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From island biogeography to landscape and metacommunity ecology: A macroecological perspective of bat communities

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Abstract

The equilibrium theory of island biogeography and its quantitative consideration of origination and extinction dynamics as they relate to island area and distance from source populations have evolved over time and enriched theory related to many disciplines in spatial ecology. Indeed, the island focus was catalytic to the emergence of landscape ecology and macroecology in the late 20th century. We integrate concepts and perspectives of island biogeography, landscape ecology, macroecology, and metacommunity ecology, and show how these disciplines have advanced the understanding of variation in abundance, biodiversity, and composition of bat communities. We leverage the well-studied bat fauna of the islands in the Caribbean to illustrate the complex interplay of ecological, biogeographical, and evolutionary processes in molding local biodiversity and system-wide structure. Thereafter, we highlight the role of habitat loss and fragmentation, which is increasing at an accelerating rate during the Anthropocene, on the structure of local bat communities and regional metacommunities across landscapes. Bat species richness increases with the amount of available habitat, often forming nested subsets along gradients of patch or island area. Similarly, the distance to and identity of sources of colonization influence the richness, composition, and metacommunity structure of islands and landscape networks.

KEYWORDS
area, Chiroptera, dispersal, disturbance, spatiotemporal scale, species sorting

Biogeography and macroecology are integrated disciplines that require the understanding of ecological and evolutionary concepts to define patterns and to identify their causal bases at multiple spatial scales. Processes that influence biogeographical or macroecological patterns occur at different temporal and spatial scales, and may be categorized as geoclimatic (e.g., tectonic plate movements, changes in sea level, climate, and oceanic circulation), evolutionary (e.g., adaptation, speciation, and extinction), or ecological (e.g., predation, competition, and dispersal) processes.[1] In general, these processes interact at multiple spatiotemporal scales to generate biogeographical or macroecological patterns. For example, as geoclimatic characteristics change over time, species must alter their spatial distribution to track environmental characteristics that correspond to their fundamental niche, or adapt (i.e., evolve) to new environmental circumstances while remaining competitive and avoiding predation. Ultimately, these interactions potentially result in extinction or speciation. Nonetheless, the dynamic interplay between mechanisms that operate at multiple spatiotemporal scales makes it challenging to determine the relative contributions of such mechanisms to the structure of communities.

Understanding how the geographical and environmental characteristics of islands affect the biodiversity, composition, and metacommunity structure of their biota is a major theme in ecology[2,3] and biogeography.[4–6] Understanding spatial patterns has become particularly relevant over the past century because human activities have converted native habitat to human-dominated land uses, fragmented landscapes, and created islands of isolated native habitat that is dispersed within a sea of human-dominated land uses, such as agriculture, forestry, and urban development. Moreover, the increasingly fragmented landscape structure of mainland habitats has critical ramifications to conservation biology, and biogeographical approaches provide insights regarding the mechanisms that lead to species loss. The application of island biogeographic principles to topics in biodiversity conservation, especially when confronting anthropogenically driven habitat loss, contributed to the birth of the science of landscape ecology.[7,8] In contrast, the explicit inclusion of dispersal, a biogeographical process, as a contributor to local patterns of biodiversity and species composition was foundational to the development of metacommunity ecology.[2,3] Consequently, the study of patterns and mechanisms associated with biodiversity on both oceanic and habitat islands is of interest in its own right,[9,10] and provides critical insights into phenomena that otherwise could not be studied because of logistical limitations in executing large-scale manipulative experiments.

Herein, we highlight a conceptual progression within spatial ecology, beginning with studies of island biogeography, including its adaptation and expansion to create the discipline of landscape ecology, and culminating in the formation of the disciplines of macro- and metacommunity ecology. We use a set of studies on Caribbean Islands to demonstrate how the use of concepts and perspectives from island biogeography, macroecology, and metacommunity ecology facilitates a more complete understanding of factors molding the composition and biodiversity of bats on islands as well as their distributions among islands. We then use a selection of studies in human-dominated landscapes to discuss the rise of landscape ecology out of island biogeography, as well as the importance of spatial and temporal scales, landscape perspectives, and metacommunity perspectives, for understanding the composition and biodiversity of bat communities. We do not attempt a comprehensive review of these disciplines, any one of which would require a monographic treatment. Moreover, we did not want this effort to simply revisit previous reviews of bat island biogeography. Rather, we wanted to provide a distinct perspective and use research on bat communities to demonstrate how island biogeography has contributed to the development of new disciplines in spatial ecology. Consequently, we draw on our own research on the spatial ecology of bats, while integrating the work of others, to illustrate the conceptual progression and interconnections of the aforementioned disciplines.

ISLAND BIOGEOGRAPHY AND SPECIES–AREA RELATIONSHIPS

The foundational work of MacArthur and Wilson[11,12] elevated the descriptive study of patterns of species richness on islands into a predictive quantitative science. The *equilibrium theory of island biogeography* (ETIB) predicts that larger islands maintain greater species richness than do smaller islands, and that islands more distant from a source area support fewer species than do islands closer to a source area.[11,12] ETIB posits that distance affects richness primarily by molding immigration rates, whereas area affects richness primarily by molding extinction rates. Critically, this theory is based on an equilibrial perspective, predicting stable species richness, but changing species composition on islands because of a dynamic balance between rates of immigration and extinction. The operational issue in ETIB considers the details of quantifying ecology's oldest law: von Humboldt's[13] observation that larger areas support more species than do smaller areas. In general, early research focused on questions related to the form and parameterization of species richness–area relationships as well as the causes of their variation between biota occupying the same island system or between island systems for the same biota.

At ecological time scales, the primary bases for effects of area on biodiversity are that larger areas are, on average, more productive, have greater environmental variation and habitat diversity, and can support a greater number of individuals than do smaller areas.[14] At evolutionary time scales, larger areas harboring more individuals can increase diversification rates (decreased extinction, and increased mutation and speciation), resulting in greater biodiversity compared to smaller areas that harbor fewer individuals. Low diversity on islands due to difficulty in colonization promotes in situ diversification, with more isolated and larger islands evincing larger adaptive radiations.[15] Compared to continents, the smaller areas and greater isolation of islands result in smaller local populations that are more vulnerable to extinction. Compared to continents, island systems, especially those comprising many islands of various sizes over a large spatial extent, provide biotas with opportunities for larger radiations and more frequent in situ diversification, while simultaneously exposing species to greater risk of extinction. Moreover, understanding patterns of species richness has benefited from the application of island biogeographic principles to nonisland systems, including habitat patches, lakes, caves, mountaintops, and host–parasite systems.

Contention over the utility of the ETIB persisted for decades. Detractors often tested predictions of the ETIB based on natural history data[16–18] and discredited the theory because empirical evidence failed to conform to predictions. However, the failure of these tests should not be surprising given the simplicity of the theory in contrast to the complexity of natural systems.[19] Others[20] view ETIB as a heuristic model that provides a useful framework from which to explore patterns rather than as a set of hypotheses to falsify.

