SCIENCE

Geographical Trends in Numbers of Species

Jos. J. Schall and Eric R. Pianka

Biotic communities differ dramatically in the numbers of plant and animal species they support. Moreover, taxonomic composition of communities varies considerably from place to place. These obvious, pervasive, and yet extremely perplexing phenomena are among the most

logitudinal effects (4-14). Wallace's speculative explanations for geographic patterns in species density are still echoed by modern hypotheses that generally invoke any or all of the following: historical factors (such as glaciation, ecosystem age, landform proximities),

been applied to various taxa in North America, South America, southern Europe, and Australia (5-12, 14). However, no detailed comparisons have yet been made between continents; moreover, trends among taxa have seldom been compared (but see 6, 8, 12, 14).

Tabulation of species numbers at relatively few, widely scattered points on the earth's surface has produced illuminating broad comparisons of trophic levels in vertebrates (17), avifaunal composition among biotic regions (19), and worldwide latitudinal trends in species richness of several taxa (13). In this article, we exploit the more precise quadrate technique to pursue an understanding of abiotic factors involved in geographic trends in numbers of species of American and Australian vertebrates. Inverse correlations between species numbers of different taxa, termed taxonomic complementarity (6-8, 20), are also examined; these could result from competition between higher taxa or simply from different physiological responses to environmental gradients (or both). We ask the following questions: Are geographic patterns in species richness repeated among taxa and between continents? Do various animal groups respond to geographic variation in environmental factors in the same ways in independently evolved faunas? Are trends in taxonomic complementarity repeated? Our results reveal interesting general patterns as well as some intriguing differences between continents. These patterns, not described or quantified before, are not obvious from single local site studies of many taxa or from multiple site studies of one taxon.

Summary. Geographic variation in the number of coexisting plant and animal species (species density) often follows repeated patterns; best known is the general increase in species richness from temperate to tropical latitudes. Here we undertake a quantitative analysis of geographic trends in species density for the terrestrial vertebrate faunas of the United States and Australia. Trends in numbers of species of amphibians, reptiles, birds, and mammals are described and are correlated with geographic variation in abiotic environmental measures. Intercontinental comparisons reveal general patterns as well as intriguing and profound differences in vertebrate distributions.

basic problems confronting evolutionary ecologists (1). Repeated patterns in numbers of species, variously referred to as "species richness" or "species density" (2), suggest that general explanations for such trends are possible.

A hundred years ago Alfred Wallace, codiscoverer with Darwin of natural selection, in a classic work on tropical biology (3), discussed the now much celebrated gradient of increasing species richness toward lower latitudes. Other observed trends in species numbers involve altitude, topographic relief, island size and location, peninsular effects, proximity to oceans, and even obscure

abiotic environmental factors (including climatic stability and predictability), or biological interactions among species within communities (especially competition and predation). Possible subtle and complex interactions among these various factors pervade current thinking on the subject (4, 15-17); a major challenge to modern ecology is to devise tests that will delimit each factor's importance.

A straightforward, yet extremely productive, method of studying patterns of species richness was developed by Simpson (5) and Terent'ev (9), who partitioned a map of a large landform into equal-sized quadrates and used range maps of individual species to estimate the numbers of species occurring at different areas (18). As reliable range maps have become available this method has

Techniques

We divided the contiguous 48 states of continental United States into 895 quadrates, each 1° of latitude by 1° of longitude (about 10,500 square kilometers). Distributions of 98 lizard species were superimposed on this grid and summed to obtain lizard species numbers per quadrate (21). Breeding distributions of 235 species of insectivorous birds judged to be possible competitors (22) with liz-

Dr. Schall is a National Institutes of Health research fellow in the Department of Zoology, University of California, Berkeley 94720. Dr. Pianka is a professor in the Department of Zoology, University of Texas, Austin 78712.

Table 1. Stepwise regression with the use of lizard or bird species density as the dependent variable and 11 environmental measures as independent variables. Variables are listed in order of their contribution to reduction in residual variance in species numbers.

Step	Variable	P	Multiple r^2	Simple r
		Lizards		
1	Sun	<.0001	.665	.816
2	Temp	<.0001	.803	.702
3	SumTemp	<.0001	.810	.557
4	Relief	<.0001	.814	.156
5	SWPpt	<.0001	.817	.033
6	J-JDiff	<.001	.819	−.485
7	Ppt	<.001	.821	−.129
			$\bar{X}$ = 6.6 species per quadrate	
		Birds		
1	Lo	<.0001	.216	−.465
2	Temp	<.0001	.299	.439
3	Ppt	<.0001	.314	.428
4	J-JDiff	<.0001	.325	−.252
5	Sun	<.001	.334	−.002
6	FF	<.001	.344	.344
			$\bar{X}$ = 84.7 species per quadrate	

Table 2. Correlations among the five climatic variables. North America above and Australia below the diagonal. Fisher transformation 99 percent confidence intervals on r's overlap broadly in all ten intercontinental comparisons.

	Annual temperature	Annual precipitation	Coefficient of variation precipitation	Hours of sunshine	Frost-free days
Annual temperature		.37	.24	.51	.87
Annual precipitation	.31		−.59	−.47	.40
Coefficient of variation in precipitation	.07	−.63		.77	.15
Hours of sunshine	.29	−.67	.70		.36
Frost-free days	.84	.26	.09	.19	

ards were similarly plotted and totaled (23).

