ON LATITUDINAL GRADIENTS IN AVIAN DIVERSITY

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Species diversity patterns exist on at least three geographical scales: (1) the diversity in a sample drawn from a single community, often called within-habitat diversity; (2) the diversity occurring in a collection of similar habitats within a given region, here referred to as between-habitat diversity; and (3) the total diversity to be found in all the available habitats in a fairly large geographical area. Whittaker (1960) has termed these categories alpha, beta, and gamma diversity, respectively.

The tropics contain more bird species than other regions. This statement seems to apply to diversity on all three geographical scales, although there are some exceptions in the case of alpha diversity; i.e., Cody (1966, 1968) has demonstrated that diversity in American grasslands is a function of vegetation structure, with structurally similar grasslands having similar avian diversities at all latitudes. In addition, within-habitat diversity declines with increasing altitude in the tropics, with many montane forests having avian diversities comparable to temperate zone forests (Orians 1969; Diamond 1973). It is not clear whether the decline in complexity of vegetation structure with altitude is sufficient to account for this pattern. Few data have been gathered to test whether beta diversity increases toward the tropics. But since an altitudinal transect conducted by Terborgh (1971) in Peru contained more forest species than the entire eastern United States, it is probable that some sort of between-habitat diversity gradient exists. Comparison of regional treatments such as the A.O.U. Check-list (1957), Edwards (1972), Slud (1964), and Meyer de Schauensee (1964) reveals obvious latitudinal gradients in gamma diversity.

Numerous papers have discussed the gradient in within-habitat (alpha) diversity (e.g., Klopfer and MacArthur 1960, 1961; MacArthur and MacArthur 1961; MacArthur et al. 1966; MacArthur 1969; Orians 1969; Karr 1971; Karr and Roth 1971; Schoener 1971). These studies have stressed such ecological phenomena as vegetation structure, niche overlap, habitat selection, and variation in the abundance and size distribution of food items. A few workers have approached the problem of latitudinal gradients by considering gamma-diversity patterns. Such approaches have usually resulted in hypotheses of an historical nature, stressing more rapid evolution in the tropics, less frequent and/or less rigorous climatic disturbances there, etc. (Dobzhansky 1950; Fischer 1961; Haffer 1969; Cook 1969). MacArthur (1965) has also made the distinction between theories relating to alpha- and gamma-diversity gradients.

There are a number of questions one can ask about these latitudinal diversity gradients. For instance, does diversity increase continuously and linearly from the poles to the equator, or are there plateaus or other slope changes in the pattern? The question is not trivial, since the discovery of differences in the form of the alpha- and gamma-diversity gradients might permit inferences as to the relative contributions of the various latitudinal gradient hypotheses (reviewed by Pianka 1966; MacArthur 1972). In addition, geographical regions where slope changes occur would be of particular interest. One might also ask about the form of diversity gradients during the winter. Previous investigations have dealt primarily with the breeding season, which comprises only 25–35% of the annual cycle for birds nesting in temperate latitudes, and probably little more than that for most species in the tropics (Skutch 1950). If one considers diversity from the standpoint of the community's ability to support coexisting species, then the potential importance of the nonbreeding seasons is readily apparent. Not only are winter gradients themselves worthy of explanation, but the community's ability to support a diverse breeding avifauna may be partially dependent upon the impact of transient and wintering bird populations upon its resources. Of course, local breeding populations must also be affected by mortality rates during migration and on distant wintering grounds.

Cook (1969) examined the gamma-diversity pattern for the North and Mesoamerican avifauna during the breeding season. In this paper I will present and analyze alpha- and gamma-diversity gradients for the North and Mesoamerican avifauna during both the breed-

ing and winter seasons. The implications of these patterns will be discussed, with special reference to unanswered questions in the area of bird-species diversity. Data for the construction of between-habitat diversity gradients are virtually nonexistent, but one possible use for beta-diversity studies will be explored here.

RESULTS

ALPHA DIVERSITY

Many of the breeding-bird censuses used to construct the within-habitat diversity gradient were taken from *American Birds* (1937–71; formerly *Audubon Field Notes* and *Bird Lore*). Other sources were Odum (1950), Johnston and Odum (1956), MacArthur et al. (1966), Grant (1966), Orians (1969), Pearson (1971), Karr (1971), Terborgh (1971), and Thomas Lovejoy (unpubl. data), as well as unpublished censuses conducted by the author in North Carolina (4), Georgia (2), and Panamá (1). Only censuses of forest habitats were used since data from other community types are too scanty for this type of analysis. In addition, census areas more than 2000 ft (613 m) above sea level were also excluded in order to eliminate an altitude effect which might mask the latitudinal gradient.

