SPECIAL FEATURE: Advances in Neotropical Ornithology

Insectivorous birds in the Neotropics: Ecological radiations, specialization, and coexistence in species-rich communities

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ABSTRACT

Insectivorous birds reach their highest diversity in the tropics and represent a striking variety of morphological and behavioral specializations for foraging, yet explanations for these patterns are inadequate because of both our limited understanding of the drivers of ecological diversification within and among clades and of coexistence mechanisms in particular. Here we synthesize recent information on Neotropical insectivorous birds, including their diversity, evolutionary ages and locations of origin, phylogenies, and both competitive and predator–prey species interactions. We propose a novel evolutionary hypothesis for the origin and coexistence of the phenotypic diversity of insectivore foraging morphologies in species-rich communities, based on their extraordinary food-resource specializations. Specifically, we develop the Biotic Challenge Hypothesis to explain the evolution of these specializations, and we provide preliminary evidence in support of this hypothesis based on a synopsis of both Neotropical insectivore specializations by family and arthropod antipredator adaptations by category. We argue that, from the perspective of tropical insectivorous birds, and particularly in the most species-rich, mainland Neotropical communities, the environment is an arthropod desert. Coexistence with all of the other insectivores requires feeding specialization to compete exploitatively and diffusely against evolutionarily diverse species and far less frequently against sister species. The arthropod desert arises primarily because of (1) the tactical diversity of arthropod predators as insectivore competitors and (2) the evolutionary arms races involving arthropod predators with their prey, which render many arthropods inaccessible to most insectivorous predators. Our idea provides an explicit mechanism for pervasive, diffuse tropical interspecific competition, for evolutionary specialization, and for positive feedback on speciation rates at low latitudes, thereby generating new predictions and insights into tropical life histories and the Latitudinal Diversity Gradient. Other recent ideas concerning the coexistence of Neotropical insectivores, including positive species interactions within mixed species flocks, are recognized and evaluated. We discuss ways to test predictions resulting from the new view of communities developed here, including a case study of diet specialization by Costa Rican tyrannid flycatchers. Our synthesis of the origin and nature of Neotropical insectivore communities injects new life into the "zombie" idea that evolution works differently in the species-rich tropics.

Keywords: arms race, avian ecology, coexistence, diffuse competition, insectivore, interspecific competition, Neotropical, specialization

LAY SUMMARY

- New World tropical (Neotropical) insectivorous bird communities are extremely rich in species.
- These birds are also extraordinarily diverse in how they forage, and illustrate a variety of specializations, but why?
- This paper summarizes and integrates information on the evolution of the diverse Neotropical avifauna, interspecific competition, feeding specializations in the Neotropics, and arms races of insectivorous birds with insect prey, to make novel deductions and predictions.
- Specifically, we propose the Biotic Challenge Hypothesis, which states that, from the perspective of many Neotropical insectivores, particularly those in lowland equatorial rainforests, food is relatively scarce, requiring specializations to find, capture, handle, and digest the prey, and requires energetic efficiency to compete effectively with other birds.
- These ideas have a number of implications for life histories and for the evolution of the Latitudinal Diversity Gradient, that is, the tendency for more species to coexist at low latitudes. For example, we propose that the evolution of feeding specialization is traded off in these birds for strong dispersal ability, which has contributed to relatively high speciation rate in Neotropical birds.
- The feeding specializations also have important implications for understanding a number of other aspects of Neotropical insectivorous birds, including their life histories, organization of mixed-species flocks, and their conservation vulnerability.

Aves insectívoras en el Neotrópico: Radiaciones ecológicas, especialización y coexistencia en comunidades ricas en especies

RESUMEN

Las aves insectívoras alcanzan su máxima diversidad en los trópicos y representan una variedad llamativa de especializaciones morfológicas y de comportamiento para forrajeo, a pesar de lo cual las explicaciones para estos patrones son inadecuadas debido a nuestro entendimiento limitado tanto de las causas de la diversificación ecológica dentro y entre clados, como de los mecanismos de coexistencia en particular. Aquí sintetizamos información reciente sobre aves insectívoras neotropicales, incluyendo su diversidad, edades evolutivas y ubicaciones de origen, filogenias e interacciones competitivas y depredador-presa entre especies. Proponemos una hipótesis evolutiva novedosa para el origen y la coexistencia de la diversidad fenotípica de morfologías de forrajeo de los insectívoros en comunidades ricas en especies, basada en sus extraordinarias especializaciones para aprovechar los recursos alimenticios. Específicamente, desarrollamos la Hipótesis de Desafío Biótico para explicar la evolución de estas especializaciones, y brindamos evidencia preliminar en apoyo de esta hipótesis basada en una sinopsis tanto de las especializaciones de las aves insectívoras por familia, como de las adaptaciones anti-depredador de los artrópodos por categoría. Argumentamos que, desde la perspectiva de las aves insectívoras tropicales, y particularmente para las comunidades neotropicales continentales más ricas en especies, el ambiente es un desierto de artrópodos. La coexistencia con todos los otros insectívoros requiere especializaciones en forrajeo para competir de forma explícita y difusa contra especies evolutivamente diversas, y mucho menos frecuentemente contra especies hermanas. El desierto de artrópodos surge principalmente debido (1) a la diversidad táctica de los depredadores de artrópodos como competidores insectívoros y (2) a las carreras armamentistas evolutivas que involucran artrópodos depredadores y sus presas, que hacen que muchos artrópodos sean inaccesibles para la mayoría de los depredadores insectívoros. Nuestra idea brinda un mecanismo explícito para la competencia inter-específica tropical potente y difusa, para la especialización evolutiva, y para la retroalimentación positiva en las tasas de especiación a bajas latitudes, por ende, generando nuevas predicciones y percepciones en las historias de vida tropicales y en el Gradiente de Diversidad Latitudinal. Otras ideas recientes concernientes a la coexistencia de los insectívoros neotropicales, incluyendo interacciones positivas entre especies dentro de bandadas de especies mixtas, son reconocidas y evaluadas. Discutimos modos de evaluar las predicciones resultantes de esta nueva perspectiva de las comunidades desarrollada en este trabajo, incluyendo un caso de estudio de especialización de dieta por parte de los tiránicos atrapamoscas de Costa Rica. Nuestra síntesis del origen y de la naturaleza de las comunidades de insectívoros neotropicales inyecta nueva vida a la idea "zombi" de que la evolución funciona de modo diferente en los trópicos ricos en especies.

Palabras clave: carrera armamentista, coexistencia, competencia difusa, competencia inter-específica, ecología de aves, especialización, insectívoro, neotropical

INTRODUCTION

The extraordinary diversity of tropical species and the complexity of their ecological interactions pose a formidable intellectual challenge, and, not surprisingly, these communities are relatively poorly understood compared to simpler communities such as Darwin's finches in the Galápagos Archipelago and lizards in the genus *Anolis* in the Caribbean. Nonetheless, understanding community structure in general necessitates confronting the most species-rich, continental communities, including their evolutionary origins and maintenance of ecological relationships

In an early review of mainland tropical communities, Dobzhansky (1950) championed the idea that evolution, particularly natural selection, differs in the tropics due to both its species richness and relatively constant ecological conditions (see also MacArthur 1969). For example, Dobzhansky (1950:215) argued that

"In the absence of competition a species tends to fill all the habitats that it can make use of; abundant opportunity favors adaptive versatility. When competing species are present, each of them is forced to withdraw to those habitats for which it is best adapted and in which it has a net advantage in survival. The presence of many competitors, in biological evolution…can be met most successfully by specialization."

This assertion argues explicitly that species richness can drive specialization via interspecific competition.

Schemske et al. (2009) also argue for generally stronger biotic interactions in the tropics compared to higher latitudes. Several recent empirical studies that controlled for methodology across latitudes reinforce the idea that a variety of ecological interactions differ in the tropics, namely more intense predation on caterpillars (Roslin et al. 2017), greater host plant specialization by tropical caterpillars (Forister et al. 2015), greater emphasis on secondary plant chemical defenses in tropical trees (Sedio et al. 2018), host tree seed specialization by weevils (Peguero et al. 2017), and the negative impact of trees from other trees of the same species (LaManna et al. 2017).

Janzen (1967) argued, further, that the reduced dispersal capacity of many tropical organisms may have evolutionary consequences. Jocque et al. (2010) generalized Janzen's argument about dispersal limitation in the tropics by arguing that this boosts speciation rates, helping explain the Latitudinal Diversity Gradient (LDG). Salisbury et al. (2012) also linked dispersal limitation to ecological specialization, but none of these studies explain why tropical species are relatively specialized in the first place, which we address explicitly.

The ideas that evolution may be different in the tropics and that tropical species are relatively specialized is still controversial and is caricaturized as a "zombie idea" that will not die (Moles et al. 2011, Moles and Ollerton 2016). It is important to resolve this controversy not only to understand diverse global communities, but also to better understand and possibly prevent global human impacts on tropical communities. As things stand, a temperate bias precludes our understanding of the evolution of communities generally (Raby 2017).

Here we take advantage of the extraordinary diversity of Neotropical insectivores to argue that their interspecific competition for food coupled with their coevolution with their prey necessitated the evolution of feeding specialization, which is thus more intense in the tropics. The feeding specializations that we have catalogued and explain mechanistically are important coexistence mechanisms, manifested to the maximum extent in the most species-rich environments on the planet. Understanding such specializations will help us comprehend the evolution of tropical communities, and of the concomitant diversity of species and species interactions. Understanding our arguments about the origin and maintenance of these specializations also necessitates appreciating the evolutionary history of tropical avifauna. We argue that Dobzhansky's (1950) views about the intensity of competition and specialization in species-rich communities, particularly in the most humid lowland tropical environments, were remarkably prescient. We integrate an evolutionary approach to interspecific competition—describing the origin and diversity of tropical avian insectivores along with their coevolutionary interactions with invertebrates—with an ecological approach to diets and foraging behavior. We provide both a comprehensive theoretical model and preliminary empirical evidence to explain why so many Neotropical avian insectivores are specialized, particularly in the lowland wet tropics.

Insectivorous Neotropical birds are ideal for these arguments because of their species richness resulting from multiple clades originating and coexisting in South America and adjacent land areas (del Hoyo et al. 2020)—radiations involving diverse ways to exploit insects and other terrestrial invertebrates are reviewed in Supplemental Material Appendix A. We operationally considered as insectivores those species whose diet is >70% invertebrates and focused further on species that consume primarily insects and spiders (e.g., Schoener 1971) as opposed to other invertebrates such as gastropods and crustaceans. We first argue why and how interspecific competition should lead to ecological and evolutionary specialization in proportion to the species richness of the predators, seasonal consistency of insect consumption by the predators, and the evolutionary arms race with insect prey. We provide synopses of both feeding-related specializations in Neotropical insectivore families and insect antipredator adaptations (Supplemental Material Appendixes A and B), emphasizing adaptations in the latter to visually hunting predators like birds. We then test these ideas preliminarily using diets of coexisting insectivores in a lowland Costa Rican rainforest and discuss alternative views of tropical community structure. Finally, we consider implications of insectivore specialization for tropical life histories, the Latitudinal Diversity Gradient, and conservation.

THEORY OF COEXISTENCE: EVOLUTION OF SPECIALIZATION VIA BIOTIC CHALLENGE

We begin with a few assumptions and definitions. We assume that speciation is allopatric in these birds and that

sister species resulting from speciation events are initially similar ecologically (Schluter 2000). We also assume that species are less likely to coexist locally within the same habitat the more similar they are to each other ecologically and the closer they are phylogenetically (Jankowski et al. 2010, 2012; Pigot and Tobias 2012). Sister species thus start out largely allopatric, and over time evolve differences that may allow greater coexistence—the subject of this section of our study.

Further, we assume that adaptive radiation has been important in the origination of many clades of tropical insectivores, if only because adaptive radiation has contributed to much biological diversity overall (Schluter 2000). However, because only the most rapid clade diversification constitutes adaptive radiation per se, as illustrated by some mainland South American furnariids (Claramunt 2010), and because we do not know how rapidly most insectivore clades differentiated ecologically within the mainland Neotropics, we use the phrase "ecological diversification" within clades rather than "adaptive radiation." Thus, we consider and include here diversification of species due to biological processes, especially interspecific competition, that sometimes occur slowly within clades and even among clades.

