Species richness and morphological diversity of passerine birds

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The relationship between species richness and the occupation of niche space can provide insight into the processes that shape patterns of biodiversity. For example, if species interactions constrained coexistence, one might expect tendencies toward even spacing within niche space and positive relationships between diversity and total niche volume. I use morphological diversity of passerine birds as a proxy for diet, foraging maneuvers, and foraging substrates and examine the morphological space occupied by regional and local passerine avifaunas. Although independently diversified regional faunas exhibit convergent morphology, species are clustered rather than evenly distributed, the volume of the morphological space is weakly related to number of species within both regional avifaunas and local assemblages. These results seemingly contradict patterns expected when species interactions constrain regional or local diversity, and they suggest a larger role for diversification, extinction, and dispersal limitation in shaping species richness.

Although species richness varies predictably with latitude and other environmental gradients (1, 2), the mechanisms responsible for geographic patterns in biodiversity remain poorly understood (3, 4). Classic niche-based hypotheses argue that local species richness is related to the variety of available resources, including escape space from enemies (5, 6), which are partitioned among species to reduce interspecific competition and thereby allow coexistence (7–10). Modifications of niche-based theory incorporating, for example, spatial and temporal variation in the environment (11), relax this prediction but have not been assessed by empirical studies. More recent consumer-resource models have addressed conditions for coexistence of similar species (e.g., refs. 12 and 13). These involve small numbers of species in simplified environments, although they do contain many basic elements of more complex natural systems. Alternatively, diversification-based hypotheses posit that elevated rates of species production compared with extinction within a region push up steady-state levels of diversity and pack species more tightly into available ecological space, tending to decouple the relationship between species richness and niche space (14–16). Ecologists have not evaluated these hypotheses adequately, in part because of the difficulty of measuring niche space and its partitioning among species (e.g., refs. 17 and 18), although the idea that diversity generally exists in a long-term, resource-influenced equilibrium has increasing support (19, 20).

Recent analyses of the phylogenetic structure of communities (21, 22) and the distribution of functional traits in communities (23–25) have attempted to address the roles of ecological specialization and species interactions in the assembly of local communities from regional species pools. These studies ask whether local communities are phylogenetically more clustered than expected in a random sample of species from the regional pool, indicating ecological filtering of suitably adapted species, or less clustered, suggesting competitive exclusion of close relatives (26). Both effects are present, although their magnitudes have not been evaluated.

Many processes influence species richness at each spatial scale, but the relationship between species richness and the variety of resources used has been analyzed quantitatively in few comparative studies (e.g., refs. 17, 27, and 28). Certainly, tropical species exhibit a fantastic variety of adaptations molded by their interactions with resources, competitors, and antagonists. Some comparisons suggest that such species interactions are stronger in the tropics than at higher latitudes, although the data on this point are sparse (29). One expects strong interactions to select for ecological specialization, but it is difficult to assess this without knowing patterns of resource utilization. In the case of terrestrial birds and bats, both of which exhibit strong latitudinal gradients in diversity, tropical environments support many species that use resources, such as nectar, fruit, and large insects, not perennially available in temperate latitudes (30–32). However, even among ecologically homogeneous phylogenetic groups, including many families of passerine birds, tropical regions harbor many more species than temperate regions.

Patterns of species richness across spatial scales represent a balance between the regional production of new species and the local interactions of species, primarily through competition for shared resources (33). Analysis of reconstructed phylogenetic branching patterns suggests that diversification becomes limited as a clade—the species descending from a single common ancestor—fills ecological niche space (19). The number of species in a clade also increases with the size of the region within which it occurs (16) but is independent of clade age (19, 20, 34, 35); regardless of their age, family-level clades in tropical regions tend to be more species-rich than those of similar rank restricted to temperate and boreal latitudes (15, 34). If clade size—and diversity more generally—were constrained by ecological space, one would expect more species-rich clades to occupy more ecological space, and the number of species within local areas, as well as within regions, to be related to the total ecological space available.

In this analysis, I ask, assuming that morphology indicates ecological position, whether the morphological space occupied by passerine birds (Order Passeriformes, the most species-rich ordinal clade of birds, with >6,000 spp.) increases in direct relation to the number of species at both regional and local scales. Alternatively, the larger tropical species pools might occupy similar morphological space to that of temperate species, in which case species would be more tightly packed, potentially indicating either smaller species niches or greater interspecific niche overlap.