Eleven abiotic environmental measures were determined for each square (abbreviations in parentheses): Highest (Hi) and lowest (Lo) elevation, topographic relief (Relief), sunfall (Sun), average annual precipitation (Ppt), annual temperature (Temp), summer temperatures (SumTemp), frost-free days per year (FF) (an estimate of growing season length), difference between normal January and July temperatures (J-J Diff), differences between summer and winter precipitation (SWPpt), and actual evapotranspiration (Evap) (24). These variables measure some of the factors often suggested as being involved in species density patterns (productivity, climatic variability, diversity of habitats). Stepwise regression ordered environmental variables by the extent to which they reduce residual variance in species numbers.

Because Australian vertebrate distributions are known much less precisely than those of the United States, we partitioned Australia into larger squares, approximately 240 km on a side (about 57,500 km²). To facilitate intercontinental comparisons, the United States was similarly divided in a second analysis. On both continents species densities of amphibians, reptiles, land birds, and mammals (marsupials only in Australia) (25, 26) were computed (27). Five identical climatic measures available for both continents were examined: annual hours of sunshine, mean annual temperature, average annual precipitation, average number of frost-free days, and coefficient of variation of annual precipitation (CV) (28).

Use of smaller quadrates in the first American analysis results in greater precision, especially in construction of maps presented and discussed below. However, broad patterns emerging from our analysis are very similar whether we used small or large quadrates (below). Thus, our results are unlikely to be altered by further refinements in taxonomy or known distributions of terrestrial vertebrates (29).

Geographic Trends in The United States

The western United States, as compared to the eastern portion, is generally drier, sunnier, and topographically higher and more complex. The south is
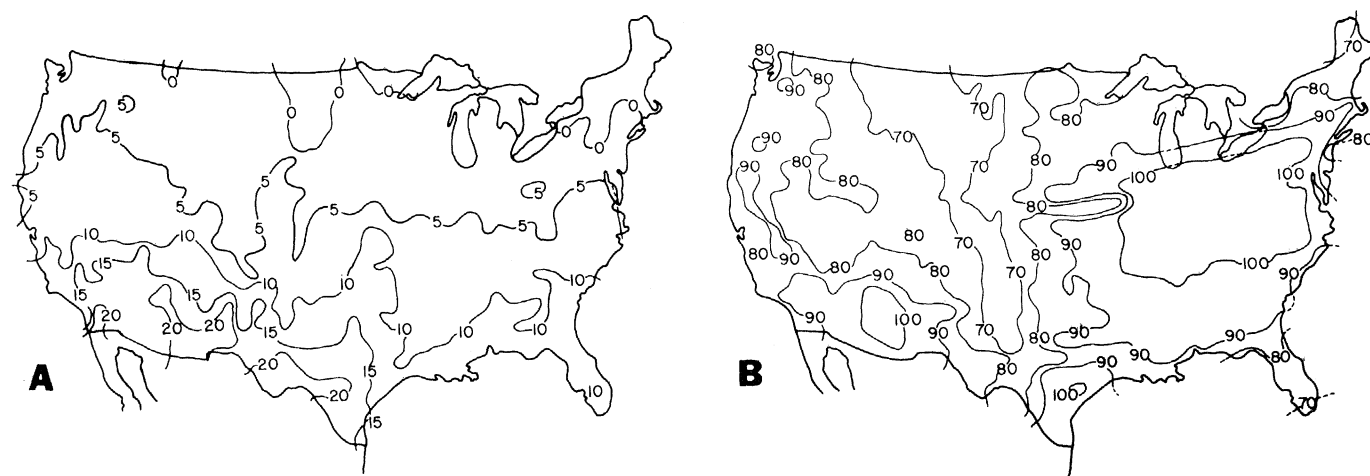

Fig. 1. Species densities of lizards (A) and insectivorous birds (B) in the United States.
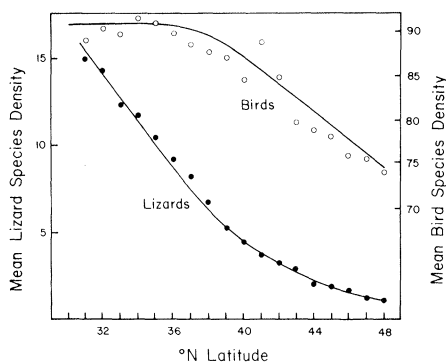
Fig. 2. Mean species density by latitude for U.S. lizards and insectivorous birds.

warmer, sunnier, and has a longer growing season, with less pronounced seasonal temperature changes, as compared to the north (30). Lizard species numbers in the United States are highest in the arid, topographically diverse Southwest but are depressed in the Rocky Mountains (Fig. 1A). Geographic patterns in species density of insectivorous birds differ from those of lizards (Fig. 1B). Highest species richness is generally at low elevation, and in wet, cool zones—conditions such as those in the mid-Atlantic states. However, a second smaller species-rich area exists in the arid, hot southwestern Sonoran desert (31). Although both lizard and bird species numbers are high in the desert Southwest, overall differences in geographic trends (Fig. 1) result in densities of lizard and bird species being only weakly correlated ($r = .28$; $P < .01$).

Latitudinal trends in the mean number of species (32) of U.S. lizards and insectivorous birds also differ (Fig. 2). From 31° to 48°N, numbers of species of both lizards and birds decrease by about 15 species although this represents a 14.4-fold decrease for lizards and only a 1.2-fold decrease for birds. Further, the density of bird species decreases less regularly than that of lizard species and, unlike the trend for lizards, levels off toward the south (33).

These results suggest that species densities of lizards and insectivorous birds correlate with, and perhaps depend on, different environmental factors. Stepwise regression confirms this, in part (Table 1). Fully 82 percent of the variance in lizard species numbers is accounted for by seven variables, 67 percent by sunfall alone. In sharp contrast, total variance in bird species numbers is reduced only 34 percent by all six significant variables and only 22 percent by the first variable, lowest elevation. The bird data fit a linear model poorly: insectivorous bird species density is pronouncedly bimodal, with high richness in both

cool-wet and hot-dry zones. Thus, compared to lizards, birds have radiated into a greater range of habitats and, as a group, appear less restricted by abiotic factors (34).