We define diffuse competition as the combined effects of 3 or more species depressing the abundance of a limiting resource sufficiently to affect the population dynamics and/or evolution of one or more coexisting species. Our definition thus explicitly includes evolutionary impacts of competitors, and relaxes the necessity for species to interact directly, pairwise, and with or without interference mechanisms. Our definition is similar to Moen's (1989) population-level diffuse competition, except that ours does not necessitate any direct behavioral (aggressive) interactions. Moen references arguments of Hubbell and Foster (1986) that "no two [rainforest] tree species encounter each other frequently or consistently enough to evolve pairwise character displacement," implicating evolutionary consequences of diffuse, exploitative competition involving many plant species simultaneously; this is similar to our conception of diffuse competition, except that insectivorous birds may "encounter" each other more frequently than tree species in terms of depressing shared resources, and in the extreme case of year-round mixed-species insectivorous bird flocks in the Neotropics, species encounter each other more or less continuously. Terborgh and Weske (1975) use a similar diffuse competition concept to ours with Andean birds, and Kricher (2017:288) recognizes, for Neotropical birds, that "the presence of many insect-eating species cohabiting a complex ecosystem generates continuous low-level (also called diffuse) competition within a species assemblage, keeping each species ecologically adapted to doing what it alone does best."

Based on these definitions and assumptions, we here provide the essence of our proposed model for the evolution of specialization in insectivorous birds coexisting in species-rich Neotropical environments. Our fundamental inference is that the resources are scarce from the perspective of insectivores in these environments, creating a metaphorical "arthropod desert" due to a combination of 2 distinctive biological challenges or resistance that species face, namely diffuse competition from a variety of birds and other insectivores and defenses evolved by the arthropod prey (Figure 1). We thus refer to this model as the Biotic Challenge Hypothesis and elaborate on these concepts and supporting evidence below. The Neotropics are particularly favorable for evolutionary specializations due to the high species richness of diverse organisms—including insectivorous birds—allowed by the large area and geological complexity, long time periods involved, and relatively stable tropical environments, particularly in lowland equatorial regions of the Neotropics. We thus argue that species richness drives specialization, as implied by Dobzhansky (1950), and as distinguished from a widely held alternative, originating in niche theory, namely that constant tropical environments allow narrow niches (i.e. resource partitioning) and large niche space, thereby allowing more species to coexist (e.g., MacArthur 1969, Orians 1969, Schoener 1971, Askins 1983). Explaining how and why relatively constant tropical environments lead to specializations, essentially narrow niches, is our purpose here.

Our model is explicitly evolutionary insofar as we view the large number of Neotropical bird species as the result of speciation rate exceeding extinction rate over long time periods (Jablonski et al. 2006, Mittelbach et al. 2007, Brown 2014). Avian studies (e.g., Brumfield 2012, Smith et al. 2014) also support this concept of the tropics as both a "cradle" (source of many species, globally) and a museum (where species persist for relatively long periods). We posit that the initial stage of community evolution is speciation, as a consequence of colonization of new regions and/or vicariant events such as continental breakup, mountain formation, or presence of large rivers that isolate populations by inhibiting dispersal. Such speciation is also facilitated by the complex geology of large landmasses like South America (e.g., Brumfield 2012, Smith et al. 2014). Extinction is assumed to be relatively low, at least over long time periods, due to the relatively benign (compared to higher latitudes) lowland tropical climate.

We argue that the kind of rapid species divergence associated with character displacement (Claramunt 2010) may be less likely in species-rich, continental tropical communities because of competition from diverse potential competitors, and thus less ecological opportunity for adaptive radiation (Schluter 2000). We argue, instead, that mainland sister species resulting from speciation tend to
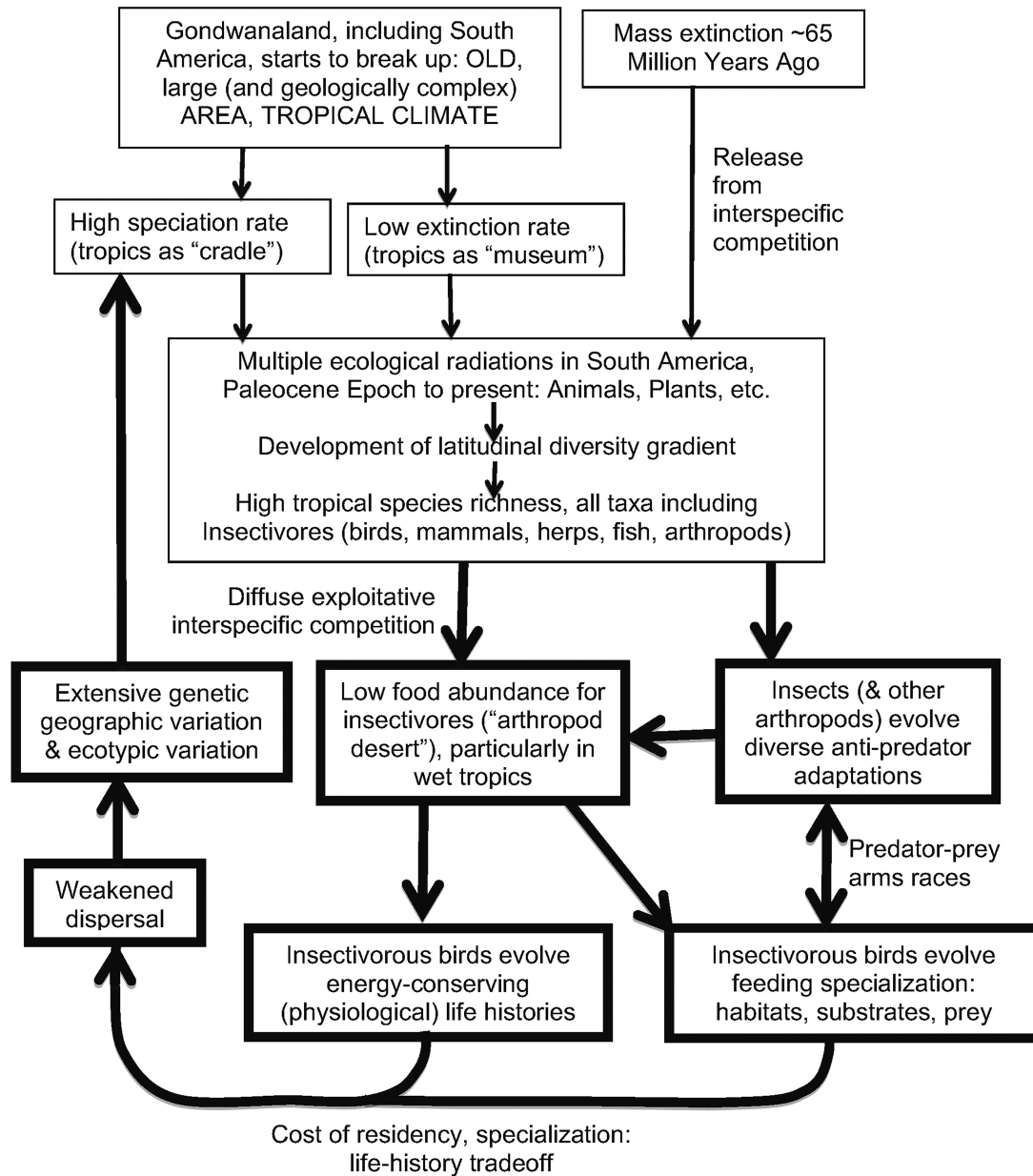
FIGURE 1. Flow diagram for the evolution of ecological specialization in species-rich tropical communities via the Biotic Challenge Hypothesis. Heavily outlined boxes represent the novel components of the theory developed here. All caps in first box (upper left of diagram) emphasize conventional contributions to high species diversity, namely large area, age of area, and tropical (relatively aseasonal) climate. Although not central to the theory of evolution of community structure via ecological specializations, diagram also indicates positive feedbacks (upward oriented arrows, left-hand side of diagram) on speciation rate at low latitudes via the consequences of specialization for life histories and reduced dispersal ability.

remain parapatric in distribution for long periods after secondary contact, only slowly evolving the kinds of ecological differences necessary for expansion geographically and eventual coexistence sympatrically (e.g., in different habitats) and eventually within habitats. The importance of sister species inhibiting each other's expansion geographically is illustrated by the fact that a third of Andean bird species are inferred to be limited in elevational distribution by interspecific interference competition from sister species (Freeman 2015), a conclusion now supported in a few cases experimentally (Jankowski et al. 2010, 2012). Similarly, diverse genera of lowland Amazonian rainforest birds maintain largely nonoverlapping distributions of sister species along successional gradients using interference competition (Robinson and Terborgh 1995). Many cases of sister species with parapatric distributions occur

throughout the Neotropics, including species abutting on adjacent sides of Amazonian tributaries (del Hoyo et al. 2020). A prominent example comes from the Furnariidae (Remsen 2003:182 and 185):

> "With the benefit of detailed recent studies of various tropical suboscine birds undertaken by Whitney, Isler and Isler, Zimmer, T. S. Schulenberg, N. Krabbe, C. Marantz, A. Aleixo and others, it can be predicted that virtually all widespread "species" of suboscines that show discrete geographical variation in phenotypic characters across major barriers to gene flow, such as Amazonian rivers and Andean dry canyons, will be found to consist in fact of multiple biological species-level taxa."

Other examples come from species abutting in the transition from secondary vegetation to primary rainforest (e.g., *Tolmomyias* and *Todirostrum* flycatchers in case study, below), and species with largely nonoverlapping foraging height distributions within rainforest (e.g., Cohn-Haft 1995). The reason these sister species pairs do not coexist to a greater extent could be direct interspecific competition, but this has rarely been tested experimentally. An exception to strict parapatry that appears to prove the rule of allopatrically distributed sister species within species-rich, mainland tropical regions involves 2 Peruvian warbling antbirds (*Hypocnemis*) that coexist via interspecific territoriality maintained by aggressive behaviors along the ecotone between bamboo and terra firme forests (Tobias and Seddon 2009, Jankowski et al. 2012). Moreover, Pigot and Tobias (2012) found in Furnariidae, a South American radiation of primarily insectivorous suboscine passerines (Supplemental Material Appendix A), that ~80% of sister species are not sympatric; of the sympatric species, rates of secondary sympatry increase with both ecological distance (measured using foraging-relevant morphological traits) and with phylogenetic distance. The time it has taken Furnariidae to evolve secondary sympatry, that is, to coexist, can be up to tens of millions of years. These authors conclude that the evolution of sympatry in species-rich adaptive radiations such as that of the Furnariidae is a complex evolutionary process—a challenging problem for the species involved, as well as for us to understand. These examples suggest that strong spatial isolation may be the norm for recently formed sister species and may persist for thousands or millions of years in species-rich environments—an important assertion for further testing. The tendency for sister species failing to become sympatric for long time periods is the fundamental challenge we address next by developing our own hypothesis for the evolution of coexistence among competing tropical mainland species.

The diversity and specialization of insectivorous Neotropical birds begins with their deep evolutionary history: the history of clade proliferation that led to their diversity and distribution taxonomically (Figure 1). Many modern (post-Mesozoic) birds originated in South America and experienced two main pulses of rapid radiation, one around the Cretaceous–Paleogene transition and another in the middle Miocene (Claramunt and Cracraft 2015, Ksepka et al. 2017). The first pulse resulted in 22 groups of Neornithes, including contemporary orders containing insectivores (Table 1), although speciation has continued steadily (e.g., in Furnariidae) into the Pliocene and Pleistocene epochs (e.g., Brumfield 2012). Moreover, many of these insectivore radiations appear to have jump-started in South America, within a large continental area of partially interconnected Gondwanan continents. Large parts of this area were tropical rainforest, in a warm, moist, and equable climate. Speciation rate increased during relatively cooler periods, when rainforest inhabitants became isolated due to forest retraction and fragmentation (Claramunt and Cracraft 2015). The ecological opportunity provided by the mass extinctions terminating the Mesozoic Era is acknowledged to have contributed to speciation rates of birds generally. We thus explicitly accept the idea that both time and area (including implicitly geological complexity) contributed importantly to the high species richness of Neotropical insectivores (Figure 1).

