

Latitudinal gradients and geographic ranges of exotic species: implications for biogeography

D.F. Sax *Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA*

Abstract

Aim To explore the biogeographic patterns of exotic species in order to discriminate between hypotheses postulated to produce several biogeographic phenomena: the latitudinal gradient in species richness, the latitudinal gradient in species geographical range size (Rapoport's rule), species geographical range boundaries and patterns of invasion in the tropics.

Location Data were taken from North and South America, Europe, Asia, Africa and oceanic islands.

Methods The latitudinal extents of the geographical range of exotic species were recorded to the nearest 1° of latitude from several published sources. Species richness was tabulated by recording the number of naturalized species present within 5° bands of latitude. Rapoport's rule was calculated by averaging the latitudinal extent of all exotic species present within 5° bands. The low-latitude boundaries of species' native and naturalized ranges were compared with the nearest 1° of latitude. These comparisons on continents were contrasted with those on islands.

Results Within the tropics, few exotic species have become naturalized and those that are have established large geographical ranges. Outside of the tropics, exotic species of birds, mammals, fishes and plants demonstrate qualitatively similar latitudinal gradients in richness and geographical range size. They show the same patterns as native species, where richness is negatively correlated and range size positively correlated with latitude. Further, the geographical ranges of naturalized species on continents rarely extend to latitudes lower than those in their native ranges. On islands (where biotic pressure is reduced) exotic species are more frequently naturalized at latitudes lower than those in their native ranges.

Main conclusions Hypotheses for the latitudinal gradient in species richness and geographical range size that are based on past glaciation events or differential rates of speciation between regions may not be necessary to explain these gradients, as exotic species are recent colonists and their patterns of distribution cannot have been directly affected by past glaciation events or differential rates of speciation between regions. Further, the low-latitude boundary of species geographical ranges may be set by tolerance for biotic pressure.

Keywords

Naturalized species, species richness, range size, Rapoport's rule, range boundaries, biotic pressure, abiotic stress, islands.

INTRODUCTION

The latitudinal gradient of species diversity is arguably the most robust pattern in biogeography. Specifically, the gradient in species richness, a negative correlation between number of species and latitude (Pianka, 1966; Rohde, 1992; Brown & Lomolino, 1998), is seen in the great majority of taxonomic groups: vascular plants, algae, birds, mammals, reptiles, amphibians, fishes, arthropods, fungi and many others (e.g. Fischer, 1959; Gaines & Lubchenco, 1982; Willig & Selcer, 1989; Currie, 1991; Rex *et al.*, 1993; Roy *et al.*, 1994; Blackburn & Gaston, 1996). There are a few exceptions, but these occur primarily at small taxonomic scales. For example, birds and trees both show the pattern, but nonrandom subsamples, such as penguins and pines, do not (Araya & Chester, 1993; Stevens & Enquist, 1998). A second robust pattern, Rapoport's rule, is characterized by a positive correlation between latitude and geographical range size. This pattern was originally observed in mammalian subspecies by Rapoport (1982) and later shown to hold at the species level for several taxa in temperate North America (Stevens, 1989). Since then, the pattern has received much attention and hypotheses to explain the pattern have generated useful discussion. Rapoport's rule appears to be robust within temperate latitudes, where it has been shown to hold for trees, birds, mammals, amphibians, fishes, arthropods and others, but to be inconsistent at tropical latitudes (Stevens, 1989; France, 1992; Rohde *et al.*, 1993; Letcher & Harvey, 1994; Ruggiero, 1994; Gaston *et al.*, 1998).

Both of these latitudinal gradients have been explained by a number of different hypotheses, with nearly 30 listed by Rohde (1992). Some of these include: availability of energy or other resources, temperature or temperature variability, environmental heterogeneity, differential rates of speciation or extinction, and the consequence of past glacial events or climate cycles. Differentiating between these hypotheses is particularly difficult for continental-scale patterns, as the quantity of appropriate data is limited, manipulative experiments are near-impossible to perform, and few replicates exist. These difficulties are further complicated by the inherent difficulty in comparing patterns among continents with different placements, shapes and histories (Brown & Lomolino, 1998). All of these difficulties inhibit an empirical approach, which in turn impede attempts to differentiate between hypotheses. Some authors have provided logical arguments why one or more hypotheses are unlikely to serve as a general explanation (e.g. Rohde, 1992; Rosenzweig, 1992). However, to address these complex issues, creative methods of analysis are needed that can differentiate between processes necessary to cause a pattern, and those unnecessary or at most accessory.

One approach is to consider whether there are any artificial experiments, containing commonalities with natural systems, that may be useful in solving these issues. Darwin (1859) used this approach when he considered the insights that artificial selection could provide towards the theory of natural selection. Obviously, artificial and natural

selection are quite different processes, yet they share some commonalities, because the organisms involved are governed by the same fundamental laws that affect all populations under a selection regime. In biogeography, the latitudinal gradients of native species are a natural system. The causes of these gradients have proven difficult to resolve for the reasons described above. Therefore, alternative evidence would be helpful in understanding the general mechanisms structuring these patterns. One possibility is to consider whether exotic species show any general patterns at biogeographic scales. This evidence would be 'artificial', but it could nevertheless assist the search for general mechanisms underlying biogeographic patterns.

Exotics are species that have been introduced by humans, or have been able to expand their range because of anthropogenic disturbances, into geographical regions where they were not historically present. The number of introductions has increased since the advent of intercontinental travel, such that thousands of exotic species have been introduced globally (Mooney & Drake, 1989). Of those species that have been introduced, only a subset establish self-sustaining populations in the absence of direct human intervention, i.e. become naturalized (Richardson *et al.*, 2000; Sax & Brown, 2000). These numbers, however, are still large. For example, over 1000 species of vascular plants have become naturalized in each of the floras of California, Hawaii and New Zealand (Webb *et al.*, 1988; Eldredge & Miller, 1998; Randall *et al.*, 1998). As these naturalized species expand their geographical ranges into new regions, they interact with the abiotic environment and with native species. Many of these interactions are strong and have been known to cause changes at the community, ecosystem and landscape levels (e.g. Elton, 1958; Carlton, 1979; Mack, 1981; Case & Bolger, 1991; D'Antonio & Vitousek, 1992; Simberloff & Stiling, 1996). Indeed, exotic species pose a serious threat to global biodiversity (Crawley, 1997).

It is because of the high number of exotic species, however, that they may prove useful in understanding biogeographic patterns and processes. It is only when many exotic species are established across a continent that emergent patterns, such as latitudinal gradients, may be examined. These patterns may be difficult to interpret because of confounding factors, but they do offer unique advantages. Unlike native species, naturalized species are recent invaders of a region, usually within the last few hundred years. Consequently, their distributions must be limited by biotic or abiotic conditions currently or recently in existence. Their distributions cannot be attributed to several of the hypotheses that have traditionally been suggested for the latitudinal gradients in richness or range size. Specifically, if there are more naturalized species, or if they have larger geographical ranges in one region than another, the explanation cannot be due to differential rates of speciation between regions, or to direct effects of Pleistocene glaciations. This powerful advantage, i.e. the ability to test the necessity of the above hypotheses, makes it worthwhile to consider whether there are general patterns in the biogeographic distributions of exotic species.