The censuses were grouped in latitude classes at intervals of 5°, from 50° N southward to the equator. Mean number of species ± 1 SE were calculated within each latitude class.

Numbers of species served as the measure of diversity in each census. Although species-relative abundances are being ignored here, I should point out that the "equitability" component of diversity (Lloyd and Ghelardi 1964) is of great importance because two communities of similar species richness may in fact have very different proportions of abundant, moderately common, and rare species. Thus species frequency distributions can reveal clues about patterns of resource partitioning among the populations sharing a community.

The main reason relative abundance is not considered here is that avian densities have not yet been accurately measured in complex tropical habitats. Tropical forest birds move about more and territorial males are less vocal than temperate-zone birds, and the complexity of vegetation structure makes accurate visual and auditory counts impossible. The studies of Terborgh, Karr, and Lovejoy involved extensive mist-netting, and probably do represent fairly accurate censuses of those species which spend a large proportion of the time
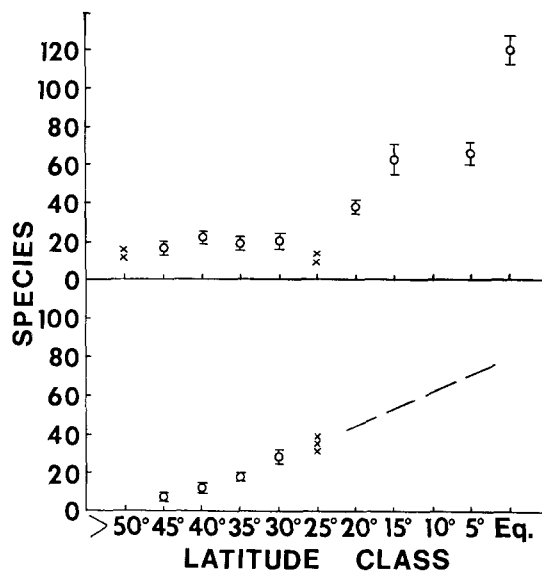

FIGURE 1. The latitudinal gradient in alpha diversity during the breeding (upper) and winter (lower) seasons. The bars encompass one standard error from the mean. Sample sizes in each latitude class range from 7 (at 45° and 20°) to 64 (at 35° during the breeding season). X's refer to single censuses.

within several meters of the ground. In any case, the available data indicate that relative abundance distributions in breeding-bird populations are fairly consistent, at least in the temperate zone (Tramer 1969). The contention that tropical communities have greater "equitability" than temperate communities appears to be largely a subjective impression which still awaits conclusive proof.

The breeding-season gradient is shown in the upper portion of figure 1. From 45° N southward to 25° N, there is no significant change in within-habitat species diversity; within this region variations in alpha diversity result from moisture and edaphic factors which affect vegetation structure (see MacArthur and MacArthur 1961). From 25° N southward, diversity increases all the way to the equator. In other words, within-community diversity does not increase as one approaches the tropics; rather, it increases after the tropics have been reached.

There is an apparent leveling-off between latitudes 15° and 5°; this is probably an artifact caused by plot-size variation since most of the censuses in the 5° latitude sample are of 5-acre (2-ha) plots. Such plots are probably too small to give a good estimate of within-habitat diversity.

Klopfer and MacArthur (1961) suggested that increased morphological similarity among closely related coexisting species accompanied

the increase in alpha diversity among tropical birds, and that this increased similarity could occur only where climatic stability insured the continuous availability of food and suitable habitat. On this basis, they selected "regions of maximum climatic stability" stretching from the lowlands of central México southward to south-central Brazil and predicted that "avifaunal diversity will show *sharp* changes at all points which cross the boundary of this area." The break in the diversity gradient in figure 1 (top) occurs at about 20°, a latitude corresponding very closely to the boundary set by Klopfer and MacArthur.

