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BIRD SPECIES DIVERSITY ON AN ANDEAN ELEVATIONAL GRADIENT¹

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Abstract. This paper analyzes patterns of bird species diversity on an elevational transect of the Cordillera Vilcabamba, Peru. Major changes in climate and vegetation are encompassed by the transect which extended from the Apurimac Valley floor at 500 m to the summit ridge of the range at > 3,500 m. Four vegetation zones are easily discerned—lowland rain forest, montane rain forest, cloud forest, and elfin forest. In progressing upwards there is a monotonic trend toward decreasing canopy stature and reduced number of plant strata.

The vegetation gradient provided the opportunity to examine the relation between bird species diversity and habitat complexity in an entirely natural setting. The decrease in forest stature with elevation was closely paralleled by decreasing **avian syntopy** (the total number of bird species cohabiting the forest at a given elevation). Bird species diversity was shown to be highly correlated with foliage height diversity, using either four or five layers in the foliage height diversity calculation ($r = .97$), and less well correlated using three layers, as defined previously by MacArthur ($r = .84$). At this superficial level the trend in bird species diversity seemed to be adequately explained as a response to the vegetation gradient.

This preliminary conclusion was found to be illusory when the elevational trend in syntopy was reexamined separately for three major trophic subdivisions of the fauna. **The number of insectivores decreased 5.2-fold from the bottom to the top of the gradient, frugivores decreased by a factor of 2.3, and nectarivores showed no change.** It was now clear that the diversity in each of these trophic categories was responsive to environmental influences other than, or in addition to, the gradient in habitat structure. Additional factors implicated by the available evidence are competitive interactions with other taxa at the same trophic level, **changing composition of the resource base as a function of elevation,** and declining productivity at high elevations.

Analysis of netted bird samples revealed an **unexpected diversity maximum in the lower cloud forest zone.** The immediate cause of this was a relaxation of the vertical stratification of foraging zones, such that an anomalously large fraction of the species present entered the nets. The excess diversity was found to consist almost entirely of insectivores. Several factors appear to contribute to the ultimate causes of the diversity maximum: greater patchiness of the montane forest due to the rugged topography, a higher density of foliage near the ground, and possibly increased resource productivity. A correlation between diversity and density in the netting results suggested a causal connection mediated via resource levels.

The conclusion is that diversity is a complex community property that is responsive to many types of influences beyond simply the structure of the habitat.

Key words: Andes; birds; ecotone; environmental gradient; foliage height diversity; Peru; species diversity.

INTRODUCTION

The species diversity problem has been under intensive investigation by ecologists and biogeographers for the past 20 yr. Yet we are still far from a global understanding of the many diversity patterns in nature. In studies involving birds, success has been limited to exposing empirical relationships that serve to predict diversity patterns within but not between biogeographic provinces. A knowledge of the foliage height profile of a habitat in eastern North America, for example, allows a fairly accurate prediction of its bird species diversity (MacArthur 1964), but the same empirical relationship fails if we use it to try to predict the bird species diversity of a tropical habitat (Terborgh and Weske 1969). Similarly, one may be able to predict the number of bird species inhabiting an oceanic island from the species-area and species-distance re-

gressions of other nearby islands (Diamond 1973), but the prediction fails if we apply it to islands in another ocean. **Clearly we have a better feeling for the environmental regulation of diversity within biogeographic provinces than we do for what causes the differences between them.**

The most thoroughly documented noninsular pattern is the positive relation between bird species diversity and measures of habitat complexity, a relation that has been shown to hold, with scaling adjustments, within several biogeographic regions (MacArthur et al. 1966; Recher 1969; Karr 1971). The notion that complex habitats provide greater opportunities for resource subdivision has intuitive appeal. Nevertheless, the causal chain that links habitat structure with consumer diversity is by no means simple, and may involve a number of branching or independent connections. Furthermore, the causal links may differ from one set of species to another. Much of the work on diversity to date has concentrated on establishing the

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empirical relations between habitat structure and diversity; the causal connections have been relatively little explored. It is this last aspect of the diversity problem that motivates the present article.

The measurements of habitat structure and species diversity come from an elevational transect of the eastern Peruvian Andes. The stature and vertical layering of the vegetation on the transect change in a systematic fashion with elevation, providing a monotonic natural gradient of habitat complexity. I will first examine the relation between avian diversity and two measures of habitat complexity: forest stature and foliage height diversity. **I will then show that a strong correlation between species diversity and these measures of habitat complexity is partly fortuitous and masks probable responses to a changing trophic organization of the community, the presence and absence of other taxa in the same trophic levels, and variations in resource productivity along the gradient.**

THE VILCABAMBA ELEVATIONAL GRADIENT

With the help of several colleagues and Peruvian assistants, I conducted an intensive survey of the elevational distribution of birdlife along a transect of the West-facing slope of the Cordillera Vilcabamba in Central Peru (approximate location, 12°35'S, 73°40'W). This was accomplished in a series of six expeditions during the period of 1965 to 1972. Descriptions of the climate and vegetation along the transect have been published in a number of previous articles, and so I will reiterate only essential points here (Terborgh 1971, 1973a; Terborgh and Dudley 1973).

Temperature is the climatic variable most closely associated with elevation ($T = -0.56^{\circ}\text{C}/100\text{ m gain in elevation}$), though the amount of cloudiness and the frequency of rainfall increase noticeably toward the upper end of the transect. Superimposed on the smooth temperature gradient are four structurally and (to a lesser degree) floristically distinct vegetation formations: lowland rain forest, montane rain forest, cloud forest, and elfin forest. They are characterized, in this order, by declining stature and reduced vertical stratification.

I concur with Richards (1952) that lowland rain forest on good sites contains five vertically distinct strata, ranging from a 50- to 60-m A-story of giant emergents down to a 0.5-m herbaceous D-story. **(One can satisfy himself of this by counting the vertically superimposed crowns beneath emergents. The most frequent number is five.)** On our transect, lowland rain forest occupied only the flat Apurimac Valley floor. (Virtually none remains at present.) **Montane rain forest (650–1,385 m) is floristically similar but lacks the emergent stratum.** Gradual trends toward reduced canopy height and increased foliage density in the understory are discernible as one climbs upward. This continues through the cloud forest belt (1,385 to roughly 2,500 m), which in the Vilcabamba is structur-

ally chaotic due to the extremely steep and irregular terrain. Frequent treefalls and landslides result in an irregular canopy that admits a great deal of light into the understory, with a consequent proliferation of climbing bamboo (*Chusquea* spp.). Elfin forest, the uppermost vegetation zone, first appears on ridge tops at $\approx 2,500\text{ m}$ in the form of stunted, nearly impenetrable thickets. On good sites, elfin forest may include three strata, corresponding roughly to trees, shrubs, and herbs, but on steep slopes or in poorly drained areas where sphagnum peat accumulates, there are only scattered low trees and a grassy understory. Elfin forest and cloud forest interdigitate on ridges and slopes between 2,400 and 2,700 m. In many places the transition between them is marked by an abrupt drop in canopy height from 20 m or so down to 8 m or less. Although the elfin forest zone is visibly patchy due to the effects of irregularities in exposure and soil conditions, the overall trend toward structural simplification and reduced stature of the vegetation continues to timberline (3,500 m).

