

# GEOGRAPHICAL VARIATION IN THE AVIFAUNAS OF TROPICAL FOREST UNDERGROWTH

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**ABSTRACT.**—The species richness and guild structure of the avifaunas of tropical forest undergrowth vary among tropical regions. Avifaunas of Central American forests are the richest, while those from Malaysia and Africa are less diverse. Dry, disturbed, and island forests in the tropics contain even fewer species. Neotropical samples contain the largest number of guilds. Guild “signatures” (distribution of species and individuals among guilds) are relatively similar among samples from the same geographic region but differ among regions. Presence, richness, and number of individuals vary from continent to continent among the guilds. The foliage-gleaning insectivore guild is invariably the most diverse guild. The irregularity of guild patterns among regions emphasizes the need to examine evolutionary pressures and their variation among guilds instead of their composite effects, which produce the entire community. Geographic proximity seems to be the primary factor producing similar guild signatures among samples, but climate (especially seasonal temperature and rainfall patterns) also produces similarities in species richness and guild composition. Nonconvergences among regions occur frequently and seem attributable to a variety of historical (e.g. Pleistocene) and biotic (e.g. coevolution, priority of arrival and diversification of several taxa) effects. Ecologists should devote at least as much effort to the explanation of the nonconvergence situations as to those demonstrating convergence. A preliminary conceptual model is proposed to help focus studies on the major variables that affect the evolution of avian communities. This model clearly demonstrates the folly of seeking a single factor as the sole determinant of avian community structure. *Received 9 July 1979, accepted 28 December 1979.*

THE most diverse terrestrial communities occur in the lowland tropics in environments with relatively stable temperatures and high humidity. These environments and their associated biotas occur in several widely separated geographic regions and exhibit a number of similarities in both structural and functional characteristics (Richards 1966). The diversity of these biotas has often been attributed to their relatively stable and benign environments.

Biotic and abiotic factors may differ among areas, however, and thus limit the extent of convergence among lowland wet-forest biotas (Karr 1976b). Important factors may include historical influences, such as accidents of biogeography (oilbirds in the neotropics), effects of geographic and topographic complexity (mountain “spine” of South America vs. uplifted plateaus of Africa), climatic effects (Pleistocene and recent), and a variety of coevolutionary patterns among organisms. Thus, we might expect both convergences and divergences among biotas of tropical regions with similar weather cycles. These differences might produce variation in community attributes such as species richness and trophic structure.

Carefully standardized surveys are needed from many study regions before the factors that produce these patterns can be characterized. Conventional survey procedures (Robbins 1978) require familiarity with the birds and their voices and extended field studies. Judicious use of mist nets provides a mechanism whereby quantitatively reliable data on the bird faunas of the undergrowth of tropical forests may be obtained (Karr 1979a). In this paper I present the results of such surveys from several tropical regions while addressing the following questions:

1. How much variation exists in species richness and trophic structure of undergrowth avifaunas within and between continents?

2. Are all guilds represented in all geographic regions?
3. Does species richness for a specific guild vary among continents?
4. To what extent is it possible to assign ecological and evolutionary reasons for the observed patterns?

#### STUDY AREAS AND METHODS

All areas were sampled using a standardized mist-net procedure originally developed in 1968–69 in Panama (Karr 1979a). Generally, I operated about twelve 12-m mist nets (36-mm mesh) for 3–5 days. Nets were located inside the forest in what seemed to be good locations based upon experience and intuition. No effort was made to keep nets in a straight line or to standardize distances between nets. In practice, inter-net distances generally were about 20 m. I avoided established trails of more than a meter or two in width or other areas where sunflecks reached the ground and thus silhouetted nets. Cutting required to clear net lanes was minimized.

Each net was set with the lower shelf at the ground through most of its length and with sufficient slack in each shelf to reduce the number of birds that bounce out of the net. Nets were opened just before first light and operated until midday, when capture rates declined (pers. obs., Medway 1969, Okia 1976). These nets captured most birds in the 5–100-g weight range; the surveys thus did not depend upon knowledge of vocalizations of birds or an ability to identify birds seen only fleetingly. All birds were released at the capture site.

I have conducted mist-net surveys in Panama, Costa Rica, Liberia, Ghana, Kenya, India, and Malaysia. Because there was some variation in the sample sizes among areas and in the habitat sampled, however, this report will emphasize results from moist lowland tropical forests. For these habitats, which were in Panama, Liberia, and Gabon, I attempted to match vegetation structure and to use areas with minimum human disturbance. My sample from suitable Malaysian forest is small, so I consider a more substantial sample from the same site provided by Dr. David Wells. As will be discussed below, the collection techniques for that sample were different from those outlined above. Descriptions of study plots have appeared previously: Panama (Karr 1971, 1976a); Costa Rica (Karr et al. 1978); Liberia, Ghana, Gabon, Kenya (Karr 1976b); India, Malaysia (Karr 1976c).