LANDSCAPE ECOLOGY

The conceptual bases of landscape ecology emerged during the 1970s as scientists struggled to understand ecological patterns and processes in human-dominated environments and endeavored to optimize anthropogenic land uses and conservation of natural habitats to preserve biodiversity in increasingly fragmented landscapes.[7] Many foundational concepts in landscape ecology arose from the ETIB[11] and were applied to habitat patches surrounded by human-dominated habitats (agriculture, pasture, urban and suburban developments) within a mainland context.[21–25] Early research in landscape ecology was relatively simple and mirrored approaches used in island biogeography that evaluated only the effects of patch size or patch isolation from potential source populations. Catalyzed by the advent of GIS, including emerging technologies and software, landscape ecology incorporated additional aspects of landscape structure (i.e., habitat composition and configuration) to understand spatial patterns of abundance, composition, and biodiversity. Effectively, landscape ecology evolved into a

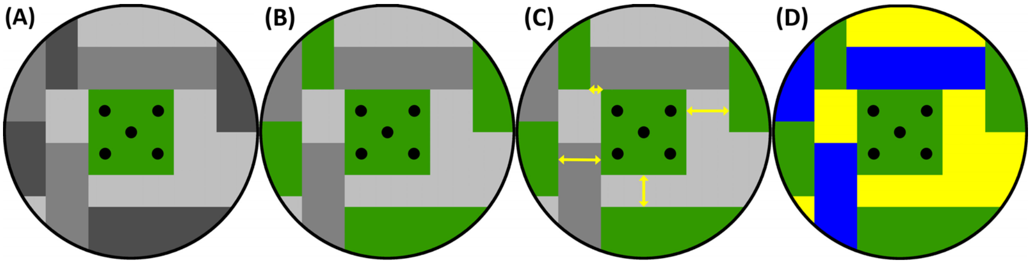

FIGURE 1 Diagrammatic representations of landscape characteristics that relate to the (A) patch area hypothesis, (B) habitat amount hypothesis, (C) habitat configuration hypothesis, and (D) multihabitat hypothesis. Shades of gray represent attributes of the landscape that are ignored for particular hypotheses. Patches are represented by polygons; land cover is represented by a color (green, blue, or yellow). Black dots represent sampling locations. Yellow arrows indicate the distance of a focal patch from other patches of the same land use

predictive and ecologically nuanced version of island biogeography to evaluate spatial dynamics at multiple scales.

Landscape ecology examines the influence of spatial and environmental heterogeneity on ecological systems (populations, communities, or metacommunities), and explicitly addresses the importance of landscape composition (the relative proportions of different land cover types within a focal area) and configuration (the spatial arrangement of land cover types within a focal area) in determining ecological patterns and processes.[26] Central to landscape ecology is the concept of the habitat patch: a relatively homogeneous area (e.g., forest patch and agricultural patch) that differs from its surroundings in ecologically relevant ways. A terrestrial habitat patch is analogous to an island, except that a patch is surrounded by a variably less hospitable terrestrial matrix rather than by uninhabitable habitat (i.e., water) for terrestrial organisms. In addition, the focal scales are different in island biogeography and landscape ecology. In landscape ecology, questions are generally about how the composition and configuration of the surrounding landscapes affects the community in a focal habitat patch. In contrast, island biogeography asks how variation among islands in their characteristics affects the communities on entire islands that contain multiple habitat types.

In general, three consequences of habitat conversion (i.e., native habitat converted to human land uses) affect the abundance and distribution of animal species: (1) loss of native vegetation, (2) fragmentation per se (i.e., formation of isolated patches of habitat), and (3) matrix (i.e., habitats that surround a focal patch) permeability or utility.[27] The loss of native vegetation and matrix effects are associated with the presence and proportion of natural and anthropogenically modified land cover types, independent of their spatial arrangement (i.e., landscape composition), whereas fragmentation per se affects connectivity and spatial arrangement (i.e., landscape configuration) of resource patches.[28] In short, the fragmentation of habitat into patches is a landscape-level process that requires a multiscale approach for understanding ecological dynamics.[28,29] Comprehensive understanding of the effects of habitat loss, habitat fragmentation, and matrix quality on the biota requires explicit consideration of compositional and configurational characteristics of landscapes (Figure 1) to resolve competing hypotheses about mechanisms underlying spatial variation in biodiversity.[8]

From a landscape perspective, the size of a core habitat patch (e.g., forest), the amount of core habitat within a focal scale, the configuration of focal habitat within a focal scale,[30] or the identity, diversity, and configuration of all habitat types within the focal scale,[31,32] may affect the abundance, biodiversity, or metacommunity structure of the biota. The most basic landscape structure hypothesis (i.e., *patch area* hypothesis) was derived from the ETIB and posits that the characteristics of diversity in a patch are determined by the area of that patch (Figure 1A). The habitat amount hypothesis challenges assumptions that patches are natural units or that patch size and isolation have distinct effects,[30] and proposes that the amount of focal habitat in a landscape is the underlying characteristic that molds patterns of biodiversity (Figure 1B). Consequently, biodiversity should increase with the amount of area represented by the focal habitat and should be independent of the size of the local patch in which diversity is measured. An alternative conceptual model (the *habitat configuration* hypothesis) integrates habitat amount with configuration of habitat patches (Figure 1C). This hypothesis proposes that both the amount and configuration of the focal habitat should have a strong influence on diversity. Finally, the *multihabitat* hypothesis predicts that local diversity is influenced by the composition and configuration of all land cover types (Figure 2D), with more heterogeneous landscapes supporting greater diversity than do less heterogeneous landscapes. In sum, these theoretical aspects of landscape ecology predict that the abundance, biodiversity, and composition of a biota in a focal patch is a function of focal patch size (Figure 1A), the total area of focal habitat in a landscape (Figure 1B), the configuration of those habitat patches (Figure 1C), and the heterogeneity, diversity, and configuration of all other land cover types (Figure 1D). Complicating matters is that landscape composition or configuration may affect attributes of biota at multiple spatial scales, depending on species-specific life history characteristics, necessitating analyses at multiple spatial scales.[28,33]

METACOMMUNITY ECOLOGY

A metacommunity perspective provides ecological insight into spatiotemporal dynamics because it explicitly considers the roles of both local and regional processes in generating mesoscale and large-scale