Three principal patterns of exotic biodiversity are possible. First, a null hypothesis suggests that no discernible patterns will exist, i.e. that richness and geographical range size of naturalized species will not vary in predictable ways across latitude. This would imply that idiosyncratic and/or stochastic processes were of principal importance in structuring the distribution of naturalized species. Second, patterns could exist that vary qualitatively among taxonomic groups or continents, e.g. mammals showing one pattern in North America and plants showing another in Europe. This would imply that the common set of factors that cause native species patterns to be qualitatively consistent among taxonomic groups and continents are not of primary importance in structuring the patterns of naturalized species. In this case, the influences of humans are probably determining the distribution and diversity of naturalized species. The most likely of these would be differential rates of introduction of exotic species across latitude, as these rates may vary among taxonomic groups and continents. Third, the patterns may be qualitatively consistent among taxonomic groups and continents. This would imply that ecological forces were causing these patterns. These forces could operate directly upon naturalized species to generate the gradients. However, they could also operate indirectly, by acting upon the legacy of processes (both ecological and evolutionary) that were experienced by naturalized species in their native ranges, or by affecting the type and number of species that are present in a place that is invaded, which in turn affects the invading species.

To differentiate among these alternative possibilities it is useful to consider not only the latitudinal patterns of richness and range size, but also one of the elements that structures these patterns, the geographical range limits of species. These limits, particularly their frequency and location across latitude, determine the form of latitudinal gradients. Dobzhansky (1950), MacArthur (1972) and Kaufman (1995) suggested that the boundaries of geographical ranges at low latitudes are generally caused by increasingly severe biotic conditions, such as competition, predation, parasitism and disease. Additionally, they suggested that high-latitude limits are generally caused by increasingly severe abiotic conditions, such as reduced energy availability, climatic variation and cold temperatures. The general role these processes have in shaping global biodiversity can be better understood by comparing range limits of species where they are native with those where they are naturalized.

With these aims in mind, the biogeographic patterns of several taxonomic groups of naturalized species were analysed for latitudinal gradients in richness and geographical range size. Specifically, I examined four taxa: two with data sets limited to specific regions, freshwater fishes in North America and vascular plants in Europe, and two with globally complete data sets, terrestrial birds and mammals. Additionally, the high- and low-latitude distributional boundaries of native and naturalized ranges of birds and mammals were examined.

METHODS

The latitudinal extent of the geographical range of exotic species of mammals and birds on continents, of freshwater fish in the United States and Canada, and of land plants in Europe were recorded to the nearest 1° of latitude from several sources (Lee *et al.*, 1980; Lever, 1985, 1987; Courtenay *et al.*, 1986; Jalas & Suominen, 1972–96). Analyses of exotic plant distributions in Europe are based on the approximately 20% of plant families (over 3000 species) whose ranges have been mapped on the continent. These families include four of 18 ($\approx 22\%$) of those families identified by Daehler (1998) as contributing a disproportionately large proportion of the total number of widespread or serious weeds in agricultural and natural areas. As such, the plant families mapped in Europe do not appear to be taxonomically biased with respect to their likelihood of having exotic species and should be qualitatively representative of overall patterns of exotic plant distributions. For all taxonomic groups: mammals, birds, fishes and plants, only exotic species that have maintained stable or growing populations for multiple generations without human assistance (i.e. naturalized species) were used in these analyses.

Species richness on continents was tabulated by recording the number of naturalized species present within 5° bands of latitude. The species richness of northern and southern hemispheres was tabulated by recording the number of exotic species on all continental landmass within 5° bands of latitude. If the same species was exotic on multiple continents, at the same band of latitude, it was only counted once for that band. Additionally, Australia was not included in counts of exotics in the southern hemisphere, because invasion patterns on that continent appear to more closely resemble those of a large island.

The gradient in geographical range size, i.e. Rapoport's rule, was calculated by averaging the latitudinal range extents of all exotic species present within 5° bands, i.e. using the method of Stevens (1989). There were a few species whose geographical ranges were less than 1° of latitude in extent, many of these were recently established species. These species were not included in the analyses of geographical range size that are presented here, but alternate analyses that included these species produced the same qualitative patterns.

LATITUDINAL GRADIENTS IN TEMPERATE ZONES

Outside of the tropics, all exotic taxa, on all continents analysed, show qualitatively similar gradients of species richness, in which richness is negatively correlated with latitude (Fig. 1). The precise latitudinal band of maximum richness varies slightly between taxa and continents, but is always the lowest or second lowest band of latitude in a temperate zone. The lowest band of latitude in the temperate zones of North America and Europe have greatly reduced land surface areas, which may explain why they

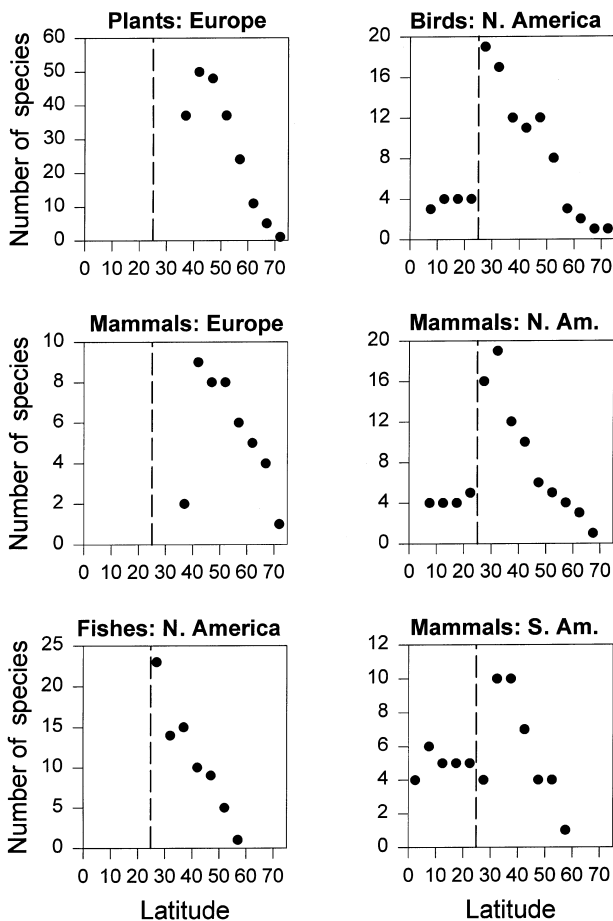


Figure 1 The species richness of naturalized exotic species in 5° latitudinal bands on continents. The dashed lines indicate the Tropic of Cancer or Capricorn, dividing tropical and temperate latitudes. Fish distributions were examined at temperate latitudes only.

sometimes have less naturalized species than the second lowest bands.