If diversity is ultimately some function of climatic "stability," one must ask why alpha diversity does not increase with decreasing latitude in the north temperate zone. Apparently some threshold of climatic stability must be attained before alpha diversity will increase. That threshold may be related to the criteria used by Klopfer and MacArthur, namely, no frost, an abundance of rainfall, and a narrow annual temperature range. Just how these climatic factors interact with the biotic community to produce increased diversity is not known, although Karr (1971) suggests that the addition of new food resources (i.e., more fruits and more large insects) may provide the link between climatic "stability" and higher bird-species diversity in lowland tropical forests. If Karr is correct, then it is possible to consider that trends toward "narrower niches" and "more niches" are operating simultaneously in the tropics.

It may be significant that diversity studies have been conducted only in the United States and from Costa Rica southward. No work has been done in the latitudinal range where the break in the within-habitat gradient occurs. Worthwhile contributions to our understanding of diversity gradients might be achieved at this apparent temperate-tropical interface.

Also of interest is the apparent increase in alpha diversity from 20° N to the equator. Are niches narrower among Amazonian forest birds than among the birds of Finca "la Selva," Costa Rica, or Palenque, Chiapas? If so, is this a reflection of historical factors or of some unknown differences in environmental predictability among these areas which are very similar in vegetation structure? Perhaps comparative analyses of feeding behavior, foraging levels, food preferences, population dynamics, and morphological variation among groups of related species in these locales would be instructive in this regard—especially if accompanied by studies of the relative abundance and seasonal availabilty of insects and edible fruits. Such a project would probably constitute a life's work for even the most energetic investigator.

An examination of the winter ranges of North American birds (from the 1957 A.O.U. Check-list) reveals that the number of North American species wintering in equatorial Brazil, Venezuela, and Colombia is somewhat lower than the number wintering in northern Central America and southern México. This presents the interesting possibility that the increase in breeding-bird diversity between 20° N and the equator is related at least partially to a reduction in interspecific competition with migrants from North America during the winter.

Another interesting possibility is that the narrowness of the Central American land bridge has inhibited the movement of Amazonian birds northward into southern México and northwestern Central America. Thus, the isthmus of Panamá may operate as a kind of sieve rather than as a "freeway" for faunal exchange.

There are few winter census data for the tropics, but one can perhaps assume that lowland tropical forests contain similar diversities at all seasons. This is because very few tropical species migrate [the Streaked Flycatcher (*Myiodynastes maculatus*) and the Yellow-green Vireo (*Vireo flavoviridis*) are rare exceptions], and because North American birds wintering in the tropics seem to be numerous only in upland areas and in disturbed habitats (Paul Slud, pers. comm.; Leck 1972). However, little is known about the ecology of North American species on their tropical wintering grounds. Obviously, the presence of millions of additional birds during a portion of the year (the dry season in many areas) must have profound consequences for the resident avifauna.

Winter plot censuses come mainly from the eastern United States. Diversity increases southward through this region (fig. 1, bottom), implying that climatic severity in some way may regulate within-habitat diversity during winter in temperate latitudes.

An analysis of the feeding habits of species listed in winter population studies published since 1964 in *American Birds* (1937–71) allows some inferences about weather phenomena which may contribute to the winter gradient. I classified the land-bird species comprising each census as either "ground feeders" or "arboreal," based on the admittedly crude criterion that a ground feeder is a species that
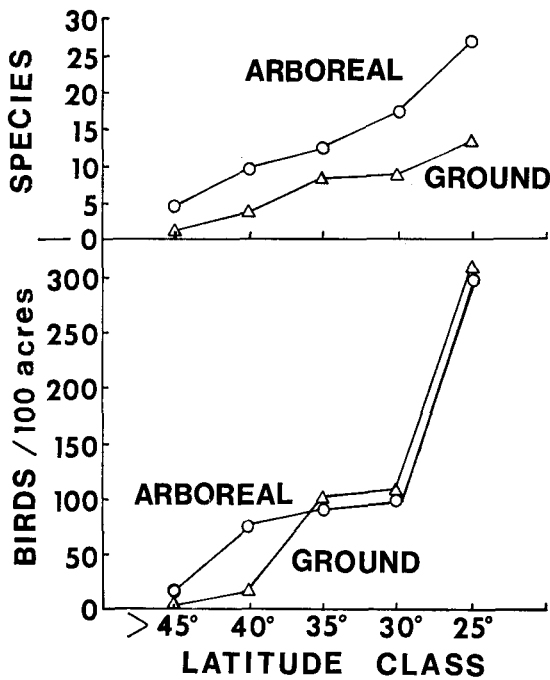
FIGURE 2. Species richness and population density of arboreal and ground-feeding birds at various latitudes during the winter.

spends at least 50% of its feeding time during winter on the ground [data on feeding habits were gleaned primarily from Bent's (1919 et seq.) life histories; for a list of ground-feeding species see appendix I].