Wallace and many later biogeographers have proposed that tropical areas support more species than temperate zones simply because they have not been glaciated and are thus ecologically older (3, 16). Although evidence is very scant, under this interpretation the observed high tropical diversity is a result of long-term undisturbed speciation. If so, the latitudinal trend in species numbers is partially attributable to a strictly geographic factor (latitude). When environmental variables are held constant by partial correlation (r_p), lizard species density is still weakly, though significantly, negatively correlated with latitude ($r_p = -.35$; $P < .01$), whereas birds are not so correlated ($r_p = -.07$). Latitude enters the stepwise regression as the fourth most important variable in the lizard analysis but does not significantly reduce variance in the density of bird species.

Sharp increases in species density from coastal to nearby inland areas have been noted in earlier studies (5, 6). However, this phenomenon could be a spurious result of the species-area effect; the area of large coastal quadrates contain much water. If we compare a series of 1° by 1° all-land coastal quadrates along Pacific, Atlantic, and Gulf coasts with similar all-land quadrates immediately inland, both lizard and insectivorous bird species densities generally increase moving inland (zero to four species for lizards and zero to nine species for birds; all comparisons, except for Atlantic Coast lizards, are significant; Wilcoxon tests, P is $< .01$). The origin of this ap-

Table 3. Approximate total number of species of various vertebrate taxa in Australia and the contiguous 48 United States. [Sources (5, 12, 21, 23, 25, 27)]

Animals	Australia	United States
Birds	650	620
Mammals	224	296
Lizards	351	99
Snakes	101	104
Turtles	16	50
Frogs	133	53
Toads	1*	23
Salamanders	0	96
Vertebrates	1476	1341
Area (10^6 km²)	7.69	7.83

*Introduced.

parent phenomenon may involve climatic or topographic gradients (Table 1), insect density, or recolonization rates from source areas still farther inland.

Comparison with Australia

Latitudes of the United States and Australia overlap by only 14° (Fig. 3), and the environments of the two continents differ in striking ways. Australia has experienced negligible glaciation, is at lower latitudes than the United States, is much flatter topographically, has much more desert and semiarid areas, and has a sharper geographical precipitation gradient. Australian rainfall is greatest along the coasts; high and low latitudes have more coastline and hence the average precipitation there is greater. Average Sun, CV, Temp, and FF are higher and Ppt is lower in Australia compared to the United States (t'-tests, all $P < .001$). Nonetheless, similarities exist. Intercorrelations among five environmental variables are virtually the same
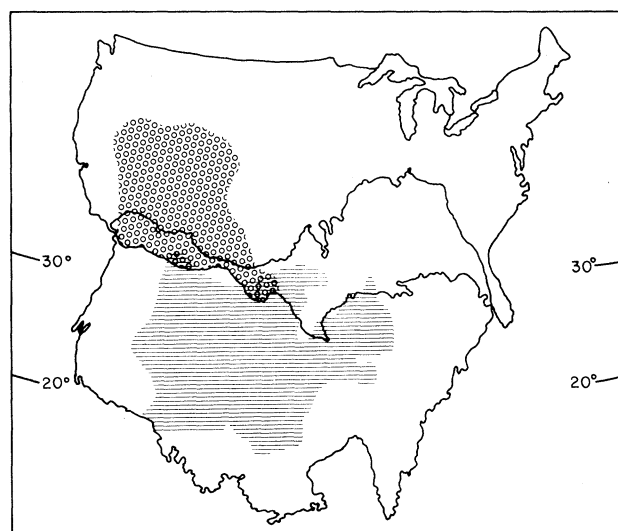

Fig. 3. Equal area projections of Australia and the United States superimposed. Latitudes and west coasts are aligned and approximate distributions of deserts are indicated by stippling.
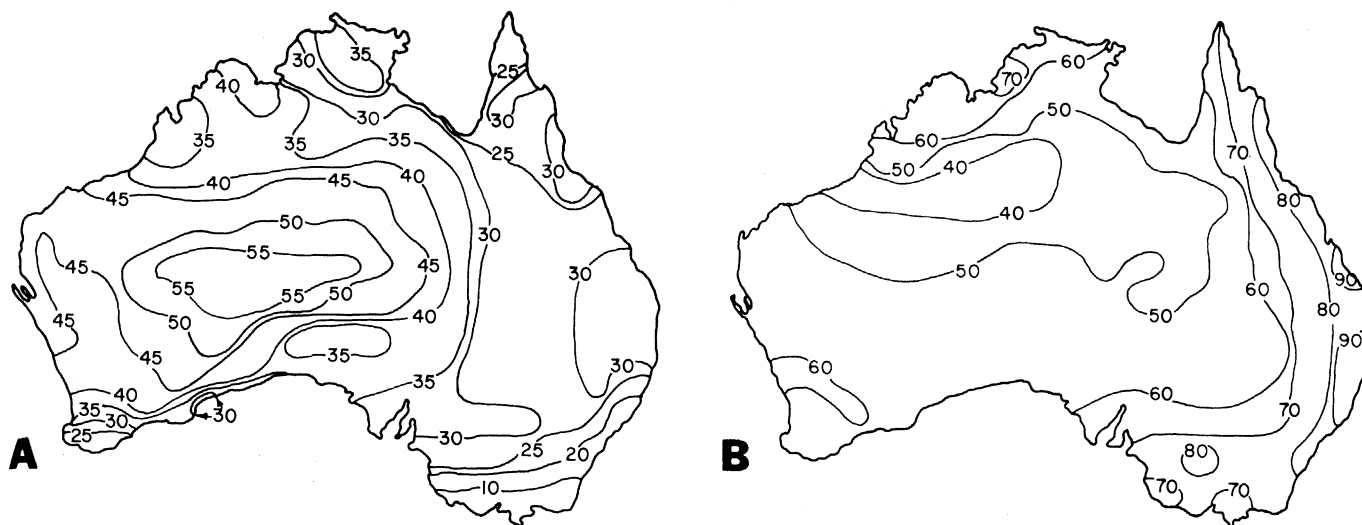
Fig. 4. (A) Species densities of nonskink lizards (36) in Australia. (B) Species densities of insectivorous birds in Australia.