In addition to patterns on single continents, the same qualitative pattern is observed for naturalized birds and mammals on all continental land mass within the temperate zones of the northern and southern hemispheres (Fig. 2).

Outside the tropics, all exotic taxa, on all continents analysed, show qualitatively similar gradients of geographical range size, in which range size is positively correlated with latitude (Fig. 3). The precise latitudinal band of smallest average range size varies slightly between taxa and continents, but is always the lowest or second lowest band of latitude in a temperate zone. The range size value from the highest latitudinal band for each taxon analysed, on each continent, is based on a single species. Therefore, variation in apparent range size at the highest band of latitude should not be taken as strong evidence for or against the generality of the patterns.

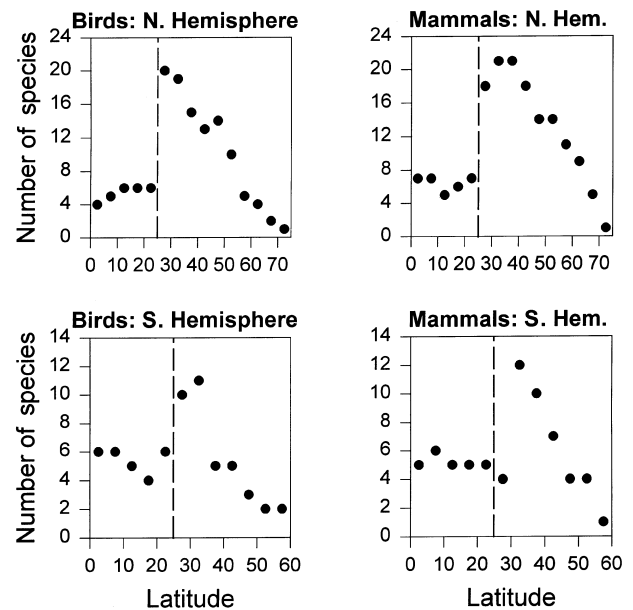


Figure 2 The species richness of naturalized exotic species in 5° latitudinal bands on all continental land mass in a hemisphere (excluding Australia). The dashed lines indicate the Tropic of Cancer or Capricorn, dividing tropical and temperate latitudes.

Human mediated processes

As patterns of richness and range size exist, the null hypothesis of no pattern can be rejected. Similarly, as the variation in these patterns is relatively pronounced and qualitatively consistent among all taxonomic groups, on all continents, it is unlikely that the patterns are the result of the proximate influences of humans (ultimately, of course, there would be no exotics without humans). This is because qualitative differences are expected in human influences upon different continents (with respect to human population distribution and patterns of land use modification), as well as upon different taxonomic groups of exotic species (with respect to rates of introduction). For example, it seems unlikely that the frequency of introduction of birds, mammals, fishes and plants in North America, South America and Europe have all been qualitatively identical. Unfortunately, it is very difficult to test this, since detailed records of introduction attempts are not usually available at continental scales. However, relatively complete records do exist for deliberate introduction attempts of birds in temperate North America (Christensen, 1963; Bump & Bohl, 1964; Long, 1981; Lever, 1987). These data show that the frequency of introduction attempts has been highest at mid-temperate latitudes, peaking at 45–50° (Fig. 4), where human population numbers are largest. This is in contrast with the maximal richness of naturalized birds, which is at 25–30° (Fig. 1), where introduction attempts have been relatively low (Fig. 4). Thus, for birds in North America this hypothesis can be rejected, i.e. the patterns of species richness are not a consequence of frequency of introduction

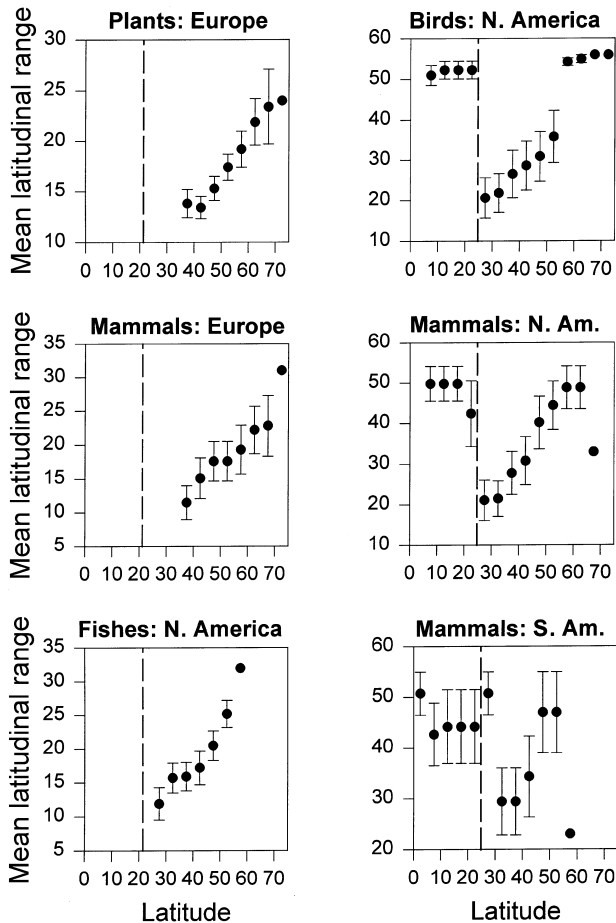


Figure 3 The mean latitudinal extent of naturalized exotic species in 5° latitudinal bands on continents. Error bars represent ± 1 SE. Points without error bars are based on a single species. The dashed lines indicate the Tropic of Cancer or Capricorn, dividing tropical and temperate latitudes.

attempts. The frequency of the introduction of exotic species are also not expected to affect patterns of geographical range size and can be rejected empirically for birds in North America (Figs 3 & 4). Two additional, but related hypotheses can also be envisioned, but both are falsified by the available data. First, if a large portion of the naturalized species introduced to a continent were from a single source area or from a restricted set of latitudes, then given certain assumptions, some of the observed patterns might be expected. However, as naturalized species on any particular continent come from several continents and a wide range of latitudes, this hypothesis is rejected. Second, small geographical range sizes of naturalized species at low temperate latitudes would be expected if the majority of introductions at those latitudes were relatively recent. As this is not the case, this hypothesis can also be rejected. However, despite all of the evidence described above, the hypothesis that biogeographic patterns of naturalized species exist because of the proximate influences of humans, while being unlikely,