The results of this analysis appear in figure 2. There is a greater diversity of arboreal species at all latitudes although the diversity of both groups increases with decreasing latitude at similar rates (upper graph). The population densities of the two groups (lower graph) are very similar below about 40° N, with a sharp rise below 30° N (i.e., in Florida) due to an abundance of insectivorous birds in those censuses.

At the 40th parallel, the two foraging groups diverge in population density. Ground feeders are extremely scarce above 45° N and comprise only about 15% of the total avifauna between 40° and 45°. Snow cover rarely persists for more than 24 hr below 35° N, but is common and persistent above about 38° N (USDA 1941). Apparently, the winter ranges of many ground feeders are limited northward by the frequency and/or duration of snow or ice cover which makes ground-feeding difficult. Indeed, examination of the censuses reveals a large number of ground-feeding species which are uncommon in winter above about 38° N, but abundant southward [e.g., Common Flicker (*Colaptes auratus*), Brown Thrasher

(*Toxostoma rufum*), American Robin (*Turdus migratorius*), Hermit Thrush (*Catharus guttatus*), and numerous Icteridae and Fringillidae].

Only 54 censuses were available for the preceding analysis; perhaps a more exhaustive examination of this gradient could be made at the gamma-diversity level utilizing the annual Christmas Bird Counts (published in *American Birds*, no. 2 in each volume).

GAMMA DIVERSITY

The method for constructing gamma-diversity gradients is a modification of that used for mammals by Simpson (1964). A grid of squares roughly 300 miles on a side was superimposed on a map of North America and the number of bird species occurring in each square was counted. Only landbirds were included, since herons, ducks, shorebirds, etc., are essentially aquatic organisms and as such are outside the scope of this paper.

The breeding-diversity gradient has already been constructed by MacArthur and Wilson (1967, fig. 37; and elsewhere) using this method and in the form of five-species-interval isopleths by Cook (1969). It will not be reproduced here although the following is offered as a review: (1) diversity gradually increases as one proceeds westward across North America; (2) in the western third of the continent diversity increases southward although the pattern is complicated by the variety of mountains, deserts, and other landforms; (3) peninsulas (Yucatan, Florida, Baja California) contain fewer species than adjacent mainland areas; and (4) in the eastern two-thirds of North America diversity is highest at the latitude of the Great Lakes (ca. 140 species per 300-mile square), but it declines southward to the Gulf Coast (ca. 90 species per square).

The westward increase in diversity in North America is probably due to a combination of the greater proximity of certain taxa of neotropical origin to their source regions and to the greater elevational amplitudes available in the mountainous western states and Canadian provinces. Squares containing largely desert or chaparral ecosystems contain fewer species, indicating a moisture effect which probably reduces gamma diversity by simplifying vegetation structure over a large geographical area.

The gamma-diversity pattern differs from the alpha gradient in both eastern and western North America. In the East, gamma diversity decreases from 45° N southward; in the West, it increases; in both cases alpha diversity re-

TABLE 1.   Per cent similarities in species composition among all possible pairs of selected censuses from the northeastern (upper) and southeastern (lower) United States.

	N.Y. a	Ohio	N.Y. b	Ill.	Mich.	N.J.	
	45.2	50.7	65.7	48.6	53.5	53.5	Conn.
		40.8	30.0	31.8	48.9	44.4	N.Y. a
	Ga. a		40.0	49.1	65.5	48.3	Ohio
Ga. b	52.4	Ga. b		32.7	35.7	42.9	N.Y. b
Ga. c	60.0	50.0	Ga. c		56.6	60.4	Ill.
N.C. a	52.8	58.2	53.9	N.C. a		55.5	Mich.
N.C. b	59.1	52.2	66.7	49.1	N.C. b		
Tenn. a	55.0	66.7	48.0	52.8	54.5	Tenn. a	
Tenn. b	56.5	58.5	67.9	64.4	64.0	60.9	

For discussion see text.

mains essentially stable through the same latitudes. In other words, throughout North America the within-habitat (alpha) diversity is not affected by the diversity available on a regional basis. This suggests that temperate forest communities are saturated with bird species—the same conclusion reached by Cody (1968) for grasslands throughout the Western Hemisphere.

