

TROPICAL BIRD COMMUNITIES

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Summary

Tropical ecosystems harbor the world's greatest diversity of avian species. Latitudinal patterns of climate and productivity, alongside historical factors, have been evoked to explain such characteristics, and there is increasing knowledge that the complex ecological interactions found in the tropical zone play a very important role in this process, regulating competition and allowing an increase in niche differentiation. As a result, several particular ecological specializations arise in these ecosystems, such as exclusive exploitation of resources that are mostly seasonal in temperate zones, such as fruits, or of resources not available in the higher latitudes, such as army ants. Less understood and recognized, however, are the considerable differences within tropical ecosystems regarding avian communities. Ecological interactions within these communities can be extremely different from one another, and these differences are crucial to the understanding of the processes that result in variances in diversity. Finally, human influence in these communities has been occurring for centuries, and still plays a major role in shaping present characteristics. It is important to recognize that, due to tropical biome particularities and to the evolutionary history that birds have been experiencing under these particularities, this influence is not a modified version of that which occurs in temperate biomes, and that the same actions may have very different impacts on different taxonomic groups and in different biomes.

1. Introduction

Birds have been used as models for the study of ecological interactions for decades, and

this is no coincidence. Being diurnal, and probably the most conspicuous (to eyes and ears) vertebrates, they have called the attention of ornithologists and bird-watchers alike to their particular habits and to how and which species compose the local scenario. Tropical birds, being so varied and unique, have also been of particular interest to ecologists, and have contributed considerably to the study of tropical diversity. The question of why bird communities vary from several dozens of species in northern North America to more than a thousand in an area of equivalent size in the Amazon or Andean forests has both puzzled and instigated researchers, and even though considerable progress has been achieved in answering this question, the puzzle remains unsolved.

The two main indexes to measure and compare communities are its richness (number of species) and diversity, which encompasses richness and relative abundance of individuals of each species, so that a community will have greater diversity when a higher number of species is present, and when less of these are rare and occur in low abundance. Estimates of worldwide tropical taxa richness are very difficult, because data are scattered in different sources and because most studies are conducted within geopolitical boundaries of countries or regions, which usually do not overlap with biogeographic ones. Nonetheless, a conservative estimate is that there are almost 10,000 bird species worldwide, between half to two thirds of which can be found in the tropical region, between the Tropic of Cancer (23° N) and the Tropic of Capricorn (23° S). Not only are the tropics richer in species, but also species are more abundant, with the total biomass of birds in a tropical area reaching fivefold that of a temperate zone of equal area. Additionally, the tropics are also quite unique: if you consider tropical rainforests worldwide, there are approximately 30 endemic families. Thus, it is important to understand which factors influence species interactions and the diversity of a given area to achieve some understanding of the complexity of ecosystems in the Tropics.

In addition to the species that constitute a community, the nature of the interactions among them and the properties that emerge from these interactions are the key to understanding why they are there in the first place. For birds, as for many other taxa, the main kind of interaction shaping communities is competition among species for access or monopoly of resources. Whenever organisms overlap in their needs and in how they exploit their habitat, there will be a negative outcome and displacement to some degree between competitors. In the case of competing populations of different species, the way in which the species interacts with both biotic and abiotic factors is termed its *niche*. Though the concept might seem simple at first, it is a multi-dimensional attribute of each species that allows for many different comparisons. For example, one may consider that the most important niche dimensions for birds that might overlap and result in competition are foraging, nesting, and courtship. The foraging niche, however, may be subdivided in several dimensions: What does it eat? How does it seek its food? At which time of the day? Similarly, subdivisions occur in other niche dimensions, leading to a very complex array of possible interactions, and the net result of the interactions of all dimensions for all species in competition will define the community of an area. Due to the principle of competitive exclusion, different species cannot coexist in a community if they completely and simultaneously occupy the same niche.