between North America and Australia (Table 2). Thus, across an environmental gradient in any variable, the other four variables change in similar ways on both continents.

We have presented maps (12) of species richness and plots of mean species density by latitude for Australian vertebrate taxa. Figures 4 and 5 are analogous to Figs. 1 and 2 for North America. Monotonically increasing latitudinal gradients in species densities toward lower latitudes, often heralded by investigators (16), are neatly demonstrable in the United States; mean species densities of most vertebrate taxa are tightly correlated with latitude (35). However, such

trends are practically nonexistent among Australian terrestrial vertebrates (12) (Figs. 4 and 5). Distinct latitudinal patterns in species densities presumably are related to trends in annual rainfall described above. Nonscincid lizards (12, 36) are most diverse in the dry interior deserts, whereas there are more species of most avian groups, skinks (36), and amphibians in wet coastal regions. Patterns of species richness of Australian lizards somewhat resemble those of North American birds, with zones of high diversity in both arid and mesic habitats. Other vertebrate groups have either relatively constant mean species densities over the latitudinal gradient

(for example, snakes and turtles) or are actually most diverse in the temperate south (marsupials).

To determine whether vertebrate groups are more diverse in the wet Australian tropics than in wet temperate regions, we compared the two regions but found no consistent trend in numbers of species (12). The tropics support as many species of amphibians, birds, and lizards as the temperate zone, whereas other reptiles are more diverse in the tropics and marsupials are actually richer in the temperate region. This is surprising in view of the large source area of tropical vertebrate species to the north of Australia but lack of a similar temperate source area in the south. Also, within the past million years, Australia has been more mesic and heavily vegetated (37, 38).

Although greater species richness at lower latitudes is often considered a general, worldwide rule (13, 16), the lack of such latitudinal trends such as described here for Australian vertebrates may actually be fairly common (11–13). Lack of clear-cut temperate-tropical trends warrants further scrutiny, and such "exceptions to the rule" merit a greater role in theoretical speculations on Wallace's phenomenon (39).

In terms of total numbers of species, the faunas of the United States and Australia are remarkably similar for birds, mammals, and snakes (Table 3). Turtles and amphibians are more diverse in the United States, whereas there are 3.5 times as many species of lizards in Australia. Are there more species of lizards in Australia simply because there is much more desert on that continent? In an attempt to answer this question, we compared selected quadrates with crude-

Table 4. Correlations between species density of various vertebrate taxa and five climatic measures for Australia (A) and the United States (U.S.). Order in which variables were entered into the stepwise regression (in parentheses) and cumulative r^2 (Cum r^2) also given. Fisher transformation 99 percent confidence intervals on r's do not overlap in 25 of the 45 intercontinental comparisons (indicated with boldface type).

Area	Animals	Sun	Ppt	CV	FF	Temp	Cum r^2
U.S.	Frogs	−.30 (4)	.80 (1)	−.49 (3)	**.49** (5)	**.52** (2)	.753
A	Frogs	−.56 (5)	.73 (1)	−.44 (3)	−**.10** (2)	**.04** (4)	.648
U.S.	Reptiles	.34 (3)	.37 (4)	.15 (2)	**.72** (5)	**.86** (1)	.774
A	Reptiles	.24 (5)	.02 (4)	.21 (2)	**.18** (3)	**.30** (1)	.163
U.S.	Lizards	**.74** (1)	−.25 (3)	.66 (4)	**.56** (5)	**.71** (2)	.836
A	Lizards	**.44** (1)	−.37 (3)	.40 (2)	**.04** (5)	**.09** (4)	.222
U.S.	Turtles	−.20 (4)	.73 (1)	−.34 (3)	.55 (5)	.60 (2)	.675
A	Turtles	−.45 (4)	.77 (1)	−.45 (5)	.20 (3)	.30 (2)	.621
U.S.	Snakes	.22 (3)	.46 (4)	−.002 (2)	**.65** (5)	**.78** (1)	.692
A	Snakes	−.18 (2)	.57 (1)	−.18 (3)	**.28** (5)	**.43** (4)	.449
U.S.	All birds	**.19** (4)	−**.70** (1)	**.34** (3)	−**.50** (5)	−**.54** (2)	.605
A	All birds	−**.63** (5)	**.69** (1)	−**.43** (3)	**.11** (4)	−**.07** (2)	.594
U.S.	Insectivorous birds	**.15** (4)	.25 (3)	.06 (5)	.27 (2)	.45 (1)	.292
A	Insectivorous birds	−**.60** (1)	.57 (2)	−.32 (4)	−**.27** (5)	−**.25** (3)	.600
U.S.	Seed-eating birds	**.12** (4)	−**.71** (1)	**.29** (3)	−**.53** (5)	−**.62** (2)	.682
A	Seed-eating birds	−**.48** (5)	**.80** (1)	−**.43** (2)	**.26** (4)	**.33** (3)	.658
U.S.	Mammals	**.55** (4)	−**.73** (1)	**.63** (2)	−.34 (3)	−.21 (5)	.657
A	Marsupials	−**.67** (1)	**.54** (3)	−**.39** (5)	−.30 (2)	−.33 (4)	.604