The insectivore diversity encompassed by avian taxa recognized today (Table 1) suggests many independent origins and adaptive radiations. By our criterion for insectivore (70% invertebrates in diet), the Neotropics contain 2,079 resident insectivorous species, detailed in the synopsis of Neotropical insectivorous birds (see Supplemental Material Appendix A). What is important to recognize here about these diverse insectivore clades, involving 15 avian orders, is their ecological diversity, including nocturnal, crepuscular, and diurnal predators; aerial and terrestrial species; species feeding on foot as well as aerially; large-insect specialists (Bucconidae puffbirds and various raptors) and some of the smallest birds globally (pygmy-tyrants and tody-flycatchers); solitary and mixed-species flock participants; predators in every habitat of the Neotropics from the lowlands to high elevations; and even aquatic feeders (e.g., rails, Rallidae; torrent tyrannulets, Tyrannidae; and one dipper, Cinclidae). This ecological diversity has had several important consequences for the evolution of specialization.

Our most novel theoretical proposition is that diffuse interspecific competition locally from dozens to hundreds of species strongly selects for specialized feeding adaptations (heavy-lined boxes in Figure 1). Diffuse competition in our conception results in the depression of food resources by many species, including phylogenetically unrelated predators, sufficiently such that each species competes simultaneously with many others (e.g., Sherry et al. 2016b). La Selva Biological Station of Costa Rica provides an example

TABLE 1. Number of species of primarily insectivorous birds by order and family, and categorized as Neotropical endemics, species inhabiting Neotropics plus Nearctic (mostly migratory), and totals of these groups. For each of these 3 categories, number of species that are primarily insectivorous (estimated to be ≥70% of diet) and totals for all diets including insectivorous species. Data are from Handbook of the Birds of the World and BirdLife International (2018) (del Hoyo et al. 2020) and a regularly updated global database of the ecology and life history traits of the world's bird species described in Şekercioğlu et al. (2004, 2019).

Orders	Families	Neotropical endemics		Neotropics + Nearctic		Total	
		Insectivores	All diets	Insectivores	All diets	Insectivores	All diets
Tinamiformes	Tinamidae	2	48			2	48
Galliformes	Odontophoridae	1	26		3	1	29
Caprimulgiformes	Nyctibiidae	7	7			7	7
	Caprimulgidae	42	42	6	6	48	48
Apodiformes	Apodidae	26	26	5	5	31	31
	Trochilidae	1	351		11	1	362
Cuculiformes	Cuculidae	25	30	3	3	28	33
Gruiformes	Heliornithidae	1	1			1	1
	Rallidae	29	43	5	10	34	53
Charadriiformes	Burhinidae	2	2			2	2
Strigiformes	Strigidae	28	56	5	7	33	63
Accipitriformes	Accipitridae	9	50	2	15	11	65
Trogoniformes	Trogonidae	8	26		2	8	28
Coraciiformes	Todidae	5	5			5	5
	Momotidae	11	13	1	1	12	14
Piciformes	Galbulidae	19	19			19	19
	Bucconidae	37	38			37	38
	Ramphastidae	1	50			1	50
	Capitonidae	1	18			1	18
	Picidae	106	114	9	11	115	125
Cariamiformes	Cariamidae	1	2			1	2
Falconiformes	Falconidae	3	22		1	3	23
Passeriformes	Sapayoidae	1	1			1	1
	Thamnophilidae	241	241			241	241
	Conopophagidae	12	12			12	12
	Melanopareiidae	4	4			4	4
	Grallariidae	55	55			55	55
	Rhinocryptidae	60	60			60	60
	Formicariidae	12	12			12	12
	Furnariidae	326	331			326	331
	Pipridae	5	52			5	52
	Cotingidae	1	67			1	67
	Tityridae	34	49			34	49
	Tyrannidae	399	425	24	24	423	449
	Vireonidae	40	44	12	13	52	57
	Laniidae			1	1	1	1
	Corvidae	18	35	1	5	19	40
	Paridae			2	2	2	2
	Donacobiidae	1	1			1	1

TABLE 1. Continued

| Orders	Families	Neotropical endemics		Neotropics + Nearctic		Total	
		Insectivores	All diets	Insectivores	All diets	Insectivores	All diets
	Hirundinidae	29	29	4	4	33	33
	Aegithalidae			1	1	1	1
	Certhiidae			1	1	1	1
	Sittidae			2	2	2	2
	Polioptilidae	11	11	2	2	13	13
	Troglodytidae	82	82	6	6	88	88
	Cinclidae	2	2	1	1	3	3
	Mimidae	16	24	3	4	19	28
	Turdidae	26	65	9	10	35	75
	Regulidae			1	1	1	1
	Peucedramidae			1	1	1	1
	Motacillidae	7	8			7	8
	Rhodinocichlidae	1	1			1	1
	Passerellidae	57	94	2	22	59	116
	Zeledoniidae	1	1			1	1
	Teretistridae	2	2			2	2
	Icteridae	58	95	7	14	65	108
	Parulidae	69	70	50	50	119	120
	Phaenicophilidae	4	4			4	4
	Nesospingidae	1	1			1	1
	Calyptophilidae	2	2			2	2
	Mitrospingidae	1	4			1	4
	Cardinalidae	21	38	5	14	26	52
	Thraupidae	117	404			117	404
	Grand total	2,081	3,315	171	253	2,252	3,568
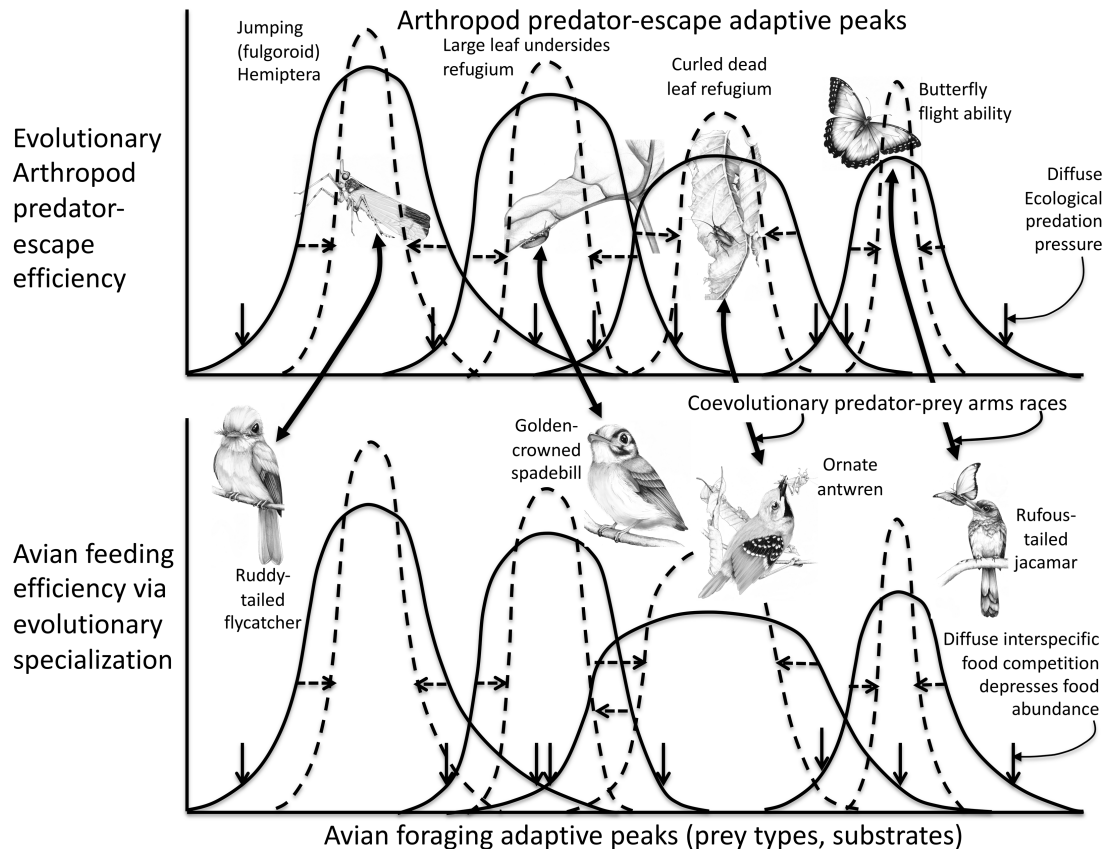
FIGURE 2. Coupled evolution of stronger arthropod antipredator adaptations and arthropod predator specializations (i.e. coevolutionary arms races [heavy double-headed arrows]) in response to intensification of diffuse predation and diffuse interspecific competition (solid downward arrows in both panels) in the species-rich Neotropical equatorial wet forests. Horizontal dashed arrows associated with 4 representative adaptive peaks indicate increased specialization by arthropods and by avian arthropod predators in response to the intensification of predation resulting from diverse adaptive radiations of insectivores in the Neotropics. All animal illustrations by Margaret (Meg) Maurer. See text for further explanation.

of 53 coexisting resident insectivorous bird species potentially involved in diffuse competition. This number comes from the list by Sigel et al. (2010) for this field station and includes the intersection of species that are year-round residents, forest-based, and "invertebrate" (i.e. insectivore) feeders. A second example comes from upland (terra firme) forests near Manaus, Brazil, with 121 species (Cohn-Haft et al. 1997) and includes species at the intersection of terra firme inhabitants ("1") or primarily terra firme forest species plus second-growth ("1,2") habitat classifications; common, uncommon, or rare in abundance; and "invertebrate" (insectivore) feeders. This list does not include waterbirds, swifts, or other birds that do not feed primarily within terrestrial vegetation. These large numbers of species coexist, we argue, largely indirectly by evolving efficient adaptations to exploit a particular resource such as a prey taxon, habitat, or microhabitat (Figure 2), rather than competing directly with, or evolving in response to, any other particular insectivore species, simply because the most closely related species such as sister species tend

not to coexist in the same geographic area or habitat, as discussed above. We argue that these specializations constitute the primary mechanisms of species coming to coexist sympatrically within species-rich communities. We are not arguing that the 121 insectivore species in a Manaus, Brazil, forest, for example, overlap in feeding on all the same insects, but we do argue that overlaps are high, even on some of the same prey types and prey species; for example, the synopsis of insectivorous Neotropical birds (Supplemental Material Appendix A) mentions diverse katydids and other Orthoptera in the diets of the large majority of families and species mentioned, suggesting diffuse competition for these insects; additionally, ants, termites, and beetles are all mentioned in the diets of hundreds of Neotropical insectivorous species, many mentioned in Supplemental Material Appendix A.

We argue on both empirical and theoretical grounds that diffuse competition favors evolutionary specialization. First, we distinguish 2 potentially confusing definitions of specialization. A widely applied definition is

the narrowing of the breadth of limiting resources arising from character displacement associated with speciation, as illustrated by the divergence of beak sizes to partition seed sizes by Geospizinae ground finches in the Galápagos Archipelago (Grant 1986, Grant and Grant 2006). This is also known as the ecological theory of character displacement resulting from divergent natural selection (Schluter 2000). A second definition of specialization, which we emphasize in the present study, is the increasingly restricted ecological attributes compared to availability—including habitat, microhabitat, and prey taxa (Sherry 1990, Irschick et al. 2005)— evolved in relation to all the other species, not just in relation to a sister species.

The empirical argument for the evolution of ecological specialization, using the second definition, builds on the idea of competitive release, or the tendency for organisms to evolve greater niche breadth within species when fewer species compete. An empirical avian example of competitive release is Ricklefs's synthesis of Caribbean and Panamanian studies (building on earlier work by Robert MacArthur and colleagues), in which controlling for elevation, latitude, and largely for geology, reveals that the more depauperate the Caribbean island community, the greater the local population density per species and the broader the habitat niche (Figure 3; see references in figure legend).