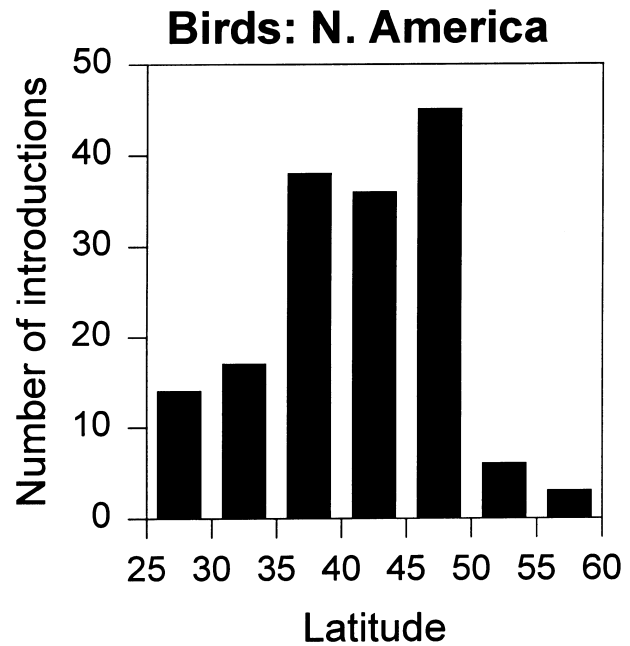


Figure 4 The recorded number of bird species that have been deliberately introduced outside of their native geographical range in the United States and lower Canada. Note that the pattern of introductions does not correspond to the number of species that have become naturalized at these same latitudes (Fig. 1).

cannot be completely rejected as other unknown and indirect consequences of humans may affect these patterns.

Contemporary ecological processes

Given the great qualitative similarities in the patterns of naturalized species among taxonomic groups and regions, and the similarity of those patterns to native ones, it is likely that the same set of biological processes determine both native and naturalized patterns. The only biological processes that could be directly affecting the distribution of naturalized species are contemporary ecological ones (I will return to the subject of indirect effects later). So, the direct influences of past glacial events or differential rates of speciation between regions cannot have affected them, as naturalized species have been present on foreign continents for only a relatively short period of time. Therefore, this hypothesis suggests that the invasion success of naturalized species, and their subsequent patterns of abundance and distribution, are affected by conditions currently experienced in invaded environments. These conditions include both abiotic pressures, such as climatic regimes and availability of resources, as well as biotic interactions, such as the presence of competitors, predators, parasites and diseases. This explanation is most likely valid because the possibility that any species, including naturalized ones, are affected by neither abiotic conditions nor biotic pressures seems extremely improbable. Indeed, there is a very large body of literature supporting the fact that naturalized species interact

with the biota and environment of invaded regions (op. cit.). Therefore, while this hypothesis is difficult to directly test, it is the one that remains by default after all of the other likely hypotheses have been rejected. If it is correct then contemporary ecological conditions must be sufficient to generate diversity gradients for both native and naturalized species.

The legacy of lineage

There is, however, another possibility. The influence of past glaciation events and differential rates of speciation, as well as ecological processes, could manifest themselves indirectly upon naturalized species. This could happen if processes that operated in the past, on a species in its native range, limit the location and size of the naturalized range of that species, i.e. if aspects of species geographical distributions are persistent species characteristics, *sensu* Lawton (1993); I shall hereafter refer to this processes as the legacy of lineage. So, if the distribution of a species in its native range is limited by tolerance for general environmental conditions, and not just by site-specific variables or historical accidents, then this tolerance should also limit or constrain the distribution of this same species in its naturalized range. If these processes are general enough, then naturalized species gradients should 'mirror' native ones. For example, fewer exotics might be present at high latitudes because the potential colonization pool of native species, i.e. those that can tolerate environmental conditions at high latitudes, may be relatively small (as there are few natives at high latitudes). Similarly, more exotics might be present at low latitudes because the potential colonization pool of native species is relatively large (as there are many natives at low latitudes). Likewise, patterns of geographical range size could be similarly affected if species from high latitudes with large ranges become naturalized at high latitudes and species from low latitudes with small ranges become naturalized at low latitudes.

To evaluate the importance of this legacy, I examined the latitudinal boundaries of geographical ranges of bird and mammal species that are naturalized in the northern hemisphere. Specifically, I compared the highest latitude reached by species in their native and naturalized ranges. These analyses (which are presented in detail in the section on geographical range boundaries) indicate that constraints on high-latitude distributions are present, but that they are relatively weak.

As constraints on high-latitude distributions are not strong, neither the presence nor absence of constraints on low-latitude distributions would lead to naturalized distributions that mirror native ones. This can be illustrated by imagining the exclusive influence of these forces in the absence of all others that might typically be expected to influence the probability of an introduced species becoming naturalized. So, in the absence of other forces, if strong constraints were present on low-latitude distributions, but not on high-latitude ones, then the reverse of the actual gradient in richness of naturalized species would form, with highest diversity at high latitudes. This is because species would be prevented from becoming naturalized closer to the

equator than their native ranges, but would not be prevented from becoming naturalized closer to the poles. Similarly, if constraints on neither low-or high-latitude distributions were present, then in the absence of other forces, no pattern of richness should be expected. Therefore, given the available evidence, the legacy of lineage hypothesis does not appear sufficient to explain the empirical patterns of naturalized species richness.

The legacy of lineage hypothesis could also affect gradients of range size. However, in order for naturalized patterns to mirror native ones, both the size and placement of geographical ranges must be duplicated. A strong correspondence in only one of these two factors would be insufficient. For example, as high-latitude range limits are not strongly constrained, low-latitude species with relatively small ranges could conceivably exist at high latitudes. Nevertheless, the correspondence between native and naturalized range sizes were examined for birds and mammals. This was carried out by comparing the largest latitudinal extent of a species native range (within a single hemisphere), with the largest latitudinal extent of a species naturalized range (within a single hemisphere). This yielded significant linear regressions (birds, $R^2 = 0.13$, $P < 0.01$, and mammals, $R^2 = 0.29$, $P < 0.01$). These results suggest that geographical range size may be a persistent species characteristic, which is consistent with other studies that have found comparable results (Forcella & Wood, 1984; Rejmánek, 1995, 1998; Duncan *et al.*, 1999). However, despite the significance of these relationships, the amount of variance in naturalized range size that is explained by native range size is relatively small. This suggests that the legacy of lineage, especially in the context of the varying positions of range placements, is not a sufficient explanation for the existence of pronounced gradients in geographical range size, and that some other factor, or set of factors, must be of greater importance.

The legacy of place

One final hypothesis remains to be evaluated. This hypothesis, the legacy of place, is closely linked to the hypothesis of contemporary ecological processes. It suggests, that the place or region being invaded determine patterns of naturalized species abundance and distribution. Obviously, if the place being invaded has an effect on the species that are invading, then it does so because of the contemporary ecological processes present in that place. Thus, these two hypotheses seem identical. However, there is a subtle, but significant difference that once again will affect whether conclusions can be drawn about the generation of gradients, or merely their maintenance.