#### RESULTS

*Species richness.*—One index of community structure is the number of species found in an area (species richness). A convenient estimate of species richness ( $S$ ) is the number of species included in a standard sample of 100 captures ( $N$ ) from a species-sample curve analogous to the species area curve of plant ecology (Mueller-Dombois and Ellenberg 1974). Only a few days are required to accumulate 100 captures, and results are consistent among samples from the same location as well as among regions (Fig. 1). Using the four tropical forest sites (Panama, Liberia, Gabon, Malaysia), I found that correlation coefficients for the power function [ $\ln(S) = A + Z \ln(N)$ ] are higher (0.98–0.99) than for exponential [ $S = A + B \ln(N)$ ; 0.92–0.96] and linear (0.95–0.99) functions ( $S$  = number of species,  $N$  = number of captures, and  $A$ ,  $B$ , and  $Z$  are fitted constants). The same pattern is true for a much wider array of sites, including second-growth, disturbed, island, and temperate samples. This suggests that  $S$  continues to increase with  $N$  and, at least for 100-bird samples, does not approach an asymptote. The largest available sample (Panama forest—1,286 captures) yields a correlation coefficient for the power function (0.983) that does not differ ( $P > 0.10$ ) from the exponential function (0.989), illustrating that an asymptote is approached with a very large sample size.

$S(N)$  is, of course, affected by the species-abundance distribution. This could lead to spurious differences when unusually rare or abundant guilds affect  $N$  and  $S$  of other guilds, because  $N$  is not related to area or capture time. Two alternatives exist to solve this problem. First, I might examine communities using capture time rather

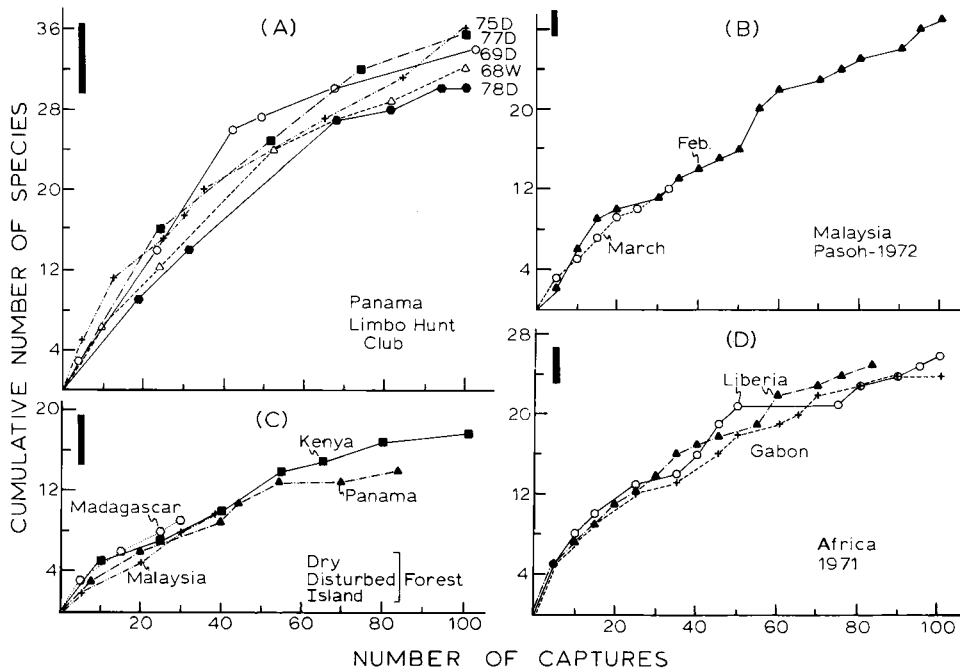


Fig. 1. Cumulative number of bird species captured in undergrowth mist nets. **A.** One wet (W) and four dry (D) seasons at Limbo Hunt Club, Pipeline Road, Panama. **B.** Two 1972 samples, Pasoh Forest, Malaysia. **C.** Selected dry, disturbed, and island forests. **D.** One Gabonaise and two Liberian forest samples. Note that the number of species in 100-bird samples varies among regions (dark bars).

than  $N$ . This has the disadvantage of richness and guild comparisons becoming more a function of absolute density than of richness and trophic structure. Further, at least among my lowland forest sites, the time required to accumulate 100 captures is very similar (Panama—288 net hours, Liberia—287; Gabon—290), suggesting that these are truly species-time curves.

A second alternative involves obtaining larger sample sizes ( $N$ ). This could be done by deploying more nets over a larger area or by sampling for a longer period in the same study site. Both have major disadvantages. Deploying more nets involves sampling from a wider array of microhabitats, thus increasing species richness for other reasons. This may be the reason for the high slope of the accumulation curve in a Malaysian sample (Fig. 1b) and its higher linear correlation coefficient ( $r = 0.985$ ). Large sample sizes could also be obtained by netting for a longer sequence of days or by halting netting operations and returning several weeks later. Capture rates decline to near zero after the third day (Karr 1971, 1979a), and thus the value of continued netting is minimized. Netting after a period of several weeks results in increasingly diverse samples because of the temporal shifts in avifaunal composition (Karr et al. 1980), especially when sampling periods overlap two major seasonal periods (dry-wet transition) or periods before and after local or long distance migrations (e.g. arrival of birds that breed in temperate zones). In my experience, a 100-bird sample is a suitable compromise in light of these conflicting problems. O. Järvinen (pers. comm.) has reached the same conclusion in studies of Finnish birds.