ly comparable climatic conditions on both continents, including both arid and mesic areas (12). In 15 such matched pairs of quadrates, the number of species of lizards is consistently higher in Australia than in the United States (mean = 3.1 times, range 2.0 to 5.8 times). Ground-level studies in the Australian desert have demonstrated that four times as many lizard species coexist on areas as in North America (38, 40). Lizards in North America are ecologically more homogeneous than those in Australia. Australian lizards occupy a broad range of niches, having usurped the ecological roles of some North American mammals, snakes, and perhaps arthropods (38). For example, in the great central deserts, large intelligent varanid lizards are important tertiary predators, a role filled by carnivorous mammals in North America (41).

In the same 15 pairs of climatically matched quadrates, insectivorous birds average 1.6 times as many species in the United States as in Australia (range 1.2 to 2.2). Similarly, species numbers of turtles are consistently lower in Australia than in the United States. This is expected considering the overall greater number of turtles in the United States (Table 3). However, snakes are equally diverse on the two continents (about 100 species), but average 1.6 times as many species in the matched quadrates in the United States than in Australia. In all quadrates, snake species density is significantly greater in the United States (t'-test, P < .005). Both continents also have similar numbers of mammal species but mean species density in all quadrates of marsupials (which make up about half of Australian mammal species) is only a seventh that of American placentals. Thus, compared to those in the United States, Australian snakes and mammals seem to have smaller average geographic ranges and these ranges may overlap less (42).
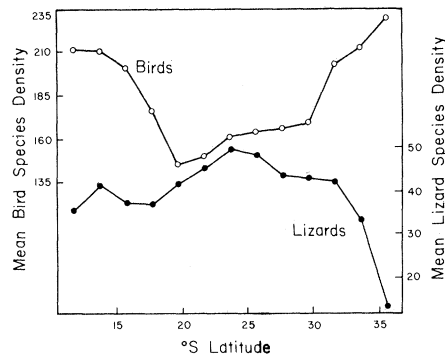

Fig. 5. Mean species density by latitude for Australian lizards and birds (all species).

Correlations between species richness of various taxa and identical environmental measures on the two continents reveal intriguing patterns (Table 4). Because Australian lizards and American insectivorous birds have large components of both xeric-adapted and mesic woodland species, they do not fit a linear multiple-regression model. For example, cumulative reduction in variance (r^2) in species numbers of the Australian lizard fauna is only 22 percent compared to 84 percent in the U.S. fauna. Since most (75 percent) Australian reptile species are lizards, cumulative r^2 for the Australian reptile species density analysis is also low compared to that for the U.S. analysis. Despite these differences, U.S. and Australian reptiles, lizards, and turtles are alike in that correlations have similar signs, and variables are entered into regression equations in approximately parallel order. Thus, the same abiotic environmental factors may well have influenced present diversity of reptile species on the two continents.

Results, however, for mammals and all birds differ between continents. Densities of American mammal species showed negative correlation with precipitation but positive correlation with hours of sunshine, whereas densities for Australian marsupials show the opposite

trend. The American desert and semi-desert support a rich assemblage of mammalian species; but mammals, both marsupials and placentals, are conspicuously depauperate in the Australian deserts (26). Species numbers of the total Australian avifauna correlate positively with average annual precipitation, whereas the total number of U.S. birds varies inversely with precipitation. Nevertheless, the five climatic variables enter into multiple regressions in nearly the same order and reduce overall variance in species density by similar amounts. North American seed-eating birds are more diverse in relatively drier environments, whereas species density of insectivorous birds is positively correlated with precipitation (Tables 1 and 4). In contrast, numbers of species of seed-eating and insectivorous birds in Australia show positive correlation with all five climatic measures in similar ways. Thus, Table 4 shows that, of 45 United States–Australia pairs of correlation coefficients, 99 percent confidence intervals on 25 pairs do not overlap.

Taxonomic Complementarity

Most field studies of competition deal with the examination of systems of closely related species. However, interest in possible competition between higher taxa has been growing (43). Negative correlations between species densities of two taxa, or taxonomic complementarity, may reflect ongoing competition or historical displacement (or both). For example, species densities of North American reptiles show negative correlation with those of bird species (44) (see Table 5); nevertheless the most likely competitors among reptiles and birds—that is, lizards and insectivorous birds—correlate weakly and positively. What is the origin of this anomaly?

Table 5. Correlations among species densities of various vertebrate taxa. North America above and Australia below the diagonal. Fisher transformation 99 percent confidence intervals on r's do not overlap in 24 of the 36 intercontinental comparisons (these are indicated with boldface type).