The first three patterns in the breeding gradient (reviewed above) have been discussed adequately elsewhere. However, the decline in gamma diversity between 45° N and the Gulf of Mexico remains puzzling. Why, for example, should Georgia have several dozen fewer breeding landbirds than Vermont, a state which is one-sixth as large, lacks a seacoast, spans 2 fewer degrees of latitude, contains less elevational amplitude, and is 1000 miles further from the species-rich tropics? Cook (1969) suggests an historical explanation based on repeated Pleistocene glaciations which forced the Tertiary biota southward and ultimately wiped out that portion of the eastern North American avifauna which was not adapted to temperate (particularly coniferous) forest ecosystems. The temperate-adapted elements then presumably shifted northward during glacial retreats, leaving behind a hiatus of avifaunal impoverishment which has been cut off from invasion of tropical and subtropical birds by arid grasslands to the west and ocean to the south and east.

Unfortunately, it is difficult to design empirical tests for hypotheses which involve events that took place thousands of years ago. In addition, paleontologists now seem to agree that there was considerable "telescoping" of plant communities in the southeastern United States during glacial periods (Ellis Yochelson, pers. comm.), indicating that subtropical communities may not have been "pushed off the edge" of eastern North America after all. In any case, the original cause of the impoverish-

ment of the southeastern U.S. avifauna can only be inferred. However, the mechanisms which operate to *maintain* that pattern—especially those which prevent the extension of breeding ranges from the north—should be investigated.

Since within-habitat diversity is virtually constant in forests of similar vegetation structure throughout the eastern United States, the gamma-diversity gradient may operate in two ways: (1) some of the available species may be spread through a wider range of habitats in the Southeast; or (2) the Southeast may actually contain fewer avian habitats than regions further north. Situations (1) and (2) are by no means mutually exclusive. Evidence for (1) might imply the existence of conditions at some time in the past which impoverished the southeastern avifauna, thus permitting gradual niche expansion by some of the surviving species. If niche expansion is the *sole* mechanism maintaining the gradient, alternative (2) must be proven false.

It is at this point that an investigation of the beta-diversity pattern would be useful, for if alternative (1) is true, bird censuses in the southeastern United States should be more similar in species composition (i.e., should have lower *beta* diversity) than plots in the Northeast. To test that possibility I took 14 forest censuses, 7 from each region, from recent issues of *American Birds*. The plots ranged in size from 13.2 to 60 acres (5.34–24.3 ha; examination revealed no correlation between plot size and number of species). The southeastern censuses were of areas in Georgia, Tennessee, and North Carolina, and spanned 4° in latitude. The northeastern censuses were from Illinois, Michigan, Ohio, New Jersey, New York, and Connecticut, and spanned a latitudinal range of a little over 3°. All plots were less than 2500 ft (760 m) above mean sea level.

For each pair of censuses a measure of per cent similarity in species composition was cal-

culated; this is $2w/(a + b) \times 100$, where w is the number of species the two censuses have in common, and $(a + b)$ is the sum of the number of species in each of the two census areas. Table 1 shows the per cent similarities for all possible pairs of northeastern and southeastern censuses (for full identification of the censuses used see appendix II). The mean per cent similarity in the northeast is 48.56%; in the southeast the mean is 57.31%. A t-test on the null hypothesis that the means are equal was rejected at the 0.05 level (d.f. = 20), indicating that there is a significant difference in redundancy of species composition between breeding-bird populations in the southeastern and northeastern United States.

This finding provides circumstantial support for "historical" factors, but the possibility that the southeastern United States provides fewer types of habitats for passerine birds should not be discounted. Anyone who has flown over the southeast Coast Plain and Piedmont in a light plane is soon aware of the extensive stretches of young pine (mostly either *Pinus palustris* or *P. taeda*) which cover thousands of square miles. These pine forests often lack a well-developed understory and consequently support a poor bird fauna. Whether they are extensive enough to affect the diversity in a 300-mile square is open to conjecture.