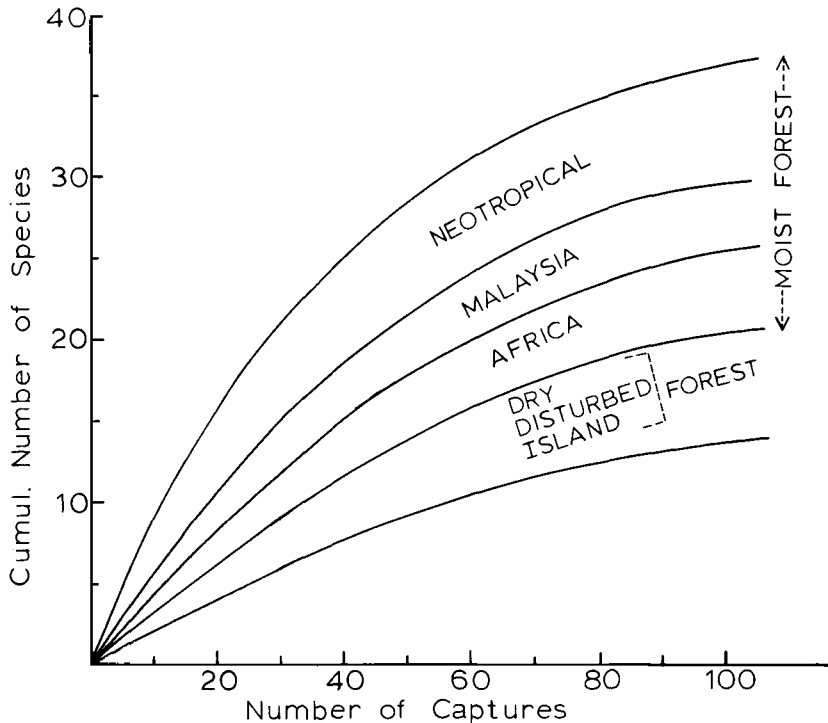


Fig. 2. Generalized diagram showing geographic variation in the species richness of the avifaunas of tropical forest undergrowth.

Thus, I have opted to use the  $S(N)$  function as a somewhat flawed but functional measure of the community attributes of interest.

In addition to similarities in the species-sample curves within a site (Fig. 1a), wet forests within a biogeographic region have similar numbers of species in a standard 100-bird sample (Fig. 1b, d). The accumulation of species is not consistent among the biogeographic regions, however, either graphically, by inspection of Fig. 1, or statistically. The slope of the power function and, thus, the species accumulation rate are higher ( $P < 0.05$ ) for the Panama forest ( $Z = 0.718$ ) than for the African study sites (Liberia:  $Z = 0.646$ ; Gabon:  $Z = 0.639$ ). The slope for the Malaysian forest ( $Z = 0.754$ ) is higher than that for the African samples ( $P < 0.05$ ) but not significantly different from the Panama sample. The intercept of the Malaysian forest ( $-0.089$ ), however, is below that for Panama ( $0.372$ ). The effect of the larger number of nets and their distribution over a larger study plot in the Malaysian forest almost certainly produces the higher rate of accumulation of species (slope) for that plot, as discussed briefly above.

In summary, the species richness of undisturbed forest in Central America is highest, while Malaysian and African forests contain fewer rich undergrowth avifaunas (Fig. 2). Undergrowth avifaunas of South American forests are the richest in the world (Terborgh and Weske 1969, Novaes 1969). Less complete samples from dry, disturbed, and island forests in several tropical regions contain even fewer species (Fig. 1d). Because many of the latter samples contain fewer than 100 captures, they will not be considered further here.

*Trophic structure.*—Another index of community structure can be obtained by examination of the trophic structure of the avifauna. Species richness varies within a community among the feeding guilds (Fogden 1972, Karr 1976b, Pearson 1977). In addition, the species richnesses of these trophic groups are not quantitatively consistent among the geographical regions. For example, 29% (16 of 56) of forest residents in Panama depend upon fruit resources to a major extent, while only 16% (8 of 50) of the forest residents in a Liberian forest depend upon fruits as a primary food resource (Karr 1976b). The differences in species richness of guilds among regions seem to be due to a complex of historical influences and to differing potentials for diversification among resource types (especially food types). Thus, community comparisons among geographical regions must include an analysis of other community characteristics in addition to number of species (Karr 1976a, b; Terborgh 1977).

The birds of tropical forest undergrowth consume a variety of resources, with foraging behavior and substrate utilization varying among species. Ten primary guilds are recognizable in the size range of birds readily captured in mist nets, and several other guilds are represented sporadically (see Appendix). Sporadically captured guilds (lumped as "Msc.") include species of irregular occurrence or of a size that makes them difficult to capture in 36-mm mesh nets. Carnivores, nocturnal insectivores, and piscivores are examples of such guilds. These and the primary guilds should be considered as generalized groups, because detailed food-habits information is available for few tropical forest species. I depended upon personal experience, various published sources, and the advice of experts from each geographic area in the assignment of species to a specific guild.