AVIAN SYNTOPY AND HABITAT COMPLEXITY

We recorded syntopy as the total number of bird species regularly using the forest within $\pm 30\text{ m}$ elevation of our 9 bush camps. The lists were compiled from sight, sound, and netting records, as described previously (Terborgh 1971). Only forest-dwelling species were counted. Thus the totals for each site omit a few species that were obvious vagrants from other habitats or that use the forest discontinuously along stream margins or in treefall openings. Although the syntopic species at any elevation differ greatly in abundance, from large eagles with territories of several square kilometres to common small passerines, all coexist in the matrix of the forest. In compiling the results my colleagues and I invested a total of 13 party-months on the transect, including 3 wk or more at each of the 9 bush camps. The thoroughness of the effort can be judged by the fact that the final expedition in 1972 added only two new species to a cumulative total of 600.

Figure 1 reveals that forest stature and avian syntopy vary with elevation in a strikingly parallel fashion. The parallelism falters only at the lowland forest-montane forest ecotone where the giant 60-m emergent stratum drops out of the vegetation. However, 60-m trees are rare, even in the best lowland stands, and nowhere does a closed canopy form at heights $>30\text{--}40\text{ m}$. A biologically more realistic index of the stature of the lowland forest would be a weighted mean of the heights of unshaded canopy trees. This would fall in the range of 30–45 m and would preserve the parallelism with the syntopy curve over the entire gradient.

As discussed above, the number of vertically superimposed plant strata in the Vilcabamba vegetation formations is closely correlated with the overall

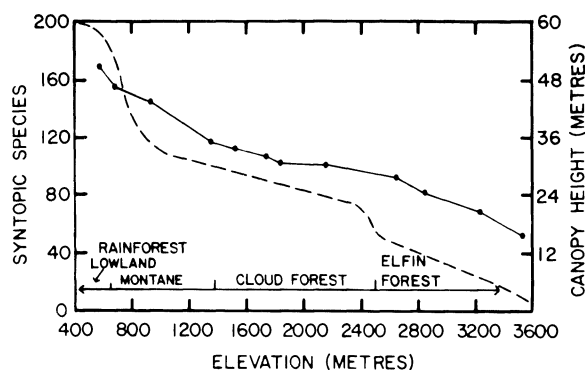


FIG. 1. Avian syntopy (solid line) and forest stature (dashed line) vs. elevation in the Cordillera Vilcabamba. Vegetation zones indicated above the abscissa. Syntopy is the number of species regularly using the forest within ± 30 m of each station. Canopy height represents the mean height of the tallest tree stratum.

stature of the forest. Thus, the data associate the richer low-elevation communities with a taller, more complex and highly stratified habitat. Expressed in this form, the results suggest nothing new.

Bird species diversity vs. foliage height diversity

To see whether the conclusions reached using a crude and easily obtained measure of habitat complexity—stature—would hold up under more conventional methods of analysis, we determined the foliage height profile of the forest at seven elevations. Foliage densities were measured with MacArthur's checkerboard technique (MacArthur and MacArthur 1961) up to 6 or sometimes 9.14 m [20 or 30 feet], which is as high as we could elevate the checkerboard. **Educated guesswork served to fill in the rest of the profile.** (For some examples, see Terborgh and Weske 1969.) Foliage height diversities were then computed on the basis of 3 layers (0–2', 2–25', >25'), 4 layers (0–2', 2–10', 10–50', >50'), and 5 layers (0–2', 2–10', 10–30', 30–90', >90'). The intervals for the 3- and 4-layer calculations were those used by MacArthur et al. (1966), while those for the 5-layer calculations were based on Richard's (1952) description of the 5 strata of lowland rain forest.

Bird species diversity is not directly measurable in tropical forest because of the presence of many cryptic species that are rarely observed, and because there is little diurnal or seasonal overlap in the vocal activity periods of many species. Thus it was necessary to estimate bird species diversity from syntopy values by assuming that community equitability is constant at all elevations. Some confidence in this procedure can be obtained from the fact that the species equitabilities of netted samples cluster tightly in the range of 0.7 to 0.8 with no apparent elevational trend (Fig. 6, and see Table 1 in Terborgh and Weske 1975). Because large birds, which are poorly sampled by nets, tend to be

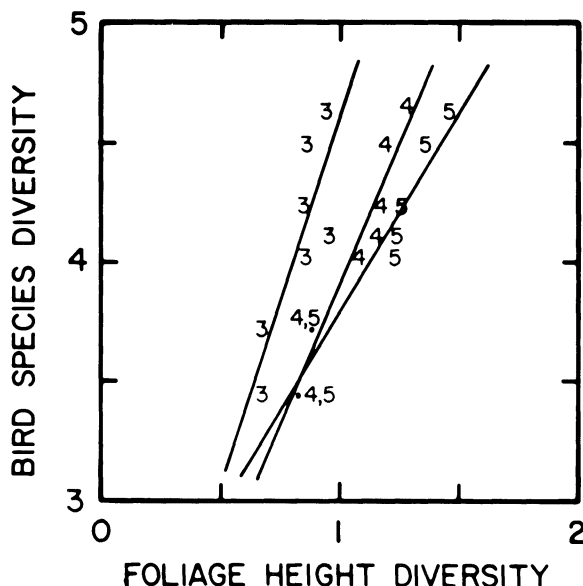


FIG. 2. Bird species diversity vs. foliage height diversity in the Cordillera Vilcabamba. Numbered points refer to the number of foliage layers used in computing the foliage height diversity. Lines represent least squares regressions with correlation coefficients, $r_3 = .84$; $r_4 = .97$; $r_5 = .97$. Further methodological details in text.

less common than small ones, a lower value, arbitrarily set at 0.6, was used to convert syntopy values to estimates of the number of equally common species. The natural logarithms of these estimates represent bird species diversity. (Letting $H = \sum p_i \ln p_i$, \exp^H gives the number of equally common species and $\exp^H/S =$ equitability, where $S =$ the total number of species in the sample.) We have just obtained estimates of H by proceeding through this backwards, i.e., $H = \ln (0.6S)$. Even if equitability does vary somewhat from station to station, most of the variation will be wiped out by taking the logarithm.