Because of their wide range in overall diversity and degree of endemism, the avifaunas of the biogeographic regions of the earth permit comparison of largely independent outcomes of diversification at the regional level, and of species sorting

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through niche relationships and species interactions at the local level, to produce observed patterns of species diversity (36, 37). I focus on passerine birds (Order Passeriformes) because their relatively uniform morphology permits meaningful comparison of similar structures. The distribution of passerine species in ecological space has not been measured, and so I use morphological distance as a proxy for ecological relationship (38–40) to address global relationships between species richness at local to regional scales and the occupation of morphological (= niche?) space. The distributions of species in morphological space based on external measurements of the wings, legs, and beak are directly related to diet, foraging substrate, and foraging movements (41, 42) (SI Appendix, Relationship of morphology to ecology).

The core finding of this analysis is that the dimensions of occupied morphological space are weakly related, or unrelated, to the number of species within family-level evolutionary clades, biogeographic regions, and local assemblages. Thus, classical hypotheses based on competition theory and limiting similarity (43), which posit that local partitioning of the overall resource niche space constrains coexistence and that species richness consequently reflects the variety of available resources, are not clearly supported for passerine birds.

**Results**

The classic ecological precept of resource partitioning resulting from evolutionary adaptation to minimize competition suggests that species should tend toward even spacing and uniform density in ecological (and morphological) space (43, 44), although patterns of niche packing would also reflect underlying patterns of resource availability, mechanisms of diversification, and statistical central tendencies. In this analysis, passerine species are clustered toward the center of morphological space (Fig. 1 and SI Appendix, Distribution of species in PC space and Fig. S2). All seven original measurements and principal components (PCs) exhibit mild positive kurtosis, which indicates a flattened distribution compared with the normal distribution, but the tendency is not marked (SI Appendix, Principal component analysis), and the density of species packing in morphological space falls off quickly with distance from the passerine centroid (Fig. 1).

The principle of adaptive radiation states that as evolutionary lineages split and the species richness of a clade increases, the descendant species diversify ecologically to reduce competition and more fully use available resources (41, 45, 46). A taxonomically nested analysis of variance revealed that between 60% and 89% of the variance in the PC scores reflects differences between genera within families and between families within the order Passeriformes. This greatly exceeds the proportion of variance at higher taxonomic levels for population abundance and geographic and ecological distribution (47) and is consistent with early morphological diversification of the major passerine lineages and subsequent evolutionary conservatism of their morphology (48, 49) (SI Appendix, Nested taxonomic analysis of variance).

The dimensions of the log-transformed morphological space occupied by individual taxonomic families of passerine birds increases one-tenth to one-quarter as rapidly as the log-transformed number of species per family over the seven PC axes (Fig. 2 and SI Appendix, Morphological space and global family species richness). The relationships between the dispersion of species on the axes of this morphological volume and the logarithm of species richness across families are noisy, and they are triangular in form (i.e., the upper quantiles of the distributions vary little in relation to the number of species per family, and the positive regression slopes are caused by smaller families that exhibit little morphological variation among species). When the relationship between axis length and number of species was analyzed with families having 10 or more species, the slope of the relationships between the SD on axis i (s_i) and number of species per family did not differ significantly from 0 [71 families, P > 0.10, except for s_1 (overall size), P < 0.01, b = 0.152 ± 0.055], although all slopes were positive (0.046-0.095; binomial P = 0.008).

Many families of birds have global geographic distributions, and overall species richness does not reflect the number of species that compete locally for potentially shared resources. Locally, however, species do interact, and niche-based community-assembly theory combined with limiting similarity would predict that families with many locally cooccurring species occupy more ecological (and morphological) space than smaller families. Among the passerine birds in a 97-ha flood-plain forest plot at Manu, Peru (50), the relationships between number of species and SDs of species scores on the PC axes were not significant for the 10 families with more than two species (total, 129 species), although all estimated slopes were positive (SI Appendix, Morphological space and family species richness at Manu, Peru).

Morphological space seems to increase with the approximately one-fifth power of the number of species in taxonomic families, suggesting that species diversification and morphological diversification go weakly hand in hand. To what degree does this relationship apply to the major biogeographic realms, which differ widely in number of passerine species, paralleling the generally higher diversity in tropical regions and in regions with larger geographic area? The number of passerine species in the major continental biogeographic regions varies from approximately 300