Another example of ecological release is the Cocos Finch (*Pinaroloxias inornata*), the single geospizine finch outside the Galápagos, endemic to isolated Cocos Island, Costa Rica (Werner and Sherry 1984, Sherry 2016). As a population, this species eats an extraordinary variety of foods from diverse substrates, including nectar, fruit, and diverse arthropods, and from all available substrates from ground to treetops. Individual finches probably compete most intensely intraspecifically, because Cocos Finches are by far the most prevalent birds encountered in all Cocos Island terrestrial habitats. This example illustrates how relatively strong intraspecific relative to interspecific competition can favor generalist diet and foraging behaviors (i.e. ecological release as a species) facilitated by individuals competing by specializing behaviorally as individuals relative to conspecifics, possibly to confer efficiency. Greenberg (2016) gives many additional examples of ecological release in birds, particularly in island species.

Ecological release can occur either in ecological time (without any genetic change) or evolutionarily, the latter likely the case in the 2 specific examples just given, as suggested by the endemism of the species involved. An example of ecological release in ecological time involves army ant–following birds in Panama. Touchton and Smith (2011; see also Jankowski et al. 2012) took advantage of the extirpation of the large, socially dominant Ocellated Antbird (*Phaenostictus mcleannani*) from Barro Colorado Island,
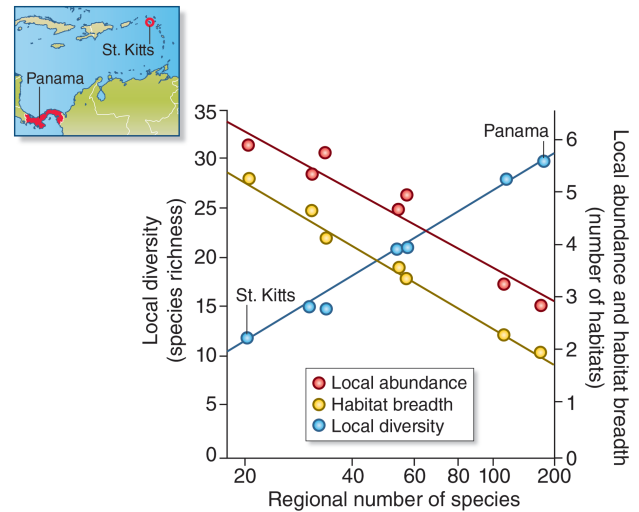

FIGURE 3. Ecological release and habitat breadth. As both the local (blue line) and regional number of species increases going from a species-depauperate island like St. Kitts to mainland Central America (Panama), the breadth of habitats occupied (yellow line) and local abundance per species (red line) both decrease. This pattern is consistent with the idea that species are "released" from competition in species-poor regions, leading to increased strength of within-species competition for food resources compared to between-species competition. From Sherry 2016, adapted from Ricklefs and Cox 1977, reproduced with permission from John Wiley and Sons; and Wunderle 1985, reproduced with permission from The Wilson Bulletin.

following its isolation by Lake Gatun in constructing the Panama Canal. In response, Spotted Antbirds (*Hylophylax naevioides*) quickly expanded their foraging niche and increased in abundance as predicted by release from a competitor.

If ecological release occurs over evolutionary time in depauperate communities, as illustrated by the examples above (Figures 3, 4), then it must also be the case that ecological contraction evolves in the presence of multiple competitors. Although specialization is discussed in the literature in a variety of contexts, the idea of competitive contraction in response to competition as a mechanism for the evolution of specialization is discussed less frequently, to our knowledge. Competitive contraction is simply competitive release viewed in the opposite direction. Competitive contraction can involve adaptation to specific habitats (Figure 3), which in the Neotropics include elevations (e.g., Terborgh and Weske 1975), heights in forests (Terborgh 1980, Cohn-Haft 1995), seasonal forest types (including deciduous woodlands, *Caatinga*, *Cerrado*, *Llanos*, and *Pantanal*), plant formations such as bamboo (Kratter 1997) and physically stunted white sand soil plants (Alonso et al. 2013), flooded vs. non-flooded forests, and river islands (G. H. Rosenberg 1990). Competitive contraction should logically extend to specialization on microhabitats for feeding and even to particular prey or food types within
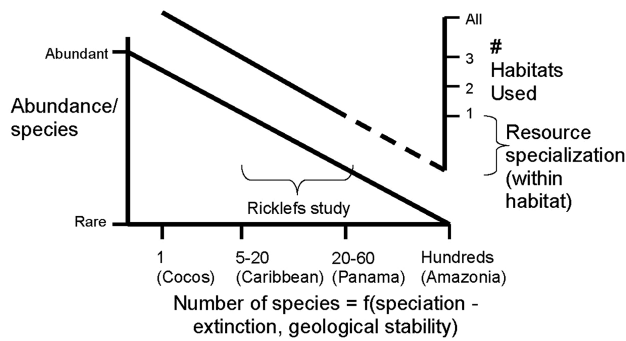
FIGURE 4. (left) Hypothetical ecological release and (right) ecological contraction = specialization, as a function of number of species present in fauna, illustrating increased levels of specialization (e.g., to microhabitats, and to particular prey types) in increasingly species-rich Neotropical habitats. Cocos refers to Cocos Island, Costa Rica, an extremely depauperate, isolated island in the Eastern Pacific Ocean in which the Cocos Finch has an extremely broad niche in the almost complete absence of competition from other bird species. "Ricklefs study" refers to the results in Figure 3.

increasingly species-rich communities (Figure 4). As various lineages diversify and exceed their extinction rates, species will accumulate and become adapted to conditions with an increasing number of sympatric and competing species, which will favor feeding efficiency, unless extinction rate of these specialists increases to match speciation rate (Figures 1, 2).

The second, theoretical argument for why we predict consumers should evolve greater ecological specialization in species-rich communities at low latitudes derives from low resource accessibility year-round in response to diverse consumers in relatively aseasonal habitats (Ashmole's [1963] Hypothesis, as extended and tested by Ricklefs 1980). The basic idea is that populations in seasonal environments are limited primarily by survival of individuals during the nonbreeding season, and that at the equator, where seasonality is minimal, this limitation is continuous. Ironically, according to this idea, resource accessibility for insectivores should be most restricted in the most ecologically productive (lush) and least seasonal lowland humid forests, because populations of consumers should tend to be at the level at which their survival is limited by food. Predator populations such as birds should be best able to track their arthropod prey populations numerically under such circumstances, at or near the food-determined carrying capacity for the environment. We emphasize that this argument is theoretical and needs testing against alternatives such as population limitation via nest predators or parasites.

However, additional factors should greatly exacerbate food limitation, including competition from other species. The more species that are present the more likely they are to compete diffusely for resources (Figures 1, 2), particularly during seasons when resources are relatively scarce. This will be particularly acute in areas of the wet tropics during the rainiest periods (which can occur year-round right at the equator), when birds may have difficulty finding enough food to survive, and when cloud cover may suppress photosynthesis, particularly in forest understory (e.g., Fogden 1972, Foster 1974). Moreover, insects constitute a rich source of protein, making them an attractive resource to diverse organisms besides birds, including other insects, arachnids, amphibians, reptiles, mammals, and even some plants. Mammals are a particularly important group of insect predators because they are warm-blooded (necessitating continual feeding while active) and include diverse insectivorous bats, many of which forage as aerobatically as some birds, and diverse rodents and small primates that also rely heavily on arthropods and search in diverse ways, day and night. Most of these predatory taxa reach their peak species richness in the humid tropics, with the consequence that not only the number of species, but also the ways these insect predators hunt and consume insects, peaks there. These insect-depressing impacts should combine to reduce ongoing, average resource availability via diffuse competition (Figures 1, 2).

A community with many insectivores is also likely over evolutionary time to drive selection for antipredator defenses in the prey on which predators feed most heavily, making these prey less accessible to most predators. This heavily sustained predation on arthropods by diverse insectivorous birds creates a powerful arms race between insectivore predators, including birds, and their prey. This arms race likely contributed to the effective scarcity of arthropods from the perspective of insectivorous birds, an important contributor to the arthropod desert (Figure 1), as elaborated in Supplemental Material Appendix B. Resource scarcity from intraspecific and interspecific competition coupled with arms races with arthropods should favor those predators with the most efficient adaptations for foraging, which we define to include finding, capturing, processing, and digesting available arthropods and life-history traits that involve optimizing the expenditures of the energy acquired (Figure 1). This should favor specialization as a means to increase efficiency. For example, a butterfly predator with greater perceptual ability to distinguish edible from inedible (e.g., distasteful, model butterflies), and with greater ability to attack and capture evasive prey, will have access to relatively more prey (Sherry 2016), providing a competitive advantage. Specialization for one prey type will often result in other prey types being less easily detected, captured, or handled by a particular species, forming an evolutionary tradeoff. For example, the long, thin beaks of jacamars that help capture relatively

soft-bodied flying insects like butterflies and dragonflies are poorly adapted for larger, harder insects more efficiently consumed by puffbirds. Specialization should also be penalized if the abundance of prey on which the specialist depends decreases. Evolutionary specialization should thus be favored in the least seasonal environments in which the specialists can survive year-round on the particular habitats, substrates, or prey types to which they have become evolutionarily specialized.

By specialized diets we do not mean specialization via divergence involving character displacement (e.g., Schluter 2000, Tobias et al. 2013a), the first definition given above. This is because sister species tend to co-exist relatively rarely within large, species-rich faunas to the extent that new species are more likely to arise with allopatric distributions, according to the allopatric speciation model, and remain parapatric for long periods of time, as argued above. Accordingly, the large majority of competitors exploiting a habitat or microhabitat may not be closely related (e.g., see MacArthur 1969), but nonetheless these competitors should all depress the abundance of shared prey such as arthropods (e.g., Gradwohl and Greenberg 1982, Michel 2012). The consequence of these circumstances is that within species-rich communities such as Neotropical rainforests, each species potentially competes not just with closely related species as often assumed (e.g., Jankowski et al. 2012), but also with other, diverse, more distantly related taxa. Tropical communities often contain a variety of coexisting congeners, such as antwrens in the genus *Myrmotherula*, which might appear to contradict our assertion above about most competitors being non-sister species; but, until we have better data on these species' diets where they coexist, coupled with phylogenies, it will be difficult to evaluate the strength of direct competition among species with different degrees of genetic relatedness. Competition with sister species where their ranges abut may be strong, and competition with other sympatric species should generally be weak. Such diffuse competition should not cause divergence involving particular species pairs so much as the evolution of independent evolutionary adaptations by each species to compete against all the other species feeding on similar resources, that is, feeding specialization on particular substrates or prey taxa (Figure 2). This diffuse competition involves not just the more than 100 other species of coexisting bird species in some parts of the Neotropics, but also interclass competition such as with insectivorous lizards and mammals (e.g., Wright 1979, 1981; Hasegawa et al. 2009). Specialization should also be necessitated by, and evolve in relation to, particular prey taxa with distinctive antipredator adaptations, as reviewed in Supplemental Material Appendixes A, B.

We argue that the best way to define specialization (Figures 1, 2) as an evolutionary process is the adaptation of behaviors to exploit particular prey types or prey substrates via feeding-related structures (or cognitive or sensory traits) that enhance the efficiency of feeding, and that are reflected by repetitive use of foraging behaviors, to detect, capture, handle, and/or digest particular prey (i.e. stereotypy). By this definition, specialists may or may not restrict the breadth of prey taxa, and thus our definition provides a better indicator of evolutionary specialization than simply restricted breadth of diet or foraging behavior (Sherry 1990). A potentially confusing aspect of specialists by our definition is that they can feed predictably either on a wide breadth of prey taxa—because of a restricted habitat or microhabitat (like aerial leaf litter)—or alternatively on a particular prey taxon using one or a variety of foraging tactics. Another potentially confusing aspect of specialization is that specialists can retain their ability to consume relatively profitable prey (i.e. act as generalists when the favorable prey are available; Robinson and Wilson 1998), and thus compete diffusely with many other species for such favorable prey. In tropical rainforests profitable prey might include relatively conspicuous (low search time), abundant, and easy-to-catch prey like ants and beetles, important taxa for many flycatcher species (Sherry 1984).