Bird species diversity correlates well with foliage height diversity on the Vilcabamba gradient, regardless of how many layers are used in computing the latter (Fig. 2). A better fit is obtained with 4 or 5 layers because foliage height diversity measurements based on 3 layers do not discriminate between forests in which most of the foliage is above 7.6 m.

Variation in habitat complexity explains a large fraction of the variance in avian syntopy/diversity on the Vilcabamba elevational gradient, whether one takes into account the details of the vertical organization of the vegetation, as with the foliage height diversity index, or uses only the simple metric of overall forest stature. Investigations in other parts of the world have frequently, though not invariably, produced similar results, except that values of bird species diversity corresponding to a given foliage height diversity have in general been much lower (MacArthur 1964; MacArthur et al. 1966; Recher 1969; Terborgh and Weske

1969; Karr and Roth 1971). It is likely that regional differences are better explained by evolutionary histories of their samples than by postulating as yet undiscovered distinctions in the quality of habitats (Vuilleumier 1972; Cody 1975; Karr 1975; Pearson 1976, and later discussion).

At this point one could easily close the paper with the statement that the Vilcabamba results have merely confirmed a common empirical relationship. When one examines the underlying details, however, a much more complicated picture emerges.

*Trophically independent subdivisions
of the avifauna*

Instead of looking at the very broad pattern described by the entire forest-dwelling avifauna, it is of interest to examine its component subdivisions to see whether they all respond similarly to the gradient. Discounting raptors and vultures, tropical avifaunas can be fairly discretely partitioned into three trophically distinct subdivisions: insectivores, frugivores (including granivores), and nectarivores. A minority of species that feed on nearly equal mixtures of insects and fruit (mainly tanagers and some honeycreepers), or of fruit and nectar (certain honeycreepers) were split evenly between the respective categories. Species that feed on markedly uneven mixtures were assigned to the category representing the major component of their diets. For example, flycatchers that seasonally take some fruit were nevertheless included as insectivores, and some manakins and certain cotin-gids that occasionally catch insects were classified as frugivores. To a first approximation at least, the subdivisions are trophically, and therefore competitively, independent of one another. Now, if structural complexity of the habitat were the controlling factor in the diversity of birds in general, the three major subdivisions of the avifauna should all respond in a like manner to the vegetational gradient. But they do not (Fig. 3). The trends are strikingly different. Syntopy among insectivores undergoes the greatest change with elevation (>5-fold). Frugivores decline less sharply (2.3-fold) while syntopy in nectarivores is entirely independent of the gradient.

The simple parallelism between vegetational complexity and avian syntopy has vanished, leaving in its place a trio of contrasting cases to be examined individually in the light of the special circumstances pertaining to each. My interpretations, while largely anecdotal, are nevertheless based on what I regard as sound biological evidence.

Insectivores.—Why should insectivores decline most precipitously with elevation? The answer to this seems to be compounded of several trends. First, it could be expected that insectivores would be most severely affected by structural simplification of the habitat. While fruit and flowers can be carried on a plant in only a limited number of ways, insects can

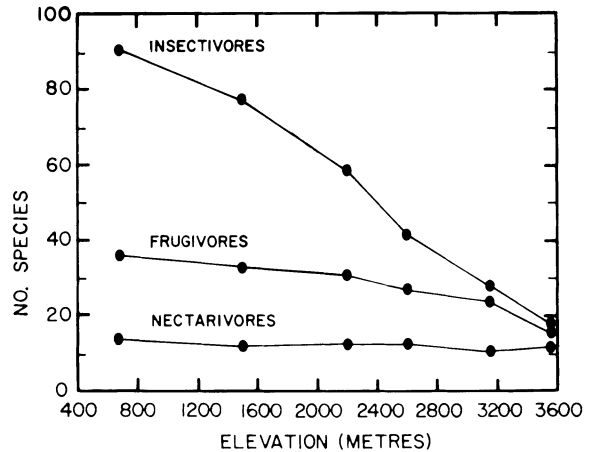


FIG. 3. Number of syntopic species in three trophic guilds vs. elevation in the Cordillera Vilcabamba. From the bottom of the gradient to the top, syntopy in the guilds decreases by the following factors: insectivores 5.1-fold; frugivores (including granivores) 2.3-fold; nectarivores 1.2-fold. Further details in text.

conceal themselves or escape by a great variety of means. Diamond (1973) has shown, for example, that fruit-eating birds in the southwest Pacific sort mainly by size, while, in contrast, it is routine to find several like-sized insectivores sharing the same habitat and segregating by subtle behavioral differences (MacArthur 1958). The simple fact that most avifaunas contain much larger numbers of insectivorous species and families than of taxa specialized on other types of resources testifies to the vast array of behavioral and morphological specializations that can be effectively employed in pursuit of insect prey (Lein 1972; Keast 1972).

Beyond the obvious generalization that structurally complex vegetation offers more opportunities for specialized techniques of harvesting insects, one can make a few more particular statements about how such opportunities decrease on the Vilcabamba gradient. One clear case is that of bark-feeding birds (woodpeckers, Picidae, and woodcreepers, Dendrocolaptidae). As many as 30 species in these two families can be found in a single locality in the lowlands where the variety of bark substrates is impressive: giant trunks, tiny twigs, swinging vines, bamboo canes, termite nests, bromeliads, rotting knot holes, etc. Near timberline the situation is drastically different. The trees are low, spindly, and nearly uniform in size, and moreover, because of the festoons of mosses and lichens that cling to most trunks and branches, there is very little exposed bark. Here the bark-feeding "guild" is comprised of a single small woodpecker. Terrestrial insectivores that forage in the leaf litter are another case. A dozen or more species may coexist in the lowlands, while above 2,400 m there is only one, a species of antpitta (*Grallaria*). The floor of the upper montane forest is a cold damp carpet of sphagnum;

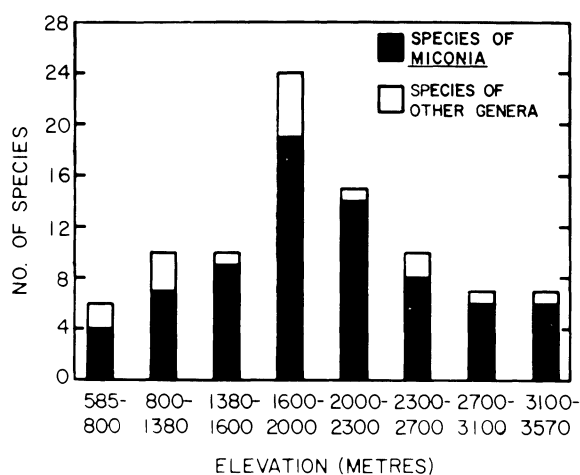


FIG. 4. Number of species in the ornithochoric plant family Melastomataceae occurring in eight arbitrary elevation zones in the Cordillera Vilcabamba. *Miconia* is the predominate genus at all elevations. Redrawn from Mardres (1970).

there scarcely is any leaf litter. One can search through the sphagnum at length without finding any arthropods at all (Terborgh and Weske 1972).