The distinction is that the legacy of place hypothesis considers the possibility that a portion of contemporary ecological processes, namely the biotic portion, may have been affected by past glaciation events or differential rates of speciation, and not just by ecological processes. Therefore, the distribution of naturalized species may be affected by past processes that are manifested through the place being

invaded. This means that the influence of species richness upon exotic species cannot be viewed solely as a contemporary ecological force. This raises the question of whether species richness, in isolation of abiotic factors, have a significant effect on the naturalization success of exotic species. The answer is probably yes, but to what extent, and whether in a positive way, through facilitation, or negative way, through resistance or exclusion, is not clearly known. A large body of work has addressed these issues. On the one hand, theoretical reasoning and modelling work by researchers (e.g. Elton, 1958; Case, 1991) has suggested that species rich communities should be more difficult to invade than species poor ones. While on the other hand, empirical evidence shows that species-rich communities are often invaded by more species than species-poor ones (Lonsdale, 1999; Sax, 1999; Stohlgren *et al.*, 1999; Levine, 2000).

Hence, with the available evidence it is difficult to clearly know what effect species number alone may be having on patterns of naturalized species abundance and distribution on continents. A simple linear relationship between native and exotic richness, in the absence of other forces, could not have generated the observed gradients. This is because if the relationship is negative then naturalized diversity should peak at arctic latitudes, whereas if it is positive it should peak at tropical latitudes. Together, the evidence suggests that the legacy of place (specifically the biotic component of it) is probably insufficient in isolation to be the entire explanation for the gradients observed, but its potential influence cannot be rejected.

GEOGRAPHIC RANGE BOUNDARIES

Understanding the mechanisms responsible for setting the limits of range boundaries is integral to understanding the

processes that govern patterns of species abundance and distribution. Abiotic stresses at high latitudes and biotic pressures at low latitudes have been postulated (*op. cit.*) to limit geographical ranges. Little direct evidence, however, has been provided to support these hypotheses. Evidence for or against these hypotheses can be evaluated by comparing the high- and low-latitude limits of species native and naturalized ranges. These comparisons, particularly of high-latitude limits, also provide evidence that is inconsistent with strong support for the importance of the legacy of lineage hypothesis in structuring the latitudinal gradients.

High-latitude limits

The high-latitude boundaries of the geographical ranges of bird and mammal species that are naturalized in continental regions of the northern hemisphere were compared with the high-latitude boundaries on continents where these species are native. These comparisons were performed on all naturalized species, irrespective of the continent they are native to. For example, some species were native to Eurasia and others to North America. For an illustration of this technique see Fig. 5. The regression analyses are significant for both taxa (birds, $R^2 = 0.46$, $P < 0.001$, and mammals, $R^2 = 0.38$, $P < 0.001$; Fig. 6). This result shows that there is a correspondence between the range boundaries of species' native and naturalized ranges. This suggests that range boundaries may be affected by persistent species characteristics, which is consistent with the hypothesis that high-latitude range limits of naturalized species are determined by the same kinds of ecological forces that limit native species. However, it does not suggest that naturalized species are influenced strongly enough by these characteristics to determine their gradients of richness. This is because, although

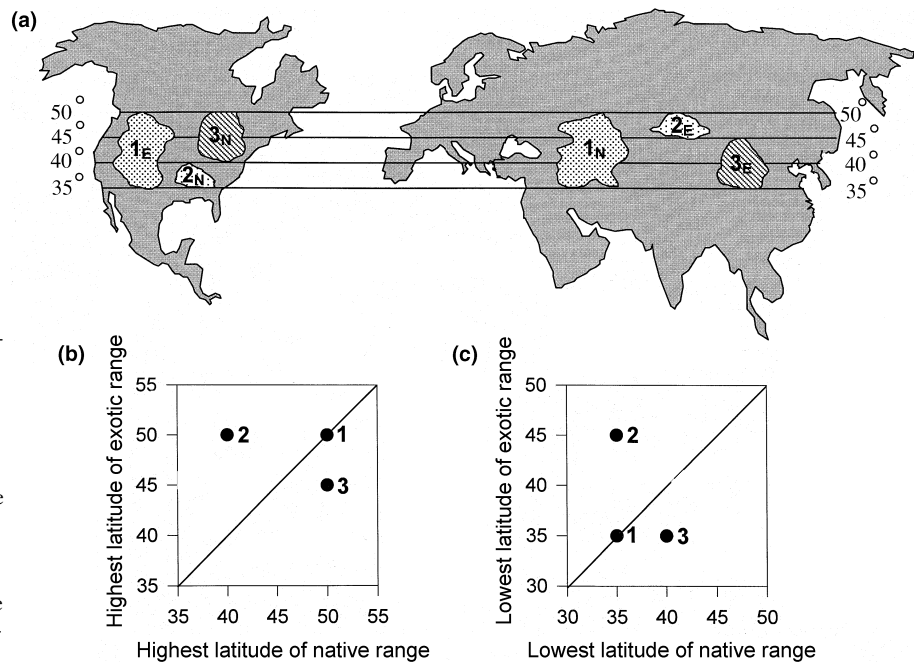


Figure 5 (a) The distribution of the geographical ranges of three hypothetical species. Species 1 is native to Eurasia and exotic in North America, while species 2 and 3 are native to North America and exotic in Eurasia. (b) Comparisons of the highest latitude in species native and exotic ranges. The diagonal line is the line of equality between native and exotic latitudes. (c) Comparisons of the lowest latitude occupied in species native and exotic ranges. The diagonal line is the line of equality between native and exotic latitudes.

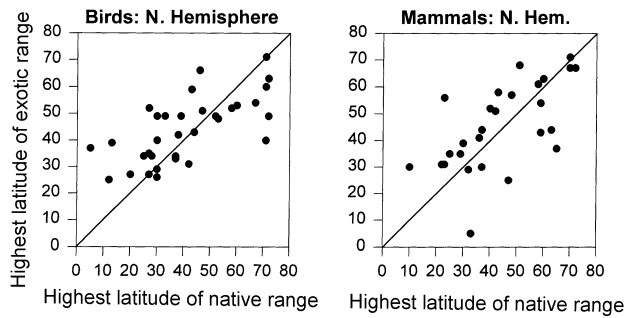


Figure 6 The relationship between highest latitude of the native range and highest latitude of the exotic range for individual species of mammals and birds on continents in the Northern Hemisphere. The line in each graph is the line of equality between native and exotic latitudes.

the regression relationships are significant, the majority of variation in the high-latitude boundaries of naturalized species ranges are not explained by native ranges. Further, species are distributed on both sides of the line of equality, which is in sharp contrast to low-latitude boundaries (described below). This means that naturalized species often exceed the high-latitude distributional boundary of their native ranges. Some have done this by more than 20° of latitude, which is the difference in distance between Miami and Montreal or Athens and Stockholm. This implies that while the legacy of lineage has some influence on the latitudinal gradient of species richness in naturalized species, that it is not the dominant force structuring these patterns.

Low-latitude limits

The low-latitude boundaries of geographical ranges of bird and mammal species that are naturalized in continental regions of the northern hemisphere were compared with the low-latitude boundaries on continents where these species are native. For an illustration of this technique, see Fig. 5.

