

THE LATITUDINAL GRADIENT IN GEOGRAPHICAL RANGE: HOW SO MANY SPECIES COEXIST IN THE TROPICS

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The tendency for species richness to increase with decreasing latitude is well known (Wallace 1878; Dobzhansky 1950; Fischer 1960; Pianka 1966; see also tables 1–4) but poorly understood. Its impact on the thinking of biologists is reflected in the large literature associated with the gradient and in the current debate over the 12 possible explanations for the phenomenon (the 10 listed in Pianka 1978, one in Huston 1979, and one in Terborgh 1985). Since most ecology textbooks (MacArthur 1972; Colinvaux 1973; Emlen 1973; Krebs 1978; Ricklefs 1979; Brown and Gibson 1983) review this debate, there is no need to rework that here. My intent is to introduce a simple observation into the discussion to suggest a new approach to the problem.

After presenting evidence for a second important latitudinal correlate (called “Rapoport’s rule”), I give an overview of the data that form our perception of the latitudinal gradient in species richness. This overview emphasizes the exceptions to the gradient and demonstrates that Rapoport’s rule and the latitudinal gradient in species richness have coincident exceptional taxa. Given this coincidence, I hypothesize that both are an outcome of the same process. Focusing attention on Rapoport’s rule, instead of the more complicated question of species richness, sheds light on the origin of both latitudinal gradients.

THE LATITUDINAL GRADIENT IN SIZE OF GEOGRAPHICAL RANGE, OR RAPOPORT’S RULE

When the latitudinal extent of the geographical range of organisms occurring at a given latitude is plotted against latitude, a simple positive correlation is found (figs. 1–5). This pattern can be found by rounding to the nearest 5° the northernmost and southernmost extremes of the geographical ranges of individual species and then calculating the average north-to-south extent of species found at each 5° band of latitude. I suggest that this correlation between geographical range and latitude be called “Rapoport’s rule” after Eduardo H. Rapoport, who made passing reference to the correlation while describing the degree of geographical overlap between the distributions of subspecies (Rapoport 1975, 1982). Remark-