This brings up another probable cause for the decline in insectivores: a scarcity of insects at high elevations. Several major groups including ants and termites appear to drop out altogether above 2,500 m, while others (Lepidoptera, Orthoptera, Diptera, Coleoptera, Hymenoptera) are conspicuously less abundant. Netting yields indicate that the biomass of insectivorous birds drops some 20- to 30-fold between midelevations ($\approx 1,500$ m) and timberline, as will be shown later. Reduced syntopy among insectivores at high elevations can thus be explained as a response both to simplified vegetation and to a reduced food resource base.

Frugivores.—Syntopy among fruit- and seed-eating birds shows a more moderate 2.3-fold decrease with elevation. It could be that this merely reflects reduced opportunities for vertical partitioning of resources, though I believe that other factors are involved as well. For one, the availability of fruit crops is considerably more seasonal in the lowlands (Smythe 1970) than it appears to be at high elevations where many plants bear fruits and flowers continuously for long periods. For another, the bulk of the lowland fruit crop is harvested by mammals. At one site in the Peruvian lowlands we found that the biomass of frugivorous primates was approximately 400 kg/km^2 , a value that is well above any reasonable estimate of the biomass of frugivorous birds in the same forest (Janson 1975). But this is by no means the whole picture, as other less easily censused mammalian groups may consume more fruit than do the primates, e.g., bats, rodents, peccaries, marsupials, procyonids. Most of these animals drop out of the Andean fauna below 2,000 m, and many of them below 1,000 m. In spite of their powers

of flight, frugivorous bats respond more like other mammals than like birds. Below roughly 1,300 m our mist nets (on the few occasions we left them open) captured more frugivorous bats at night than birds of all species by day. Above this level the reverse was true and we routinely left nets open at night. These observations suggest that birds, by default, harvest a much greater proportion of the fruit crop at middle and upper elevations than they do in the lowlands. Moreover, it is possible that more suitable fruit is available, as the incidence of several ornithochoric plant families increases sharply in the upper montane forest (e.g., Ericaceae, Rubiaceae, Melastomataceae—Fig. 4).

Why then, if all these things are true, does the number of frugivorous bird species not increase with elevation? Although the proportion of fruit-eating birds in the community does increase markedly, the number of species does not. Part of the answer may lie with the reduced potential for spatial partitioning of the resource in structurally simplified vegetation. (Terrestrial frugivores, for example, drop out entirely above 2,800 m—because of the sphagnum?—though lowland forests may accommodate as many as 6 or 8.) There may be other influences as well, such as declining plant productivity at high elevations. Though the elevational variation in syntopy among frugivorous birds plots as a deceptively simple monotonic trend, it is clear that the underlying causality is complex and still largely unresolved.

Nectarivores.—The situation with regard to nectar-feeding birds is also complex. In the lowlands there is a pronounced vertical stratification of species. Nets capture little else than hermits (subfamily Phaethorninae) while several genera of trochiline hummingbirds and a number of honeycreepers occupy the canopy. Conditions in the lowland forest militate against high densities of nectarivores. Flowering tends to be markedly seasonal, and only a few species are in bloom at any time (Janzen 1967; Frankie et al. 1974). A large majority of the plants are entomophilous (Faegri and Pijl 1971). All these circumstances are reversed at high elevation. The climate is much less seasonal, a large proportion of the plants have flowering periods that last for months (Nevling 1971), and the flora is rich in ornithophilous genera and families (e.g., Ericaceae, Loranthaceae, Loganiaceae, Onagraceae, Bromeliaceae, Verbenaceae, etc.). Whereas hummingbirds and honeycreepers usually comprise $<10\%$ of the individuals in lowland net samples, these 2 families frequently constitute half of the catch near timberline. The roughly constant number of nectarivores over the whole gradient may result from a fortuitous balance of two countervailing influences: greater opportunities for vertical partitioning of nectar resources in the lowland forest vs. more abundant and more constant supplies of these resources at high elevations.

In summary, we first found that the overall trend in avian syntopy along the elevational gradient closely paralleled a gradual telescoping of the forest. However, a very rudimentary trophic breakdown of the fauna clearly demonstrated the folly of taking a good correlation too seriously in the absence of compelling *a priori* logic. Each trophic subdivision of the fauna responds to the gradient in a strikingly individualistic fashion. In every case the causal mechanisms seem to be compounded of several more or less independent influences. The structure of the habitat seems to play a role in every instance, but superimposed on it are effects that derive from major decreases (insects) or increases (nectar) in the availability of food resources, or from the dropout of a major class of competitors (frugivorous mammals). The structure of the habitat *per se* is by no means the only determinant of avian diversity.

DIVERSITY IN NETTED POPULATION SAMPLES

Now that we have examined the pattern of avian syntopy on the elevational gradient, we can ask whether a similar pattern holds for the component of the fauna that frequents the forest understory. First, a few methodological comments.

Netting method

Mist nets capture birds using the airspace between 0.1 and 2 m above the ground. The size we use (12 m long, 36 mm mesh) is maximally efficient for birds in the 8- to 60-g range; smaller species occasionally slip through the mesh and larger ones frequently bounce out without becoming entangled. Our standard procedure is to construct long end-to-end lines of 20 or more nets (up to 50) and to operate them for periods of 4 to 8 consecutive days. At the end of such a run, >80% of the resident population will have been captured, as can easily be verified by checking for bands on birds observed in the vicinity. Population density estimates can be obtained by making use of the fact that daily catch rates (of previously unmarked individuals) decline in a log-linear fashion with time. Regression analysis then yields a statistic that we call the projected population per net (see caption of Fig. 8 and Terborgh and Faaborg 1973 for further details).

As a sample accumulates the number of species captured increases, rapidly at first, and then gradually to a plateau because of the many inefficiently trapped terrestrial and canopy-dwelling species present at most sites. Diversity estimates that are statistically independent of the density measurements are obtained by basing them on the first 100 individuals captured. (More than 100 individuals are always contained in the density estimates.)