To document the arms race involving insectivorous Neotropical birds we catalog the birds involved (Supplemental Material Appendix A) and describe some of the most prominent defenses of arthropods against birds (Supplemental Material Appendix B). This arms race involves the greatest concentration of insectivorous birds globally. The Neotropics contain 3,315 endemic bird species in total, of which 2,081 species (just over 60%) are insectivores (Table 1). Including species that are both Neotropical and Nearctic, which adds mostly migrants spanning both regions, boosts these numbers to 3,568 and 2,252 for totals and insectivores (63%), respectively. Considering just the Neotropical endemic insectivores, 367 species (~18%) are non-passerines (in 14 orders). Of these resident non-passerines, insectivores are concentrated in woodpeckers, nightjars and nighthawks, and puffbirds; and to a lesser extent in owls, swifts, cuckoos, jacamars, and rails. The other 1,714 (82.2%) species of endemic Neotropical insectivores are passerines. Of these passerines, 1,148 species (almost 67%) are non-songbird perching birds (i.e. suboscines), which evolved and are endemic primarily in the Neotropics. The most species-rich of these suboscine families (and insectivore families generally) are the New World flycatchers, ovenbirds and woodcreepers, and antbirds. The other 556 species of passerines (33%) are oscines, or songbirds, of which the most species-rich insectivore families are tangers, wrens, and New World wood warblers. Many other Neotropical birds eat some insects, albeit not qualifying as insectivores by our definition, including many granivores, frugivores,

nectarivores, and carnivores. For example, although hummingbirds are generally considered nectarivores, they nonetheless consume insects frequently (e.g., Stiles 1995).

Besides the diversity of Neotropical species attacking insects, the diverse and often complementary ways predators forage for prey is also extraordinary. This has the consequence that natural selection for predator-avoidance mechanisms to avoid one group of predators favors prey traits that could be exploited evolutionarily by another kind of predator. For example, jumping mechanisms by Hemiptera to escape predators feeding primarily on foot (e.g., foliage-gleaning birds, lizards, and frogs) appears to have created a feeding opportunity for predators able to pursue these insects in flight after the jump (Sherry 1984). Prey that hide effectively from diurnal predators and become active at night create an opportunity for nocturnal and crepuscular predators, and vice versa. Thus, in a long-term evolutionary perspective, diverse insect predators select for diffuse enhancement mechanisms among predators, which should in turn create additional antipredator adaptations on the part of the prey. These coevolutionary arms races, including insectivorous birds and their prey, are crucial to understanding the arthropod desert from birds' perspectives, hence the need to detail the specializations by the birds (Supplemental Material Appendix A) and antipredator adaptations by the insects and a few other arthropods (Supplemental Material Appendix B). Understanding the ecological diversification and specialization of insectivorous birds also necessitates appreciating the evolution of their prey, and we refer to these reciprocal coevolutionary relationships as predator–prey arms races (Figure 2). To the extent that insectivorous birds as predators are evolutionarily specialized on particular prey substrates and taxa, as we argued for diverse Neotropical insectivores (Supplemental Material Appendix A), it seems inescapable that their prey would have needed to evolve diverse and effective antipredator defenses, including defenses specialized against particular predators. Coevolution in the context of an arms race necessitates both that a predator has evolved traits in response to a particular prey taxon, and that the prey taxon has evolved defenses in response to the predator (Janzen 1980), for example, antwrens (Thamnophilidae) specialized to forage on the arthropods hiding in dead leaves. Bird adaptations likely include the ability to recognize dead leaves as a foraging substrate, agility to hang onto the substrate so as to be able to grab an insect within the dead leaves, a beak size and shape to catch and hold onto particularly rewarding prey such as Orthoptera and cockroaches, and flocking behavior to gain protection against predators, to which they are vulnerable while peering myopically into the leaf substrates. Reciprocal adaptations by the insects might include brown coloration for camouflage in the leaves, selection of leaves alone as a diurnal resting place

to protect against many kinds of predators, and ability to escape leaves when under attack.

Another kind of evolutionary species interaction, whether or not it qualifies as co-evolution, is enhancement (Charnov et al. 1976), in which the defense evolved by a prey taxon against one predator type creates a new resource to be exploited by another predator type, an evolutionary opportunity. For example, the evolutionary defense by particular orthopterans and cockroaches that hide in suspended dead leaf clusters to escape predators searching green leaves and twigs provided the evolutionary opportunity that is exploited by the dead-leaf foraging thamnophilids and a few other species. Other examples of enhancement are implicit in insect defenses described in Supplemental Material Appendix B.

To summarize the foregoing considerations, foraging specialization should evolve and persist under the following conditions: high species richness of competitors, including birds and other taxa; diverse consumer types present consistently, year-round depressing prey abundance in a variety of ways (the birds emphasized here; see Supplemental Material Appendix A); long time periods for evolution of divergence in traits that allow coexistence and thus for coevolution with the prey or food resource (see Supplemental Material Appendix B); and prey type availability relatively constant and predictable year-round, and over long time periods (e.g., Lijtmaer et al. 2011). All of these conditions should be maximized in ancient, large, continental, wet lowland and low-latitude tropical regions, such as characterize large expanses of equatorial South America.

TESTING THE HYPOTHESIS: ARE TROPICAL INSECTIVORES EVOLUTIONARILY SPECIALIZED?

Ecologists have addressed the question of specialization for decades in attempting to understand geographic patterns of species richness and specifically why more species coexist in the tropics than at higher latitudes (e.g., Hutchinson 1957, 1959; MacArthur 1969, 1972). Diverse empirical studies have addressed this question from different perspectives, using a variety of taxa, as illustrated by the references in the Introduction. Ecological niche theory has motivated many such studies, for example, tests of hypotheses about the possible occurrence of narrower niches in terms of tropical prey taxa and/or foraging microhabitat breadth (e.g., Orians 1969, Askins 1983, Marra and Remsen 1997) as evidence of specialization. Another approach to specialization comes from optimal foraging theories, which assume a particular phenotype such as morphology and ask how the organism makes decisions given various optimization schedules and constraints (see Sherry 2016 for a review using avian examples). Both niche theory and optimality approaches have effectively used

experimental field and lab studies to test for how animals feed and compete. Some ecologists have even argued that interspecific competition is best studied experimentally and cannot be demonstrated without conducting experiments (e.g., Connell 1980, Schoener 1983, Dhondt 2012). Sherry (1990) distinguished these ecological approaches to specialization, namely niche theory and optimal foraging, from evolutionary approaches, and argued for the importance of distinguishing the two. For example, ecological specialization in diet is often identified by the use of a subset of prey compared to what is available, whereas evolutionary specialization is identified in relation to phenotypic traits of some predators in comparison with others.

Our approach to interspecific competition here, and the resulting community structure of species-rich Neotropical regions epitomized by lowland wet forests, is evolutionary and comparative (Figure 2). Manipulative experimental tests of the effects of interspecific competition in such communities will probably be insufficient alone for at least 2 reasons: First, evolutionarily specialized and stereotyped feeders may not respond quickly, if at all, to manipulations of other competitors or even prey abundance. Their feeding stereotypy will probably render such predators relatively less able to respond opportunistically or quickly to changes in their communities compared to resident higher latitude birds and migratory species (e.g., Sherry 1984, Sherry et al. 2016a). Second, to the extent that tropical insectivores compete with many other species diffusely and exploitatively, as argued above, manipulations of one or a few insectivore species' abundances will also likely have little detectable impact on the multitude of other coexisting species. The community response involving dozens to hundreds of species sharing resources may be effectively impossible to monitor, at least in any simple field experiment (Cody 1974:131; Prins 2016). Thus, in addition to experiments, comparative approaches are needed that take advantage of natural experiments and natural variation, illustrated by studies of interclass competition (e.g., Wright 1979, 1981) and isolated geographic regions (Terborgh and Weske 1975).

Most studies of specialization have used surrogates for the actual resources, such as foraging behavior or morphology, which is risky because surrogates may tell a different story than actual resources consumed (e.g., Poulin and Lefebvre 1996, Gordon et al. 2019, Kent and Sherry 2020). Diet studies that include more than just one or a few species simultaneously, and that thereby control for available prey, are rare. We expand next on Sherry's (1984) study of 16 Costa Rican lowland rainforest flycatchers to address the question of dietary differences and ways in which these species have evolved dietary specializations, and why. In subsequent sections, we discuss briefly other ways to test the ideas presented in this paper.

Case Study: Aerial Flycatcher (Tyrannidae) Specialization in Lowland Costa Rican Rainforest

Sherry's (1984) study compared and contrasted 16 species of sympatric, aerially foraging insectivorous tyrannids (including upward strikers, aerobatic pursuers, and hawkers) coexisting within the lowland wet tropics and focused on multiple habitats in Caribbean Costa Rica. All of the birds were collected for diet information while foraging actively (as the only way to secure stomachs of most of the species, due to their rarity and/or foraging behavior high in the canopy), 3–10 individuals per species were sacrificed, cut open immediately, and stomachs preserved in alcohol to halt digestion; samples were later sorted into arthropod taxa and identified in the lab with the help of a variety of arthropod identification guides.

Sherry (1984; see also Sigel et al. 2006) showed that these aerially foraging tyrannid species, although sympatric, differed in habitat (rainforest, vine tangles along streams, forest edge, and open country with varying amounts of shrubbery and isolated or patchy trees) and microhabitat, prey taxa, degree of prey taxon homogeneity (among different individual stomach samples), degree of prey taxon restriction, "clumpedness" (i.e. patchiness) of the prey, and other ways that helped elucidate how these species foraged and differed ecologically, thus potentially facilitating coexistence. The samples controlled for season insofar as they were obtained during 3 consecutive years during the post-breeding, wet season months (October–December) when interspecific competition was considered maximized by reduced prey abundance or accessibility, due to rainy, cloudy (dark) conditions, for example. Such conditions might impede foraging in some birds.

Although the original study (Sherry 1984) considered individual variation within species, it did not test for prey taxa differences among species. To address this question as one way to test for specialization in these birds, here we reanalyzed the same samples, using ordination methods and nonmetric multidimensional scaling axes (methodological details in Sherry et al. 2016a) to ask if prey taxa differences among species exceed the variation within a species. (We are unaware of any other sample of the diets of multiple coexisting Neotropical insectivorous birds, controlled for time and place, other than diets of migratory warblers currently under study by TWS and CMK). We included just the resident, nonmigratory species here.

First, considering just the 7 aerially foraging flycatcher species that coexisted strictly within rainforest (Table 2), and could all theoretically be detected at the same point in space, diets differed statistically significantly (PERMANOVA, $F = 11.5$, $P < 0.001$), also indicated by their 95% confidence ellipses for the mean prey taxa being almost completely nonoverlapping (Figure 5; stress

TABLE 2. Species names and codes used in case study of aerially foraging tropical flycatchers (Tyrannidae).