Once again, birds represent a very interesting model for the study of interspecific

competition because, due to morphological and behavioral adaptations, they can quite easily be classified in *guilds*, or groups of species in a community that are ecologically similar, in the sense that they explore the same resources in similar ways. Given the above-mentioned competitive exclusion principle, this is only possible if there is some type of niche segregation between species of a guild, that is, if species specialize in exploiting different resources or in ways of exploring such resources, such as food size, foraging location, nesting in specific tree species, and so on. These interactions may also lead to niche shifting, a good example of how competition within a community may affect the evolution of different populations. Niche shifting occurs when populations of the same species, but in different communities, occupy different niches as a result of competition and interaction with the different species composing these communities.

A classical example can be found in the Galapagos Islands, where several species of *Geospiza* finches have been studied for decades. Since birds are morphologically constrained due to flight adaptations (wings are not good for grasping food!), most of the foraging ecology of a species can be inferred from beak characteristics, such as beak depth, which is a reliable indicator of gape (and thus size of food that may be ingested). Certain species of seed-eating finches, when occurring alone in islands, have a much broader range of beak depths than when cohabiting in islands with other finch species. This indicates that competition pressures lead to specialization on certain sizes of seeds to minimize niche overlap, and that when these pressures are absent, the species that inhabits the island alone may feed on a much broader range of seeds.

1.1. Trends in Species Richness

Returning to the question about differences between tropical and temperate zone ecosystems in species richness and community composition, it is important to determine how these differences relate to ecological characteristics that might explain such trends. The latitudinal pattern in diversity is far from exclusive to birds, and extends to most groups of animals and plants. However, latitude alone cannot explain such patterns, as there is no recognizable logical causal path between latitude and species richness. Thus, it is important to identify other factors that change with latitude and that may interfere with richness in a predictable manner.

There are four paths by which richness may vary among areas: (1) with more available resources, more species may coexist, simply because quantitatively there is more to be exploited; (2) if species are more specialized (have a narrower niche), more species can coexist because they compete less; (3) if species are more generalist (have a broader niche), with a reasonable area without overlap, they may coexist since they can exploit multiple resources, thus also reducing competition; and (4) if species explore more fully the available resources (thus saturating the community), it will also have more species coexisting than a community with similar, but more unexploited, resources. It is important to notice that, if there is no increase in available resources, scenarios (2) and (3) may lead to greater diversity, but with lower productivity (and thus abundance) of each species. Therefore, to recognize patterns of avian richness globally, it is important to understand how tropical areas provide more resources, more opportunity for specialization, for coexistence while exploring the same resources, or why they can be

more saturated than their temperate counterparts.

Differences in productivity between regions may also affect their diversity. Generally, it is considered that increases in productivity will lead, at least to some extent, to increases in diversity, and there are several pathways as to how this may occur. Greater productivity may simply lead to more abundant resources, thus reducing competition and allowing for the habitat to accommodate more species – as in (1), above. However, it is important to note that such increase in productivity, yielding higher availability of resources but not of resource diversity, increases diversity not through addition of new species, but because species exploring those resources will have more similar abundances. Another possibility is that an increase in productivity may lead to an increase on the abundance of otherwise rare resources, and thus species that are specialized in such resources may find the necessary conditions to exist in such a community. Nonetheless, the relationship between productivity and diversity and richness is not straightforward. For example, if a given resource is no longer limiting for a few species (due to increases in productivity), they may exclude other, less competitive species, while at the same time other species may still be limited by different resources that have not increased in availability. In this case, a decrease in diversity would follow an increase in productivity.