Species diversity in net samples

Now let us attempt to anticipate how diversity, as sampled with mist nets, might vary with elevation. Re-

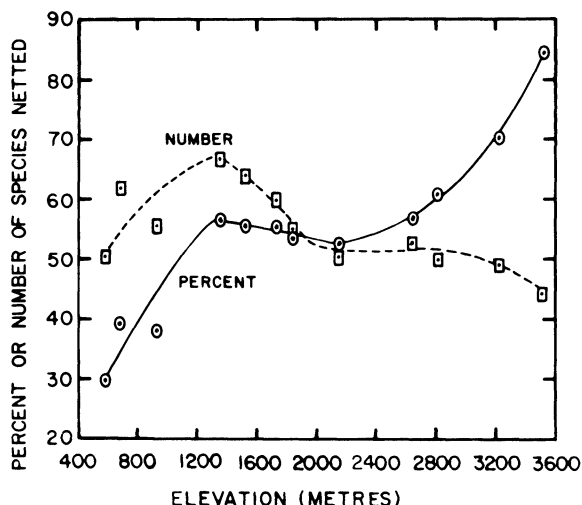


FIG. 5. Number of species contained in samples of 300 mist netted birds (dashed line), and the percent this represents of total syntopy (solid line) vs. elevation in the Cordillera Vilcabamba.

call first that the total number of species present (syntopy) declines from 170 in the lowland forest to 52 at timberline, a 3.3-fold decrease. However, the stature of the habitat also decreases by an equal or greater factor, suggesting that the concentration of species in a standard vertical slice of the forest may not change very much. Moreover, we can expect the nets to capture a much higher proportion of the whole community toward the upper end of the gradient where the vegetation is low.

This does indeed happen, but with some unanticipated kinks. The fraction of the entire syntopic community that is captured in a standard net sample of 300 individuals increases from $\approx 30\%$ in the lowlands to $>85\%$ at timberline. But instead of rising as the mirror image of the forest stature curve, as might be expected, the curve displays a prominent shoulder between 1,200 and 2,000 m (Fig. 5). In the absence of any major changes in forest stature in this region, the result is puzzling. An anomalously large fraction of the community is captured in the lower cloud forest zone with the consequence that netted species diversities rise to a pronounced peak (Fig. 6). The high diversities are not due to the presence of additional species, as the syntopy curve (Fig. 1) clearly shows, but rather to an unexpected local relaxation in the vertical stratification of the community. Neither is the high diversity explained simply by an increased incidence of canopy species in the samples, because the inclusion of inefficiently captured species results in reduced equitabilities and little or no change in diversity. To the contrary, equitabilities are high in the region of the diversity peak. Elsewhere on the transect the results are much as anticipated; comparing the bottom and the top of the gradient, the net samples contain roughly equal diversities, in spite of the large difference in syn-

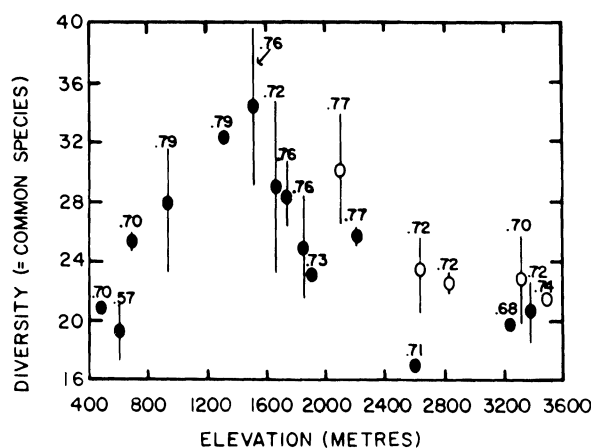


FIG. 6. Number of equally common bird species ($= \exp - \sum p_i \ln p_i$) contained in netted samples of 100 individuals vs. elevation in the Cordillera Vilcabamba. Vertical bars represent the range of values obtained at stations sampled on 2 or more yr. Open points indicate lines where nets ran along exposed ridgetops (cejas) as distinguished from broad slopes or level ground (closed points). Numbers give the mean equitability ($= \exp - \sum p_i \ln p_i / S$) of the sample(s) at each station.

topy. The problem that remains is how to account for the anomalous midelevation peak.

The midelevation diversity peak

An increased concentration of foliage at the level of the nets might contribute to greater coexistence, as has been demonstrated in some other studies (Karr and Roth 1971; Willson 1974). There may be some evidence for this, as shall be discussed later. However, the elevational patterns do not accord. **Netted bird diversity is at a maximum between 1,400 and 1,600 m while the thickest understory occurs between 2,000 and 3,000 m.**

Though the structure of the habitat may be of some ultimate significance in regulating the diversity pattern, it is possible that better insights may be derived by examining the more proximal clues offered by the organization of the avian community itself. The community undergoes pronounced compositional shifts as its trophic structure changes, and as a result of a nearly constant rate of species turnover with elevation (Terborgh 1971). Whole guilds wax and wane, or drop out altogether. Obligate army ant followers are a good example. Members of this guild are among the commonest species in lowland net samples. Their relative abundance and the number of species decline steadily with elevation until the last of them drops out near 2,000 m. Earlier I mentioned the cases of the bark-gleaning guild and terrestrial insectivores. There are many more examples, including ones that entail increases with elevation, as well as decreases.

Given that such marked compositional shifts involve guilds that depend on a wide range of distinct food and habitat resources, it is at least conceivable that there

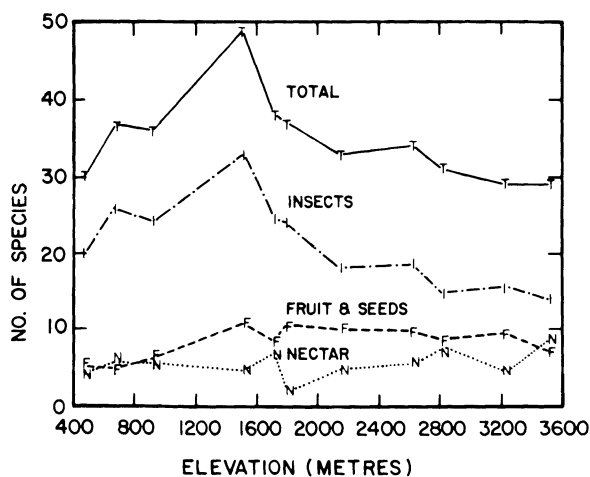


FIG. 7. Trophic composition of net samples vs. elevation in the Cordillera Vilcabamba. Criteria are the same as in Fig. 3.

might be some point on the gradient at which the spectrum of available resources allowed a maximum number of guilds to coexist.

Equitability of faunal components

Using the same rough breakdown of the fauna into insectivores, frugivores, and nectarivores, we note the surprising result that the midelevation diversity peak is almost entirely attributable to an increased concentration of insectivores (Fig. 7). At this crude level at least, enhanced equitability of trophic guilds is not the answer.