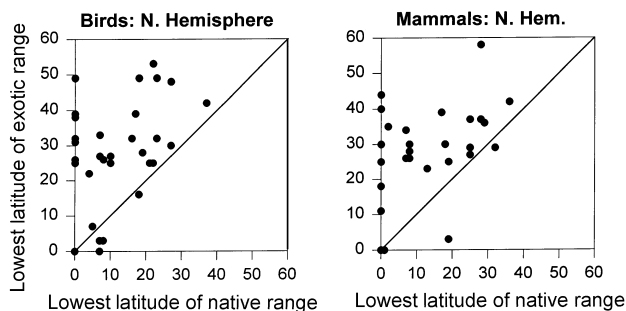


Figure 7 The relationship between lowest latitude of the native range and lowest latitude of the exotic range for individual species of mammals and birds on continents in the Northern Hemisphere. The line in each graph is the line of equality between native and exotic latitudes. Both plots show a greater proportion of points above the line of equality than expected by chance.

This relationship was evaluated for birds and mammals. Unlike high-latitude boundaries, regression analyses of low-latitude boundaries revealed much weaker relationships (birds, $R^2 = 0.13$, $P < 0.05$, and mammals, $R^2 = 0.16$, $P < 0.05$; Fig. 7). Note, however, that in sharp contrast to high-latitude limits, where a relatively even proportion of points fall on both sides of the line of equality (Fig. 6), with low-latitude limits only a strikingly small number of points occur below the line of equality (Fig. 7). This means that only a small proportion of bird and mammal species extend to a lower latitude in their naturalized range than in their native range. Further, this proportion is much smaller than expected by chance (χ^2 tests of an equal distribution about the line of equality rejects at $P < 0.001$, for both birds and mammals). These relationships are consistent with the hypothesis that low-latitude range limits are determined by contemporary ecological forces. If the ecological forces of importance at low latitudes are biotic pressure then the importance of these pressures should be reduced on islands relative to continents. This is because islands have lower species diversities, and consequently are postulated to have lower biotic pressures, than equal-sized areas at similar latitudes on continents (MacArthur & Wilson, 1967; Brown & Lomolino, 1998). This leads to the prediction that naturalized species should have lower latitudinal boundaries on islands than continents.

To examine this hypothesis, the low-latitude boundaries of geographical ranges of all naturalized birds throughout the globe were compiled for both islands and continents. These values were then compared with their low-latitude boundaries where they are native (Fig. 8). Both comparisons show significantly fewer points below the line of equality than expected by chance (χ^2 tests, $P < 0.001$). However, the proportion of points substantially below the line of equality, defined here as being five or more degrees of latitude, is significantly higher on islands than on continents (χ^2 test, $P = 0.05$). This means that on average exotic species have

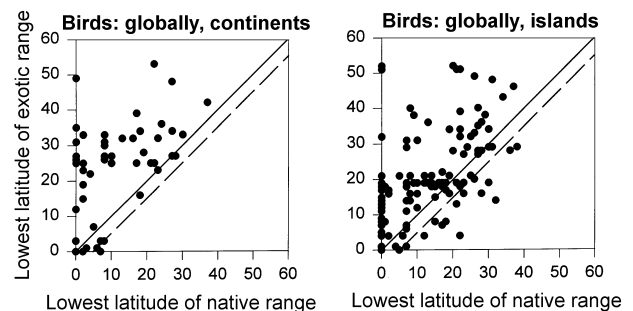


Figure 8 The relationship between the lowest latitude of the native range and the lowest latitude of the exotic range for birds on continents and islands throughout the world. The solid line in each graph is the line of equality between native and exotic latitudes. The dashed lines are parallel, but 5° below the lines of equality. Both plots show a greater proportion of points above the line of equality than expected by chance. However, a greater proportion of points is below the dashed line on islands than on continents.

become naturalized at significantly lower latitudes on islands than on continents. This supports the hypothesis that low-latitude boundaries are set by biotic pressures.

An alternative is that islands at a given latitude are more easily invaded because of less stressful abiotic conditions associated with maritime climates, and not because of reduced biotic pressure. However, if this were the case, then we would also expect to see naturalized species extending to lower latitudes along the coasts of continents. As most naturalized ranges of birds and mammals on continents include coastal regions, but nevertheless do not extend to lower latitudes along these coasts, it appears that abiotic conditions are not the factor facilitating island invasions. A second alternative is that exotics have become naturalized at lower latitudes on islands more often than on continents because a greater number of introduction attempts have occurred on islands than continents (Whittaker, 1998). While this certainly seems probable on an equal area basis, it does not seem as probable at the scale of latitude. Given the much greater quantity of land area and people inhabiting continental regions, within most bands of latitude, an equal or greater total number of introduction attempts are expected there.

PATTERNS OF SPECIES INVASION IN THE TROPICS

Few species of birds or mammals have become naturalized in continental environments of the tropics, so that naturalized richness is uniformly low (Figs 1 & 2). Those species which have naturalized, also have uniformly large geographical ranges (Fig. 3). This is in contrast to the gradients in richness and range size observed in the temperate zones. The consistently large geographical range sizes of naturalized species in the tropics can be explained by the status of most of these species as human commensals, i.e. species that inhabit anthropogenic environments. As such, they have broad geographical ranges that are linked with human distributions. The low richness of naturalized species in the tropics is most likely the result of one or both of two factors. First, that few species have been introduced to the tropics, or second, that contemporary ecological conditions are excluding them.

It is possible that few attempts to introduce species into the tropics have occurred, but this seems unlikely given the evidence available. Tropical regions, such as central Mexico, at 15–20° latitude, have had a long history of occupation by Europeans, particularly the Spanish, in which time introduction attempts would have undoubtedly been attempted. Indeed, the Spanish were highly successful at introducing exotic species into temperate regions that they colonized (e.g. Lever, 1985). Further, islands in the Caribbean Sea, within the same band of latitude as central Mexico, 15–20°, have had many introduction attempts, as is evident by the many naturalized species of birds and mammals that have become established (≈ 40). Finally, if introduction rates have been the limiting factor within the tropics, then it is noteworthy that they have been uniformly low throughout

the tropics of North America, South America, Africa and Asia.

A second possibility for the low number of naturalized species in the tropics is that some contemporary ecological force is excluding them. This force does not appear to be abiotic, or similar patterns would be expected on islands and coastal environments of continents. Furthermore, most organisms can tolerate the abiotic conditions of the tropics, as witnessed by the ability of most plants to grow in 'tropical' greenhouses. Instead, the discrepancy between many naturalizations on islands and few on continents suggests that this force may be biotic.

It remains unclear, however, why continental gradients of naturalized richness and range size should exhibit such sharp breaks at the tropics of Cancer and Capricorn. Although this is illustrated by only two groups in this study (birds and mammals), a similar pattern has been observed for vascular plants, with few species becoming naturalized on continents in the tropics (Rejmánek, 1996). One speculative explanation for this apparently sharp demarcation is that there is a threshold in biotic pressure located near the border of the tropic and temperate zones, beyond which many species are excluded from becoming established.