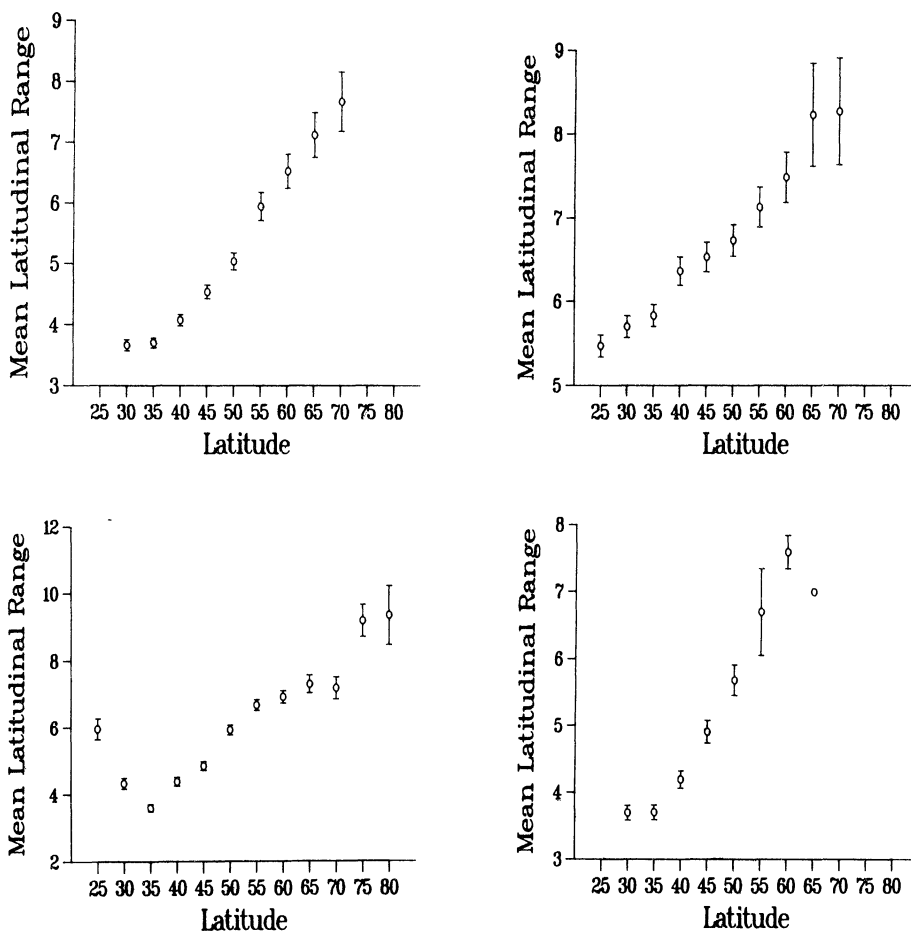


FIG. 1 (*top, left*).—Mean latitudinal extent of North American trees native to various latitudes. Sample sizes (left to right): 267, 324, 273, 182, 118, 47, 29, 17, 6. Latitudinal extent in this and all subsequent figures is the number of degrees of latitude, rounded to the nearest 5°, through which the native geographical range of the species passes. The error bars are one standard error of the mean. Data from Brockman 1968.

FIG. 2 (*top, right*).—Mean latitudinal extent of North American marine mollusks with hard body parts. Sample sizes (left to right): 510, 474, 467, 266, 203, 181, 133, 97, 41, 40. Annotations as in figure 1. Data from Rehder 1981.

FIG. 3 (*bottom, left*).—Mean latitudinal extent of North American freshwater and coastal fishes. Sample sizes (left to right): 147, 362, 588, 435, 302, 162, 107, 79, 51, 41, 6, 3. Annotations as in figure 1. Data from Lee et al. 1980 et seq. The apparent increase in the mean latitudinal extent of fishes in the southern United States is due to an edge effect. At the southernmost sites of the United States (at about 30° to 25° latitude), there is little land per latitudinal band and few freshwater species. As a result, most of the species listed are coastal (often marine) and have wide ranges.

FIG. 4 (*bottom, right*).—Mean latitudinal extent of North American reptiles and amphibians. Sample sizes (left to right): 205, 210, 145, 80, 38, 10, 5, 1. Annotations as in figure 1. Data from Conant 1958.

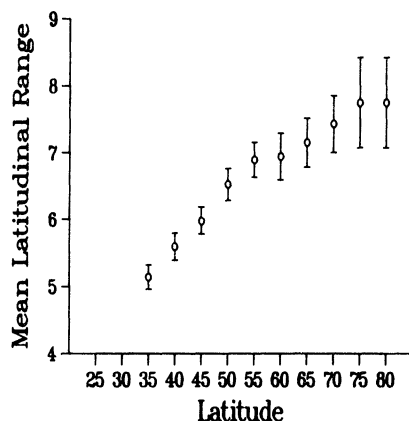


FIG. 5.—Mean latitudinal extent of North American mammals. Sample sizes (left to right): 214, 176, 148, 117, 95, 71, 53, 40, 8, 8. Annotations as in figure 1. Data from Burt 1964.

ably, this correlation (i.e., Rapoport's rule) is found in all higher taxa whose geographical ranges are well known (except migratory birds; a fact discussed later). This is not to say that all low-latitude organisms have small geographical ranges (e.g., *Bufo marinus*, the marine toad, is a good counterexample to that claim), but on the average, the ranges of organisms decline with declining latitude.

The aspect of size of the geographical range that is being compared is the length of the north-south axis. Total areal extent does not yield as clear a correlation as does latitudinal extent, possibly because the area of the geographical range does not reflect the climatic challenges a species must face as well as does latitudinal extent. Two points separated only by longitudinal differences do not as consistently show climatic differences as two points separated by degrees of latitude. To see this, consider how climatic variables change with latitude. Temperature extremes show a simple relation with latitude (fig. 6); the range in temperature readings over the course of many years is a positive function of latitude. Rainfall as a function of latitude is more complicated (figs. 7, 8), but there is still an easily explained pattern. The range in annual precipitation values for a single station over many years shows the greatest absolute range of values in the tropics (fig. 7), but this is a consequence of the magnitude of accumulated rainfall. A better measure of the environmental stresses faced by a resident at the different latitudes might be the variation relative to the mean experienced at that site (fig. 8). In any case, the point is that climatic variables show a rather simple relationship with latitude. Similar plots of longitude versus climatic conditions do not yield such regular patterns. For this reason, the width of the geographical range contains little information about climatic variability within the range of a species. Therefore, the north-south axis of the geographical range was used as the major information-containing variable in this analysis.

