

## THE ROLE OF COMPETITION IN STRUCTURING TROPICAL BIRD COMMUNITIES

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**Resumen.** – El papel de la competencia en la estructura de comunidades de aves tropicales. – A pesar de muchas décadas de intenso estudio, el papel de la competencia como una fuerza estructuradora de comunidades ecológicas continúa siendo controversial. En este artículo resumimos las presentaciones de un simposio enfocado en examinar el efecto de la competencia interespecífica en la distribución y abundancia de las especies de aves en ecosistemas tropicales, en los cuales posiblemente las interacciones bióticas son las más intensas debido a la alta diversidad en ambientes estables. Describimos una serie de estudios independientes, cada uno enfrentando preguntas aún no resueltas utilizando o combinando técnicas modernas y recursos que no eran disponibles en las décadas anteriores. Estos trabajos incluyen estudios a largo plazo que monitorean cambios en la abundancia y el comportamiento, pruebas experimentales de segregación mediada por comportamiento, la aplicación de mapeo intensivo de territorios, el uso de isótopos estables y datos de sensores remotos para cuantificar nichos y hábitats, y métodos de comunidades en un contexto filogenético para evaluar patrones de co-ocurrencia dentro de clados. Colectivamente, estas aproximaciones ofrecen alternativas para evaluar la importancia de competencia entre especies y clarificar su efecto sobre la estructura de comunidades a escalas locales y regionales.

**Abstract.** – Despite several decades of intense scrutiny, the role of competition as a force structuring ecological communities remains controversial. Here we summarize a symposium focused on examining the effect of interspecific competition on the distribution and abundance of bird species in tropical ecosystems, where biotic interactions are likely to be most intense because of high diversity in stable environments. We outline a series of independent studies, each tackling long-standing questions by utilizing or combining modern techniques and resources that were largely unavailable in previous decades. These include long-term datasets tracking changes in abundance and behavior, experimental tests of behaviorally-mediated segregation, application of intensive territory mapping, stable isotopes, and remotely sensed data to measure habitat niches, and community phylogenetic methods for assessing patterns of coexistence within larger clades. Collectively, these approaches offer rich potential for evaluating the strength of competition between interacting species and clarifying its effect on the structure of communities at local and regional scales.

**Key words:** avian, community assembly, elevational gradient, interspecific aggression, natural experiment, Neotropical forest, niche segregation, phylogenetic structure

## INTRODUCTION

The study of interspecific competition as an ecological mechanism has a long history (Darwin 1859), yet there is little consensus about its role in shaping community structure. Much recent work has shown that plant community assembly can be explained by neutral models, or else by deterministic models that emphasize niche-based processes such as habitat filtering and dispersal limitation (Hubbell 2001, Rosindell *et al.* 2011, Weiher *et al.* 2011). These findings suggest that competition is a relatively weak ecological force at the community level. However, their generality is difficult to assess as many tests struggle to discriminate between models (Chisholm & Pacala 2010), and in any case competition seems likely to be elevated in other systems, such as vertebrates. In particular, tropical birds may compete strongly because of factors such as low dispersal, narrow niches, large numbers of sympatric congeners, and intense interspecific territoriality and aggression (MacArthur 1964, Cody 1974, Graves & Gotelli 1993, Tobias & Seddon 2009, Jankowski *et al.* 2010). Most of these factors are well established, yet the extent to which they influence range boundaries and patterns of diversity and abundance in tropical avifaunas remains controversial (Wiens 2011).

At least three patterns, which have often been documented in the Neotropics, have historically been considered evidence of interspecific competition: overt interspecific aggression at spatially concentrated resources, resource partitioning among coexisting species, and segregation of ecologically similar species along environmental gradients. These observed patterns capture different avenues by which competitive interactions among species could either permit or prevent species coexistence (e.g., forbidden combinations *sensu* Diamond 1973). Interspecific aggression at spatially concentrated resources and patterns of resource partitioning are necessarily ob-

served at local spatial scales and are typically studied in the context of community assembly. The segregation of ecologically similar species along environmental gradients occurs at both local and regional scales, depending on the spatial extent of a given gradient. Accordingly, patterns of segregation can be examined in the context of the interactions influencing community assembly, the maintenance of local distributions across habitats, and the reinforcement of range boundaries at larger scales.