*Guild "signature."*—In addition to variation among the areas in the number of species represented in 100-bird samples, the number and diversity of guilds represented also varies. Nine guilds (seven samples) are always represented in the Panama forest (excluding the Msc. category). The two African forest samples contain 6 and 8 guilds, while the Malaysian sample includes 6 guilds.

The distribution of species (Fig. 3) and individuals among guilds is relatively stable among samples from the same geographic region but differs among regions. The configuration of the bar graphs (the "guild signature") is similar among samples from Panama (Fig. 3). The Costa Rican samples from midelevation forest (San Vito) and from wet lowland forest (Osa Peninsula) have a more equitable distribution among guilds than do samples from Panama, perhaps due to their more uniformly wet climates.

Two guilds (undergrowth insectivore-frugivores and bark insectivores) are represented by one species each in the Gabonese sample but are not represented in Liberia; otherwise, the ecological structures of the two African samples are very similar. Comparison of these guild signatures for African and neotropical forest parallel the patterns described earlier for these two regions (Karr 1976b, Pearson 1977; e.g. reduced diversity of frugivores and bark gleaners in Africa as compared in neotropical sites).

The Malaysian sample is noteworthy in several respects but especially in the lack of undergrowth frugivores. (Recall that this discussion is concerned with the undergrowth avifauna. Canopy frugivores are common in the Malaysian forest.) The reasons for this are not clear but are supported by the independent development of the same conclusion by Janzen (1980) following a survey of Malaysian forest.

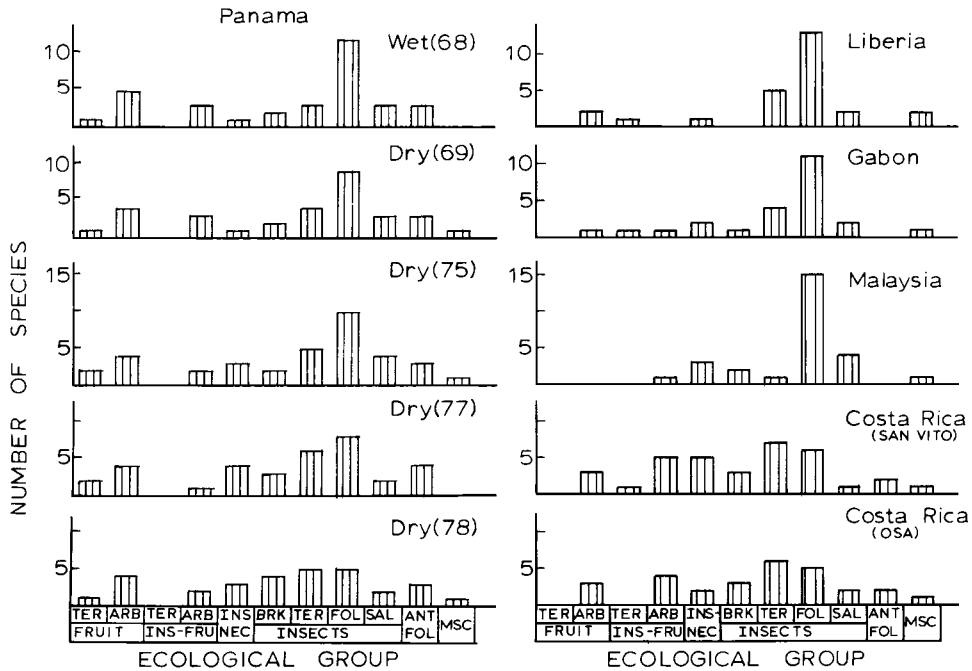


Fig. 3. Guild signatures (number of species in each ecological group) represented in 100-bird mist-net samples from the undergrowth of tropical forests. See Appendix for description of guilds.

The low diversity of terrestrial insectivores in Malaysia is also in sharp contrast to African and Neotropical samples. Presumably this is due to some characteristic of leaf litter dynamics. Diurnal termite activity (outside of covered runways) is common in Malaysian forest, but I have never observed similar behavior in Africa or the Neotropics. Could bird evolution be affected by changes in termite evolution and, therefore, leaf litter dynamics?

Another striking divergence among the geographic regions is the presence of professional ant-followers only in the New World. No species follows raiding columns of ants in Southeast Asia, while several species follow driver ants in Africa. My experience in Africa, however, suggests that these ants are a much less reliable resource for birds than their New World counterparts, the army ants (Willis and Oniki 1978), primarily because of differences in the seasonal and diurnal pattern of raiding (Karr 1976b; see also Wilson 1971 for more details of ant biology). No African birds seem to be totally dependent on ants for their food supply, but several New World genera (e.g. the antbirds *Gymnopithys*, *Phaenostictus*) are.