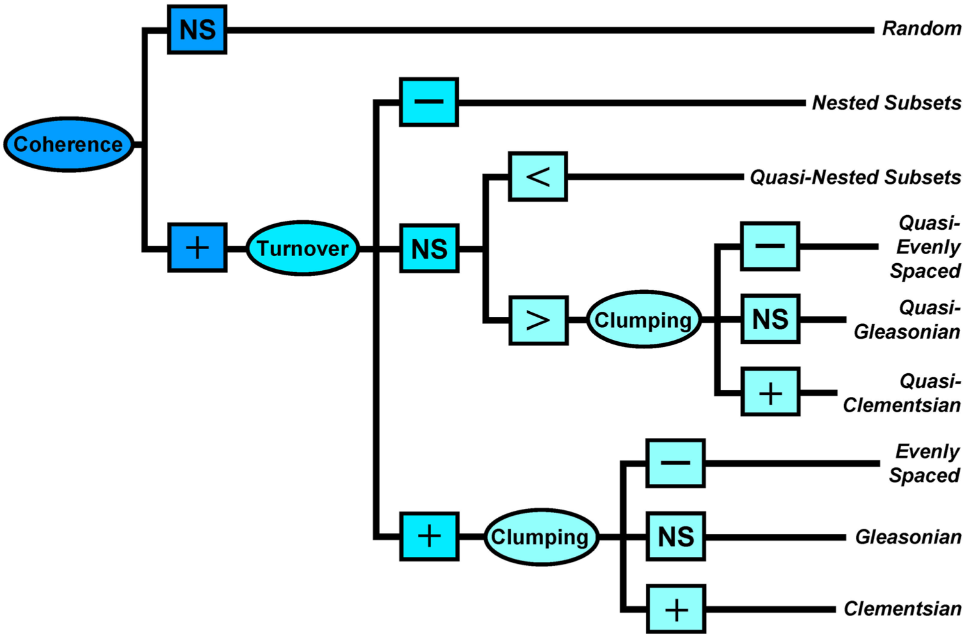

FIGURE 2 A diagrammatic representation of combinations of the three elements of metacommunity structure (ovals) that differentiate among five idealized metacommunity structures and four quasi-structures. Possible results for tests for each element appear in squares: a positive sign (+) indicates results consistent with greater coherence, range turnover, or range boundary clumping than expected by chance, a negative sign (–) indicates results that are consistent with less range turnover or range boundary clumping than expected by chance, and NS indicates results that are indistinguishable from chance expectations. Quasi-structures arise when the range turnover is less than (<) or greater than (>) the mean from the simulations, but not significantly so

patterns (i.e., those beyond local patterns) and the emergent system-wide structures that arise from species distributions along environmental gradients.[3] More specifically, a metacommunity is a network of communities that occur at sites that are connected to each other via dispersal of individuals among constituent communities.[34] The connection of communities via dispersal intimately ties metacommunity ecology to island biogeography, but the former is focused more on the role of environmental and spatial factors in affecting species distributions and variation in the composition among communities than on variation in species richness among communities. Local emigration and immigration, when coupled with other spatially explicit ecological processes (e.g., species sorting, habitat filtering, priority effects, and interspecific competition), imbue metacommunities with an emergent structure associated with underlying environmental gradients.[2,35]

In general, two complementary approaches are used to study metacommunities: one that focuses on processes that structure communities (i.e., mechanisms that generate variation in species composition) and one that focuses on emergent patterns in species distributions that are generated by those processes. The framework of the process-based approach is built on four archetypical mechanistic models (i.e., neutral theory, patch dynamics, species sorting, and mass effects). These models differ in their assumptions about the role of particular processes (e.g., competition and dispersal) and sources of variation (e.g., habitat heterogeneity and species-specific capacity) to make predictions about species distributions and community composition.[3] Current perspectives on metacommunity theory do not pit one hypothesis against another; rather they attempt to evaluate the relative contributions of spatial and environmental factors to metacommunity structure (i.e., variation in species composition and the spatial structure of that variation).[3,36–38] Significant environmental effects (on species composition) are consistent with species sorting, significant spatial effects are consistent with neutral theory, significant environmental and spatial effects are consistent with mass effects, and significant spatial effects that are temporally dynamic are consistent with patch dynamics.

A pattern-based approach in metacommunity ecology identifies emergent structures (e.g., nestedness, Clementsian, and Gleasonian) that are defined by relationships among the distributions of species along environmental or spatial gradients.[34,39–41] Because these structures reflect large-scale patterns that emerge from multiscale responses to variation in island or landscape characteristics, metacommunity approaches are complementary to traditional analyses of island biogeography and landscape ecology. Several conceptual models characterize the patterns of species distribution along gradients. Clements[42] described a metacommunity structure based on shared evolutionary history of species and interdependent ecological relationships, resulting in coincident range boundaries for groups of species along different portions of a gradient. Each set of communities that harbors a relatively exclusive group of species represents a compartment,[43] with compartments replacing one another along the gradient. In contrast, Gleason[44] described a structure arising from idiosyncratic species-specific responses to the environment, with local coexistence arising as a byproduct of similarities in ecological requirements or abiotic tolerances (i.e., niche characteristics), with species distributions occurring independently along the gradient. In situations where strong interspecific competition exists, trade-offs in competitive ability may result in environmental distributions that are evenly spaced along gradients.[45] Finally, species-poor communities may form nested subsets of increasingly species-rich communities,[46,47] with predictable patterns of species gain associated with variation in species-specific characteristics (e.g., dispersal ability, habitat specialization, and abiotic tolerance). These idealized structures form the framework representing a continuum of possible structures,[34,39,48] from those with high species turnover (e.g., as described by Clements or Gleason) to those with low species turnover (e.g., nested subsets), and from those structures characterized by coincident range boundaries (i.e., as described by Clements) to those characterized by hyperdispersed range boundaries (i.e., as described by Tilman).

The common conceptual aspect to all nonrandom metacommunity structures is that the distributions of species are molded by a common environmental gradient, with sites reflecting environmental variation along that gradient. This reflects a fundamental principle in ecology that species ranges should be *coherent*, constituting continuous distributions along environmental gradients (e.g., a species that occurs at temperatures of 10 and 15°C should also occur at all temperatures between those values). For a metacommunity to exhibit coherence, the distributions of a preponderance of species must be associated with the same environmental gradient.[34,39] However, the extent and location of species distributions will differ along the gradient, such that coherent metacommunities may evince many different structures. In contrast, if the distributions of a preponderance of species do not respond to the same environmental gradient, coherence is not achieved, and structure is considered to be random.[34] Importantly, random structure does not mean that species occur at random, only that their distributions are not aligned with the same environmental gradient.

The elements of metacommunity structure (EMS) comprise three attributes of species distributions (i.e., coherence, species range turnover, and range boundary clumping) that combine to discriminate among metacommunity structures (Figure 2).[34,39] EMS uses reciprocal averaging (also called *correspondence analysis*) to determine the gradient along which both sites and species are organized. These gradients represent variation in biotic and abiotic environmental factors that are important for defining the distributions of species. Typically, subsequent analyses (e.g., canonical correspondence analysis, variation partitioning, or general linear models) are used to determine the relationship of the gradient to environmental factors that define the distributions of species.[48–57]

Patterns that manifest at one scale may be the result of mechanisms that operate at other spatial scales.[58] Consequently, it is generally advantageous to explore patterns at local and regional scales to understand the relative contribution of various mechanisms to community or metacommunity structure. The combination of tools and concepts developed to study island biogeography, landscape ecology, macroecology, and metacommunity ecology combines to provide a broad spatiotemporal perspective (and analytical tool kit) from which to understand how mechanisms at local and regional scales create local and regional patterns of biodiversity and species composition.