Common name	Code	Latin name	Latin Code	No. stomach samples	No. prey identified
Coexisting rainforest species					
Black-capped Pygmy-Tyrant	BPYT	*Myiornis atricapillus*	MYIATP	12	205
Eye-ringed Flatbill	ERFL	*Rhynchocyclus brevirostris*	RHYBRE	3	43
Golden-crowned Spadebill	GCRS	*Platyrinchus coronatus*	PLACOR	10	212
Long-tailed Tyrant	LTTY	*Colonia colonis*	COLCOL	11	364
Ruddy-tailed Flycatcher	RDTF	*Terenotriccus erythrurus*	TERERY	9	65
Sulphur-rumped Flycatcher	SRFL	*Myiobius sulphureipygius*	MYISUL	7	153
Yellow-margined Flycatcher	YMFL	*Tolmomyias assimilis*	TOLASS	10	263
Additional sympatric species					
Black-headed Tody-Flycatcher	BHTF	*Todirostrum nigriceps*	TODNIG	10	157
Common Tody-Flycatcher	COTF	*Todirostrum cinereum*	TODCIN	10	289
Northern Bentbill	NOBE	*Oncostoma cinereigulare*	ONCCIN	6	98
Slate-headed Tody-Flycatcher	SHTF	*Poecilotriccus sylvia*	POESYL	5	128
Yellow-olive Flycatcher	YOFL	*Tolmomyias sulphurescens*	TOLSUL	6	163
Tropical Pewee	TROP	*Contopus cinereus*	CONCIN	9	184
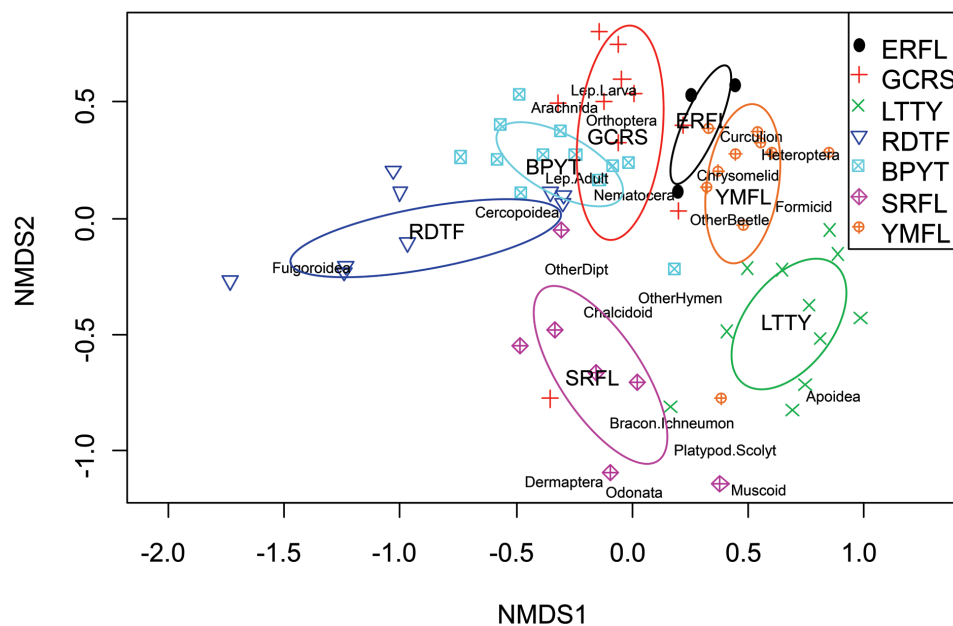
FIGURE 5. Differences in prey taxa consumed by aerially foraging insectivores coexisting within rainforest habitat in Costa Rica (see case study, in text). These 7 species truly coexist (i.e. can be observed in theory at the same places). Ellipses represent 95% confidence ellipses for the mean of each species within nonmetric multidimensional scaling space; locations of arthropod taxa are also shown in this space to help interpret dietary specializations of the insectivore species. Species codes along with common names and Latin binomials for all species are given in Table 2.

for this ordination = 0.20). The 2 most distinctively specialized species (i.e. relatively low distances from a species centroid = relatively tight clustering of individual bird data points) were Ruddy-tailed Flycatcher (See Table 2 for Latin names of species in this section) on fulgoroid and cercopoid (jumping) Hemiptera, which the bird pursues aerobatically in flight, and Long-tailed Tyrant primarily on stingless bees (Apoidea, Hymenoptera). The other aerobatic pursuer, Sulphur-rumped Flycatcher, pursues diverse hymenopteran, some dipteran, and odonate (damselfly) prey, probably aided in detecting prey by routinely following understory mixed-species antwren flocks that flush some of these prey to the benefit of a species such as *Myiobius* that captures flying (fleeing) prey. The other 4 species are upward-strikers: Black-capped Pygmy-Tyrant is one of the smallest birds globally, considered a surprise-attack forager (Sherry 1982, 1984); Yellow-margined Flycatcher and Eye-ringed Flatbill both tend to feed on relatively slow-moving and probably conspicuous prey such as ants and beetles, the former flycatcher typically in the company of canopy mixed-species flocks (comprising vireos in the genus *Hylophilus* and other species) and the
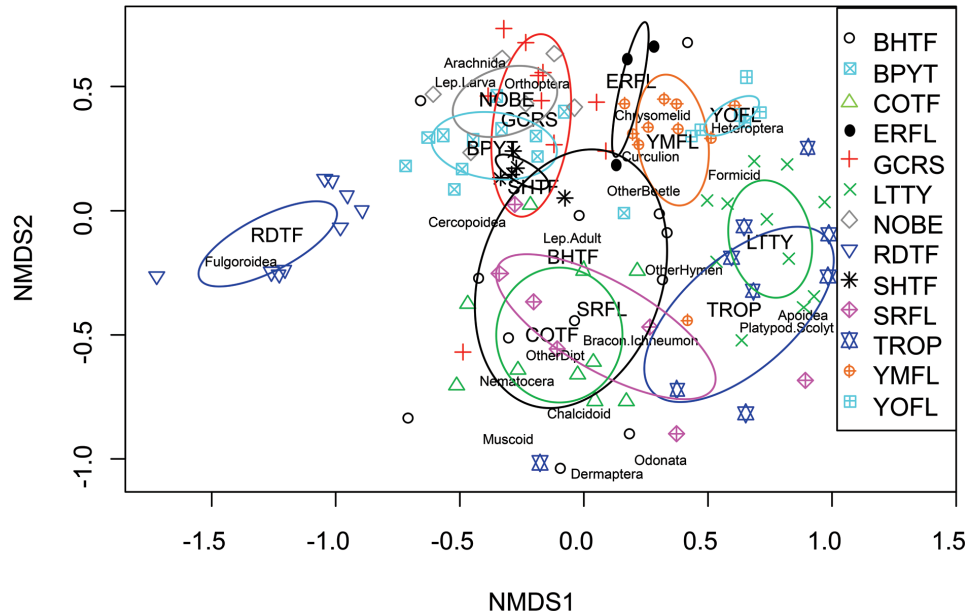
FIGURE 6. Locations of all 13 species of aerially foraging, insectivorous flycatchers from the Costa Rican case study within the same nonmetric multidimensional scaling space as in Figure 4, except with added sympatric species found in different habitats from the species in Figure 4. See case study in text.

latter typically solitarily (Sherry 1984); and the Golden-crowned Spadebill is an upward striker that tends to feed in understory vegetation, on prey underneath large leaves such as palms and aroids, eating a wide variety of insect taxa. Body sizes also differed considerably in these upward-strikers (5.3, 8.8, 14.5, and 22.9 g body mass in the pygmy-tyrant, spadebill, Yellow-margined Flycatcher, and flatbill, respectively; Sherry 1984, TWS personal observation), thus likely contributing to the distinctiveness in prey taxa. Besides the largely distinctive diets (Figure 5), these 7 species have morphological traits that facilitate their distinctive foraging modes (Leisler and Winkler 1985): relatively large wings and tails (low wing-loading), plus prominently stiffened rictal bristles in the case of the 2 pursuers, Ruddy-tailed Flycatcher and Sulphur-rumped Flycatcher; short, wide, and flat beaks in the 3 larger-bodied upward-strikers; and a small body size, long and spatulate beak, and reduced wing and tail area plus relatively long tarsi in the surprise-attacker pygmy-tyrant. Despite coexisting within rainforest habitat, these 7 species also exhibited subtle differences in microhabitats, from understory to canopy, and in the case of the Ruddy-tailed Flycatcher and spadebill, a tendency to select vine tangles, probably associated with regenerating tree-fall gaps (Michel et al. 2015). Thus, these specializations in diet and microhabitat involved morphological differences not just in body size, but also in shape of wings, beaks, tails, tarsi, and probably visual acuity (e.g., for dark understory vs. open canopy; Stratford and Robinson 2005). Some of these specializations involved

narrow, restricted prey taxa (e.g., *Terenotriccus*, *Colonia*), whereas other specializations involved diverse prey taxa and consistently the same prey taxa among individuals of the same bird species, but within restricted microhabitats or because of stereotyped foraging behaviors, as illustrated by upward strikers like *Platyrinchus* in the present study (see also Traylor and Fitzpatrick 1982).

Adding in the other 5 resident sympatric, aerially foraging flycatchers gave the same pattern of species differences as with just the 7 species (PERMANOVA, $F = 10.5$, $P = 0.001$; Figure 6, with stress for this ordination = 0.23; see also diet overlaps, Table 3), but also documented a pattern of multiple species, often congeners, eating similar prey types in different habitats or microhabitats. For example, 2 flycatchers in the genus *Todirostrum* (Black-headed and Common) that are surprise-attack foragers, with overlapping diets due to the number of Diptera and small, parasitic wasps they both eat, foraged in different habitats from any of the other small-bodied upward-strikers. The Black-headed Tody-Flycatcher foraged high in the canopy, in the narrow rainforest–open country ecotone; the Common Tody-Flycatcher was widespread in open country, foraging at a range of heights and situations. Two canopy-foraging flatbills in the genus *Tolmomyias*, Yellow-margined and Yellow-olive, had similar diets of primarily beetles and ants (Figure 6; Sherry 1984), but were nonoverlapping spatially because the former foraged with mixed canopy flocks in rainforest, the latter solitarily in pasture, open woodland, and seasonal woodlands in lowland Costa Rica, and never

TABLE 3. Pairwise diet overlaps of 13 species of resident Neotropical flycatcher included in case study. Overlaps ≥0.5 are highlighted in bold.

	Myiobius barbatus	*Myiornis atricapillus*	*Terenotriccus erythrurus*	*Todirostrum sylvia*	*Todirostrum nigriceps*	*Todirostrum cinereum*	*Oncostoma cinereigulare*	*Rhynchocyclus brevirostris*	*Platyrinchus coronatus*	*Tolmomyias assimilis*	*Tolmomyias sulfurescens*	*Colonia colonis*
Myiornis ecaudatus	**0.63**											
Terenotriccus erythrurus	0.24	0.41										
Todirostrum sylvia	**0.54**	**0.84**	**0.63**									
Todirostrum nigriceps	**0.59**	0.49	0.14	0.48								
Todirostrum cinereum	**0.69**	**0.59**	0.25	**0.62**	**0.66**							
Oncostoma cinereigulare	0.35	**0.8**	0.3	**0.83**	0.4	**0.52**						
Rhynchocyclus brevirostris	0.48	**0.61**	0.14	**0.57**	0.37	**0.5**	**0.53**					
Platyrinchus coronatus	0.46	**0.78**	0.14	**0.78**	0.44	**0.59**	**0.92**	**0.7**				
Tolmomyias assimilis	0.47	**0.57**	0.04	**0.5**	**0.52**	**0.67**	**0.52**	**0.71**	**0.62**			
Tolmomyias sulfurescens	0.38	0.4	0.02	0.42	0.45	**0.64**	0.4	**0.65**	0.46	**0.91**		
Colonia colonis	**0.72**	0.34	0.02	0.13	0.33	0.24	0.1	0.23	0.13	0.17	0.21	
Contopus cinereus	**0.78**	0.4	0.03	0.25	0.45	0.45	0.16	0.28	0.21	0.38	0.46	**0.92**

within continuous rainforest. Four sympatric euscarthmine (subfamily) flycatchers all had overlapping diets due to similarly explosive upward-strike foraging tactics, but in different situations: Black-capped Pygmy-Tyrant in rainforest canopy, Golden-crowned Spadebill in rainforest understory, Northern Bentbills restricted to areas of dense vine tangles, especially along small streams and old second growth, and the Slate-headed Tody-Flycatcher (*Poecilotriccus*) in dense, short vegetation in more open habitats than rainforest (e.g., dense shrub patches in overgrown pastures). Thus, a variety of congeneric species groups (*Todirostrum*, *Tolmomyias*) and other relatives (euscarthmine upward strikers in general) appear to have coexisted by adaptation to different habitats and microhabitats. Many of these species share sister species in different geographic locations (e.g., Golden-crowned Spadebill replaced higher in elevation by a spadebill congener), a common pattern in the tropics (Jankowski et al. 2012).