Some of the earliest studies of tropical avian guilds showed evidence consistent with competition playing a role to structure species assemblages at local scales. In their study of army-ant followers, Willis & Oniki (1978) showed that interspecific dominance based on body size enabled some species to gain preferential access to the most productive microhabitats at the leading edge of army ant swarms. Yet, there was also resource partitioning within the ant following guild based on differential use of perch types. Nectarivorous hummingbirds also show a combination of patterns consistent with a competition-structured bird community, with behaviorally dominant species monopolizing clumped flowers, exploitative competition for more dispersed flowers, and coexistence of species with different bill types that enable them to use different flowers (Feinsinger 1978, Feinsinger & Colwell 1978, Pimm *et al.* 1985). Some of the most specialized foraging behaviors observed are those of insectivorous tropical birds, especially among species that forage in mixed-species flocks (Snow & Snow 1971, Jones 1978, Pearson 1977, Munn 1985, Naoki 2007). Such specialization has been argued to reduce competition within flocks and may determine the “rules” underlying community assembly in which each flock can only contain one species per foraging niche (e.g., insectivores that search suspended dead leaves; Munn 1985, Pierpont 1986, Graves & Gotelli 1993). Extreme foraging specialization has also been associated with

the evolutionary divergence of lineages within the mega-diverse flycatcher (Tyrannidae) family in which morphological adaptations associated with particular foraging tactics such as bill shape (Fitzpatrick 1985) and divergence in diet (Sherry 1984) may enable as many as 50 flycatcher species to coexist in a single community without overlapping significantly in resource use. Whether competition was a primary driver of such divergent foraging behavior, versus a mechanism involved in ecological sorting, remains a contentious issue.

Additional correlational evidence for an important role of interspecific competition has come from studies showing segregation of closely related species along environmental gradients in the tropics (Terborgh 1971, 1985). Studies of species replacements along elevational gradients in the Andes suggest that direct interference competition limits elevational distributions of one-third of species along these gradients (Terborgh 1971, Terborgh & Weske 1975). Furthermore, a comparison of the principal Andean gradient with an isolated mountain range in which high-elevation congeners were absent revealed that even species without species replacements along the principal gradient showed an expansion of ranges upslope, suggesting that both direct competitive interactions as well as diffuse competition among species may limit up to two-thirds of montane birds. Comparable replacement of similar-sized congeners along successional gradients (Terborgh 1985) also provides evidence for a role interspecific competition, including experimental evidence that habitat segregation along the gradient is maintained by interspecific territoriality (Robinson & Terborgh 1995).

Although each of these studies has demonstrated patterns consistent with competition as a dominating force in tropical bird communities, none of these studies has provided proof that interspecific competition structures bird communities or that it promotes or maintains Neotropical bird species diversity. Thus, even

after four decades of research, these questions remain elusive within fields of tropical ecology and evolution. Here we describe a number of innovative approaches and tools that have allowed us to refine our assessment of the role of competition operating to structure communities. One of these approaches is the identification of landscapes that have undergone local extinction of species, which may include the loss of dominant competitors. Of course, this opportunity is conditional upon the availability of a historical catalogue of communities. Other approaches incorporate the use of isotopes and remotely sensed data for better quantification of niche and habitat overlap between species, studies of behavior that can serve as surrogates of competitive pressure, and the application of phylogenetic relationships and trait information to test hypotheses of how communities should be assembled if competition constrained species coexistence. Further application of such methods across tropical communities should permit a more comprehensive synthesis of the role of competition in shaping community composition and species distributions.

#### NATURAL EXPERIMENTS: ECOLOGICAL OPPORTUNITY FOLLOWING EXTINCTION

Thus far, much of the evidence presented for competition as a dominant force structuring tropical bird communities has been provided through indirect measures. One direct test of the impact of competition is to perform species addition or removal experiments and examine subsequent shifts in resource use of species (e.g., Martin & Martin 2001, Bolnick *et al.* 2010); however, such experiments are seldom realistic in tropical bird communities, as large-scale alterations of bird communities are generally logistically unfeasible and are often considered unethical. An undervalued alternative to such removal experiments is to

take advantage of species losses due to fragmentation, particularly in locations that have previous baseline data on community structure (Terborgh *et al.* 2001). Exceptionally valuable are areas that also contain quasi-controls — locations that did not undergo the same species loss as nearby experimental fragments. The responses of remaining species in such quasi-experiments enable an assessment of the degree to which competitors may constrain niche boundaries of other species.