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Fig. 1. Distribution of species in morphological space exhibits a strong central tendency. Left: Symbols represent 500 points whose x and y coordinates were drawn at random from bivariate normal distributions, each axis having a mean of 0 and SD of 1. The circles outline concentric shells with diameters 1, 2, or 3 SD units. Points and densities are shown for 0.5-SD-thick bands. Center: The number and density of random points at Left within 0.5-unit-thick concentric shells around the centroid. Right: Number and density of species of passerine birds within 0.5-SD-unit-thick concentric shells around the centroid of the seven-dimensional morphological space. The volume of progressively more distant concentric shells increases as the power of the number of dimensions. Although the number of species in these shells initially increases with distance from the centroid, the density of species decreases monotonically.
in the Nearctic to almost 2,200 in the Neotropics. Smaller, isolated areas, such as New Zealand and Madagascar, have many fewer species. Nonetheless, the occupation of morphological space by passerine birds within regions is unrelated to the number of species in the region (Fig. 3 and SI Appendix, Comparison of the morphological volume between regions). Morphological variation in overall size is lowest in the Ethiopian region (e, Subsaharan Africa), and it is highest in New Zealand (az), which supports the least diverse avifauna; variation in the shape axes exhibits similar absence of a relationship to species richness across regions. Moreover, neither region area nor the distinction between primarily tropical and primarily temperate environment has a significant influence on passerine morphological volume (SI Appendix, Morphological volume in relation to size and latitude of region).

The volume of morphological space occupied by species in local assemblages differs little from that of the species within entire biogeographic regions. For example, SDs of the PC scores for 34 species in eucalypt woodland near Armidale, northeastern New South Wales, Australia (51), 43 species in deciduous forest in Connecticut (Plot CT2778262 of the Breeding Bird Census) (see ref. 52), and 139 species in a flood-plain forest plot in Amazonian Peru (50), approximate those of the larger region in which each of these local areas occurs (Fig. 3 and SI Appendix, Relationship of regional to local morphological variance).

Although the morphological volumes occupied by passerine birds in the different regions are similar, the spaces for each region are displaced to varying degrees (SI Appendix, Discriminant analysis of morphological space among regions). A discriminant analysis revealed significant differences between the regions, with Australia and New Zealand being particularly distinctive; however, differences between regions represent only 4.4% of the total variance in morphology. On average, only 27% of species were uniquely assigned to their native region by discriminant analysis. Fewer than 10% of species were placed correctly in each of the large tropical regions (Neotropical, Ethiopian, Oriental), indicating the nearly complete overlap of their morphological spaces, whereas 65% of the New Zealand species, including old, endemic lineages such as the New Zealand wrens (Acanthisittidae) and wattlebirds (Callaeidae), were uniquely assigned to that region (SI Appendix, Discriminant analysis of morphological space among regions). The striking morphological similarity among the avifaunas of the large tropical regions in this analysis belies their different origins and evolutionary diversification (36). For example, although 25 families of passerine birds are shared by both the Ethiopian (41 families in total) and Oriental (47) regions, of
the 34 Neotropical families only 5 and 10 families, respectively, are shared with these other Old World tropical regions.

Discussion
The striking convergence of morphological diversity between regions, despite the partially independent origins of the avifaunas of each region, suggests that ecological relationships play a strong role in matching morphological adaptations within regional species pools and local assemblages to similar arrays of foraging substrates and food resources. That morphology reflects diet and foraging maneuvers is a cornerstone of evolutionary ecology (38, 41, 45, 53). However, to the extent that position in morphological space reflects position in ecological space, the observations related here are inconsistent with some predictions of classical niche-based hypotheses concerning patterns of biodiversity. First, although competition is generally thought to be the driving force behind phenotypic diversification (45), the present analysis provides no evidence that morphological diversification has tended to fill morphological space evenly. Instead, passerine birds are clustered toward the center of their morphological space, and most species seem to have a generalized morphology suited to a variety of foraging substrates and movements, as well as prey items. Second, number of species and volume of morphological space occupied per family are weakly related, and morphological space bears no correspondence to the number of species within large regions or local assemblages, the size of the region, or whether it is located within predominately temperate or tropical latitudes.

How one interprets these observations depends on the predictions one develops from niche-based and diversification-based hypotheses for the generation and maintenance of patterns of species richness. To the extent that the utilization of resource space is expressed in the morphological adaptations of consumers, the packing of species in morphological space should reflect the underlying distribution of resource qualities. Accordingly, the strong central tendency in passerine morphology suggests either that resource qualities themselves have a strong central tendency or that a generalized morphology permits exploitation of resources across a broad range of resource qualities. This dichotomy seemingly cannot be resolved without knowing the qualities of the resource space itself.

To some degree, tropical environments support more species because they offer a broader array of resources. This is reflected in the greater number of orders of birds in tropical compared with temperate regions, as pointed out long ago by many naturalists. However, the higher species richness of the order Passeriformes in the tropics is not matched by increased morphological diversity compared with temperate regions. Thus, species either are packed more densely into a similar resource space in the tropics, perhaps supported by higher productivity or resulting in lower average population densities, or a generalized morphology permits efficient exploitation of a wide variety of resources in the tropics. Certainly, the same resource—a seed, for example—can be consumed by many organisms, including birds, rodents, and ants (54).

