect range limits. Changes in distributions for any particular species could be due to many ecological processes:

- Is the species absent because it has not been able to move to an area (dispersal limitation)?
- Is the species absent because it does not recognize the habitat as suitable?
- Do other species prevent colonization (parasites, predators, pathogens)?
- Are there limiting physical or chemical factors (temperature, water, oxygen, soil, pH)?

Changes in distribution because of climatic warming can be accepted only if the first three questions are carefully considered.

Large-scale patterns can obscure some of the observed shifts in range

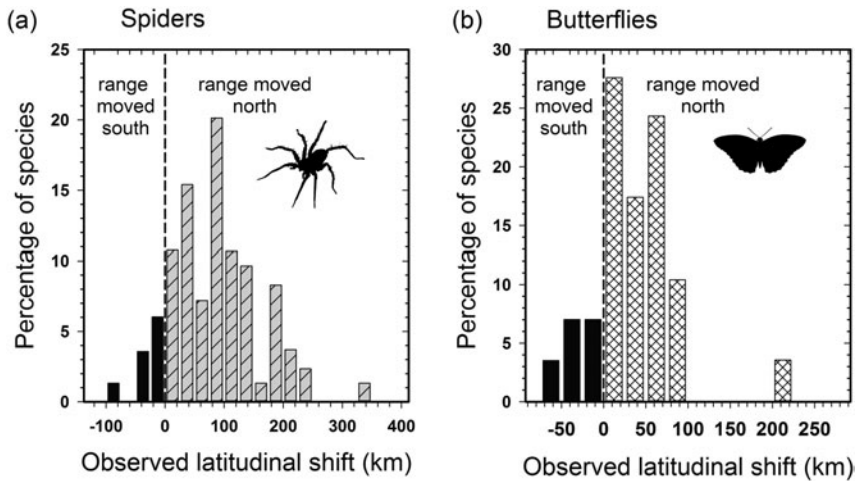


Figure 1.6 Observed latitudinal shifts in the range boundaries of (a) spiders (85 species) and (b) butterflies (29 species) studied over 25 years in Britain. The dashed line marks the point of no range change, and the black bars indicate species that have shifted south, contrary to predictions. (Modified from Chen et al. 2011.)

limits. The simple model for climatic limitation is that geographic ranges for all species should be shifting poleward. But, for example, in an analysis of 764 individual species from a variety of taxonomic groups, Chen et al. (2011) found that 22% of the species moved their ranges in an opposite direction from that predicted by this simple climate change model. One important concept in work on changing climate is to map the rate at which climates are changing in relation to the movement of geographic range. VanDerWal et al. (2013) did this for 464 species of Australian birds over the time period 1950 to 2010. They measured the climatic zone in which each bird species lived. They then mapped the observed shift in this climate zone and compared it to the observed change in the same species distribution from bird observation records over the 60 years. The result was that species were shifting their ranges faster than climate was changing, so they could readily keep up with climate change in Australia. This does not of course mean that if climate shifts become faster this generalization will be correct. While many of the Australian birds were moving in the “correct” direction with respect to climate change, some were not, and these species need additional study.

On a local scale many biological interactions such as competition can affect the distribution of a species. Many plants and microorganisms use chemical warfare to suppress possible neighbors that might harm them.

A well-known example of chemical warfare is the action of penicillin, the secretion of a fungus, on other microorganisms. The soil fungus *Penicillium* excretes this antibiotic to protect itself against bacteria. Humans have simply learned to use this chemical for our own protection against disease. The study of human disease is essentially a study of colonization (by microorganisms) of new environments (people), and thus differs only in scale from the starling's colonization of North America. At some time in our lives most of us owe a debt to the chemical warfare of an antibiotic against some disease organism, and the restriction and elimination of the invading microbe in our bodies. Many plants secrete toxic chemicals that inhibit other plants or the animals that try to feed on them. Most of the spices we use in cooking were evolved by plants to stop herbivores from eating them.

Stream fishes provide an interesting case study in changing geographical distributions because they are constrained by stream geography. In France a survey of the range shifts for 32 stream-dwelling species over a 30-year time frame from 1980 to 2009 has illustrated both the altitudinal changes as well as the upstream-downstream changes. In general, with water temperatures rising, the prediction is that stream fish will tend to move upstream to stay within their temperature zone. Comte and Grenouillet (2013) found that fishes in these French streams shifted upstream on average 14 m in elevation per decade, which averaged 0.6 kilometers in distance per decade. For these streams they found that the rate of range shifting was not keeping up with the temperature changes within the streams, and thus range shifts were lagging behind what is needed to adapt to ongoing water temperature increases.

Mangroves are intertidal trees and shrubs that grow around the Earth along coastlines in tropical and warm temperate areas. Mangroves grow in salt water and are sensitive to cold, so they are a good index of changes associated with ocean warming. Mangrove species have expanded their geographical range toward the poles on five continents over the past half century, at the expense of salt marsh (Saintilan et al. 2014). One common species of mangrove, *Avicennia germinans*, has extended its range along the USA Atlantic coast and expanded into salt marsh as a consequence of lower frost frequency in the southern USA. This genus has also expanded into salt marsh at its southern limit in Peru, and on the Pacific coast of Mexico. Mangroves of several species have expanded in extent and replaced salt marsh where protected within mangrove reserves in Guangdong Province, China. In southeastern Australia, a strong expansion of mangroves

into salt marshes is now occurring. These changes are consistent with the poleward extension of temperature thresholds coincident with sea level rise, although the specific mechanism of range extension might be complicated by limitations on dispersal. The shift from salt marsh vegetation to mangrove dominance on subtropical and temperate shorelines will have effects on other species in the intertidal community. Larvae from many species of fish rear in mangrove areas, and, from a practical point of view, mangroves protect shorelines from catastrophic wave action during tsunamis (Alongi 2008).

CONCLUSIONS

The ecological processes limiting the geographic distribution of most species of animals and plants are poorly understood. On the global scale geography and climate are the two main limiting factors. While we recognize well the fauna and flora of different continents, we do less well at the local level to understand, for example, why a particular plant occurs in one woodland but not in an adjacent one. Changes in historic geographic ranges are now being caused by two main processes—human introductions and climate change. The general prediction that in a warming world most species will move their geographic ranges toward the poles is now validated in many cases, but some species do just the opposite and move the “wrong” way for reasons that are not understood. We know from bitter experience that moving species willy-nilly from one continent to another is a serious error without very careful study, and yet we allow plant stores and pet shops to sell species well known to be major pests, should they escape confinement. We know enough to do much better.