One could potentially ascribe these dietary differences (particularly by the 7 species coexisting within rainforest habitat) to "resource partitioning." To examine this further we used Pianka's (1974) overlap index. Overlaps in diet (Table 3) appear consistent with resource partitioning. For example, specialists such as the Ruddy-tailed Flycatcher (*Terenotriccus*) had many low diet overlaps with other species (e.g., 0.14 [3 cases], 0.04, 0.03, 0.02 [2 cases]). Similarly, the next most specialized species dietarily, Long-tailed Tyrant (*Colonia*), had one overlap value of 0.72, the rest <0.5, and a couple of 0.1 or less, which are low overlaps overall. The highest pairwise overlap values overall were 0.92 (between the spadebill and bentbill, and between *Colonia* and Tropical Pewee) and 0.91 between the 2 flatbills (*Tolmomyias*) where 1.0 is the maximum possible value. Two of these cases, the first and third, involved species that are upward-strikers in different habitats; the second involved 2 sallying species that forage at different heights above ground (i.e. different microhabitats where they coexist in open-country habitats: *Colonia* forages high above ground both in rainforest and in scattered trees in more open habitats in the Sarapiqui lowlands of Costa Rica; Sherry 1982, 1984). The majority of the pairwise species dietary overlaps (56%) were <0.50. Nonetheless, we hesitate to interpret these overlaps as "resource partitioning," other than the cases of habitat partitioning, because there is no simple ecological resource spectrum implicit in Figures 5 and 6. Also, the species that actually co-occurred in the same habitat (Figure 5) were not partitioning resources with each other (many close-to-zero overlaps), but rather specializing on different prey taxa evolutionarily (Figure 2), independently of the other avian competitor species—"resource partitioning" implies a response to another competitor either ecologically or evolutionarily, as opposed to an evolutionary response to a prey type or substrate. Interestingly, diet overlaps

appear to be greatest in these tyrannid species in cases involving congeners and otherwise closely related species. This observation suggests the prediction that closely related, evolutionarily more recent species pairs will tend to overlap more dietarily and behaviorally, showing niche conservatism.

The species-rich mainland Costa Rican case study included just the aerially foraging flycatchers for which we had stomach contents. Several other aerially foraging, resident flycatchers (Tyrannidae) co-occurred with the species in Table 2 but were too rare to allow collecting enough stomach samples for meaningful comparisons: Royal Flycatchers (*Onychorhynchus coronatus*) occur throughout the Caribbean lowlands, but are rare, pursuing prey aerobatically, and primarily along streams. This species is phylogenetically related to the other 2 genera that forage similarly aerobatically with conspicuous rictal bristles (*Myiobius*, *Terenotriccus*; Ohlson et al. 2008), and diet data are scarce but include Homoptera, Lepidoptera, Odonata, and Orthoptera (Sample et al. 2016). Tawny-chested Flycatcher (*Aphanotriccus capitalis*) is also rare by virtue of its restricted habitat of second-growth flood-plain forests at La Selva (much like Varzea and Igapó specialists in South America); stomach contents of 2 individuals (TWS personal observation) included diverse beetles and ants, suggesting that it is a typical upward-striker such as *Tolmomyias* and *Rhynchocyclus* species, neither of which co-occurs in the same floodplain habitat as *Aphanotriccus*.

In addition to these aerially foraging tyrannids, a variety of other insectivores coexist sympatrically and presumably have competed with these aerial insectivores over evolutionary time, helping shape the lowland rainforest community. These other species include insectivorous cuckoos, raptors, potoos, nightjars, swifts, jacamars, puffbirds, woodpeckers, ovenbirds, treecreepers, antbirds and antwrens, non–aerially foraging tyrannid flycatchers, and diverse other passerines—in other words, most of the insectivore groups covered in Supplemental Material Appendix A (for detailed species listing for La Selva Biological Station, where our diet study was based, see supplementary information for Sigel et al. 2010). Based on Supplemental Material Appendix A, many of these other bird families overlap taxa consumed by the tyrannid flycatchers studied here (e.g., ants, beetles—especially Chrysomelidae and Curculionidae—and miscellaneous Orthoptera; see Sherry 1984 appendix). Orthoptera such as katydids, cockroaches, and crickets are also listed as prey for many different families covered in Supplemental Material Appendix A. Thus, La Selva has a rich insectivorous avifauna, much like that of rainforests in Amazonia, if not quite as species-rich; any competition for food is likely to be diffuse based on how many different predator species eat similar prey taxa.

Testing for Evolutionary Feeding Specialization Generally

First, it is important to recognize a variety of spatial scales (and relevant habitats) over which birds, or any other taxon, might vary in degree of species richness, prey types available, and thus ecological or evolutionary specialization. Great attention has been devoted to latitudinal gradients and to mainland–island comparisons. Other tropical gradients are also likely important to recognize, albeit relatively less well studied, including forested to open-country habitats, continuously wet to more seasonally wet–dry tropics (the latter in South America include seasonally deciduous woodlands, *Caatinga*, *Cerrado*, *Llanos*, *Pantanal*), elevational gradients (e.g., Londoño et al. 2015, 2016), and even the gradient from tropical rainforest understory to canopy vegetation (Cohn-Haft 1995). The Neotropics includes all of these habitats, and the tropics in general includes African rainforests and grasslands with historically very different faunas, to Bornean and Indonesian island "continents," to smaller rainforested regions of northern Australia. Because the number of species, and the range of foraging behaviors as illustrated here in insectivorous birds, vary considerably at all of these spatial scales, the argument above that species diversity drives degree of interspecific competition suggests that the degree of diffuse interspecific competition and different degrees of co-evolutionary arms races vary along these gradients. Any comparisons of specialization and evolutionary pressure must be careful to account for such variation. For example, a latitudinal gradient in the Old World (with Borneo as the wet tropical forest endpoint) may be very different from the Neotropical gradient: geography and history matter.

Mindful of these provisos, we predict that insectivorous avifaunas will show greater habitat and dietary specialization, as well as greater diffuse competition, in proportion to the number of species present, to the predictability of the resource environment, and to the age and diversity of the taxa competing for insects and other arthropods—and not just in the tropics as niche theory has often argued. Controlling somewhat for history by making comparisons just in the Americas, say, we predict greater diffuse competition, and greater habitat and diet specialization in the Amazonian tropics than Central America, and in Central America compared with Mexico, and compared to regions at yet higher latitudes and compared to islands. We would predict that adjacent islands, controlling for area and latitude, will have fewer species that are less specialized, and encounter less diffuse interspecific competition compared to adjacent mainland areas. Similarly, Madagascar should have far less evolutionary specialization in birds than mainland Africa due to its relatively fewer species overall, and Borneo far less than in Neotropical regions like South America that are characterized by much larger area, far

greater species richness, and phylogenetically older and more diverse avian clades. Thus, we predict that tropical regions generally have more species and more intense ecological interactions, in part because of lower extinction rates than higher latitudes; but that, in addition, history and geography contribute to the variability in species richness and in turn to the degree of evolutionary dietary specialization. Thus, we predict that the Neotropical LDG will be steeper than that in the Old World land areas just because the tropical endpoint in the Americas is so rich in species for a variety of geographical and historical reasons.

Many aspects of how tropical birds forage and select prey are readily testable, even experimentally, as illustrated by several studies involving Neotropical insectivorous birds, such as large-insect specialists (Sherry and McDade 1982), suspended dead-leaf foragers (Rosenberg 1997), and butterfly specialists (Pinheiro and Campos 2019).

Evolution of Tropical Life Histories
Another test of our hypothesis for the evolution of specialized diets (Figures 1, 2) in the humid tropics is the application of the idea of the arthropod desert to explain inadequately understood life-history traits. For example, another effective strategy to survive resource scarcity from an arthropod desert—besides feeding specialization—is to economize in the use of resources (Figure 1). Some tropical insectivores are known for such strategies, including low metabolic rates (e.g., Steiger et al. 2009, Londoño et al. 2015); the ability physiologically to undergo torpor daily, even in species residing in the "warm" tropics (e.g., Bartholomew et al. 1983, McKechnie et al. 2007); and low-stamina flight capacity (Moore et al. 2008) possibly via the reduction of costly-to-maintain flight muscle mass. Sit-and-wait foraging behavior of many "lethargic" tropical birds such as puffbirds is another potential energy-conservation adaptation. Many rainforest interior birds, especially insectivores, are notoriously poor dispersers (Stratford and Robinson 2005, Claramunt et al. 2012), probably in part due to poor stamina for longer distance flights, including across dangerous habitat (e.g., Woltmann et al. 2012a, 2012b; see also Mittelbach et al. 2007, Salisbury et al. 2012). Adaptation to the low light conditions and high humidity within lowland rainforest interior may also cause birds to become disoriented and vulnerable to predation when venturing outside forest, making such species ill adapted to cross barriers such as rivers and forest openings (Stratford and Robinson 2005). Other energy-efficient, and thus energy-conserving, feeding strategies prevalent in the Neotropics include the use of other animals as "beaters" such as those described in Supplemental Material Appendix A for a variety of species that follow understory antwrens and canopy mixed-species flocks, army ant–following birds, and species that use cattle, monkey troops, and other animals to flush and thus reveal arthropod prey.

Martin (2015) provides important recent insights into the evolution of life-history strategies with latitude in birds, and particularly clutch size differences. He argues that tropical songbirds have a slow pace of life, with relatively high adult survival driving reproductive strategies. Furthermore, this research emphasizes nest predation, well known to be important in the tropics, and predation on fledglings as well, factors favoring previously unappreciated latitudinal differences in body mass vs. wing growth strategies. Our view of tropical communities is not incompatible with these views in several respects: Martin's comparisons involved songbirds, which are only about a third of endemic passerines, and an even smaller component of endemic Neotropical insectivores (Table 1), necessitating more information on the life histories of birds other than songbirds, and particularly the extraordinarily species-rich and successful suboscine passerines. Second, our view of communities emphasizes the diversity of tropical habitats, and particularly the potential differences between lowland wet tropics and other habitats, differences given insufficient consideration to date in most life-history studies. Thirdly, our view of the wet tropics as an arthropod desert provides a compelling alternative to nest and fledgling predation as an evolutionary constraint on provisioning of food to offspring and fledglings, a key part of Martin's (2015) scheme. The idea that relatively higher annual adult survival in the tropics (e.g., Johnston et al. 1997, Muñoz et al. 2018) could also result from the arthropod desert is counterintuitive, but could result indirectly from conservative energetic investment, low basal metabolic rate, and low movement (dispersal) rates in these birds, just discussed. Our Biotic Resistance Hypothesis, at the very least, suggests the need to better integrate effective food availability with various life-history traits so as to advance understanding of distinctive tropical life histories.

Evolution of the Latitudinal Diversity Gradient
The potential value of our model is reinforced by its contribution to explaining the Latitudinal Diversity Gradient (LDG; Figure 1). The LDG results fundamentally from evolutionary processes and specifically speciation exceeding extinction rate more at lower than higher latitudes (Mittelbach et al. 2007, Salisbury et al. 2012). The important question, and a fundamental contribution of our ideas presented here, is explaining why speciation rate should be higher in the tropics than at higher latitudes (e.g., Ricklefs 2006; see also Rolland et al. 2014 for mammals). We propose a positive feedback loop that arises primarily from reduced dispersal capacity in many tropical birds, particularly insectivores, which leads to greater rate of genetic differentiation geographically and ultimately to a higher rate of speciation (Stratford and Robinson 2005, Jocque et al. 2010, Claramunt et al. 2012, Harvey et al. 2017). Jocque et al. (2010) proposed a tradeoff between ecological specialization and dispersal ability, leading to higher

speciation rate and diversity in the tropics facilitated by stable climate; our study identifies the ecological driver of this tradeoff, and its source in diffuse, pervasive interspecific food competition in the tropics. This intense competition, implicit in our concept of the arthropod desert in the case of insectivorous birds, necessitates specialization in diet and energy-conservation mechanisms as discussed above. Moreover, particular foraging modes, such as surprise-attack and upward-striking flycatchers, and other common Neotropical foragers with short and rounded wings (like many Furnariidae and Thamnophilidae), probably contribute to many of these tropical insectivores having relatively poor dispersal and thus greater speciation rate (Claramunt et al. 2012, Salisbury et al. 2012), in part due to inefficiency of low aspect ratio wings for long-distance or high-speed flight. At the other extreme of wing shapes, relatively large wings (low wing loading) and tail should also be relatively inefficient for long-distance flight due to the high drag forces. Weaker dispersal should contribute to a greater rate of ecotypic variation and other mechanisms of population differentiation within species (Salisbury et al. 2012). Thus, the LDG should be viewed, we argue, as the result of a complex set of coevolutionary feedbacks in which more coexisting species, particularly in mainland tropical regions, favor specialization as a coexistence mechanism, and this specialization comes at the cost (tradeoff) of dispersal ability, which in turn feeds back positively on speciation rate. In other words, the LDG is argued here to result from geography (area), history (for multiple ecological radiations), coexistence mechanisms such as the kind of ecological specializations highlighted in our study (Mittelbach et al. 2007), and the consequent impacts of life histories that then feed back further on speciation and extinction rates (Figure 1). These arguments should apply most strongly to forest interior insectivores, and especially the species-rich suboscine families (Table 1) and lowland rainforest families in general, where the processes in Figure 1 are likely to be strongest. An interesting exception is the suboscine family Tyrannidae, which have evolved diverse migratory species, and species that dispersed across water to islands such as the Greater and Lesser Antilles—an exception begging explanation, but beyond the scope of our study.