BATS AS A STUDY TAXON

Bat populations and communities have qualities that make them ideal for large-scale ecological and biogeographical studies. Bats are highly mobile and can travel long distances between roosts and foraging sites, making them efficient seed dispersers, pollinators, and predators of insects or small vertebrates.[59] High mobility also makes bats among the most effective animals at tracking resources through space and time, including long-distance migration and dispersal to oceanic islands or to isolated patches of habitat. Indeed, bats are the only endemic mammals on Caribbean or Hawai'ian Islands.[60] In general, bats are landscape species because home ranges of individuals include ecologically heterogeneous areas (i.e., individuals use multiple habitat types). Bats belong to many foraging guilds (i.e., frugivores, nectarivores, carnivores, insectivores, sanguinivores, and omnivores), perform a variety of ecosystem functions, and provide many ecosystem services. Bats are the sole or primary agents of pollination or seed dispersal for many early and mid-successional plant species,[61] promoting secondary succession and regeneration of disturbed areas,[62] especially in the tropics, suggesting that the use of landscapes by bats may influence temporal changes in landscape structure (i.e., the types and distributions of habitats). Consequently, bats have been a focus of study by biogeographers as well as by macro-, metacommunity, and landscape ecologists. Early studies of landscape ecology of bats employed an island biogeographical approach focusing on effects of habitat area and isolation to understand the consequences of habitat fragmentation.[63–66] Hereafter, we leverage a diverse array of bat research to illustrate the interplay of principles and concepts from island biogeography, macroecology, metacommunity ecology, and landscape ecology to advance the scientific understanding of spatiotemporal dynamics.

CARIBBEAN BATS: FROM ISLAND BIOGEOGRAPHY TO METACOMMUNITY ECOLOGY

The Caribbean is an area of high species richness and endemism.[67–69] Despite the relatively small amount of land represented by these islands (266,500 km^2, about the size of the state of Colorado), the Caribbean harbors 7000 endemic vascular plants and ~800 endemic vertebrates, making it one of the hottest of hotspots,[70] especially for bats.[71–76] Both historical (e.g., geological and evolutionary) and ecological (e.g., island size and distance to mainland) factors contribute to complex patterns of endemism and richness.[66,69,77–79] Moreover, changes in climate during the late Quaternary modified the distribution, size, and abiotic characteristics of caves, significantly altering the distribution of bats in the Caribbean.[79,80] Flooding associated with rising sea levels or erosional collapse caused widespread extinctions of cave-dwelling species on small islands (e.g., Bahamas and Cayman Islands). Nonetheless, caves represent an important island characteristic that molds assemblage composition and distinguishes it from mainland assemblages.[79,81] Moreover, the biota of the Caribbean is a conservation concern because of accelerating rates of anthropogenic activity that threaten the persistence of species.[69] Indeed,

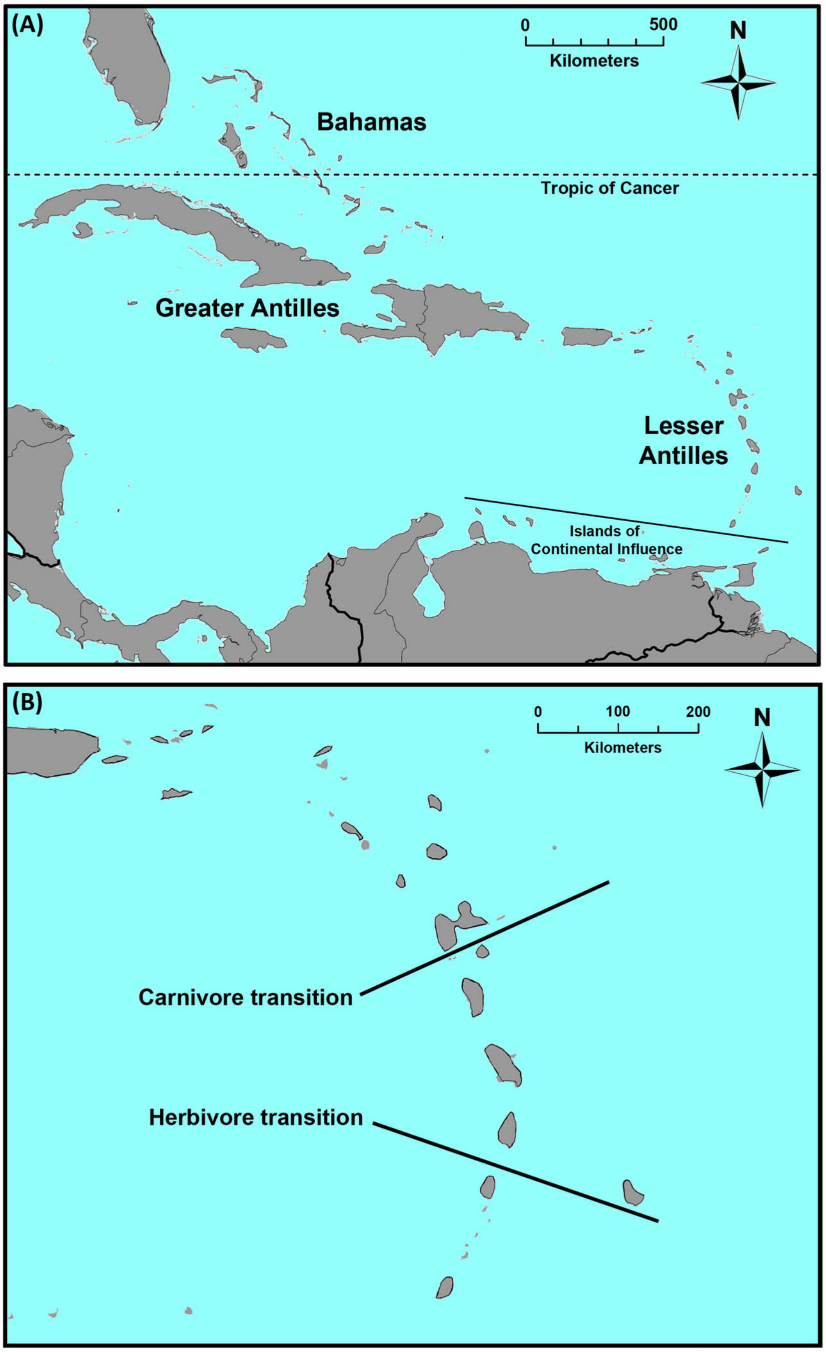

FIGURE 3 Maps of (A) the Caribbean Islands, indicating the locations of the Bahamas, Greater Antilles, and Lesser Antilles in relation to continental America, and (B) the Lesser Antilles indicating the different locations of transitions between northern and southern compartments associated with carnivorous and herbivorous bats in their respective Clementsian structures. Islands so close to mainland South America (south of line) were omitted from consideration as their proximity to the mainland effectively makes these bat communities part of the mainland fauna

primary vegetation of Caribbean Islands covers <10% of its original extent,[67] representing a constraint to the long-term persistence of bat populations,[69] especially given the likelihood of climate-induced increases in the frequency and intensity of high energy storms and droughts in the region.