Rapoport (1975) compared the geographical distributions of mammalian subspecies of the same species and found that subspecies at lower latitudes tend to have smaller distributions than their higher-latitude counterparts. His compari-

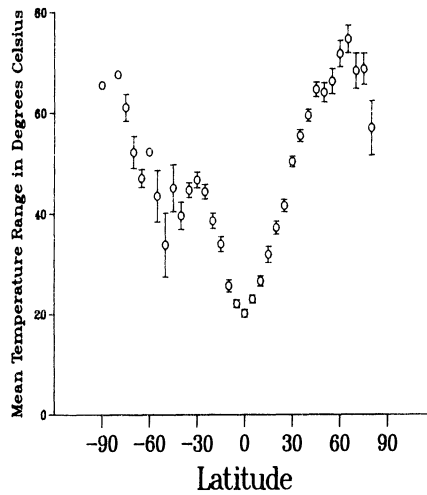


FIG. 6.—Mean of absolute range in temperature as a function of latitude. Negative latitudes are in the Southern Hemisphere. The data represent record highs and lows (not maximum daily extremes) over 30 yr (1931 to 1960) or less (then up to 1970) depending on the particular station. Annotations as in figure 1. Data are from 1056 stations (slightly biased toward European stations) spread over the globe and compiled in Müller 1982.

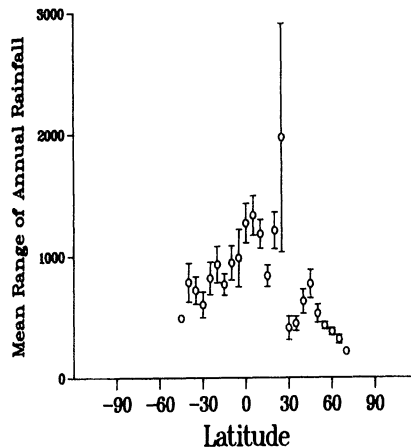


FIG. 7.—Mean of absolute range in accumulated annual rainfall as a function of latitude. Periods of data collection and annotations as in figure 6.

sons included 136 species from North America, 30 from Central America, and 31 species whose ranges entered both North and Central America. Rapoport restricted his analysis to mammals that had been well studied in order to avoid major biases resulting from differences in the completeness of mammalian censuses in different latitudes. His work confirms the pattern presented in figures 1–5 and also allows the correlation shown by those figures to be extended to tropical latitudes. Since the range limits of tropical organisms are less well known than those of

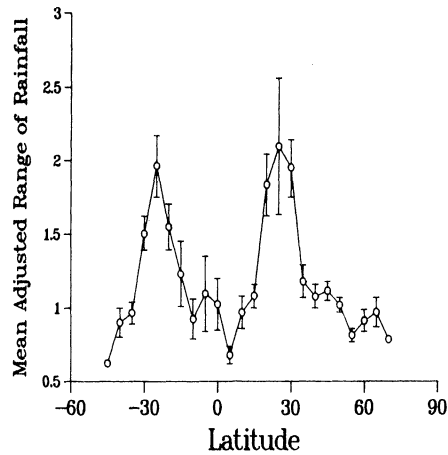


FIG. 8.—Mean of relative range in accumulated annual rainfall expressed as the difference between the annual maximum and annual minimum divided by the mean annual rainfall. Data and annotations as in figure 6.

North American organisms, estimates derived from plots like those found in figures 1–5 would tend to be misleading if broadly applied to tropical organisms. For example, using the distributional data from Holdridge and Poveda (1975) for trees of Santa Rosa National Park in northwestern Guanacaste Province, Costa Rica (ca. 10° N latitude), an average of 11.45° ($N = 73$) of mean latitudinal extent is found. This value is certainly overinflated, because narrowly distributed species are those most likely to have missing data. Yet 11.45° is less than that found for any of the other latitudes presented in figure 1. Rapoport's method is the only way of extending my survey into tropical latitudes without introducing unacceptable error into the correlation. His method succeeds because it is applied only to subspecies whose geographical ranges are well known.

Rapoport's work (1975) also provides evidence that the smaller geographical ranges of tropical organisms are not an outcome of the smaller landmass of tropical lands (i.e., Central America). By plotting the average meridional expansion of mammals throughout the North American continent, he found that the percentage of the width of the landmass used by the average mammal decreases from 93.1% in the far north to 64.2% in Costa Rica (noted in another context in McCoy and Connor 1980). Thus, the reduction in the size of the geographical range of mammals is not exclusively due to the reduction in the landmass of North America toward the tropics. Marine mollusks show the same pattern as terrestrial organisms (fig. 2), also suggesting that Rapoport's rule is not a simple matter of the size of the landmass.