Animals	Frogs	Reptiles	Lizards	Turtles	Snakes	Birds All	Birds Insectivorous	Birds Seed-eating	Mammals or marsupials
Frogs		**.61**	−.002	.81	.69	**−.74**	.34	**−.77**	**−.65**
Reptiles	**.19**		**.68**	.76	**.96**	**−.60**	**.56**	**−.71**	−.06
Lizards	−.23	**.85**		.11	**.50**	−.02	.38	−.14	**.40**
Turtles	.80	.29	−.20		.80	**−.80**	.42	**−.85**	**−.65**
Snakes	.67	**.59**	.09	.79		**−.65**	.54	**−.75**	**−.30**
All birds	**.83**	.08	−.32	.76	.60		**−.18**	**.95**	.70
Insectivorous birds	**.77**	.15	**−.19**	.65	.56	**.93**		−.47	**.05**
Seed-eating birds	**.78**	.15	−.30	**.79**	**.71**	**.84**	.76		.61
Mammals or marsupials	**.71**	.05	**−.19**	**.44**	**.37**	.72	**.76**	.60	

A Non-Lizard Reptile Species

r = -.657

B Turtle Species

r = -.735

C Snake Species

r = -.578

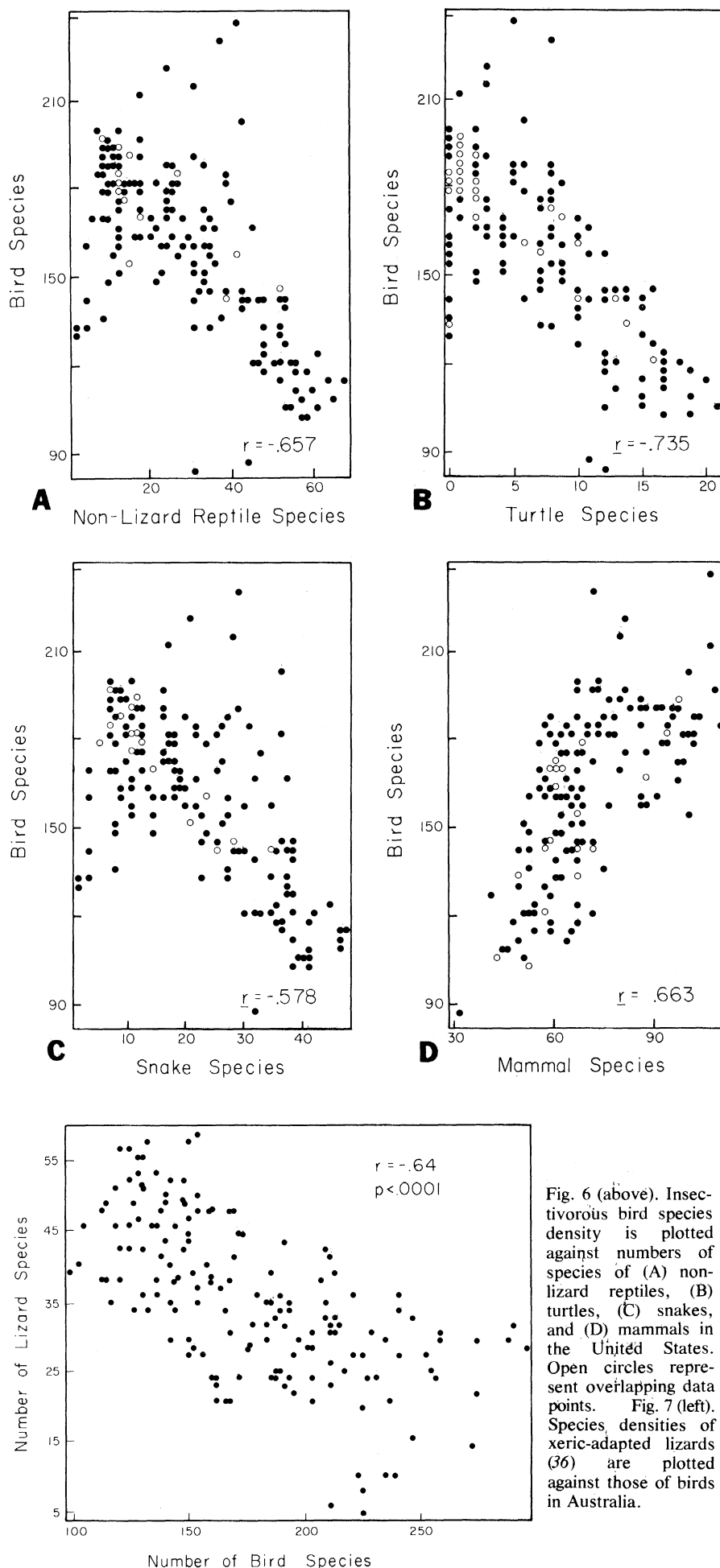**D** Mammal Species

r = .663

r = -.64
p<.0001

Fig. 6 (above). Insectivorous bird species density is plotted against numbers of species of (A) non-lizard reptiles, (B) turtles, (C) snakes, and (D) mammals in the United States. Open circles represent overlapping data points. Fig. 7 (left). Species densities of xeric-adapted lizards (36) are plotted against those of birds in Australia.

Partitioning reptile species numbers into those for lizards, turtles, and snakes (Table 5) demonstrates that total bird species density is not correlated with lizard species number, but species densities of birds do vary inversely with those of reptiles other than lizards (Fig. 6). In general, turtles and snakes are unlikely to compete with birds for foods or any other conceivable resource. In the United States, species numbers of lizards, seed-eating birds, and all birds correlate negatively with precipitation whereas species densities of turtles, snakes, and insectivorous birds all correlate positively with precipitation (Table 4).

Thus, inverse correlations between species densities should not be taken as unequivocal evidence for or against intertaxa competition. Various taxa may have simply diversified in habitats favoring their particular morphological and physiological plan. Likewise, random historical factors may play an important role. Species densities of frogs are much greater in Australia than in the United States, whereas salamanders are diverse in North America but absent in Australia (Table 3). Although anurans and salamanders may compete as larvae in small ponds (45), species densities of U.S. salamanders and frogs are actually positively correlated ($r = .80$). The richness of the Australian frog fauna undoubtedly has little to do with the absence of salamanders on that continent.