To pursue the matter further we focus on insectivores, in particular, the six most important families: Tyrannidae (flycatchers)—59 spp.; Formicariidae (antbirds)—43 spp.; Furnariidae (ovenbirds)—26 spp.; Dendrocolaptidae (woodcreepers)—16 spp.; Troglodytidae (wrens)—8 spp.; and Parulidae (warblers)—8 spp. (Numbers are all species inhabiting the gradient; many are not readily captured in nets.) Significantly, each of the four largest of these families possess a distinctive and characteristic type of foraging behavior. There are a few exceptions in each family, but to a first approximation woodcreepers glean the bark of trunks and major limbs, antbirds are foliage gleaners, ovenbirds have a creeping habit and are partial to searching through epiphytes and dead leaves, and flycatchers hawk or hover-snatch. The deployment of such conspicuously different foraging techniques probably implies differential resource utilization, as Hespenheide (1975) has shown for a number of tropical and temperate insectivores. It is not immediately obvious, however, why the proportions of these families should vary so strongly with elevation (Table 1). Antbirds predominate in the lowlands, contributing more species to the net samples than the other five families combined. But by 2,500 m they have virtually dropped out of the fauna. Flycatchers and ovenbirds, on the other hand, prevail near the top

TABLE 1. Representation of major insectivorous families in Vilcabamba net samples (first 300 individuals). Number of species

Family	Elevation (m)									
	585	685	930	1,350	1,520	1,730	1,835	2,215	2,640	3,510
<i>Dendrocolaptidae</i>	4	4	4	3	2	1	3	3	0	0
<i>Furnariidae</i>	4	4	5	10	9	8	7	4	5	3
<i>Formicariidae</i>	15	12	9	8	9	8	6	4	1	0
<i>Tyrannidae</i>	4	9	11	10	11	8	9	6	10	6
<i>Troglodytidae</i>	1	1	1	3	2	3	2	3	1	0
<i>Parulidae</i>	0	2	2	1	3	3	2	3	3	1
Total	28	32	32	35	36	31	29	23	20	10

of the gradient. The unexpectedly high net diversity at midelevations is clearly a consequence of the good and strikingly equitable representation of all the families of insectivores. Since each of the distinctive family foraging modes requires appropriate substrates, the key to the problem lies in understanding how the midelevation forest provides such a wealth of foraging opportunities.

Structural heterogeneity of the midmontane forest

Mid- and high-elevation forests are far more heterogeneous in the horizontal plane than are lowland forests. In part this is an inevitable consequence of mountain topography, with its ridges, slopes, and ravines. The continuity of the forest is frequently interrupted by landslide tracks and deep stream gorges; tree heights vary greatly between sheltered ravines and exposed ridgetops. All these irregularities create a variety of "edge" situations that are exploited by flycatchers. Climbing bamboos (*Chusquea* spp.) invade old landslides and treefalls, forming impenetrable thickets that are the home of certain ovenbirds, antbirds, and wrens. Where rising air currents are deflected by slopes and ridges, the forest becomes choked with a profusion of mosses and other epiphytes that carpet all exposed surfaces, both vertical and horizontal. The thick mats of mosses, lichens, and ferns offer a novel substrate that is exploited by a great array of creeping birds, notably ovenbirds and certain wrens. In addition, the forest harbors a full spectrum of the more conventional types of bark and foliage gleaners that are so prevalent in the lowlands. In sum, the steep terrain, irregular canopy, and an extraordinary variety of arboreal substrates all contribute to the microspatial heterogeneity of the midmontane forest of the Cordillera Vilcabamba. Lowland forests, in contrast, are more regularly stratified in the vertical plane, and less heterogeneous in the horizontal plane. (Such structural differences between forests, while potentially important to bird diversity, are not registered in foliage height diversity measurements because horizontal variation in foliage density is averaged in the computation.)

Is the elevational pattern of bird species diversity

adequately explained by the structural heterogeneity of the midmontane forest? No. What does seem to be accounted for is the more equitable representation of the principal families of insectivores. But there are other features of the pattern that are not explained, such as why there are decidedly fewer insectivores at 2,200 m than at 1,500 m (Table 1), even though at the higher elevation the forest still contains large trees and remains extremely heterogeneous, as is affirmed by the high family equitability. For the answer to this question we must inquire into the causes of the declining role of insectivory toward the upper end of the gradient. This will be taken up in the next section.

AVIAN DENSITY, SPECIES DIVERSITY, AND RESOURCES

Population density estimates derived from 4-day net runs yield an elevational pattern that closely parallels the trend in species diversity (Fig. 8). A high degree of correlation between the two sets of results is confirmed by plotting them together in a scatter diagram (Fig. 9). Maximum levels of both density and diversity coincide in a narrow elevational belt corresponding to lower cloud forest. Two quite independent questions are posed by the findings: (1) is a causal interrelationship implied by the correlation of density and diversity, and (2) what features of the changing conditions on the gradient could account for the pattern of avian abundance in the understory? These questions will be taken up in order.

Density and diversity

Our earlier experience with the parallelism between syntopy and forest stature provided a trenchant reminder to proceed with caution in the interpretation of correlations. In the present case it is not even clear which is the independent variable. There are plausible arguments on both sides. At one extreme, it could be held that the number of individuals in a community is a function of the number of species it contains. This is what one could expect if avian niches were rigidly unresponsive to variations in the intensity of interspecific competition. Though something like this may occur in the impoverished Pacific islands studied by Diamond (1971b), a large body of evidence indicates that in gen-

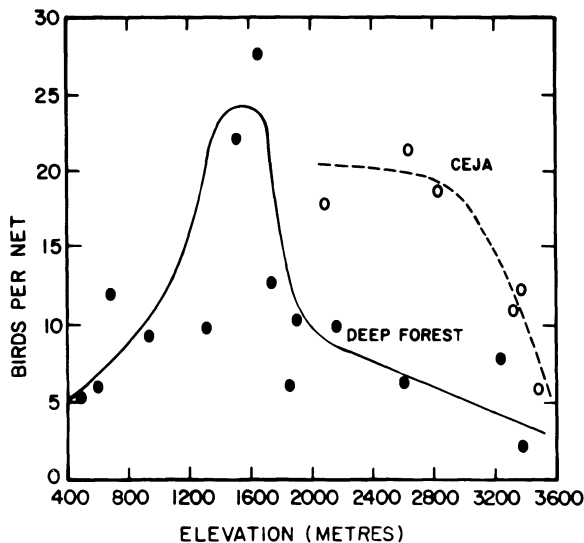


FIG. 8. Avian population density vs. elevation in the Cordillera Vilcabamba. The ordinate gives the projected population per net, computed from the first sample taken at each station as $[N/n]/[1 - (C_f/C_o)]$, where N = the number of different individuals in the sample, n = the number of nets used, C_f = the final and C_o = the initial capture rates (in birds per net-day). C_f and C_o are taken from the log-linear regression of capture rate vs. accumulated net-days of sampling. Further details on this method are given in Terborgh and Faaborg (1973). Open points represent ceja lines, as described in the caption of Fig. 6. Single values only are given for each station because banded birds are adept at avoiding nets, hence lower values are obtained when repeat measurements are made on subsequent years.

eral birds are capable of almost unlimited competitive release (Crowell 1962; Diamond 1971a; MacArthur et al. 1972, 1973). Indeed, our own efforts to determine the limits of competitive release among Caribbean birds have been notably unsuccessful. Tiny islands with only 10 or 12 species support avian biomasses that equal or exceed those of much larger species rich islands (Terborgh and Faaborg 1973; Terborgh et al. 1977). Among Caribbean bird communities at least, densities are more or less constant over a wide range of diversities. Thus it seems doubtful that diversity could be the independent variable in Fig. 9.