In this symposium, Touchton presents an example of a quasi-experiment within a three-species guild of ant-following birds that had been studied extensively in lowland forests of Panamá on both Barro Colorado Island (BCI; Willis 1967, 1972, 1973) and on the nearby mainland in Soberanía National Park (Styrsky 2003). On BCI, socially dominant Ocellated Antbirds (*Phaenostictus mcleannani*) went extinct in 1969 (Willis 1974, Willis & Eisenmann 1979) but remained common on the mainland. The other two species, Bicolored Antbirds (*Gymnophiys leucaspis*) and Spotted Antbirds (*Hylophylax naevioides*), have remained at both sites (Robinson *et al.* 2000, Robinson 2001). This situation permits a direct comparison of Bicolored Antbird and Spotted Antbird population densities and microhabitat use between current BCI (dominant guild member absent) and the mainland (dominant guild member present) to historical data gathered from BCI in the 1960s when the dominant guild member was present. Touchton found that the island-wide density of Spotted Antbirds has more than doubled since the loss of Ocellated Antbirds, despite similar levels of foraging resources (Touchton & Smith 2011). Additionally, Spotted Antbirds functionally overcompensated for consumption of resources that were historically monopolized by Ocellated Antbirds (Touchton & Smith 2011). In order to exploit these newly available yet patchy resources, some Spotted Antbird individuals relaxed their territoriality by expanding their

home ranges and exhibited higher reproductive output than their counterparts even in the face of moderately higher rates of nest predation (Touchton & Wikelski in prep). Despite having a foraging strategy more similar to Ocellated Antbirds than to Spotted Antbirds, Bicolored Antbirds did not respond with rises in density or microhabitat shifts akin to Spotted Antbirds, perhaps a result of other limiting factors such as predation (Touchton & Smith 2011). These results indicate that interspecific competition can restrict foraging niches in coexisting bird species, and highlight the role of competition in microevolutionary processes.

#### BEHAVIORAL EXPERIMENTS: COMPETITIVE INTERACTIONS, RANGE BOUNDARIES AND RE- GIONAL DISTRIBUTIONS

Interspecific competitive interactions, as expressed through territorial aggression, may play a role in reinforcing the distributional limits of competing species at large spatial scales, particularly when ranges of competitors are largely parapatric (Jankowski *et al.* 2010). In birds, such elevational replacements are found repeatedly along tropical mountainsides and have long been thought to be a product of direct competition (Terborgh & Weske 1975). Using heterospecific playback experiments along an elevational gradient in the Tilarán range of Costa Rica, Jankowski *et al.* (2010) showed that behavioral interactions between species with elevational replacements were present in two genera of montane birds. Additionally, the responses to congener song stimuli changed over small spatial scales, diminishing as one moved away from contact zones to regions within the elevational ranges of either congener. This work suggested that behavioral interactions were likely a learned response, which was conditional upon having sufficient encounter rates between species in order to develop and be maintained.

In this symposium, Jankowski and Robinson follow up on Jankowski *et al.* (2010) to demonstrate that across two elevational gradients (one in Costa Rica and one in the southeastern Peruvian Andes), there is considerable variation in the strength of interspecific aggression found between species for a range of tropical montane genera, ranging from very strong responses toward congener stimuli to no detectable response. Using the modeled probability of occurrence for congeners at the contact zone as a surrogate for likely encounter rates between species, they find a negative relationship between aggression toward congeners and probability of occurrence of the congener. Cases of strong interspecific aggression were only observed when the probability of occurrence of the congener at the range boundary was greater than approximately 40%. This lends support to the idea that the strength of competitive interactions as a mechanism maintaining elevational replacements may depend upon local densities of species at contact zones, and accordingly, any environmental factors that affect those densities by influencing species responses to environmental gradients. Furthermore, although competition may affect range boundaries of common species, this work suggests that such interactions may have little impact on distributions of rare species, which represent a considerable portion of tropical communities.