Correlations of species numbers among taxa for the United States and Australia are compared in Table 5: the matrix is notably asymmetric with correlation values and even signs differing (two-thirds of them differ significantly at the 99 percent level). For example, insectivorous birds and seed-eating bird species densities are similarly correlated with other taxa in Australia, but the two groups differ in North America. Also, bird and lizard species densities, unlike the positive correlation for these taxa in the United States, are weakly negatively correlated in Australia. When skinks (36) are excluded, the number of xeric-adapted lizard species is much more strongly negatively correlated with bird species density (Fig. 7).

Community Convergence

Notions that the structure of entire biotic communities may converge in similar but geographically distinct environments have become popular (46). Occasionally, pairs of species in such communities are apparent ecological equiva-

lents, and very rarely such pairs may be morphologically almost indistinguishable (47). However, considerable evidence, both empirical and theoretical, argues against the existence of convergence of entire communities (48). A major unsolved problem in evolutionary ecology is in predicting the degree of similarity expected in the structure of possible convergent communities. That is, how can we recognize convergence at the community level? Clearly, Australian and American vertebrate faunas are, in the broadest sense, similar. Both have frog, bird, lizard, snake, turtle, and mammal species, and species numbers of these taxa are similar on the two similarly sized continents (Table 3). In fact, even taxa with great disparity in species numbers (lizards, frogs) could be used as evidence for convergence because the difference in species density between continents is much less than even an order of magnitude.

However, despite similarities between the two continents in the total number of species, land area (Table 3), climate (Table 2), and latitude (Fig. 3), our results (Tables 4 and 5) demonstrate profound ecological differences between terrestrial vertebrate faunas of the United States and Australia. Morton (26) also documents major differences in the organization of desert mammalian communities on the two continents.

Ectothermy Versus Endothermy

Despite differences between continents noted above, one trend appears consistent. On both continents, lizards have diversified most in hot arid desert regions and birds tend to be more diverse in cool, wetter zones. Endothermic birds maintain thermal homeostasis by costly metabolic mechanisms; fully 80 to 90 percent of incoming energy is consumed by thermal homeostatic processes (49). Ectothermic lizards, however, rely on external heat sources and behaviorally regulate body temperatures by shuttling, basking, and posturing (50, 51). Compared to birds, lizard activity times are relatively constrained by ambient thermal conditons, but metabolic savings of ectothermy allow a much greater proportion of food energy to be utilized for growth and reproduction (52).

Activity periods for thermophilic lizards in sunny, warm places would be longer and, probably of more importance, they would be more predictable than those in cooler and less sunny areas. In times and environments where thermoregulation has high costs, lizards

reduce or even abandon thermoregulation (51). In sunny, warm environments lizards can maintain high optimal body temperatures for long periods inexpensively, facilitating specialization on particular microhabitat and food resources. Thus, ease of thermoregulation may partially account for lizard diversity in sunny, warm zones (53).

Likewise, deserts generally have low, unpredictable productivity and periodically extremely hot and dry conditions. The saurian tactic under harsh conditions is to reduce or eliminate dietary requirements by lowering body temperatures, usually through entering deep burrows. In fact, a major advantage of ectothermy is this ability to reduce metabolic processes when their maintenance would lower lifetime reproductive success (54). Under harsh desert conditions the lizard tactic may well be at an advantage over that of birds which must weather out unfavorable periods at considerably higher metabolic cost (55).

Conclusions

During the century that has elapsed since Wallace (3) first focused attention on geographical patterns in numbers of species, distributions of many species have been mapped precisely enough to allow quantitative analysis of geographic trends. Here we undertake such an analysis for the terrestrial vertebrate faunas of the United States and Australia (about 2500 species). Trends in numbers of species are correlated with geographic variation in climatic measures. Species densities of vertebrates in North America increase toward lower latitudes; those of Australian vertebrates generally do not. Correlations between species densities and abiotic environmental factors for birds and mammals differ on the two continents: correlations are often opposite in sign.

On both continents, lizards have diversified most in arid sunny regions, probably partially because costs of thermoregulation are low for ectotherms in such environments. Moreover, the ability to become inactive during periods of stress confers ectotherms with an advantage over endotherms in unpredictable desert environments. Lizards in North America are less diverse ecologically than those in Australia, and species densities are much lower in North America. Correlations among taxa in numbers of species differ between the two continents. Despite some biological and environmental similarities between the continents, ecological differences be-

tween terrestrial vertebrate faunas of the United States and Australia are profound.

As reliable range maps become available for these and other taxa from other parts of the world, extension of this sort of analysis should allow us to gain further insights into the complexity of interactions that determine global patterns in species richness.

References and Notes

1. Factors influencing geographical variation in numbers of species are actually included in a more general problem in biology: Why are there so many species [G. E. Hutchinson, *Am. Nat.* **93**, 145 (1959)]? This question is fundamental in evolutionary biology.
2. Species diversity includes the relative abundance of each species as well as number of species. Diversity and species density are usually strongly correlated [E. J. Tramer, *Ecology* **50**, 927 (1969); and see (44)].
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18. This analytical technique combines both the within- and between-habitat components of species richness [R. H. MacArthur, *Biol. Rev.* **40**, 510 (1965)]. As an analogy, the quadrate method presents an aerial overview whereas field ecology provides a ground-level view of biotic communities.
19. M. R. Lein, *Syst. Zool.* **21**, 135 (1972).
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21. Range maps used here for all taxa are smoothed, best fit, approximations derived from spot maps of actual collection data. Error sources in using such maps have been discussed (6). Reptile range maps are from R. Conant [*A Field Guide to the Reptiles and Amphibians* (Houghton Mifflin, Boston, ed 2, 1975)], R. Stebbins [*A Field Guide to Western Reptiles and Amphibians* (Houghton Mifflin, Boston, 1966)], and our own unpublished observations. Reptile distributions are rather well known in the United States, and their movements are restricted; estimates of species densities are therefore quite reliable.
22. "Possible competitors" are insectivorous land birds feeding on the ground or from the surface of vegetation, excluding, for example, raptors, woodpeckers, swallows, and most sparrows. Many species classed here as "seed eaters" also consume insects although they are most efficient at granivory (19), and patterns of their species richness follow different trends than do those of insectivorous birds.
23. Considering avian mobility, bird distributions can be only approximations. Our sources, however, are among the best and most recent available [C. S. Robbins, B. Brown, H. S. Zim, A.