Guild signatures based upon number of individuals illustrate the varying patterns of relative abundances per species among the guilds (Table 1). The foliage-insectivore guild has the highest species richness in all four tropical forests, while the richness of the arboreal frugivores is lower. In contrast, the number of individuals (total and per species) is relatively low among the foliage-insectivores but high among the arboreal frugivores. As Diamond (1973) has demonstrated for New Guinea fruit pigeons, the major axis of segregation among species is by size of fruits. The undergrowth of tropical forests generally has a very restricted range of fruit sizes.

TABLE 1. Species richness and number of individuals per species for foliage-insectivore and undergrowth-frugivore guilds in four tropical regions. Based on 100-bird mist-net samples.

Study area	Number of species		Number of individuals per species	
	Foliage-insectivore	Undergrowth-frugivore	Foliage-insectivore	Undergrowth-frugivore
Panama	9	4	2.0	8.3
Liberia	13	2	2.3	11.5
Gabon	11	1	3.8	15.0
Malaysia	15	0	4.7	—

Thus, the potential for frugivore diversification is low. The high abundance of fruits when they are present, however, supports relatively high abundances of frugivorous birds.

In contrast, foliage-gleaning insectivores diversify rapidly along size, foraging location (dead leaf clumps, living leaves, etc.), and foraging behavior (searchers, pursuers, sit-and-wait pouncers, etc.) axes. This proliferation is probably related to the specialization required for efficient foraging in a variety of places on food items (insects) that are under strong selection for protective coloration and behaviors (in contrast to fruits, which are advertised). The resource quantity per specialized species is low; thus the abundances per species tend to be low. In addition, the fact that fruits are one or two trophic levels lower than insects on the trophic web may account for increased total abundances of frugivores. Other guilds (especially insectivores) exhibit intermediate tendencies in the interaction of richness and total abundance.

Although these general patterns remain consistent, the relative abundances per species do not remain consistent within a single guild for Africa and the Neotropics. (Recall that the numbers of net hours required to accumulate 100-bird samples are very similar among these three major sample areas.) The number of individuals per species is higher in Africa than in Panama for the arboreal frugivores (13.3 vs. 8.3), insectivore-nectarivores (9.0 vs. 3.4), and ground insectivores (4.5 vs. 2.3), respectively (Mann-Whitney *U*-test,  $P < 0.05$ ). Undergrowth insectivore-frugivores are captured more rapidly per species in Panama (2.5) than in Africa (1.0). No significant patterns exist between the two regions for the other guilds. Presumably the captures per species vary geographically because of varying availability of resources.

*Similarity among samples.*—The analyses of the guild signatures suggest that there are consistent patterns of similarities among samples from the same geographic region and differences among samples from different geographic regions. A cluster analysis (weighted pair-group method using arithmetic averages, Sokal and Sneath 1963) using Horn's (1966) information-theory based, ecological-overlap index demonstrates the affinities of the guild signatures among the samples (Fig. 4). The first major cluster is the five samples from Limbo Hunt Club in Panama. The next group to join the Panama cluster contains the two samples from Costa Rica. Much later, the two ecologically similar African samples join and, finally, the very different Malaysian sample is added. This provides a quantitative demonstration of the differences observable by examination of the guild signatures of the communities (Fig. 3).

When the number of individuals is considered, the clustering of samples is similar, except that the African areas fuse with the Neotropical areas in a somewhat unex-

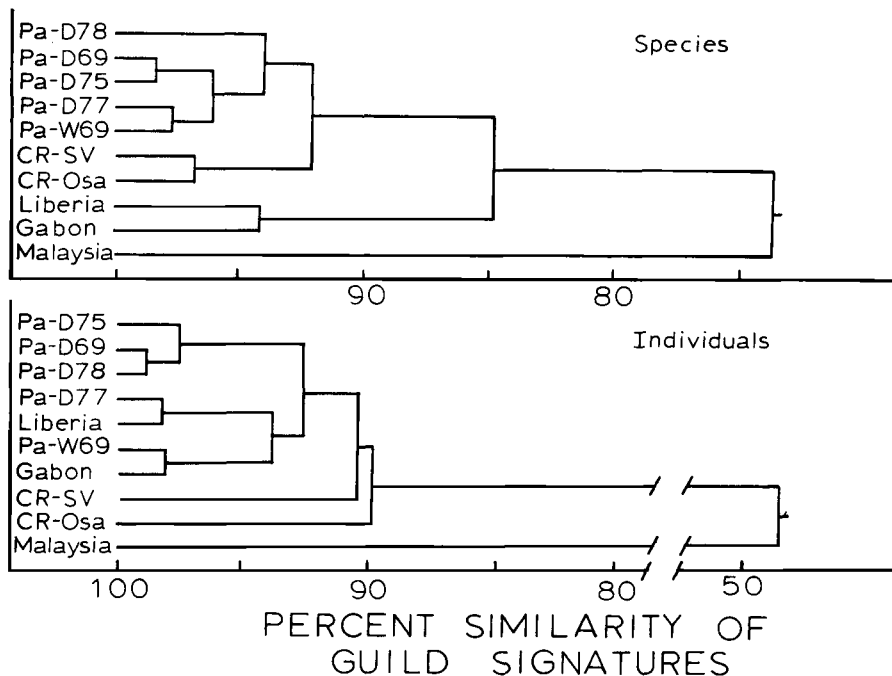


Fig. 4. Dendrograms for percent similarity of guild signatures for 100-bird samples from lowland tropical forests. Pa = Limbo Hunt Club, Panama; CR-SV = San Vito, Costa Rica; CR-OSA = Osa Peninsula, Costa Rica; D78 = Dry season 1978; W69 = Wet season 1969; etc.