Alternatively, species richness might not be strongly constrained by competition for limiting resources, but rather species are packed into limited resource space in response to the pressure of diversification within regions. Accordingly, species richness within regions and local assemblages alike would primarily reflect diversification rather than species interactions. Of course, independently of the predictions of resource-based and diversification-driven hypotheses, the morphological measurements used in this analysis undoubtedly are inadequate, or at least incomplete, indicators of niche relationships. In regard to diet and foraging maneuvers, additional attributes of beak mechanics, gut physiology, and locomotory adaptations, not to mention the ways that species vary with respect to their annual cycles, including seasonal movements, might tell a different story. Furthermore, the positions of species in morphological space might not be linearly related to their positions in niche space, such that distance near the center of the morphological space would correspond to greater niche differentiation than distance toward the periphery of morphological space.

In the absence of more complete measures of ecological niche space, the morphological distributions of passerine birds provide, at best, ambivalent support for niche-based determination of species richness. This is consistent with several observations that are enigmatic in the context of niche theory, namely (i) most of the variance in the abundance and distribution of populations resides between closely related species that should otherwise be ecologically similar; and (ii) the geographic distribution, ecological distribution, and abundance of populations are independent of the number of closely related (confamilial) species within a region or local area (55, 56).

Although species clearly are adapted morphologically to exploit different parts of the resource niche space, their competences in this regard may be broadly similar over large parts of this space, particularly its densely occupied center (57). Moreover, each species is represented by a point in morphological space, but a volume in ecological space. One could imagine a core of resources that are abundant and readily exploitable by individuals with a generalized morphology, but that species differ ecologically primarily with respect to peripheral resources. In this scenario, morphology would reflect selection for the ability to exploit common resources, leading to a central tendency in morphology, balanced by selection to specialize with respect to some particular peripheral resource. This could explain the observed central tendency in morphology but allow sufficient specialization to permit stable coexistence of a large number of species when peripheral resources are diverse or can be finely subdivided (Fig. 4).
The analyses described here point to a need for more thorough characterization of niche space, and the manner in which species both occupy and partition niche space, to distinguish among the most basic mechanisms that shape patterns of species richness. At present, however, mechanisms of niche-based community assembly do not seem to constrain species richness at local to continental scales. Regional influences on the dynamic balance between species formation and extinction, as well as historical contingency, would appear to dominate.

Materials and Methods

Samples and Measurements. No live animals were involved in this research; all measurements were taken from museum specimens. Seven measurements of external appendages (lengths of the wing, tail, tarsus, middle toe, and the length, width, and depth of the beak) (40) were taken on two to four specimens of one or more populations of each of 1,642 species (27%) of passerine birds (Order Passeriformes) in 775 genera and 118 families (SI Appendix, Taxonomy and distribution, Sample, and Measurements).

PC Analysis. Analyses are based on species averages of the seven measurements. Log_{10}-transformed measurements were subjected to a PC analysis based on the covariance matrix (40). Principal components are orthogonal, synthetic axes that are linear combinations (i.e., representing products and ratios) of the original variables. PC1 is a general size variable; PC2–PC7 represent aspects of shape that are associated with different qualities of foraging substrates, foraging movements, and prey. The morphological space maps fairly well onto a space constructed from the variety of foraging substrates and manuevers used by passerine birds (42).

Morphological Space. In the present analysis, dimensions of the morphological space are the square roots of the eigenvalues of the PCs. Thus, these axis lengths are the SDs of the positions of each of the species in log-transformed morphological space projected onto each axis. Because the scaling of individual PCs with respect to ecological niche dimensions cannot be quantified (SI Appendix, Relationship of morphology to ecology), the PCs are analyzed independently (cf. 58). Details of the PC analysis are presented in SI Appendix, Principal components analysis, Nested taxonomic analysis of variance, and The morphological space.

Statistical Analyses. The relationship between species richness and each morphological dimension was evaluated by linear regression of the log-ratios of the number of species within (i) families of passerine birds globally and within regions, (ii) the passerine faunas within large biogeographic regions, and (iii) the passerine faunas in local assemblages in several of the regions (Results). All analyses were performed with SAS 9.2 software (SAS Institute).

Caveats. Because local and regional species richness are strongly related, no measure provides an indication of diversifying selection by cooccurring competing or potentially competing species. Although morphology is evolutionarily conservative (SI Appendix, Nested taxonomic analysis of variance), rapid morphological diversification in some island radiations, such as the Hawaiian honeycreepers (59, 60), demonstrates that conservatism is not an intrinsic feature of avian morphological evolution (45). Accordingly, I have not applied phylogenetically explicit analyses that take into account evolutionary relationships of species. My goal in this analysis was to determine how the density of morphological space filling is related to number of species. How species have diversified morphologically is an equally interesting, but different, issue.

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