Caribbean Islands and their bats

The Caribbean harbors more than 7000 islands (Figure 3A), islets, reefs, and cays that differ greatly in size, elevational variation, topographical relief, sources of colonization, isolation, geological history, and exposure to hurricane-induced disturbances, making them an ideal albeit complex setting in which to study the effects of island biogeography and environmental variation on species composition, biodiversity, and metacommunity structure. Based on biogeographical considerations, islands are classified into three major groups: Bahamas, Greater Antilles, and Lesser Antilles.[71] The Bahamas (Figure 3A) are low-lying islands (63 m maximum elevation) formed from the carbonate banks of the Bahamas platform of the North American tectonic plate. In contrast, Antillean Islands were formed by andesitic volcanism, and have mountainous terrain and caves that serve as roosts for bats.[82] Islands of the Greater Antilles range from Cuba in the west to Anegada in the east, and the islands of the Lesser Antilles range from Sombrero in the north to Trinidad in the south (Figure 3A). In our consideration, we excluded the bat faunas of Trinidad and Tobago, as well as islands along the northern coast of South America (e.g., Isla de Margarita, Isla de Tortuga, Isla La Orchila, Gran Roque, Isla La Blanquilla, Curaçao, and Aruba) because the proximity of these islands to the South American mainland essentially makes their bat communities part of the mainland fauna (Figure 3B).

There are three primary sources of colonization of Caribbean Islands by bats: subtropical North America, the Yucatán of Central America, and northern South America.[71] Interisland distances can affect biodiversity as well as compositional similarity.[49,83–86] Importantly, strings of islands can act as steppingstones for colonization from the mainland or can act as sources of recolonization after local extinction events.[24,87] This is particularly important in disturbance-mediated systems, where many islands are relatively small, harbor small populations, and are exposed to large-scale disturbance events (i.e., hurricanes). These factors combine to increase extinction risk.

Reliable data for bat species composition and selected environmental characteristics exist for 65 islands throughout the Caribbean, including 19 in the Greater Antilles, 23 in the Bahamas, and 23 in the Lesser Antilles.[86] Land area of these islands spans ~5 orders of magnitude (from 5 km^2 on East Plana Cay to 114,524 km^2 on Cuba) and elevation spans ~3 orders of magnitude (from 5 m on Grand Bahama to 3175 m on Hispaniola). Although the age of islands could affect the identity of species that occupy them, such considerations were beyond the scope of this review. Because bats are highly vagile and effective dispersers to islands, variation among islands in age is unlikely to be a major factor associated with variation in bat biodiversity or composition among islands.

Fifty-eight species and 7 families of bats are documented from this group of islands, including 13 species and 5 families from the Bahamas, 38 species and 6 families from the Greater Antilles, and 24 species and 7 families from the Lesser Antilles. Families of bats that occur on Caribbean Islands include the Emballonuridae (1 species), Phyllostomidae (24 species), Noctilionidae (1 species), Mormoopidae (5 species), Natalidae (7 species), Molossidae (7 species), and Vespertilionidae (13 species). Caribbean bats occupy many trophic guilds, including piscivores, gleaning animalivores, aerial insectivores, open-space insectivores, nectarivores, and frugivores. However, some species (e.g., *Brachyphylla cavernarum*, *Erophylla bombifrons*, *Erophylla sezekorni*, *Lonchorhina aurita*, and *Micronycteris megalotis*) are not classified easily into guilds because they forage on multiple resource bases and are broadly omnivorous. Although responses by bats to particular island characteristics may be guild specific, many islands harbor few bat species and many guilds are absent from most islands. Consequently, broad categorizations are necessary to evaluate trophic-based responses to interisland variation. Broad feeding classes were defined to include carnivores (i.e., insectivores, piscivores, carnivores, animalivores, and omnivores) and herbivores (i.e., nectarivores and frugivores), with most species clearly belonging to only one of the classes. Detailed information on the physical characteristics of islands and the composition of their bat communities are available in extensive appendices elsewhere.[86]

Island biogeography

The ETIB[11,12] provides a basis to evaluate responses of species richness to variation in island characteristics (i.e., area and distance from source populations) that affect rates of immigration, emigration, extinction, and diversification. In general, Caribbean Islands that are larger or that have greater elevational heterogeneity harbor more bat species and guilds than do smaller or low relief islands.[86] Effects of area manifest for each island group, whereas effects of elevation occur only in the Greater and the Lesser Antilles. Bahamian Islands exhibit little elevational variation, making it unsurprising that species and guild richness of these islands are not influenced by elevation. Moreover, distance from mainland source populations, interisland distances, and historical hurricane-disturbance regime do not appreciably affect species or guild richness on Caribbean Islands as a group or within any of the three constituent island groups.

Area

Effects of area can be confounded because of positive associations among environmental variation, habitat diversity, and area.[11,83,88] Habitat diversity on islands increases with variation in elevation due to gradients of temperature and precipitation that are associated with changes in elevation as well as with aspect and prevailing wind patterns. In addition, habitat diversity generally increases with island area because habitats change predictably with distance from the coast. Maximum elevation is correlated positively with island area in the Greater and the Lesser Antilles (but not in the low-lying Bahamas), such that their effects are confounded. Importantly, the *unique* variation from a statistical analysis that is attributable to area (or to any particular environmental characteristic) does not equal the effects of area (or to any particular environmental characteristic), per se. This occurs because all important characteristics are not included in particular analyses or because included characteristics may be measured at spatial or temporal scales that are different from those to which species respond. Consequently, changing the characteristics included in a model can change the unique variation associated with all other included characteristics. The confounded nature of variation in environmental characteristics in empirical studies (e.g., correlation between area and maximum elevation for Caribbean Islands) prevents discernment of the ultimate mechanism responsible for variation in any particular dependent variable (e.g., species richness).