#### NEW INSIGHTS INTO THE DYNAMICS OF COMPETITION AND NICHE SEGREGATION AT LOCAL SCALES

Previous authors have challenged the view that spatial segregation and behavioral aggression are sufficient tests of competition (e.g., Murray 1976, Cadena 2007). The main arguments are, first, that spatial segregation (e.g., low territory or range overlap) can reflect subtle habitat partitioning, and second that aggressive responses

to social signals (e.g., song) can reflect recent ancestry and misdirected aggression (phylogenetic conservatism). Even where the intensity of aggressive responses peaks at territory or range boundaries, presumably as a result of learned recognition mechanisms, it can be argued that stronger interspecific aggression is merely a correlate, rather than a cause, of spatial patterns. This raises the question of whether spatial patterns and competitive interactions actually reflect underlying niche overlap.

In this symposium, Tobias presented a range of data from a multi-year study of antbird communities in Amazonian Peru, focusing on the question of whether aggression between the Peruvian Warbling-Antbird (*Hypocnemis peruviana*) and the Yellow-breasted Warbling-Antbird (*H. subflava*) is directly shaped by resource competition. Previous work has shown that these two forms co-occur with strong interspecific responses to territorial songs (Tobias & Seddon 2009, Tobias *et al.* 2011). The level of aggression predicts that territory overlap should be low, and this is confirmed by mapping of >5000 GPS-point localities collected over 5 years. Several techniques were adopted to assess niche overlap. Stable isotope analyses suggested that dietary niches of the two forms were divergent, although it is likely that this reflects different isotopic signatures of bamboo and *terra firme* forest rather than different insect prey. Foraging behavior, including foraging strata, showed broad overlap between species. Vegetation surveys (conducted at numerous points within ~10 territories per species) suggested that, although core habitats were different, there was a large degree of habitat niche overlap, a result confirmed by analysis of remotely sensed light detection and ranging (Lidar) data collected from aerial overflights by G. Asner and colleagues (Carnegie Airborne Observatory). Vegetation profiles extracted from all GPS localities revealed that although mean habitats were significantly different between species, the range

of habitats utilized was broadly overlapping. Direct competition between species was further demonstrated by sequential occupation of territories in two instances, one species was replaced by the other on the same territory. They concluded that both species compete directly for a broad range of intermediate habitats such as secondary growth, riverine vegetation, and bamboo-forest ecotones.

Although competition between Peruvian and Yellow-breasted Warbling-Antbirds is intense, the spatial pattern of territory occupancy is a loosely packed mosaic. This pattern offers insights for studies of competition in general. First, it suggests that strong competition does not necessarily predict abrupt parapatric range boundaries, particularly where high habitat heterogeneity allows competitors to occur broadly in sympatry. Second, it demonstrates that strongly competing species can exclude each other at fine scales (e.g., home range), yet coexist locally. Both species were often audible from the same point and thus essentially coexist at the site or plot scale. This sounds a note of caution regarding the scale-dependence of assumptions in community ecology. It is often proposed that competition has little explanatory power at larger scales, and that the likelihood of competitive exclusion is maximized at small scales. Work on these Warbling-Antbirds has shown that even when survey plots are of minimum size (i.e., a single point in space) the presence of two putative competitors does not necessarily imply that competition is weak.

#### PHYLOGENETIC SIGNALS OF COMPETITION: INFERENCES FROM EVOLUTIONARY RELATIONSHIPS AND TRAITS OF CO-OCCURRING SPECIES

Phylogenetic community structure, especially when combined with information on functionally relevant traits, can provide some insight into the relative importance of biotic in-

teractions, environmental filtering and random chance in structuring local assemblages (Webb *et al.* 2002). Biotic interactions, such as competitor or enemy-mediated negative density dependence, should result in co-occurring species that have relatively different trait values, which should lead to evenly spaced morphologies within a local assemblage (Ricklefs & Travis 1980). If traits important in biotic interactions (such as beak length in hummingbirds) are conserved, such that close relatives have similar trait values, then assemblages composed of relatively distantly related species (i.e., showing a pattern of phylogenetic evenness) would have relatively different trait values; a phenomenon that would be consistent with biotic interactions influencing assemblage structure (Webb *et al.* 2002). If functional traits are not conserved, however, then there is no expected match between phylogenetic and phenotypic structure.