pected manner. The two African samples and five Panamanian samples cluster together. These are joined by the two Costa Rican samples. All of these fuse by about the 90% level and are joined much later by the Malaysian sample at somewhat below 50%.

These results demonstrate that the similarity of species richness and trophic structure among samples from a single area is striking when different geographic areas are broadly compared. More detailed comparisons, however, show considerable dynamics over time within a single fauna. Over a series of five dry-season samples from a Panama forest site, the number of species (range 30–38) is inversely correlated with March (the sample month) rainfall (Kendall's  $\tau = 0.80$ ,  $P = 0.042$ ). Further, there are changes in species composition and guild structure that seem to be attributable to changes in weather between years (wet vs. dry dry season) and to changes in vegetation structure, especially increased area of treefall gaps (Karr 1979b, Karr et al. 1980). Such patterns, while not the central theme of this paper, are relevant to the caution of Connell (1978) against assuming that tropical forest communities are stable over time.

#### DISCUSSION

These results show clearly that the avifaunas of moist tropical forest undergrowth differ among continental areas in both species richness and trophic structure. It is also true that moist tropical forests support more species than do dry or island forests in the tropics. The general similarity in the 100-bird samples within each zoogeo-



graphic region illustrates that faunas on the same continent (and under similar ecological conditions) are more similar to each other in species richness (Fig. 2) and trophic structure (Fig. 3) than to faunas on the other continents. These similarities are presumably due to common ecological and evolutionary history. Although Malaysia and Africa are broadly connected by an overland route and the taxonomic composition of the faunas is similar at the family level, they are not more similar to each other than either is to the Neotropics, especially for trophic structure (Figs. 3, 4). This suggests that factors in addition to biogeographic affinity, a component of evolutionary history, are important in influencing community structure.

General similarities among the faunas can also be discerned for both species richness and trophic structure, presumably due to environmental factors such as similarity in physical (climatic) conditions. The degree of convergence is less than perfect, however, as there are small but consistent differences in the number of species among tropical regions. More important, it is manifest in faunas with differing trophic structure. The variables that produce these intercommunity differences are at best very difficult to segregate. Notable among these is a complex of biotic interactions that may, in part, be subsumed under historical factors but are also of sufficient significance that they should be discussed in their own right. Within this class I include the presence of ants with a natural history suitable to the support of professional ant-followers, and the apparent lack of suitable fruits and, therefore, of frugivorous birds in Southeast Asia. In the latter case, the periodic mast of the dominant plant family in Asian forests may limit fruit availability in the undergrowth and thus limit the potential evolution of the undergrowth frugivore guild. Nonavian competitors for a variety of food resources may also be important in biotic interactions, as has been indicated by Pianka and Huey (1971), Karr (1976b), and Pearson (1977).

#### DIRECTIONS FOR FUTURE STUDIES

The past decade has seen a tremendous proliferation of studies on the evolution of avian communities. Many have been descriptive, while others have set out to test hypotheses about the importance of a variety of factors (predation, competition, etc.) as determinants of community structure. Some have taken a broad-scale, geographic pattern as their focus, while others have examined a successional pattern or a pattern among a series of similar vegetation types. Each approach has yielded insights into avian community organization, but there have been relatively few efforts to synthesize this disparate literature.

A review of that literature leads me to propose a complex of factors (and their interactions) as the primary determinants of avian community structure (Fig. 5). From left to right in Fig. 5, time and geographic scale decrease and the local, short-term dynamics become more important. The following discussion highlights selected studies that demonstrate the relevance of each factor as a determinant of avian community structure. In addition, I try to show some of the important interactions among factors. Clearly, this brief review must be superficial in many respects. It is simply not possible to cite more than a few relevant studies for each subject. My apologies to those whose work is both relevant and significant but has not been cited.

I propose this general and very tentative model in hopes of stimulating a more organized and systematic approach to the study of avian community structure. It

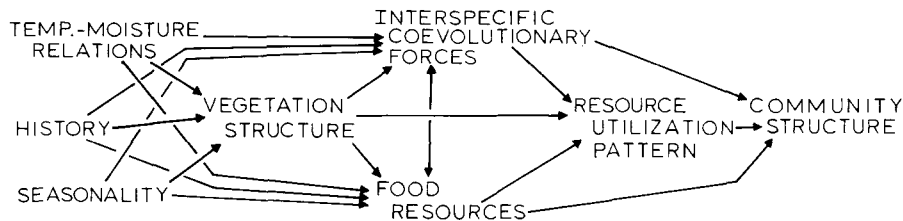


Fig. 5. Conceptual model showing the primary variables (and their interactions) that govern the development of avian community structure.

might also be useful as a foundation in organizing thoughts on the determinants of community structure among other taxa.