An intermediate proposition would be the following. Since we have already noted that the equitability of insectivorous families increases sharply from the lowlands to middle elevations, apparently in response to a greater structural heterogeneity of the habitat, it is possible that a broader spectrum of foraging opportunities could contribute to an increase in both density and diversity. Though this cannot be rejected as a partial explanation, there are additional facts that remain unresolved. One is the decline in number of insectivores between 1,500 and 2,200 m, a zone in which family equitability is high and within which there is little perceptible change in the character of the forest.

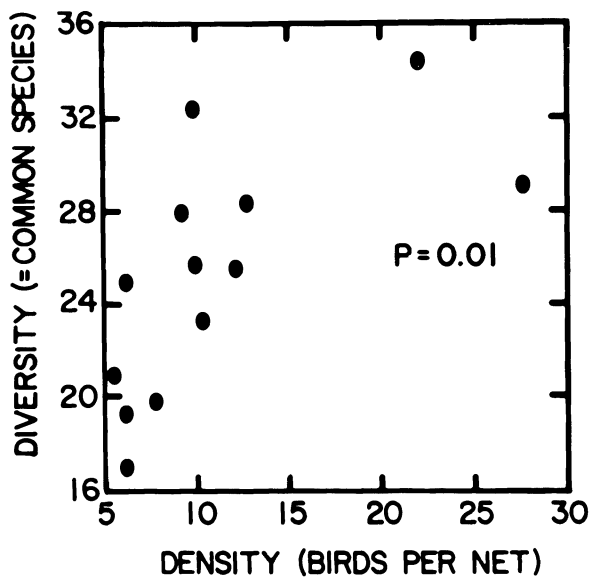


FIG. 9. Scatter plot of bird species diversity vs. population density in Vilcabamba net samples. Values were taken from the closed (deep forest) points in Figs. 6 and 8. The correlation is highly significant, $P = .01$.

Another is that the relative increase in density in Fig. 9 exceeds the relative increase in diversity. If the high diversity of the lower cloud forest region were simply a response to the presence of additional foraging opportunities, one would indeed find more species, but the average abundance per species would remain the same or decrease; certainly it would not increase. But in our results it does. To account for this it seems necessary to postulate that at least some of the extra diversity is a consequence of increased density.

An increased density of birds in the understory could result from a greater concentration of foraging substrate (foliage), reduced mortality (predation, disease, etc.), or a higher productivity of food resources. Greater amounts of foliage in the understory might result in increased foraging activity at net level, though, as mentioned above, maximum foliage densities near the ground are attained above 2,000 m where both density and diversity are declining. We have no information on mortality factors, nor is it clear what effect local variations in predators, parasites, etc. would have on diversity. Specialized bird hawks (*Microrastur*, *Accipiter*) occur in low numbers over the entire gradient. To me the most plausible cause of the midelevation "hot spot" is a greater abundance of food resources.

A more productive environment could support both a more numerous and more diverse community because it could provide essential food resources in greater amounts and in greater variety. But why should avian resources, especially insects, reach a peak in the lower cloud forest zone? Most of what follows is admittedly a *a posteriori* rationalization,

though some of the corroborative evidence is independently derived.

Productivity and the environmental gradient

The problem has two parts: why do bird densities increase from the lowlands upward into the cloud forest, and why do they then decrease at still higher elevations. In discussing this I shall assume only that there is some proportionality between the density of bird populations and the productivity of the resources that sustain them.

Taking the second part of the problem first, what is the evidence that the availability of insects may decline toward the upper part of the gradient? (1) Subjective impressions. Ants, termites and flying insects—hymenoptera, flies, cicadas, lepidoptera—are omnipresent in low-elevation forests. At night there is a constant din of insect noise, and heaps of scorched bodies accumulate under the pressure lantern. In contrast, the nighttime silence at high elevation is broken only by an occasional owl or frog. The lantern attracts nothing more than a few moths. During the day one sees no ants or termites and only an occasional butterfly during the brief periods of sunshine. (2) The number of syntopic insectivores decreases by a factor of 5 between the bottom and top of the gradient. (3) The rate at which nets capture insectivorous birds decreases by more than 10-fold between 1,500 and 3,500 m (Fig. 8). If we take into account the fact that nets sample a much larger fraction of the high-elevation community (Fig. 5), the disparity becomes something like 20- to 30-fold. (4) Janzen (1973b) has shown that arthropod density and diversity decrease sharply at high elevations in Costa Rica. While these are all statements of circumstantial evidence, taken together they argue plausibly that the decrease in diversity of insectivorous birds above 1,500 m is due at least in part to a declining resource base.

The evidence that insect densities increase upwards from the lowlands to a midelevation maximum is far less compelling. (1) There is no corresponding increase in the number of avian insectivores, only in the overlap of their foraging zones. (2) The increased capture rates could be at least partly an artifact of this and other circumstances, such as the irregular terrain. (3) Greater concentrations of foliage near the ground could result in increased foraging activity at net level in the absence of any real increase in bird numbers. (4) Still another possibility is the preemption of resources that are harvested by other taxa at lower elevations. Highly insectivorous squirrel monkeys (*Saimiri sciureus*) abound in the undisturbed lowland forest, but these animals drop out at the base of the mountains around 600 m. In the one locality for which we have reliable census data, the squirrel monkey population ($\approx 80/\text{km}^2$) has a biomass roughly equal to that of all avian insectivores in the same forest (Janson 1975). Thus, though the densities of insectivorous birds do

appear to increase at midelevations, there is little in our experience to suggest that insects do also. (5) The only direct evidence comes from Janzen's (1973a,b) sweep net survey of an elevational transect in Costa Rica in which he found maximum numbers of arthropod species and individuals in lower montane forest between 1,000 and 1,500 m. Indeed, the elevational pattern of arthropod density and diversity in his sweep net samples parallels that of our mist net results so closely as to merit further discussion.