Among bird groups, hummingbirds provide an ideal system for studies of community ecology and biotic interactions because, for years, ornithologists have carefully documented their behavior, morphology and patterns of co-occurrence, yielding both a rich empirical dataset as well as a strong theoretical basis for hypotheses testing (e.g., Feinsinger & Colwell 1978, Altshuler *et al.* 2004, Gutiérrez-Zamora *et al.* 2004, McGuire *et al.* 2006, Stiles 2008, Temeles *et al.* 2009). Using information on 236 hummingbird assemblages (126 species) across two major gradients in northern South America: elevation and precipitation, Graham and Parra evaluated whether trait structure could be predicted, assuming that environmental filtering or biotic interactions are working primarily on phylogenetically conserved functional traits. They found that the distribution of trait values within assemblages generally did not correspond to those predicted based on phylogenetic signal and phylogenetic structure. For some traits, however, their results supported a key prediction in community

ecology that dates back to Darwin; the more closely related species are, the more strongly they will compete (Graham *et al.* in press). Furthermore, by combining patterns from both phylogenetic structure and the spacing of morphological traits, they could better evaluate potential mechanisms influencing local assembly structure (also see Swenson & Enquist 2009, Mayfield & Levine 2010).

As a cautionary note, although results from phylogenetic and trait-based analyses can be consistent with potential mechanisms, such as competition, they are by no means proof that such mechanisms are governing patterns of assemblage structure (e.g., Kembel 2009). Such results, however, do provide the basis for generating new hypotheses about interactions among specific species and in different regions (i.e., along environmental gradients; Parra *et al.* 2010) that can be studied with field based observational or experimental studies such as those highlighted elsewhere in the symposium (Tobias & Seddon 2009, Jankowski *et al.* 2010).

#### FUTURE DIRECTIONS FOR ASSESSING THE ROLE OF COMPETITION

The complementary presentations of this symposium show that combining tools and approaches from different disciplines can provide unique and promising avenues for elucidating the ecological and evolutionary mechanisms that influence patterns of community structure and distributions in tropical birds. There are, however, a number of opportunities for further development, and we mention a few of these here.

Much of the work presented in this symposium has focused on interactions among closely related species. As suggested by Graham and Parra, however, functional similarity in species may not always have a strong phylogenetic signal, so the assumption that the most likely competitors within a community are the closest relatives may not always be satisfied.

Future work may therefore consider aspects of resource overlap across distinct avian groups that nevertheless share similar requirements. Likewise, an assessment of the extent of resource overlap with increasing phylogenetic distance among species would directly test these assumptions.

As climate change and habitat degradation continue to affect species ranges and reshuffle the composition of communities, long-term datasets that document distributional shifts may be especially useful “natural experiments” for testing hypotheses of the importance of competition in the ecological sorting of local assemblages and reinforcement of range boundaries (Touchton & Smith 2011, Forero-Medina *et al.* 2011). For example, in cases of upslope range shifts along elevational gradients, perhaps we would expect range contractions of low-elevation limits to be more common for species that have congeners with abutting ranges downslope (Jankowski *et al.* 2010). Tests of the importance of competition acting on range boundaries may also be placed in the context of expected range breadths based upon independently measured aspects of species fundamental niche (Jankowski *et al.* in review), such that species whose ranges abut those of congeners should exhibit more compressed elevational ranges than predicted by their physiological tolerances (Gifford & Kozak 2011).

Finally, any study focused on the role of competition in structuring communities will benefit from increased knowledge of the local and regional distributions, natural history, and specific requirements of species by enabling us to test patterns of resource overlap and niche use in putative competitors. Even for the best known taxonomic groups, such as birds, the lack of data on ecology, behavior and distributions of species continues to be a major hurdle to achieving a consensus on the way that competition, as well as other biotic interactions, structure tropical communities.

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