Mixed-species Flocks of Insectivores in the Lowland Tropics

Several recent studies of mixed-species foraging flocks of birds (primarily insectivores, at least in the understory and mid-story mixed-species antwren flocks, discussed above and in Supplemental Material Appendix A) have proposed that positive interactions among flock species members are underappreciated, and may be important in explaining the existence of these flocks (e.g., Goodale et al. 2010, Sridhar et al. 2012, Sridhar and Shanker 2014,

Martínez and Robinson 2016). This view contrasts with the negative ecological interactions associated with interspecific competition for food that constitute the focus of the present study. One kind of positive association accrues to species adapted to pursue and exploit insect prey flushed by the rummaging activities of other flock members, although this benefit accounts typically for relatively few flocking species (Sridhar et al. 2012, Sridhar and Shanker 2014, Martínez and Robinson 2016). Our synopsis of avian foraging specializations (above) acknowledges this beater function of other flock members, and of army ants, monkey troops, and a variety of other animals whose activity reveals insects to foraging birds.

More importantly, the Biotic Resistance Hypothesis provides new perspectives on mixed-species insectivore flocks, particularly the antwren flocks in lowland wet tropical rainforests. First, we argue that flock members compete for food within these flocks diffusely—and intensely, the result of a long evolutionary history—and that to coexist birds need to have evolved sufficient foraging differences behaviorally and morphologically to allow feeding on distinctive resources, either substrates or prey types. This diffuse competition occurs both with other flock members and with any other non-flocking birds overlapping the flocks that eat some of the same insects. Thus, we argue that interspecific competition is not necessarily any stronger or different among flock members than between flocking and non-flocking insectivorous birds (and other insectivores). Although Sridhar et al. (2012) emphasize the positive associations of flock member species compared to null hypotheses, they also acknowledge the important, and still largely unexplored, possibility that flock member species are specialized dietarily. We note that even the most species-rich Amazonian mixed-species bird flocks are composed of species foraging in diverse ways, including walking on the ground, gleaning from foliage, foraging in aerial dead leaf clusters, tree-creeping in various ways in vine tangles and on tree trunks, and pursuing insects flushed by other flock members. The benefit of joining a flock—what accounts for their cohesion—we argue is primarily protection from predators. This is particularly important for any species myopically searching particular substrates, such as suspended dead leaves, vine tangles, and various leaf and tree trunk surfaces—all activities that could render small birds vulnerable to attack by diverse predators such as mammals, snakes, and raptorial birds. If our view about competition is correct, we predict that future studies of species foraging even in the most speciose and predictable mixed-species bird flocks will verify subtle dietary differences among all flock members (and non-flock members) that correspond with differences in morphology and foraging behavior, and that involve distantly related taxa whose most recent common ancestor may be millions of years old. Although many studies have

interpreted species differences among flock members as examples of pairwise resource partitioning, we argue that an equally plausible alternative is that species have evolved specializations in response to many other diffuse competitors, rather than in response to each other (pairwise), calling into question the methods of generating null hypotheses to test for positive or negative associations among flock species members, methods that assume pairwise species interactions (e.g., Sridhar et al. 2012). We urge future studies to quantify diets of both flocking and sympatric non-flocking species to provide a better basis with which to evaluate species adaptations and coexistence mechanisms.

Our argument for the importance of food specialization, particularly in the most species-rich Neotropical insectivorous bird flocks, does not preclude other factors simultaneously structuring these assemblages, including various forms of social cohesion and facilitation that could favor protection against predators, or adaptations for nesting and reproductive success (e.g., Goodale et al. 2010, Sridhar et al. 2012).

Alternatives to Diffuse Food Competition in Community Organization

Tobias et al. (2013a) recently tested competing theories of species interactions in adaptive radiations using 350 lineages of Furnariidae. Natural selection should favor divergence ecologically (and morphologically) among sympatric sister taxa, but older radiations might be expected to converge in response to common environmental factors. Their study compared predictions from these 2 ideas and found little support for continued ecological (morphological) divergence in ancient radiations. Sister taxa in their study differed significantly, and more in sympatry than allopatry, with respect to beaks (related to food competition), tarsi (related to foraging), and song, but these differences can be explained by the fact that closest relatives living sympatrically were ~2.3 times older phylogenetically than closest relatives living in allopatry. This is also consistent with our argument that a considerable amount of time may be required for species to evolve the morphological shape and associated foraging behavioral differences needed to coexist sympatrically, and this is consistent with the tendency for sister taxa to be largely allopatric (see also Lovette and Hochachka 2006 for North American parulid warblers, and Graham et al. [2009] for lowland—but not higher elevation—Neotropical hummingbirds). Tobias et al. (2013a) argued that character displacement does not seem to be a force driving ecomorphological divergence in Furnariidae, whereas they found evidence for convergence of vocal behavior, leading to the conclusion that convergent signaling is more important over long evolutionary time periods than ecological segregation. However, their procedure of controlling for lineage age is problematic because it assumes that species only diverged morphologically in species-rich faunas as a result of character displacement, rather than in response to diffuse competition with many competitors. If the morphological feeding-related species differences they studied evolved in response to diffuse competition with many competitors, then the results of interspecific competition may not be readily detectable using methods motivated by character displacement.

Another confusing aspect of birds' morphological traits is that factors other than competition for food are also relevant. For example, beak size and shape have consequences for functions other than just feeding, such as vocal behavior and thermoregulation (Navalón et al. 2019). Body size in homeotherms such as birds can also be shaped by a variety of selective factors. These may all influence phenotypes in species-rich tropical avifaunas, and increasingly over time, in ways that complicate the interpretation of putative feeding adaptations—but these influences are beyond the scope of our study. Moreover, species reproductive differences via egg size and shape, nesting behavior, incubation and nestling durations, and parental care are also important and may well be involved in species' ability to coexist but are also beyond the scope of the present study. We are not arguing that the only adaptations necessary for coexistence are foraging related, but rather that alternative ways to look at foraging and competition may go a long way toward helping us understand specialization, species richness, and coexistence.

SUMMARY AND CONCLUSIONS

We have developed here the Biotic Challenge Hypothesis to help understand the evolution and coexistence of tropical bird species that feed primarily on insects and spiders, and in species-rich environments. We have argued specifically that tropical communities of birds, particularly those in the most continuously humid lowland Neotropics, are "different" than those of other regions, and that evolutionary forces are different, at least in degree, if not kind. Synergistic evolutionary effects of diffuse food competition and arms races, involving dozens to hundreds of species, especially over the relatively long time periods and relative environmental constancy that tropical environments have persisted at low latitudes in the Neotropics, have added up to more than the sum of their parts. There is a lot more to tropical avian life-histories than clutch size and nest (and adult) predators. Our results suggest that it is risky to generalize from simple communities (such as islands and archipelagos) and from higher latitudes to mainland tropical communities. Our results support some of the inferences of Dobzhansky (1950) quoted in the Introduction, about the intensity of competition for food in the tropics, the intensity and ubiquity of biological interactions, and the importance of relatively stable (seasonally, and over long time periods) tropical habitats, especially humid forests (Figure 1). This idea of strong

tropical species interactions is reinforced both by our arguments for strong interspecific competition driving evolutionary feeding specializations as well as by evidence for evolutionary predator–prey arms races involving avian insectivores and their arthropod prey. These latter interactions appear to contribute to the existence of an arthropod desert from the perspective of many Neotropical insectivores. Our results support the idea that insectivores in these highly species-rich communities compete diffusely and exploitatively with many other species simultaneously. Speciation contributes sister species, leading initially to allopatric and parapatric distributions. Allopatric speciation certainly contributes to our understanding of species diversity at large, for example, continental scales, but is insufficient to understand the mechanisms that allow tropical coexistence locally, for instance, within species-rich mainland rainforest habitats and microhabitats. Some of these coexisting insectivores may be competing with many dozens, if not >100 other insectivorous birds, not to mention bats and other mammals, amphibians, reptiles, and arthropods. Our results suggest that interspecific competition is indeed pervasive among these insectivores, but probably has been largely overlooked, and will not be easily detected using traditional approaches such as manipulative experiments, because of the degree of evolutionary specialization resulting in stereotyped foraging coupled with specialized morphological features for detecting, capturing, handling, and digesting different prey types from diverse substrates.

We thus argue that diffuse interspecific competition in species-rich communities must be understood at least in part as an evolutionary phenomenon, and largely remains to be integrated with evolutionary theory addressing diversification of coexisting species. We envision species richness as an important driver of evolutionary specialization. The so-called "zombie idea," that evolution may be different in the tropics, is anything but dead, and would benefit from testing in the context of arguments about evolutionary specialization in the present study.

Our view of community evolution in the tropics has important implications for a number of long-standing questions involving tropical communities, including tropical life histories, dispersal capacity, the latitudinal diversity gradient, interspecific competition, and the strength of biotic interactions.

Our view of communities also has important conservation implications. Increased specialization in birds increases extinction risk (Şekercioğlu 2011), and as tropical communities disintegrate due to intensification of agriculture and forest exploitation, tropical forest loss, fragmentation, and loss of top predators, among other factors, the lowland tropical specialists should be particularly vulnerable to the altered environmental conditions, including changes in prey (Stratford and Robinson 2005). All of these

factors will be exacerbated by declining populations of arthropods independently of these factors (e.g., Sánchez-Bayo and Wyckhuys 2019, Wagner 2019, van Klink et al. 2020). Thus, our study provides a compelling explanation for why tropical insectivorous birds appear to be particularly sensitive to various types of human disturbance such as logging and rainforest fragmentation (Şekercioğlu et al. 2002, Sigel et al. 2006, 2010; Şekercioğlu & Sodhi 2007, Tobias et al. 2013b, Michel et al. 2015), although other factors than just feeding specialization undoubtedly contribute (Visco et al. 2015).

The widespread disintegration of tropical communities due to all of these human activities will also make it difficult to study the predictions arising from our study, because many of the competitors have already been widely extirpated, including from La Selva Biological Station, Costa Rica (Sigel et al. 2006, 2010), the focus of the case study presented above. The disappearing species will also change the selection pressures that at one time appear to have favored the evolution of specialization, weakening these selection pressures for specialization, and in time favoring communities with fewer forest specialists and more generalists and open-country species (e.g., Şekercioğlu et al. 2019, Stouffer 2020).

Disappearance of insectivore specialists will also have impacts via trophic cascades. For example, some of the tropical insectivores most specialized on large herbivorous Orthoptera may alter population pressures and even selection pressures on these insects. Tropical insectivores are likely important providers of ecosystem services (Şekercioğlu 2006, Şekercioğlu et al. 2016, Michel et al. 2020), and the loss of these species from tropical ecosystems is likely to have diverse, cascading impacts on tropical arthropod and plant communities.

SUPPLEMENTARY MATERIAL

Supplementary material: Supplementary material is available at *The Auk: Ornithological Advances* online.

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