CONCLUSIONS

At tropical latitudes, naturalized species richness is uniformly low and range sizes are uniformly high. However, at extratropical latitudes, naturalized species of plants, fishes, mammals and birds all show essentially the same latitudinal gradients of species richness and range size (Rapoport's rule). Species richness peaks in the subtropics and declines with latitude, while range sizes are smallest in the subtropics and increase with latitude. These latitudinal gradients are present on multiple continents in both hemispheres. Some irregularities exist, but these irregularities do not appear fundamentally different than the irregularities shown by gradients with native species (e.g. Stevens, 1989; France, 1992). The qualitative similarity of these gradients to those of native species can potentially be explained by several hypotheses. Available evidence suggests that the most reasonable of these hypotheses is that naturalized species interact with their environments, sorting into the patterns of distribution and diversity for the same reasons that native species do. This in turn suggests that these patterns can be formed in the absence of past glaciation events and differential rates of speciation, and that contemporary environmental conditions (such as productivity, abiotic stress and biotic pressures) must be sufficient to generate them. It should be strongly noted, however, that this 'conclusion' is largely an interpretation of the available evidence, and that other interpretations are possible. Therefore, it warrants some caution, especially given the number and complexity of hypotheses that may affect the biogeographic patterns of naturalized species, and the difficulty in equivocally rejecting several of the hypotheses that are alternative to contemporary ecological forces. As such, evidence that corroborates this conclusion is desirable.

The palaeontological record, with regard to glaciation events, does just that. It shows that latitudinal gradients of species richness have existed in geological periods that preceded Pleistocene glaciation events (e.g. Stehli *et al.*, 1969). While these same palaeontological studies do not examine variation in geographical range size, the results of this study predict that Rapoport's rule should also be detectable in the palaeontological record prior to the Pleistocene. Unfortunately, the palaeontological record cannot address whether differential rates of speciation are necessary to form these patterns. As such, while the necessity of glaciation events in structuring latitudinal gradients can probably be rejected, the paired conclusion that gradients of diversity can form in the absence of differential rates of speciation should be viewed tentatively until further evidence is available.

One subject that was not fully explored in this study is the legacy of lineage hypothesis. It was examined, but only in regard to its relevance in structuring the latitudinal gradients. In this regard it was shown to be of minimal importance. However, the persistent species characteristics that affect range boundaries may map poorly onto latitude. This may be the case as latitude is only a rough estimate of biotic and abiotic conditions experienced at a particular place. It could be that some other factor (e.g. the number of frost free days per year) would show a stronger correspondence between native and naturalized ranges. This means that the legacy of lineage hypothesis could potentially be shown to have more support, but still be of little importance in structuring the latitudinal gradients of naturalized species. Undoubtedly, further work in this area is necessary and should prove to be insightful.

The difference between the low-latitude boundaries of species native and naturalized ranges suggests that there is some ecological factor influencing the establishment of species at low latitudes. Based on the difference between the distribution of naturalized species on continents and islands, this ecological factor appears to be biotic pressure. This implies that the low-latitude boundaries of species' geographical ranges (both native and naturalized) are determined by their tolerance for biotic pressure. Therefore, the greater the amount of biotic pressure that a species can tolerate, the lower its latitudinal limit should be.

The decreasing number of naturalized species with increasing latitude in the temperate zone, despite a large number of introduction attempts (at least with birds) suggests that some ecological pressure also prevents the naturalization of exotic species at high latitudes. This pressure may be abiotic conditions, which have been postulated to become increasingly severe with increasing latitude (op. cit.). Although the majority of variance in the high-latitude limit of geographical ranges was not explained by native range limits, the fact that there were significant relationships is consistent with the interpretation that abiotic factors may limit high latitude distributions. Further work is needed to substantiate the importance of abiotic stress and biotic pressure, as well as to more finely characterize how they may influence biogeographic patterns.

ACKNOWLEDGMENTS

I thank B. Enquist, J. Hamilton, D. Kaufman, E. Siemann, A. Kodric-Brown, H. Hansen, T. Lowrey, T. Case, G. Stevens, J. Brown, two anonymous reviewers, and a graduate seminar at UCSB for helpful discussion and comments on the manuscript. This is contribution number 32 of the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO): A Long-Term Ecological Consortium funded by the David and Lucile Packard Foundation.

REFERENCES

- Araya, B. & Chester, S. (1993) *The birds of Chile: a field guide*, p. 400. LATOUR, Santiago, Chile.
- Blackburn, T.M. & Gaston, K.J. (1996) Spatial patterns in the species richness of birds in the New World. *Ecography*, **19**, 369–376.
- Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn, p. 691. Sinauer Associates, Sunderland, MA.
- Bump, G. & Bohl, W.H. (1964) Summary of foreign game bird propagation and liberations 1960–63. *US Fish and Wildlife Service Special Scientific Report*, **80**, 1–48.
- Carlton, J.T. (1979) Introduced invertebrates of San Francisco Bay. *San Francisco Bay: the urbanized estuary* (ed. T.J. Conomos), pp. 427–444. American Association for the Advancement of Science, Pacific Division, San Francisco.
- Case, T.J. (1991) Invasion resistance, species build-up and community collapse in model competition communities. *Metapopulation dynamics* (eds M.E. Gilpin and I. Hanski), pp. 239–266. Academic Press, London.
- Case, T.J. & Bolger, D.T. (1991) The role of introduced species in shaping the abundance and distribution of island reptiles. *Evolutionary Ecology*, **5**, 272–290.
- Christensen, G.C. (1963) Exotic game bird introductions into Nevada. *Nevada Fish and Game Commission Biological Bulletin*, **3**, 1–66.
- Courtenay, W.R. Jr, Hensley, D.A., Taylor, J.N. & McCann, J.A. (1986) Distribution of exotic fishes in North America. *The zoogeography of North American freshwater fishes* (eds C.H. Hocutt and E.O. Wiley), pp. 675–698. John Wiley & Sons, New York.
- Currie, D.J. (1991) Energy and large scale patterns of animal and plant species richness. *American Naturalist*, **137**, 27–49.
- Crawley, M.J. (1997) Biodiversity. *Plant ecology* (ed. M.J. Crawley), pp. 595–632. Blackwell Science, Oxford.
- D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63–87.
- Daehler, C.C. (1998) The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. *Biological Conservation*, **84**, 167–180.
- Darwin, C. (1859) *On the origin of species*, p. 360. Murray, London.
- Dobzhansky, T. (1950) Evolution in the tropics. *American Scientist*, **38**, 209–221.
- Duncan, R.P., Blackburn, T.M. & Veltman, C.J. (1999) Determinants of geographical range sizes: a test using introduced New Zealand birds. *Journal of Animal Ecology*, **68**, 963–975.