Hardwood forests have a spotty distribution in this region, and are often restricted to river bottoms. These patches of hardwood forest may function as islands (or, at least, peninsulas) in that their small size, narrowness, and their isolation from one another and from the more continuous hardwoods further north make them unavailable to many forest or forest-edge species which breed further north [e.g., the Black-billed Cuckoo (*Coccyzus erythropthalmus*), White-breasted Nuthatch (*Sitta carolinensis*), Warbling Vireo (*Vireo gilvus*), Ovenbird (*Seiurus aurocapillus*), American Redstart (*Setophage ruticilla*), Northern Oriole (*Icterus galbula*), and Rose-breasted Grosbeak (*Pheucticus ludovicianus*)]. Some assessment of this possibility might be gained by censusing hardwood swamp forests in river bottoms from Virginia southward along the Coast Plain to Florida. If the river-bottom hardwoods act as "islands," the plots should become more impoverished and less variable in species composition as one moves southward. Some support for this idea is already supplied by the fact that many of the above-mentioned species do occur further south in the Mississippi Valley where hardwood forests are more extensive.
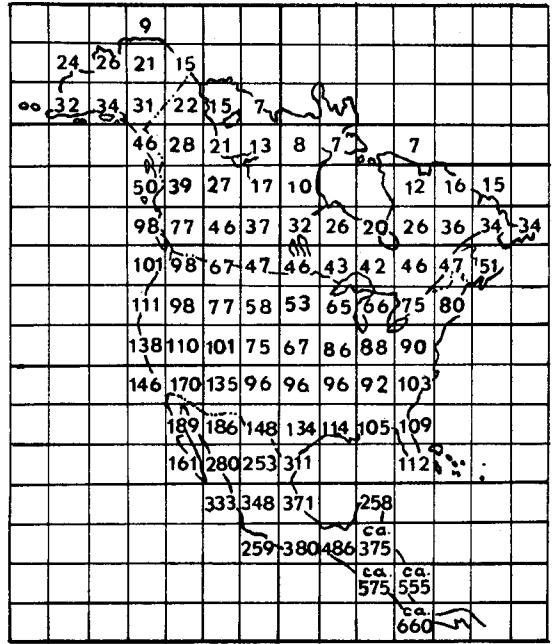

FIGURE 3. Species density of North and Meso-american landbirds during the winter. Each square is 300 miles (500 km) on a side.

Finally, mention should be made of the "coastal hiatus" (Lowery 1945). The majority of spring trans-Gulf migrants continue inland to the northern Gulf states or beyond before alighting; as a result, a large number of passerine species are rather scarce on the southeast Coast Plain during migration. This curious pattern, which possibly originated during Pleistocene interglacials when sea levels were high and parts of the Coast Plain were inundated, may also contribute to the maintenance of the Southeast's impoverished condition during the breeding season. Landbirds are considerably more catholic in their choice of habitats during migration than during the breeding season, so the maintenance of the "coastal hiatus" migratory pattern is probably not related to a paucity of habitat types in the Southeast, and is itself an ornithological problem worthy of investigation.

The winter gamma-diversity gradient is presented in figure 3. The winter ranges of landbirds given in the A.O.U. Check-list (1957) were used to compile the gradient. In general, diversity increases southward and toward the seacoasts. As in the case of the breeding gradient, diversity in the western United States is heightened by the variety of landforms in each square and by proximity to the Neotropics. However, since coastal areas have milder winters than inland areas at the same latitude, the overriding impression is that cli-

matic severity is the primary factor determining the form of the winter-diversity gradient. In fact, since the winter ranges of some species [e.g., Tufted Titmouse (*Parus bicolor*), Mockingbird (*Mimus polyglottos*), Cardinal (*Cardinalis cardinalis*), and Northern Oriole] have recently expanded northward due to the availability of food at backyard feeding stations, it is possible to say that winter ranges are largely determined by the effects of winter climate regimes on the availability of food.

Thus, it appears that during the winter both alpha- and gamma-diversity gradients are correlated with climate patterns, at least in the temperate zone. The effects of biotic interactions such as competition and predation seem to be tied closely to the constraints imposed by climate upon the food supply (e.g., Johnston 1942; Morse 1970). Historical factors affecting the winter gamma-diversity pattern would include those which influenced the evolution of migration in the North American avifauna. Since the pattern is largely a reflection of present-day climate regimes, one can assume that the evolution of migratory movements among birds wintering in temperate regions results from the net benefits gained by moving into an area where a milder climate permits higher resource levels (Cox 1968). These higher resource levels, in turn, permit the coexistence of more species.