From an ecological perspective, island area affects species or guild richness via two primary mechanisms. First, larger areas can support a greater number of individuals and, therefore, sustain larger population sizes that reduce the risk of stochastic extinction. Second, larger areas generally harbor more habitat types of sufficient size to maintain viable populations of species that are habitat specialists. Moreover, larger islands have greater habitat diversity associated with coast-to-inland and elevational gradients. Elevational variation and associated climatic gradients (e.g., solar insolation, temperature,

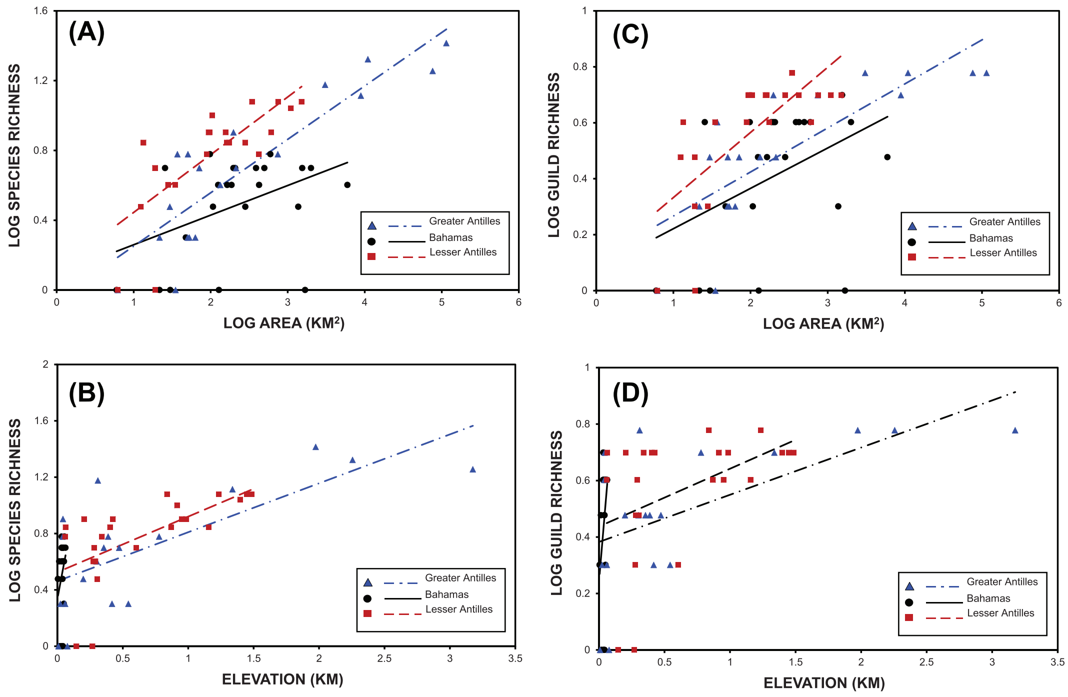

FIGURE 4 Scatter plots of log species richness (left column, A, B) and log guild richness (right column, C, D) as a function of log island area (top row, A, C) and elevation (bottom row, B, D) for Caribbean Islands

and precipitation) also increase habitat diversity, which can increase species and guilds richness. In addition, the geological processes that produce elevational relief enhance the likelihood of cave formations that can be used as roosts by bats.[81] Caves augment species richness by providing suitable roosts for many Caribbean bats, including *Artibeus* spp., *Brachyphylla* spp., *Chilonatalus* spp., *Eptesicus* spp., *Erophylla* spp., *Monophyllus* spp., *M. blainvillei*, *Natalus* spp., *N. leporinus*, *Pteronotus* spp., *S. rufum*, and *T. brasiliensis*, and by buffering such species from the immediate negative effects of hurricanes.[60,81] The combined effects of area and elevation result in greater rates of increase in species richness with increasing area for islands in the Greater Antilles and the Lesser Antilles compared to that in the Bahamas (Figure 4). However, the effect of island size and elevation only manifests for species richness. Larger islands appear to provide the necessary resources to harbor all foraging guilds, with the identity of species changing along elevational gradients, but without the addition of new feeding guilds along such gradients.

From an evolutionary perspective, larger populations on larger islands provide greater opportunity for the evolution of new species (more individuals provide greater opportunity for beneficial mutations to arise) and larger islands are also more likely to have physical barriers (mountains and large rivers) that facilitate allopatric speciation. Island size also reduces the likelihood of chance extinction of species by supporting more individuals, enhancing the likelihood that newly evolved species persist and immigrate to other islands. Indeed, the large number of endemic species on Caribbean Islands, most of which originated on large islands, suggests that this is an important mechanism that contributes to the regional species pool.

Latitude

Because bat species and trophic richness increase toward the equator at rapid rates on the New World mainland over the range of latitudes that characterize Caribbean Islands,[89–92] we expected latitude to have a similar effect on island biodiversity. However, only species richness for the Greater Antilles evinced a significant response to latitude, but with richness increasing with increasing latitude, an opposing pattern to that on the mainland.[86] This opposing pattern occurs in the Greater Antilles because the larger, more species-rich islands (e.g., Cuba and Hispaniola) occur further north than do small, less species rich islands (Figure 3A). The variation among islands in salient characteristics (e.g., area, elevational relief, and distances to source populations) is sufficiently strong to override any effects associated with latitude that mold spatial patterns of bat biodiversity on the mainland.

Disturbance, dispersal, and isolation

Caribbean Islands support disturbance-mediated ecosystems that are episodically affected by major hurricanes with great variation among islands in historical exposure to these disturbances. Nonetheless, the history of hurricane-induced disturbance on islands is not significantly associated with bat biodiversity.[86] Any effect of such storms on bat biodiversity appears to be short term, suggesting that resident populations have mechanisms for persisting despite intermittent, major, widespread disturbances that can result in the temporary loss of habitats from entire islands. Because bats must be highly effective at dispersal and colonization to have populated oceanic islands, even when high energy storms cause local extinctions, rescue effects from nearby islands likely make such phenomena transitory. Alternatively, persistence through evolutionary time in disturbance-mediated environments may have selected for species with greater niche breadths compared to taxa in less disturbance-prone environments. Consequently, the species pool for Caribbean bats necessarily comprises species that are resistant and resilient to local disturbance regimes. In addition, long-term effects of hurricane-related disturbance may depend on island size. Biodiversity on large islands may be enhanced by hurricanes, as these disturbances effectively maintain or increase habitat heterogeneity, prevent competitively dominant species from driving other species extinct, and have relatively low likelihoods of causing island-wide extirpation of species. In contrast, the effects of hurricanes may be devastating over the short-term on small islands, causing high local extinction rates. However, interisland recolonization may ameliorate such effects in an island-specific manner depending on proximity to source populations. Because bats have exceptional dispersal abilities, interisland distances in the Caribbean may not be sufficiently great to influence bat species richness at large temporal scales (i.e., interisland dispersal may be accomplished effectively regardless of interisland distance). Importantly, hurricanes have been replaced by anthropogenic activities as the dominant force of disturbance on Caribbean Islands.[70] Habitat loss due to human activities has reduced local bat species richness, caused extinction of endemic species, and reduced the distribution of many species on Caribbean Islands.[69,93]