*History.*—Since Darwin's pioneering studies in evolution, the primary role of history in biotic evolution has been recognized. The distribution and abundance of dispersal barriers are obvious examples. More recently, the dynamics of climatic cycles have been emphasized as determinants of avian evolution (Moreau 1966, Haffer 1969). Other examples illustrating the role of history relate to the occupation of trophic roles by different taxonomic entities on different continents and the geographic extent of habitat "islands" in determining community structure on oceanic islands (Diamond 1972, Cox and Ricklefs 1977) and continental areas (Howell 1971, Cody 1975, Karr 1976b).

*Temperature-moisture relations.*—That temperature and moisture conditions play a major role in biotic evolution is widely recognized. Chronic environmental hardships associated with cool environments at high elevation generally result in depauperate avifaunas (Terborgh 1977). More subtle influences of temperature-moisture relations include weather-dependent foraging (Grubb 1975), bird size and energetic relationships (James 1969), and alteration of breeding periodicity (Balda 1972). At the community level, grasslands at low rainfall sites support fewer species and lower biomass than mesic sites (Wiens 1973). The guild structure of coniferous forest avifaunas varies as environmental conditions (especially rainfall) become more severe (Wiens and Nussbaum 1975).

*Seasonality.*—The temporal dynamics of environmental conditions have also been shown to play a role in avian evolution. Both the amplitude of environmental fluctuations and their predictability are of special significance to organisms. Seasonal patterns of weather determine the timing of migration with variation in the precision of that timing between spring and fall (Buskirk 1980). Numerous studies have demonstrated the importance of seasonal rhythms in determining breeding seasons (Immelmann 1971). Tramer (1969) first suggested the role of seasonal mediation of species diversity patterns; diversity changes with richness in stable, benign environments near equilibrium but varies with evenness under unstable, rigorous conditions in which populations are held below equilibrium. More recently, this hypothesis has been used to explain long-term yearly and/or large-scale geographic variation in local community structure (Rotenberry et al. 1979). The concept of "lean season" (Fogden 1972) is relevant when events recur in each annual cycle or in the "bottleneck" (Wiens 1977) concept over longer temporal cycles. The seasonal dynamics of weather on food resources has been stressed for entire communities (Kricher 1972, 1973) as well as for various species exploiting specific food resources and/or microhabitats (Wolf 1970, Leck 1972, Karr 1976b, Foster 1977). Seasonal patterns may directly

affect shifts in foraging behavior or location (Willson 1970, Grubb 1975) or may be linked to complex food-resource and competition dynamics.

*Vegetation structure.*—The most extensively documented determinant of avian community structure is vegetation structure. Although the principles of this relationship were recognized several decades ago (Pitelka 1941, Beecher 1942, Kendeigh 1945), modern emphasis on this subject was stimulated especially by the work of MacArthur and MacArthur (1961). Numerous subsequent studies implied causal but typically unexplained relationships between foliage structure and bird-species diversity. Some researchers encountered difficulties in detecting simple relationships (Balda 1969, Lovejoy 1975, Tomoff 1974) and thus proposed other patterns, such as plant-species diversity (Lovejoy 1975), physiognomy, and horizontal heterogeneity (Blondel et al. 1973; Wiens 1973, 1974; Roth 1976), as well as foliage volume (Karr 1968, Balda 1969, Karr and Roth 1971). Foliage volume may be an especially useful concept in producing a biological explanation for the habitat structure–avian diversity relationship (Willson 1974). The importance of foliage structure in habitat selection (“the niche gestalt”) was clearly demonstrated by James (1971). More recently, Holmes et al. (1979) have demonstrated that height-related matters contribute to initial segregation by avian guilds, followed by location relative to tree trunks, with each region being exploited by species with special morphology and behavior (see also Willson 1974).

*Interspecific coevolutionary forces.*—The importance of competition as a determinant of avian community structure has been a dominant theme for a number of years (MacArthur 1972, Cody and Diamond 1975). Recently, Wiens (1977) has argued very cogently that support for the competition theory “seems largely based on intuition and indirect evidence.” The arbitrary and often subjective combining of resource axes has been a point of contention for some time. Some of the best evidence of the importance of competition derives from studies of niche shifts on islands (MacArthur et al. 1972, Diamond 1970). Others have drawn attention to the need to consider competitive effects with other taxa, such as primates (Pearson 1975), bats (Fenton and Fleming 1976), and spiders (Pearson 1977). Some deny or minimize the importance of predation (Fogden 1972), while others emphasize the importance of predation as a determinant of community structure (Connell 1975, Oniki 1979).

Finally, the network of interconnections to coevolutionary pressures is clear from studies of nectarivores (Feinsinger 1976) and frugivores (Leck 1972, Howe and Estabrook 1977, Thompson and Willson 1979). In the aggregate, these and other coevolutionary pressures play a major role in structuring avian communities.