- Eldredge, L.G. & Miller, S.E. (1998) Numbers of Hawaiian species (Suppl. 3), with notes on fossil species. *Bishop Museum Occasional Papers* 55, 3–15.
- Elton, C.S. (1958) The ecology of invasions by animals and plants, p. 181. Methuen and Co. Ltd., London.
- Fischer, A.G. (1959) Latitudinal variations in organic diversity. *Evolution*, 14, 64–81.
- Forcella, F. & Wood, J.T. (1984) Colonization potential of alien weeds are related to their 'native' distributions: implications for plant quarantine. *Journal of Australian Institute of Agricultural Science*, 50, 35–41.
- France, R. (1992) The North American latitudinal gradient in species richness and geographic range of freshwater crayfish and amphipods. *American Naturalist*, 139, 342–354.
- Gaines, S.D. & Lubchenco, J. (1982) A unified approach to marine plant herbivore interactions. II. Biogeography. *Annual Review in Ecology and Systematics*, 13, 111–138.
- Gaston, K.J., Blackburn, T.M. & Spicer, J.I. (1998) Rapoport's rule: time for an epitaph? *Trends in Ecology and Evolution*, 13, 70–74.
- Jalas, J. & Suominen, J. (eds) (1972–96) *Atlas florae Europaea*, Vol. 1–11. The committee for mapping the flora of Europe, Helsinki.
- Kaufman, D.M. (1995) Diversity of New World mammals: universality of the latitudinal gradient of species and bauplans. *Journal of Mammalogy*, 76, 322–334.
- Lawton, J.H. (1993) Range, population abundance and conservation. *Trends in Ecology and Evolution*, 8, 409–413.
- Lee, D.S., Gilbert, C.R., Hocutt, C.H., Jenkins, R.E., McAllister, D.E. & Stauffer, J.R. Jr (eds) (1980) *Atlas of North American freshwater fishes*, p. 854. North Carolina State Museum of Natural History, Raleigh.
- Letcher, A.J. & Harvey, P.H. (1994) Variation in geographic range size among mammals of the Palearctic. *American Naturalist*, 144, 30–42.
- Lever, C. (1985) *Naturalized mammals of the world*, p. 487. Longman, Essex.
- Lever, C. (1987) *Naturalized birds of the world*, p. 615. Longman, Essex.
- Levine, J.M. (2000) Species diversity and biological invasions: relating local process to community pattern. *Science*, 288, 852–854.
- Long, J.L. (1981) *Introduced birds of the world: the worldwide history, distribution and influence of birds introduced to new environments*, p. 528. Universe Books, New York.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, 80, 1522–1536.
- MacArthur, R.H. (1972) *Geographic ecology: patterns in the distribution of species*, p. 269. Harper & Row, New York.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*, p. 203. Princeton University Press, Princeton.
- Mack, R.N. (1981) Invasion of *Bromus tectorum* into western North America: an ecological chronicle. *Agro Ecosystems*, 7, 145–165.
- Mooney, H.A. & Drake, J.A. (1989) Biological invasions: a SCOPE program overview. *Biological invasions: a global perspective* (eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek and M. Williamson), pp. 491–506. John Wiley & Sons, New York.
- Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *American Naturalist*, 100, 33–46.
- Randall, J.M., Rejmánek, M. & Hunter, J.C. (1998) Characteristics of the exotic flora of California. *Fremontia*, 26, 3–12.
- Rapoport, E.H. (1982) *Areography: geographic strategies of species*, (translation by B. Drausel), p. 269. Pergamon, Oxford.
- Rejmánek, M. (1995) What makes a species invasive? *Plant invasions – general aspects and special problems* (eds P. Pyšek, K. Prach, M. Rejmánek and M. Wade), pp. 3–13. SPB Academic Publishing, Amsterdam.
- Rejmánek, M. (1996) Species richness and resistance to invasions. *Biodiversity and ecosystem processes in tropical forests, ecological studies* (eds G.H. Orians, R. Dirzo and J.H. Cushman), Vol. 122, pp. 153–172. Springer Verlag, Berlin.
- Rejmánek, M. (1998) A theory of seed plant invasiveness: the first sketch. *Biological Conservation*, 78, 171–181.
- Rex, M.A., Stuart, C.T., Hessler, R.R., Allen, J.A., Sanders, H.L. & Wilson, G.D.F. (1993) Global scale latitudinal patterns of species diversity in the deep sea benthos. *Nature*, 365, 636–639.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, 6, 93–107.
- Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, 65, 514–527.
- Rohde, K., Heap, M. & Heap, D. (1993) Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *American Naturalist*, 142, 1–16.
- Rosenzweig, M.L. (1992) Species diversity gradients: we know more and less than we thought. *Journal of Mammalogy*, 73, 715–730.
- Roy, K., Jablonski, D. & Valentine, J.W. (1994) Eastern Pacific molluscan provinces and latitudinal diversity gradient: No evidence for 'Rapoport's rule'. *Proceedings of the National Academy of Sciences of the USA*, 91, 8871–8874.
- Ruggiero, A. (1994) Latitudinal correlates of the sizes of mammalian geographic ranges in South America. *Journal of Biogeography*, 21, 545–559.
- Sax, D.F. (1999) Native and exotic species distributions: implications for general models of diversity, from community to biogeographic scales. *Dissertation*. The University of New Mexico, New Mexico.
- Sax, D.F. & Brown, J.H. (2000) The paradox of invasion. *Global Ecology & Biogeography*, 9, 363–372.
- Simberloff, D. & Stiling, P. (1996) Risks of species introduced for biological control. *Biological Conservation*, 78, 185–192.
- Stehli, F.G., Douglas, R.G. & Newell, N.D. (1969) Generation and maintenance of gradients in taxonomic diversity. *Science*, 164, 947–949.
- Stevens, G.C. (1989) The latitudinal gradient in geographic range: how so many species coexist in the tropics. *American Naturalist*, 133, 240–256.
- Stevens, G.C. & Enquist, B.J. (1998) Macroecological limits to the abundance and distribution of *Pinus*. *Ecology and*

- biogeography of Pinus* (ed. D.M. Richardson), pp. 183–190. Cambridge University Press, Cambridge.
- Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. (1999) Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, **69**, 25–46.
- Webb, C.J., Sykes, W.R. & Garnock-Jones, P.J. (1988) *Flora of New Zealand, IV: naturalized pteridophytes, gymnosperms, dicotyledons*. Botany Division, D.S.I.R., Christchurch.
- Whittaker, R.J. (1998) *Island biogeography: ecology, evolution and conservation*, p. 285. Oxford University Press, Oxford.
- Willig, M.R. & Selcer, K.W. (1989) Bat species density gradients in the New World: a statistical assessment. *Journal of Biogeography*, **16**, 189–195.

BIOSKETCH

Dov Sax is a postdoctoral associate at the University of California, Santa Barbara. His primary research interests are the patterns, processes and mechanisms of variation in species diversity. He has just published a manuscript on 'The paradox of invasion' in *Global Ecology and Biogeography*. He is currently editing a book on the 'Foundations of Biogeography' with James Brown and Mark Lomolino. His current research projects include comparisons of marine and terrestrial biogeography, a synthetic explanation for the latitudinal gradient in diversity, and an examination of species richness on oceanic islands following the invasion of exotic species.