Singer, *A Guide to Field Identification, Birds of North America* (Golden, New York, 1966); C. S. Robbins and W. T. VanVelzen, "Breeding bird survey 1967 and 1968," special scientific report 124 (Bureau of Sport Fisheries and Wildlife, Department of the Interior, Washington, D.C., 1969); R. T. Peterson, *A Field Guide to the Birds* and *A Field Guide to Western Birds* (Houghton Mifflin, Boston, 1947 and 1961, respectively); H. C. Oberholser and E. B. Kincaid, Jr., *The Bird Life of Texas* (Univ. of Texas Press, Austin, 1974)].

24. The highest and lowest elevation (Hi and Lo) are taken from U.S. Geological Survey 1:250,000 topographic maps by J. Mulvihill where the topographical relief (Relief) is estimated as Hi minus Lo. The sunfall in kilocalories per square centimeter per year is taken from H. E. Landsberg, H. Lippman, H. Paffen, C. Troll [*World Maps of Climatology* (Springer-Verlag, Berlin, 1963)]; the annual average precipitation is taken from the U.S. Department of Agriculture [*Climate and Man* (Government Printing Office, Washington, D.C., 1941)], and other measures are from S. S. Visher [*Climatic Atlas of the United States* (Harvard Univ. Press, Cambridge, Mass., 1966)]. Error estimates for these measures are not available, except for Hi and Lo which were further measured for 41 random quadrates, allowing comparison between these and previous measures. Error was estimated as 4 to 8 percent.

25. Very little has been published concerning the number of species and the distributions of Australian placental mammals. However, areas of highest placental species richness appear to coincide with those for marsupials [W. D. Ride, *A Guide to the Native Mammals of Australia* (Oxford Univ. Press, Melbourne, 1970) and (*26*)].

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28. Australian climatic data from J. Gentilli, *Climates of Australia and New Zealand* (Elsevier, Amsterdam, 1974).

29. For example, Stehli (*13*), using old (about 1889) and recent (about 1960) data, constructed very similar worldwide maps of crocodilian species richness.

30. These generalizations are neatly supported by correlations between environmental measures and latitude and longitude.

31. The difference in distributions between insectivorous birds and lizards is reflected in the correlations between longitude and species density. For birds, $r = -.41$; for lizards, $r = .24$ ($N = 895$). Comparison of taxonomic composition of bird assemblages in cool-wet and hot-dry habitats of high species density would undoubtedly be profitable, but such comparison is beyond the scope of our study.

32. Computed as the mean number of species for all quadrates in a degree of latitude. Because lizard species density increases toward the west and we have no data for northwestern Mexico, we plot species density only as far south as 31°N.

33. Correlations for all 895 quadrates for species density by latitude are $r = -.83$ for lizards and $r = -.45$ for birds.

34. W. P. Porter and D. M. Gates, *Ecol. Monogr.* **39**, 227 (1969).

35. Lizard, snake, turtle, amphibian, and bird mean species densities are highly correlated with latitude in the United States (for lizards, $r = -.98$; for snakes, $r = -.99$; for turtles, $r = -.98$; for amphibians, $r = .99$; and for birds, $r = -.92$); whereas mammals, exclusive of bats are not [J. W. Wilson III, *Evolution* **28**, 124 (1974)].

36. We include the large genus *Ctenotus* with non-scincid lizards because, although *Ctenotus* is taxonomically a skink, ecologically it is a desert-adapted analog of American *Cnemidophorus*. Similarly, when discussing "skinks," *Ctenotus* has been excluded (*12*).

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39. It will be of interest, as distributions of Mexican vertebrates become available, to see whether latitudinal trends differ between the two continents at lower latitudes.

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41. In the geologically recent past, enormous varanids, larger than almost any American Pleistocene carnivore, roamed Australia (E. Lundelius, personal communication).

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55. Darwin, on his *Beagle* voyage, noted that lizards live in the driest and least hospitable portions of the earth [C. Darwin, *The Voyage of the Beagle* (Culburn, London, 1840; reprinted, Natural History Press, Garden City, N.Y., 1962)]. In describing the central deserts of Australia, the mammalogist Finlayson said, "to a very large extent it is a land of lizards" [H. H. Finlayson, *The Red Centre* (Angus & Robertson, London, 1943)].

56. We thank J. Mulvihill and L. Day for assistance in processing data; N. Burley, W. Cade, M. L. Cody, R. Huey, A. R. Kiester, E. Lundelius, and M. Rosenzweig for reading the manuscript and offering useful suggestions for its improvement; K. Jehn and A. Court for advice on climatological literature; C. Sexton for sharing his knowledge of bird habits; and A. Bennett for pointing out important references. R. W. Schall and E. Soderquist executed the figures. Supported largely by NSF grant BMS-74-0231. Final preparation of the manuscript was supported by an NIH postdoctoral grant to J.J.S. We acknowledge the efforts of Australian and American workers who plotted the distributions of vertebrates, for without their contributions this study would have been impossible.