Finally, two other ideas must be briefly introduced to understand patterns of global avian diversity, and further information on these topics can be found in related chapters of this volume. The equilibrium theory of island biogeography, proposed by Robert MacArthur and Edward Wilson, suggests that the number of species found in a given area should be stable and dependent on a continuous turnover of species, resulting from a balance between immigration (thus, its remoteness in the case of an island, or rates of speciation for a continent) and extinction rates. In other words, the size of an area (i.e. available habitats for colonizing and competing species) and its isolation (i.e. probability of colonization by new species) should determine the number of species a given area will have at equilibrium. Another important concept determining local species richness is habitat heterogeneity: heterogeneous habitats should be more species-rich, first because they provide different resources for species with different niches, and secondly because a patchy environment should allow different evolutionary paths for populations of the same species in the same community, leading to differentiation and, ultimately, to speciation. For animals, habitat heterogeneity is mainly defined by plant heterogeneity, and curiously, one of the first tests of this hypothesis was conducted with birds, by Robert and John MacArthur in the early 1960's, investigating how bird richness varied with different levels of vertical stratification in grass, shrubs and trees. As expected, they found a positive relation between the number of available vertical layers and the number of species in the community.

2. Factors Shaping Tropical Bird Communities

Having outlined how competition and resources may shape communities, we may now focus on how these factors differ in the tropics relative to the temperate zone, and how they shape bird communities. Several hypotheses, based on biotic and abiotic factors, have been proposed for why lower latitude regions have higher faunal diversity. The first and most obvious difference between tropical and temperate zones is climate.

Tropical areas are often called “milder”, because they have an average longer growing season and higher annual rates of heat, light and precipitation. Seasonal and nonseasonal conditions alike can be hypothesized to lead to greater diversity. Seasonal habitats provide temporal heterogeneity to an ecosystem, allowing species to specialize in different annual conditions. However, this is probably not the case for birds, since they are mostly long-lived and do not have hibernation mechanisms, which would make survival difficult during the season in which the species is not specialized.

Nonseasonal environments, on the other hand, allow for greater specialization in resources available year-round, such as fruits and nectar, and also provide further opportunities for specialization in resources that simply are not available in temperate zones, such as epiphyte probing and army ant-raid following, all of which add to tropical diversity. In fact, as will be outlined below, frugivory and nectar feeding, along with other unique characteristics made possible in a stable and predictable environment, are important components of tropical avian communities. This hypothesis also predicts several life history characteristics and adaptations found in tropical bird species that differ from their temperate counterparts, such as populations reaching carrying capacities, low adult mortality rates and distribution of reproductive effort in many, but smaller, clutches throughout the life of individuals. Also, while most examples given are related to foraging niche, it is important to remember that avian niches are broad and diverse, and specialization may also occur in, for example, nesting site or material, courtship display arenas, and so on.

The climatic characteristics described above also result in an environment of high productivity that may be related to greater diversity and abundance. In the case of avian diversity, plant diversity and heterogeneity of form and function can be particularly relevant, since these factors determine where birds live, what they eat, and where they reproduce. Great productivity and the “locking up” of nutrients in living biomass are characteristics of tropical plant ecology, which are related to plant diversity. Thus, tropical environments (especially rainforests) provide a wide vertical range of light regimes, allowing for plant specialization in different uses of this resource, which, from a bird’s-eye view, would result in a very stratified vertical habitat, and thus a greater range of possible foraging and nesting opportunities. Besides vertical variation, several characteristics of plant diversity could influence avian distribution and diversity and must be taken into consideration, such as local variation in habitat structure, percentage of vegetation cover, and plant function in the ecosystem.

Another way in which a stable climate could contribute to diversity is through the maintenance of small and restricted populations. Since there are fewer environmental extremes and less variation throughout the seasons, small populations that are the unique representatives of certain bird species (and normally very susceptible to climatic harshness) can persist without expanding their ranges but also without going extinct, thus contributing to local diversity. Among such remarkable species are the Purple-backed Sunbeam, *Aglaeactis aliciae*, a hummingbird from Peru, and the Araripe Manakin, *Antilophia bokermanni*, in Northeastern Brazil, both of which are known from only one population each, with a distribution range of about 1 km² in their respective countries. Most such populations are threatened by habitat loss and thus it is difficult to estimate how much of the restricted distribution is normal and how much is due to

human impact. BirdLife International (a renowned international partnership of conservation organizations, and official IUCN Red List authority regarding birds) has recognized 2,500 endemic bird species worldwide restricted to areas smaller than 50,000 km². They have used this criterion to determine critical conservation areas encompassing most of these birds with restricted range (called Endemic Bird Areas, or EBAs), and not surprisingly, 77% of these EBAs are located in the tropics and subtropics, which is to say that more than three quarters of all selected areas rich in birds with restricted populations occur in this region of the globe.