The emphasis on the latitudinal gradient in geographical-range size within the North Temperate Zone serves another purpose. As argued below, Rapoport's rule and the latitudinal gradient in species richness may arise from similar ecological processes. Generally, the high species richness of tropical latitudes is taken as a tropical phenomenon, something to be studied by tropical biologists. What must

be emphasized is that the processes that produce these two latitudinal correlates are at work within North America. They are not due to some abnormality of tropical climates, glacial disturbances of temperate areas, or some antibiotic agent in polar habitats. These latitudinal gradients can be studied at all latitudes.

WHY RAPOPORT'S RULE EXISTS

Consider a spruce tree living in interior Alaska. This individual tree must have the ability to survive temperatures as cold as -55°C in the winter and as warm as $+34^{\circ}\text{C}$ during the summer. The seasonal variation in temperature or moisture content of any given piece of forest precludes ecological specialization on some smaller set of climatic conditions. The tolerance of any individual organism must span the range of conditions to which it is exposed throughout its life. The large latitudinal extent of high-latitude organisms is a simple consequence of the selective advantage to those individuals with wide climatic tolerances, tolerances that are needed for the successful exploitation of any given high-latitude location. For tropical organisms, individuals that have wide climatic tolerances derive no great advantage. The full breadth of their potential tolerances are never tested by natural selection. This does not preclude the evolution of different climate-tolerant races within the total geographical range of the tropical species, but selection for wide tolerance of single individuals would not be expected. Such broad tolerances would not be selectively advantageous to the individual possessing them and might even be detrimental if they reduce the efficiency of exploitation of particular microclimatic conditions. These ideas are not new, having been discussed in reference to barriers to gene flow by Janzen (1967) and having found empirical support in the work of Huey (1978) and others (MacArthur 1965, 1969). Pielou used similar reasoning in interpreting the correlation between latitudinal and altitudinal range in *Pinus* (1979, p. 218).

It does not follow, and the biogeographers cited above did not claim, that phenotypic plasticity alone explains the boundaries of the geographical range of a species. Examples of geographical variants can be found in all the taxa listed here for both high and low latitudes. The point is that in a tropical setting, within a few kilometers, or just a few tens of meters in elevation, there exists a set of climatic conditions that the grandparents of a given organism never experienced. This situation is much more difficult to find in a temperate or an arctic area. The spatial scale of distinctively different microhabitats is smaller in the tropics. This makes the evolution of tropical geographical variants less likely. There simply is not enough physical space to support a large (and therefore persistent) population of genetically distinctive members of a microclimate-tolerant race.

In summary, two points differing in latitude are likely to experience different ranges of climatic conditions, with tropical areas showing a narrower range of temperature and rainfall and extratropical areas showing a greater annual range (at least in temperature if not in rainfall). Temperate and polar areas may experience conditions on a given day that are similar to those found in tropical areas, but their annual range of climatic conditions far exceeds that ever experienced by organisms restricted to the tropics. Natural selection favors the wide climatic tolerance

TABLE 1

COMPILATIONS OF REGIONAL SURVEYS SHOWING A LATITUDINAL GRADIENT IN SPECIES RICHNESS

Organism or Guild	Region	Source
Vertebrates		
Non-oceanic birds	New World	Dobzhansky 1950
	New World	MacArthur 1969
	New World	Cook 1969
	Nearctic	Tramer 1974
	Paleartic	Järvinen 1979
Mammals	New World	Simpson 1964
	New World	Wilson 1974
Fish	Nearctic	Horn & Allen 1978
Reptiles	Nearctic	Kiester 1971
Anurans	global	Arnold 1972
Lizards	global	Arnold 1972
	Nearctic	Schall & Pianka 1978
Snakes	New World	Dobzhansky 1950
	global	Arnold 1972
Invertebrates		
Papilionid butterflies	global	Scriber 1973, 1984
Sphingid moths	New World	Schreiber 1978
Dragonflies	global	Tillyard 1917, cited in Williams 1964
Wood-boring Scolytidae and Platypodidae	global	Beaver 1979
Planktonic foraminiferans	Nearctic	Stehli et al. 1969
Permian brachiopods	Nearctic	Stehli et al. 1969
Corals	Australian	Wells 1955, cited in Fischer 1960
	global	Stehli & Wells 1971
Tunicates	global	Hartmeyer 1911, cited in Fischer 1960
Calanid crustaceans	global	Brodskij 1959, cited in Fischer 1960
Mollusks	Nearctic	Fischer 1960
Plants		
Trees	Paleartic	Silvertown 1985
Orchids	New World	Dressler 1981