*Food resources.*—Several components of food-resource availability play major roles in determining avian community structure. These include type of resource, quantity of resource, and spatial and temporal distribution of resources (MacArthur 1972). Seasonal shifts in food availability are especially important in determining regular migration patterns (temperate-tropical) as well as local movements, which may be regular or sporadic (Keast and Morton 1980). In addition, food resources are important in determining breeding season (Beals 1969, Dingle and Khamala 1972) as well as molt. In Sarawak, for example, molt phenology varies among insectivores due to seasonal stability of food availability (Fogden 1972); molt may be arrested at the onset of the lean season. Guild addition in a successional sequence of habitat types shows the role of food resources in governing community structure (Willson 1974).

Limited availability of specific food resources (even for short periods) may limit

evolution of specialists and thus diversification in an avifauna (Karr 1976b). Seasonal shifts in food exploitation and/or foraging substrate (Anderson 1972, Wiens 1975), however, may mitigate limited seasonal availability of specific resources. While some have emphasized the importance of production (Connell and Orias 1964), others have emphasized the availability of resources above threshold levels (MacArthur 1970) as well as the diversity of resource types available (Orias 1969, Karr 1976a). Diversity of types may allow addition of new specialist species; in addition, the generalist may survive in an area by exploiting several resource types opportunistically when it would not be able to inject itself into a community because of limitation in the availability of a single resource.

The complex role of food resources as determinants of community structure illustrates the linkages among the variables in Fig. 5. The spatial and, especially, temporal distribution of resources is, to a great extent, determined by seasonal patterns. Thus, seasonality plays a role directly, as discussed above, and also with food-resource dynamics as an intervening variable. Because of the need for brevity and simplicity, the present discussion underemphasizes the complex interactions of the primary variables (Fig. 5).

*Resource utilization pattern.*—The roles of physical environment, food-resource availability, and coevolutionary forces interact in very complex ways to determine patterns of resource utilization by individual species and, in the aggregate, by communities. These interactions may be observed in the wealth of behavioral patterns within specific taxa (e.g. Tyrannidae) or in patterns of habitat selection. Both horizontal and vertical segregation have been documented among congeners (Catchpole 1973) and have been recognized in habitat mosaics such as light gaps produced by treefalls (Willson and Moriarty 1976, Schemske and Brokaw MS). At the community level, horizontal and vertical habitat segregation vary within and between habitats between tropical and temperate avifaunas, as well as among tropical habitats (Cody 1975, Karr 1976b). There is substantial evidence that rare species tend to be habitat specialists, while more abundant species are habitat generalists (Lovejoy 1975, Wiens 1975). Finally, as discussed in this paper, the food resources themselves (fruits vs. insects) may play a major role in governing resource-utilization patterns and, thus, community development.

Clearly, the process of community development involves a complex mosaic of environmental factors and biotic responses including interactions among species. The challenge is to sort out how these interactions in the aggregate have produced specific community complexes among geographic regions. The interesting question then becomes—why and how have the specific differences arisen?

Without doubt, the linkages involved vary in relative importance from place to place, even over time in the same place. This conclusion, to a significant extent, represents a divergence from the popular approach to the study of community evolution. In my opinion, too many researchers try to attribute patterns in nature to a single causal agent (e.g. competition), when in fact a complex mosaic of factors interact to produce specific communities of coexisting taxa. Detailed elucidation and comprehension of these interrelationships will, in the future, depend upon the development of innovative experimental approaches. Much can still be accomplished by examination of carefully selected plots representing a range of natural experiments, especially over extended periods that represent the range of potential environmental conditions at a site.

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APPENDIX. Primary trophic groups represented in mist-net samples of birds using the undergrowth of forest habitats.

Trophic group <sup>a</sup>	Food type	Feeding location or behavior
1. Terrestrial frugivore	Fruits	Collect and eat fruits that have fallen to the ground.
2. Undergrowth frugivore	Fruits	Glean fruits from the shrubs and branches of small trees.
3. Terrestrial insectivore-frugivore	Mixed insect, <sup>b</sup> fruit	Glean from ground.
4. Undergrowth insectivore-frugivore	Mixed insect, fruit	Glean from shrubs and branches.
5. Insectivore-nectarivore	Mixed insect, nectar	Feed in association with flowers to a major extent.
6. Bark-gleaning insectivore	Insects	Glean from trunk and large branches.
7. Terrestrial (ground-gleaning) insectivore	Insects	Glean from the ground.
8. Foliage-gleaning insectivore	Insects	Glean from leaves and twigs.
9. Flycatching insectivore	Insects	Sally forth from a branch to capture flying insects.
10. Ant-following insectivores	Insects	Accompany raiding parties of ants and feed on arthropods fleeing the ants; >50% food obtained in this way.
11. Miscellaneous	Number of species with other foods and/or foraging stations. These include raptors and fish-eaters.	

<sup>a</sup> Species for which two resources each compose >25% of the diet are placed in mixed guilds, such as insectivore-frugivore.

<sup>b</sup> Insects in this context include all arthropods.