I agree with Janzen in the feeling that the elevational pattern in arthropod abundance reflects an underlying variation in plant primary productivity. Neither of us has any direct evidence; yet there are sufficiently compelling circumstantial arguments to excuse a few lines of speculation. Janzen (1973b) maintains that net productivity can be expected to increase at midelevation because of reduced nighttime temperatures and the attendant savings in energy lost to respiration. At higher elevations, diurnal as well as nocturnal temperatures are severely depressed, resulting in lower productivity. Whether one accepts this argument or not, there are a number of additional grounds for rationalizing a midelevation productivity maximum.

First, several aspects of the lowland environment are ameliorated at midelevations in ways that would be expected to enhance photosynthetic activity.

1) Prolonged dry spells (>1 wk) are rare to nonexistent at midelevations, and accordingly there is no deciduousness, even in the tallest trees. On the other hand, droughts of a month or more are a routine annual event in the lowlands where most of the taller trees drop their leaves for some portion of the dry season, and many subcanopy species reduce their leaf volumes.

2) Middle elevations characteristically experience a propitious daily weather regimen in which the mornings and late afternoons tend to be sunny, and middays and early afternoons cloudy or rainy. Light intensity and temperature in the canopy are thus moderated through the day, mitigating the conditions that produce a midday photosynthetic depression. The Apurimac Valley lowlands, at least during the dry season, tend to be shrouded in mists for the early morning hours, and hot, dry, and sunny through the middle of the day.

3) Retarded rates of organic decomposition at middle and higher elevations may mean a more gradual release of mineral nutrients. This should imply a more continuous rate of growth than is possible in the lowlands where nutrients are released from the leaf litter in a burst at the beginning of the rainy season (Richards 1952).

4) The duff mat (25 cm thick at 1,800 m) that develops on the forest floor above 1,000 m soaks up water like a sponge, retarding runoff and buffering the superficial layers of the soil against desiccation.

Even if one were satisfied that these circumstances

pointed to rising productivity above the lowlands, it would remain to be explained why there seems to be a decline at still higher elevations. Again, there appear to be a number of contributory circumstances.

1) Reduced light intensity. The amount of cloudiness becomes extreme toward the top of the range. Even in mid dry season the summit ridge receives <20 h of sun a week, and most of this comes before 0800 when there may still be frost on the ground.

2) Low temperatures, especially low root temperatures, may adversely affect growth via retarded nutrient uptake.

3) Permanently high humidities imply low transpiration rates, another factor that could hamper nutrient uptake (Baynton 1969; Gates 1969; Weaver et al. 1973).

4) A ubiquitous carpet of sphagnum above 2,000 m lowers the pH to 4–5 in the root zone (our measurements), perhaps further exacerbating a scarcity of nutrients.

5) Drastically retarded organic decomposition at high elevations leads to the accumulation of thick peat deposits that could sequester nutrients in forms that are not readily taken up by roots.

Finally, I wish to present a piece of anecdotal evidence that to me very convincingly illustrates the existence of an optimal productivity zone in the lower montane region. It is the pattern of recent agricultural settlement in the eastern Andean sectors of Colombia, Ecuador, Peru, and Bolivia. The first colonists to arrive in an unexploited area invariably choose sites within the elevational span of 500 to 1,200 m. In most places the terrain above this level becomes too steep to cultivate easily. But even so, as the pressure of immigration continues, late-arriving settlers prefer to hack out pitiful little plots on 30 to 40 degree slopes, rather than to invade the expansive Amazonian flat lands. These people know what they are doing. It is common knowledge, gained by trial-and-error experience, that it is futile to attempt to cultivate food and cash crops much below 500 m. In Colombia, where the pressure of overpopulation is most severe, agricultural settlement has spread practically to timberline, while vast expanses of lowland forest remain virtually uninhabited. The behavior of peasant farmers is probably as good a bioassay for inherent productivity (with a correction for steepness of the terrain) as any we have.

I would not have dwelt so long on these speculative matters had I not been impressed by the striking parallels between Janzen's results and ours. In both cases maximum species diversities occurred in areas supporting maximum densities of individuals. It is tempting to imagine that an increased abundance of resources in a complex environment like a tropical forest could allow a greater array of foraging specializations to achieve profitability, thus accounting for enhanced diversity. While this interpretation has a commonsen-

sical appeal it is only suggested, not proven, by the data on hand.

BIRD SPECIES DIVERSITY IN PERSPECTIVE

The primary lesson of our examination of bird species diversity patterns in the Cordillera Vilcabamba is that diversity is a complex community phenomenon, not just a number which can be "explained" with one or another competing hypothesis. Contributory factors overlie in an intricate mosaic, so that one cannot even be assured of unidirectional trends in moving along major environmental gradients. Carefully conducted comparisons are at present our most effective means for dissecting out the important variables.

Influences of history and geography may dominate when the geographical scale of a comparison is large. Thus the factors which appear to control the trends within the 30-km Vilcabamba transect—habitat structure, abundance and qualitative balance of food resources, presence or absence of other taxa at the same trophic levels—may play minor or negligible roles in interregional comparisons. The richest mature forests in North America, for example, harbor barely half as many bird species as the stunted 4-m elfin shrubland astride the cold, mist-shrouded Vilcabamba summit ridge. Clearly the differences in habitat complexity and productivity run the wrong way to explain this seemingly paradoxical contrast. I side with MacArthur (1969) in thinking that evolutionary processes (speciation, immigration, and extinction) are largely at the root of such interregional differences, as I have already expounded elsewhere (Terborgh 1973b).

The possible causal connections between productivity and diversity remain problematical. An increased abundance of resources could provide sustenance for additional species through either or both of two mechanisms: the availability of broadened resource spectra or the availability of the same basic spectrum of resources in a greater variety of sites in a complex environment. It goes without saying that a necessary condition for a positive response to a high productivity site is the presence of appropriately adapted species in adjacent habitats. Merely fertilizing a pond or a piece of grassland may not provide an adequate test, because it creates a novel situation to which many of the species present are not adapted. Resource spectra may consequently narrow instead of broaden.

Diversity has proven difficult to study because it lies at the end of a number of interacting causal chains, often several steps removed from the things we are able to measure. Even if we could measure the whole gamut of proximate variables—the precise habitat needs of individual species, resource spectra, the pressure of interspecific competition, etc.—we would still have to contend with historical/evolutionary influences in accounting for interregional contrasts. The contribution of this work has not been in resolving issues so much as in demonstrating the composite na-

ture of the diversity problem and the essentiality of reducing it to its component parts as a precondition for further understanding.

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