of individuals in high-latitude areas and shows no preferential treatment of the same in low latitudes. As a consequence, individual organisms of high latitudes are less restricted in their habitat use; their distribution thus shows greater latitudinal extent than that of species in low latitudes.

THE LATITUDINAL GRADIENT IN SPECIES RICHNESS

There is an ecological connection between the correlation of geographical-range size and latitude with the correlation between species richness and latitude. Illustrating this connection requires a review of the data giving rise to the idea that the tropics support more species of organisms than do higher latitudes. The exceptions to this pattern deserve special attention, since I show that exceptions to one latitudinal correlation are also exceptions to the other.

From tables 1 and 2, it is clear that the latitudinal gradient in species richness applies to the same broad array of taxa in which Rapoport's rule exists. These tables divide the data into those generated by range maps (table 1) and those

TABLE 2
 COMPILATIONS OF POINT SAMPLES SHOWING A LATITUDINAL GRADIENT
 IN SPECIES RICHNESS

Organism or Guild	Region	Source
Vertebrates		
Non-oceanic birds	New World	Karr 1971
	New World	Karr & Roth 1971
	Nearctic	Tramer 1974
Mammals	New World	Fleming 1973
Lizards	Nearctic	Pianka 1967
Freshwater fish	global	Barbour & Brown 1974
Invertebrates		
Arthropod communities	Nearctic	Teraguchi et al. 1981
Litter mites	New World	Stanton 1979
Stream invertebrates	Nearctic	Stout & Vandermeer 1975
Marine invertebrates	New World	Heck 1979
Lepidoptera	New World	Ricklefs & O'Rourke 1975
Ants	global	Kusnezov 1957
	New World	MacArthur 1972
Marine copepods	Nearctic	Turner 1981
Polychaetes	global	Sanders 1968
	Old World	Ben-Eliahu & Safriel 1982
Gastropods	New World	Spight 1977
	Nearctic	MacDonald 1969
Marine bivalves	global	Sanders 1968
Epizooplankton	Nearctic	Grice & Hart 1962
Plants		
Trees	New World	Dobzhansky 1950
	Nearctic	Monk 1967
	Nearctic	Glenn-Lewin 1977

produced by counting species that occur at particular sample points (table 2). Several times (MacArthur 1965, 1969; Whittaker 1969) it has been pointed out that habitats (however defined by the investigator) in tropical latitudes generally support more species than similarly defined habitats in the Temperate Zone. Without doubt, the high species richness of tropical latitudes is due to more than just a greater variety of distinctively different habitats in the tropics. In a given tropical habitat, more species coexist than in analogous extratropical sites.

The two most frequently cited exceptions to the latitudinal gradient in species richness are both cases in which recent reviewers have failed to update the interpretations of earlier workers. According to Stout and Vandermeer (1975), the findings of Patrick (1966) probably represent incomplete sampling of rare species and should not be taken as a counterexample to the latitudinal gradient in species richness of aquatic communities. The work of Thorson (1951) is also often used as counterevidence, but he is reported to have changed his mind after more data collection (Sanders 1968). Other often-cited studies are clearly too narrow in geographical extent to be considered a test of the latitudinal pattern (e.g., the state of Texas, Rogers 1976; the deserts of the United States, Brown 1973, Brown and Davidson 1977), and the authors did not intend for their data to be used in this way.