For species migrating deep into the tropics, winter distributions must have a stronger historical component. Our understanding of the evolutionary forces responsible for the winter distributions of these long-range migrants remains poor.

SUMMARY

Latitudinal gradients in avian species diversity were constructed and analyzed for North and Mesoamerica. Diversity patterns were examined using two geographical scales: (1) the diversity in single censuses taken in a homogeneous habitat (alpha diversity); and (2) the diversity contained in squares 300 miles wide (gamma diversity). Diversity gradients for both breeding and winter seasons were investigated.

During the breeding season alpha diversity remains stable between 50° and 20° N. In the tropics, however, alpha diversity increases all the way to the equator. Apparently, some threshold of climatic stability is reached at about 20° N which allows for the coexistence of more species. How this threshold is set and why alpha diversity increases from 20° N southward are not known.

In the winter alpha diversity increases steadily from north to south, corresponding to the severity of winter climates. Ground-feeding species are particularly scarce in regions where the ground is frequently snow-covered.

Gamma diversity in summer increases from east to west in North America and from north to south in western North America, but it declines from the Great Lakes southward in eastern North America. Possible causes for these patterns are given, and tests are suggested which may help explain the failure of northeastern U.S. birds to extend their breeding ranges into the Southeast. The changes in gamma diversity occur across a region where alpha diversity is constant, indicating that avian communities in temperate North America are generally species-saturated.

In winter, gamma diversity follows climate patterns, increasing southward and toward the coasts where climates are milder. In the temperate zone winter ranges appear to be regulated by the effects of climate on food supply. In the tropics unknown historical factors may be of greater importance.

ACKNOWLEDGMENTS

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APPENDIX I.

List of species occurring in winter plot censuses considered to be primarily ground-feeders:

All Galliformes
All Columbiformes
Flickers (*Colaptes* spp.)
Red-headed Woodpecker (*Melanerpes erythrocephalus*)
Crows (*Corvus* spp.)
Brown Thrasher (*Toxostoma rufum*)
All Turdidae except *Sialia*
Starling (*Sturnus vulgaris*)
Palm Warbler (*Dendroica palmarum*)
Ovenbird and Waterthrushes (*Seiurus* spp.)
Meadowlarks (*Sturnella* spp.)
Grackles (*Cassidix* and *Quiscalus*)
Cowbird (*Molothrus ater*)
All Fringillidae except *Spinus* spp., *Hesperiphona vespertina*, *Carpodacus purpureus*, *Loxia* spp., *Pinicola enucleator*, *Zonotrichia leucophrys*, *Melospiza lincolnii*, and *M. georgiana*.

APPENDIX II.

Breeding-bird censuses published in *American Birds* which were used to compare beta diversity in woodlands of the southeastern and northeastern United States.

A. Southeastern

Ga. a	Tramer, E. (1966). Woodland swamp. 20:609.
Ga. b	Mellinger, E. (1969). Mountain ravine mixed forest. 23:711.
Ga. c	Davenport, L. (1969). Southern mixed hardwoods. 23:723.
N.C. a	Oelke, H. (1966). Oak-hickory hardwoods. 20:614.
N.C. b	Smith, W. (1969). Upland mixed habitats. 23:720.
Tenn. a	Howell, J. (1967). Ridge and valley hardwoods. 21:674.
Tenn. b	Wallace, G. (1969). 2nd growth oak-pine forest. 23:721.

B. Northeastern

N.J.	Tramer, E. (1969). Mixed hardwoods. 23:705.
Mich.	Dahlstrom, H. et al. (1969). Mixed hardwoods. 23:712.
Ill.	Franks, E., and W. Martin. (1967). Upland oak-hickory forest. 21:615.
N.Y. a	Hamel, P., and R. McCarthy. (1966). Maple forest. 20:611.
N.Y. b	Bowman, M. (1967). Upland deciduous forest. 21:613.
Ohio	Morse, R. et al. (1966). Wet 2nd growth hardwoods. 20:608.
Conn.	Magee, A., and J. Cavanaugh. (1967). 2nd growth hardwoods. 20:611.