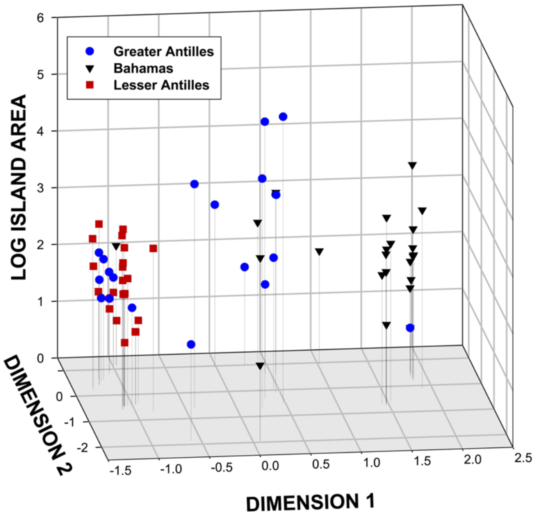

FIGURE 5 Three-dimensional representation of the relationships among islands of the Caribbean based on species composition (dimensions 1 and 2 from nonmetric multidimensional scaling) and island size (log area)

Macroecology

Although spatial attributes of islands (latitude and interisland distance) explain little variation in bat biodiversity within island groups,[86] island group itself significantly affects both bat biodiversity and bat species composition. Island group reflects geospatial location: latitude, spatial proximity to other islands, and distance from particular mainland sources of colonization. As such, each island group has a distinct species pool (Figure 5) that is reflected in the presence of endemic species and distinct groups of core species (i.e., species that occurred on a large proportion of islands in a group). Differences among island groups in their species pools arise as a consequence of the number and location of historical mainland source populations for the Bahamas (subtropical North America) versus the Greater Antilles (subtropical North America and the Yucatán of Central America) versus the Lesser Antilles (Greater Antilles and northern South America).

A secondary prediction of the ETIB[11,12] is that species turnover occurs on islands, with the identity of species going extinct or colonizing islands occurring at random. From an empirical perspective, species composition of Caribbean Islands is not primarily a product of random processes.[85] Interisland distance is the most important factor affecting variation in species composition among islands within each island group; proximate islands harbor more similar bat communities than do more distant islands. In addition, differences in island size contribute significantly to differences in species composition between islands in the Greater Antilles and the Lesser Antilles, with islands of more similar size having more similar bat communities than do islands of different sizes. Differences between islands in elevation or in hurricane history did not account for differences in bat community composition.[85] Although variation in species composition among islands is not related to interisland variation in elevation, two observations suggest that elevational relief may affect bat species composition on Caribbean Islands. First, species composition is statistically associated with island area in the Greater Antilles and the Lesser Antilles, the island groups with considerable elevational variation, but not in the Bahamas, islands with little elevational relief. Second, island elevation and area are highly correlated in the Greater Antilles and the Lesser Antilles, but not in the Bahamas.[85] In addition, maximum elevation is only a crude measure of elevational relief and associated habitat heterogeneity, which likely affects the identities of bat species that persist on an island. Consequently, the magnitude of effects statistically ascribed to island area also represents the cumulative influences of other factors with which it is correlated, including elevational relief and habitat diversity.

Predictions about the manner in which some island characteristics affect composition are biologically intuitive: islands of similar area, elevational relief, or geographical location are expected to have more similar bat assemblages than would islands dissimilar in those characteristics. In contrast, a priori expectations about the effects of hurricane-related disturbance regimes on bat composition are less intuitive for many reasons. First, the potential effects of hurricane-induced disturbances on species composition likely are contingent on island size. When hurricanes strike smaller islands, the entire island is likely to be devastated, resulting in temporary decreases in habitat diversity, habitat quality, resource abundance, and resource diversity. In addition, because average population size is positively associated with area,[14] the probability of hurricanes causing local extinctions should be correlated negatively with island size. Because hurricanes are less likely to severely impact the entirety of larger islands, disturbances created by hurricanes may increase habitat heterogeneity on large islands, resulting in the same phenomenon having opposing effects depending on island size. Second, rescue effects after hurricanes may be contingent on distances to source populations. Species extirpated from an island as a result of a hurricane may re-establish quickly on islands close to multiple source populations compared to the situation for extirpated species on more isolated islands. Moreover, hurricane-induced disturbances likely have guild-specific effects depending on how particular storms affect particular food resources on islands (e.g., fruits, flowers, and insects). Consequently, effects of disturbance on bat assemblage composition may depend on island size because of the relationship of resource diversity with island area, as well as on the ability of bats to persist until guild-specific resources are replenished.[94] Because of these complexities, the effects of particular disturbance events on bat species richness or on species composition may be difficult to predict or even detect with confidence.

Metacommunity ecology

Island characteristics influence the distributions of species within an island system (e.g., archipelago) and thus metacommunity structure on those islands. Caribbean bats have distinctive Clementsian structure, with compartments corresponding to the three primary island groups (Bahamas, Greater Antilles, and Lesser Antilles; Figure 3A). This compartmentalized structure manifests for all bat species as well as for metacommunities restricted to only herbivores or carnivores.[50] However, each constituent island group by itself has a distinctive metacommunity structure. Interestingly, the primary mechanisms that structure these metacommunities are biogeographical (e.g., spatial relationships with source populations) rather than ecological (i.e., responses to local island conditions). In addition, these metacommunities are not structured along gradients associated with island area, elevation, or historical disturbance regime.[50] Rather, each structure reflects differences in the sources of colonization and the geographical relationships of those sources of colonization to the islands (Figure 3A).

Greater Antillean bat communities are nested, with most (26 of 38) bat species from this island group having evolved on large islands, such as Cuba, Hispaniola, or Jamaica.[71] This nested structure arises from a core group of widespread species that is augmented by restricted-range species that occur only on the large islands on which they originated as well as on some nearby small islands. Moreover, the geographical configuration of the Greater Antilles may predispose the creation of nested subsets via speciation and the subsequent dispersal of those species. The greater area represented by larger islands can support more individuals and more habitat types, increasing the number of species that can maintain sustainable populations.[14] These factors increase the likelihood that larger islands serve as sites of species origination more often than do smaller islands. In addition, larger islands in the Greater Antilles are closer to continental sources of colonization (e.g., Florida and the Yucatán Peninsula) than are smaller islands. Consequently, populations on larger, western islands replace continental populations as the primary sources of colonization for smaller, eastern islands of the Greater Antilles. Differential dispersal of species, specialization on locally abundant resources, and size-mediated hierarchical habitat distributions on islands are mechanisms that likely enhance nestedness for the Greater Antillean bat metacommunity.[85] Low sea levels during the Pleistocene created *super islands* due to land bridge connections,[95] a phenomenon that could potentially contribute to nested structures. However, neither the Bahamas nor the Lesser Antilles exhibit a nested pattern despite experiencing the same phenomenon, calling into question the importance or pervasiveness of this historical factor. Importantly, the extent of island connections during the Pleistocene was relatively modest compared to the high vagility of bats that allows them to move easily between nearby islands to track spatiotemporal variation in the environment. Consequently, responses to environmental variation during the more than 10,000 years since Pleistocene sea-level changes likely have erased any effect it may have had on the current distributions of bats among islands and the resulting metacommunity structure.