TABLE 3
PSEUDO-EXCEPTIONS TO THE LATITUDINAL GRADIENT IN SPECIES RICHNESS

Organism or Guild	Region	Source
Vertebrates		
Rodents	Nearctic	Brown 1973
	Nearctic	Brown & Davidson 1977
Fish	New World	Patrick 1966, cited in MacArthur 1969
	Nearctic	Miller 1958
Reptiles	Nearctic	Rogers 1976
Invertebrates		
Freshwater invertebrates	New World	Patrick 1966, cited in MacArthur 1969
Rocky-intertidal invertebrates	New World	Paine 1966
Basommatophoran mollusks	global	Hubendick 1962
Decapod crustaceans	Neotropical	Abele 1974
Estuarine polychaetes and bivalves	global	Sanders 1968
Deep-sea polychaetes and bivalves	global	Sanders 1968
Marine infauna	global	Thorson 1951
Apoidea	global	Michener 1979

TABLE 4
EXTRATROPICAL PEAKS OR CONTRADICTIONARY PATTERNS OF SPECIES RICHNESS

Organism or Guild	Region	Source
Vertebrates		
Non-oceanic birds	Nearctic	Cody 1966
	Australia	Schall & Pianka 1978
Lizards	Australia	Schall & Pianka 1978
Invertebrates		
Ichneumonid parasitoids	Old World	Owen & Owen 1974
	Nearctic	Janzen 1981
Collembola	global	Rapoport 1975

Other pseudo-exceptions (table 3) to the latitudinal gradient in species richness include cases in which an unclear statement of the phenomenon has led to false expectations. It should not come as any surprise that some organisms (penguins, conifers, willows, brown algae, seals, etc.) have greater species richness at high latitudes than at low latitudes. These cases are not relevant to the latitudinal gradient in species richness because in each situation the particular ecological role filled by the organism is filled by many more species at lower latitudes (e.g., willows are replaced by several genera of shrubby plants at lower latitudes). The latitudinal gradient in species richness is an observation about the number of species in an assemblage of species, not the number of species in a genus. Similar but less obvious kinds of ecological replacements may account for the exceptional findings of the remaining entries in table 3. These authors have restricted their studies to narrowly defined sets of taxa without adequate study of potential ecological analogues.

The remaining exceptions (table 4) do not pose a serious threat to the generality

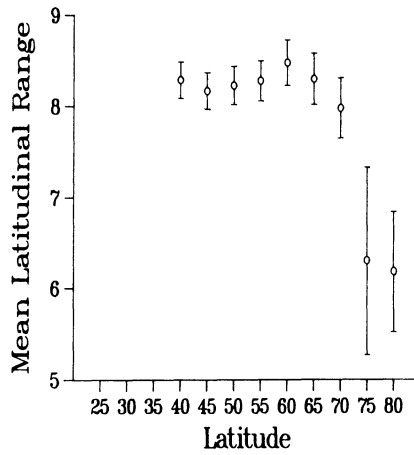


FIG. 9.—Mean latitudinal extent of the breeding ranges of Soviet non-oceanic birds as a function of latitude. Sample sizes (left to right): 440, 441, 395, 315, 254, 190, 124, 20, 11. Annotations as in figure 1. Data from Dement'ev et al. 1951–1954.

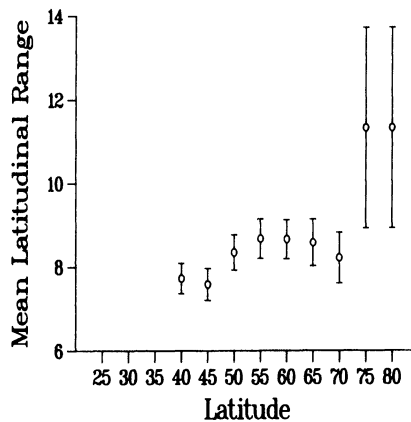


FIG. 10.—Data from figure 9 but only for nonmigratory birds. Sample sizes (left to right): 112, 97, 76, 54, 41, 31, 18, 3, 3. Annotations as in figure 1.

of the latitudinal gradient in species richness, but they are of interest because they provide a key to what types of ecological processes produce the pattern. Compare these exceptions to organisms that do not show the Rapoport phenomenon.

THE EXCEPTIONS TO RAPOPORT'S RULE

The pattern of latitudinal extent of Soviet bird breeding distributions is exceptional (fig. 9). No positive correlation between latitudinal extent and latitude can be seen when the breeding ranges of migratory and nonmigratory birds are lumped together in a single graph. When only the nonmigratory birds are displayed (fig. 10), the now-familiar Rapoport phenomenon returns. (This also shows that

Rapoport's rule applies to Old World species as well as to those of the New World.) Since migratory birds do not experience the full range of climatic conditions that a breeding ground offers over the seasons, they are not selected for the same breadth of climatic tolerance as are nonmigratory birds breeding in the same area. Migration allows birds to live in a narrow range of environmental conditions, and hence their breeding distributions do not match Rapoport's rule. The observation that organisms migrating long distances do not show the Rapoport phenomenon strengthens its climate-based explanation discussed earlier.