Together with the ecological hypotheses proposed above, there are several historical characteristics of the tropical region that must also be taken into account when trying to explain its diversity. For example, not much longer than 10,000 years ago, glaciers covered most of the temperate continents during the last of many glaciations. According to some, tropical areas were not subject to such major changes for long periods of time, providing a stable environment where species evolved without facing mass extinctions and having to go through repeated processes of colonization and differentiation. Despite the fact that tropical continental landmasses were indeed not covered with ice during recent past glaciations, assuming they were unchanged is controversial. Climatic characteristics in the tropics changed as well, and it is believed that what now are lush forests were then fragments of forest due to the expansion of grasslands. These forest “refuges”, however, could still contribute to the great diversity found nowadays. Fragmented populations in forest islands could undergo differentiation processes so that when the grasslands retreated and forests were once again continuous, these populations had become specialized and remained segregated, leading to speciation and increased diversity.

Birds also have an important characteristic when considering local diversity. Though individuals in many species are very reluctant of leaving a forest patch and crossing some grassland (or dirt roads) to reach another patch, some species take their flying ability to the extreme by migrating. As a result of this behavior, birds may take advantage of predictable variation in weather and food abundance, avoiding competition and coexisting temporally with competitively superior residents. In contrast with many temperate bird communities, in which the majority of the species are migrants, staying only for a restricted period of the year, the minority of species of most tropical communities are migrants. In fact, studies suggest that most migrant species are of tropical origin, migrating north to breed when conditions are better during summer, when insects are abundant to feed the young and where there are fewer predators. This hypothesis is derived from the fact that there are also many intra-tropical migrants, which migrate between regions within the tropics. In Central America, for example, many nectar-feeding and frugivorous birds perform the so called altitudinal migration in search of blossoming and fruiting plants. In Africa, where migration is considered to play a minor role, many forest species winter in grassland and savanna ecosystems. In Central Brazil, many flycatchers and finches that reproduce in savannas migrate north after breeding, but only as far as the Amazon or Central America. In Southeast Asia, migrants are considered to have a major impact on local communities, but the overall relationship between migrant and resident species in all tropical ecosystems still remains unsatisfactorily explored. Therefore, there are two basic migration processes that may involve tropical birds: birds that migrate to the tropics (or within different

tropical areas) to breed, such as some examples given above, and there are birds that migrate to the tropics during the high-latitude winter, for food and milder climates but that breed in the temperate zones (many times going as far as the arctic circle), which include many shorebirds such as bustards and sandpipers.

Overall, there clearly are several factors, both ecological and historical, which may have shaped avian tropical communities. Further studies are required to clarify which of these factors are most relevant, since they all correlate in some way with latitude and many may be confounding factors. Nonetheless, spatial heterogeneity plays a fundamental role in allowing the coexistence of many species of birds in the same area, in addition to the multiplicity of opportunities for specialization.

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Biographical Sketches

Rafael Maia obtained his Master's Degree at the Department of Ecology of the University of Brasília, in Brazil. His thesis focuses on visual communication and color production in birds. His main research interests are the evolution of communication, cooperation and mating systems, and he believes tropical birds are an unexplored "pot of gold" in these research topics.

Eduardo Santos is currently with the Department of Ecology of the University of Brasília, in Brazil, where he is undertaking his Master's Degree Thesis. His thesis focuses on the parental care and reproductive success of a Neotropical bird. His main research interests are the evolution of parental care and mating systems of tropical birds.