Although the data are not yet available, I would hypothesize that Rapoport's rule would not be found in organisms that act like migrants in their exploitation of the environment. Insects that are dormant for much of the year "migrate" in that they avoid some of the environmental extremes the seasons offer. Annual plants that reside in the seed stage during much of the year, or organisms that actually migrate or hibernate, should not show variation in their geographical ranges consistent with Rapoport's rule. Internal parasites that are buffered from the external environment may also not show the Rapoport phenomenon, provided that their host use is so generalized that their distribution is not limited to the distribution of a single host species. The difficulties in testing these hypotheses are that the taxa being studied must be sufficiently species-rich to allow statistical comparison and that their geographical ranges must be equally well known in all of the latitudes being compared.

HOW RAPOPORT'S RULE MAY PRODUCE THE LATITUDINAL GRADIENT IN SPECIES RICHNESS

Looking back over the counterexamples to the latitudinal gradient in species richness in table 4, it should now be noted that strongly seasonal or migratory organisms found in that table should not be expected to show the Rapoport phenomenon. Take, for example, Ichneumonidae, which do not show a simple latitudinal gradient in species richness but instead show a peak at mid-latitudes. These parasitoids make their living during the warm months of the year and, in a sense, live in the tropics, no matter what latitude they call home. Because these species are freed from selection to broaden their environmental tolerances, other ecological factors (outlined in Janzen 1981) become the major determinants of their distribution. Similar reasoning leads one to conclude that all the taxa of table 4 are groups that should not be expected to show the Rapoport phenomenon for the same reasons that migratory Soviet birds (fig. 9) are exceptional. Both the migratory birds and the exceptional taxa in table 4 experience only a small portion of the climatic variation their breeding latitudes have to offer.

The coincidence of the exceptional taxa for these two latitudinal correlates does not demonstrate that they both have the same cause, but the coincidence begs for some simple explanation. The remainder of this paper is devoted to clarifying the connection between these two latitudinal gradients.

A prediction of Rapoport's rule is that organisms from low latitudes have narrower tolerances for climatic conditions than do high-latitude species (provided that the above explanation of Rapoport's rule is correct). The consequence

of this prediction is that tropical latitudes appear as a finer mosaic of distinctive microclimates to a tropical organism than to a temperate or polar organism (or to climate generalists like humans). This difference arises because a climate change that is minor to an organism from a high latitude is a major (possibly life-threatening) change to an organism from a lower latitude, even though the magnitude of the change in climate is the same. As mentioned earlier, several reviews have made the point that greater habitat heterogeneity of tropical areas does not account for all of the gradient in species richness because even comparable habitat types support more species in tropical than in extratropical latitudes (MacArthur 1965, 1969; Whittaker 1969). The increased environmental sensitivity of low-latitude organisms does not result in an increase in the number of obvious ecotones in the tropics but produces greater heterogeneity in the success of organisms exploiting a given location. This heterogeneity may allow for species coexistence that might otherwise be impossible.

If the microhabitat requirements of tropical organisms are narrowly defined, then the dispersal powers of individuals near the edge of their preferred microhabitat may extend to unfavorable areas. Often this would result in the arrival of individuals in areas where they are able to survive but unable to maintain their population. Shmida and Wilson considered the various determinants of species richness in plant communities and presented a new category called "mass effect" (1985, p. 2). This enrichment of species number in a given habitat is the result of "the establishment of species in sites where they cannot be self-maintaining" (p. 2). From their surveys of desert washes, they found that valleys contain many species of hillside plants whose populations cannot persist in the valley bottoms without the constant input of seeds from the hillsides. This is precisely the phenomenon that I suggest inflates the species richness of tropical forests (some anecdotal evidence suggests that this inflation process occurs in low latitudes; Heck 1979).

The existence of Rapoport's rule suggests that tropical organisms have narrower environmental tolerances than temperate or polar organisms. Their narrower tolerances would lead to greater spatial heterogeneity and discontinuity of the areas where they do well. The sites where a species is successful become source areas for colonists that sometimes arrive in habitats to which they are poorly suited. Populations of these poorly suited arrivals cannot be excluded through competition with better-adapted locals because their population dynamics depend on the proximity of areas where they do well, not on local conditions (for a similar argument, see the "rescue effect" in Brown and Kodric-Brown 1977). The greater species richness of tropical habitats would then be a result of prolonging the coexistence of species whose traits would otherwise lead to competitive exclusion.

Several researchers (Connell 1978; Hubbell 1979, 1980; Huston 1979) have proposed a nonequilibrium hypothesis to account for the high species richness of tropical forests. In its usual form, this approach involves some kind of disturbance to the community. The problem for proponents of these explanations is that even with nonequilibrium conditions, competitively inferior species are eventually lost in disturbance models (see especially Hubbell 1980). The loss occurs because

these models calculate the probability that a particular species will colonize a newly open resource as a function of the local abundance of the potential colonist. When species presence is decoupled from the success or failure of propagules, even competitively inferior species can stay in the system. From the explanation of the latitudinal gradient in species richness given above, it should be noted that a mechanism for the continued existence of competitively inferior species already exists. The "rescue effect" of Brown and Kodric-Brown (1977) or the "mass effect" of Shmida and Wilson (1985), coupled with the proximity of narrowly defined source areas (as expected from the Rapoport effect), will allow more species to coexist than will considering the forest patch a closed system.

If tropical communities are more "open" than originally imagined, then a reevaluation of the boundaries of tropical communities must be considered. This reevaluation leads to several testable predictions. The sensitivity of tropical communities to isolating disturbance (i.e., the creation of habitat islands) should be higher than that of similar temperate or polar systems. A substantially larger fraction of the species in tropical communities should be very rare, and, of those species, a smaller proportion should be "globally rare" (i.e., rare in all parts of their distribution) than in other latitudes. Each of these predictions is based on the idea that many of the species in tropical communities are not locally self-sustaining but are maintained as rare populations through continued immigration from areas where they are successful.

CLARIFICATION

There are several pitfalls I have encountered in trying to present the ideas in this paper. Generally, these problems arise because an attempt is made to use the latitudinal gradient in species richness to explain Rapoport's rule instead of the reverse. There is no way to determine cause and effect here except to try it both ways and look for logical inconsistencies. At the outset, both competition and differences in stability seem to give promise of explaining Rapoport's rule, but ultimately neither explanation is satisfactory.

The existence of Rapoport's rule should not be taken as an indication that competition forces species to specialize in a way that reduces the size of their geographical range. Anderson and Koopman (1981) expanded upon Rosenzweig's (1975) suggestion that competition influences the size of an organism's geographical range, but they were unable to show that a correlation between species richness of the local community and the size of the geographical range of the interacting species was a general phenomenon. Even though it is difficult to separate the species richness of the community from latitude, Rapoport's rule should not automatically be given a competitive interpretation. Given the large number of species encountered by an organism with a large geographical range, it is unlikely that conditions in just one of the communities of which it is a part will strongly influence the evolution of the suite of traits that determine its geographical range (Janzen 1985).

Rapoport's rule also does not depend on differences in the stability of the habitats at different latitudes. It may seem that the variability in climatic condi-

tions is just another way of measuring environmental stability, but this is not my intent. Rapoport's rule tells us little about the degree of specialization expected among organisms interacting through a diverse resource base. The climate axis of the resource hypervolume itself is narrower in low latitudes, but the relative widths of exploitation of that axis by particular organisms are not. I do not predict how organisms will divide up the available resources.

SUMMARY

The latitudinal gradient in species richness is paralleled by a latitudinal gradient in geographical-range size called Rapoport's rule. It is suggested that the greater annual range of climatic conditions to which individuals in high-latitude environments are exposed relative to what low-latitude organisms face has favored the evolution of broad climatic tolerances in high-latitude species. This broad tolerance of individuals from high latitudes has led to wider latitudinal extent in the geographical range of high-latitude species than of lower-latitude species.

The existence of Rapoport's rule suggests yet another way of looking at the latitudinal gradient in species richness. If low-latitude species typically have narrower environmental tolerances than high-latitude species, then equal dispersal abilities in the two groups would place more tropical organisms out of their preferred habitat than higher-latitude species out of their preferred habitat. It is hypothesized that a larger number of "accidentals" (i.e., species that are poorly suited for the habitat) occur in tropical assemblages. The constant input of these accidentals artificially inflates species numbers and inhibits competitive exclusion.

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