The Lesser Antillean bat fauna has two primary sources of colonization, the Greater Antilles and northern South America, resulting in Clementsian structure for the bat fauna. Although two compartments characterize herbivores as well as carnivores, the influence of the two sources of colonization is not the same for each feeding class. Carnivore compartments span the northern half of the Lesser Antilles, south to Guadeloupe (bats of Greater Antillean origin) and islands south of Guadeloupe (bats of South American origin). In contrast, the transition between herbivore compartments is considerably further south, with the southern compartment restricted to Grenada, St. Vincent, and the Grenadines (Figure 3B). The unique distributional pattern of each feeding class results in three compartments when considering the entire bat fauna: (1) Grenada, St. Vincent, and the Grenadines, (2) northern islands south to Guadeloupe, and (3) islands between and including Marie Galante and St. Lucia (Figure 3B). Distinct groups of bats systematically colonized opposite ends of the archipelago until they met. In this transition area, priority effects[96] (i.e., incumbency advantage) likely prevent further dispersal of ecologically similar species.

The metacommunity structure of Bahamian bats is greatly influenced by endemic species (i.e., bats recorded from a single island). The removal of endemic species changes the structure of the entire bat fauna from Clementsian to Gleasonian, and the structure of carnivorous bats from Clementsian to random.[50] Herbivorous bats in the Bahamas exhibit random structure regardless of inclusion of endemics. Bahamian Islands are all physiographically similar (i.e., low lying with similar habitat types) and have a single colonization source (sub-tropical North America). Although a number of species originated in the Bahamas, most are distributed throughout the island system and occur idiosyncratically on islands, resulting in either Gleasonian or random structure. The random structures in this island group may represent the lack of a common gradient molding the distributions of species or incomplete data on species composition for some islands.

NEOTROPICAL BATS IN HUMAN-DOMINATED LANDSCAPES

The Anthropocene is an epoch of increasingly pervasive and dominant effects of human activities on the world's biomes.[97] The defining human activities that have created the Anthropocene include carbon emissions (climate change) and habitat conversion (land use change) to agricultural, urban, and suburban land uses. The rates of increase in these global change drivers are inextricably linked to increases in human population size[98,99] and in per capita consumption.[100] Specifically, habitat loss and fragmentation[101] have directly resulted in considerable loss of biodiversity[102] and have altered biogeographical patterns of species distributions.[103,104] Indeed, the magnitude of such effects represents the beginning of the Earth's sixth mass extinction,[105] which requires research to understand how changing landscapes affect populations, communities, and metacommunities to guide conservation, management, and policy. As mentioned above, being landscape species, bats typically use multiple habitat types in a landscape (e.g., night roosts, day roosts, flyways, and foraging sites). The earliest and most simple approaches to landscape ecology mirrored studies of ETIB, evaluating only the effect of patch area or distances to sources of colonization (fragmentation of habitat) on bat abundance or biodiversity.[8] More sophisticated approaches have been developed and applied over the past two decades, leading to deeper and broader understanding of causes of spatiotemporal variation in bat assemblages in human-dominated landscapes.

Bat populations and communities in fragmented landscapes

Bats from moderately fragmented, lowland Amazonian Forest[106,107] and from highly fragmented Atlantic Forest[108,109] respond to landscape structure at multiple spatial scales. In research using mist nets to characterize the bat fauna, species-, guild-, and season-specific responses of phyllostomids to landscape structure were identified in Amazonian landscapes.[106,107] Frugivore abundances respond primarily to variation in landscape composition (i.e., forest cover) during the dry season, whereas landscape configuration (e.g., edge density, patch shape, and mean patch proximity) elicited the strongest responses during the wet season. Gleaning animalivores exhibit opposing responses, with abundances being molded by landscape configuration during the dry season and by landscape composition during the wet season.[107] Within an island biogeographical context, this is equivalent to habitat amount (island size) molding responses of frugivores during the dry season and of animalivores during the wet season, but habitat isolation (distance from source populations) molding responses by frugivores during the wet season and animalivores during the dry season. In regions characterized by tropical dry forest, abundances of frugivores increase with increasing amounts of riparian forest, whereas abundances of nectarivores increase with the amount of dry forest.[110] In the Selva Lacandona of southern Mexico, abundance and biodiversity of frugivorous bats that forage in the canopy increase with area of old-growth forest, whereas abundance and diversity of frugivorous bats that forage in the understory increase with area of secondary forest.[111] Each of these examples of season- and guild-specific responses to landscape structure likely are associated with variation in the abundance and diversity of foods as well as with energetic constraints associated with reproduction.[107,110,111] Indeed, ecological function is commonly associated with the form of response by phyllostomids to habitat fragmentation.[112] In general, body size and trophic level are the best predictors of sensitivity to habitat fragmentation: primary consumers generally respond positively to fragmentation (i.e., increase in abundance and biodiversity), whereas secondary or tertiary consumers generally respond negatively (i.e., decrease in abundance and biodiversity) to fragmentation. In addition, roost availability may affect the abundance or distribution of bats in fragmented landscapes, as the distance species forage from their roost is limited, and species typically select roosts close to multiple foraging areas.[113,114] Loss of roosting habitat is particularly important for species that roost in the cavities of large trees in mature forests, whereas foliage-roosting bats are less limited by roost availability.[115,116]

In highly fragmented interior Atlantic Forest, forest cover, patch size, and patch density are most strongly associated with phyllostomid abundances, with abundance increasing as forest amount increases. Phyllostomid abundance and biodiversity typically are the greatest in moderately fragmented landscapes.[108,117,118] However, in regions with extensive tracts of undisturbed forest, responses of Neotropical bats to landscape structure can be highly species specific. For example, landscape composition affects the abundances of most phyllostomid species during the dry season. However, phyllostomid biodiversity is not associated with landscape composition[106] because its effects are species specific. Bat biodiversity in lowland Costa Rica is affected by landscape composition during the dry season, but was unrelated to either landscape configuration or composition during the wet season.[119] The prevalence of guild- and season-specific responses by bats in fragmented landscapes demonstrates the ability of bats to effectively track resources through time and space, and the need to consider autecological factors as well as temporal environmental variation to understand local patterns of abundance and biodiversity in highly vagile species.

In Neotropical forests, the area and configuration of mature forest are not the only important factors that affect the abundance or diversity of nectarivorous or frugivorous bats, which forage on plants that commonly occur in early successional forests or along forest edges.[119,120] Consequently, a moderate amount of forest loss and fragmentation typically has a positive effect on these populations and communities.[118,120] This response occurs in landscapes within tropical rainforest,[121,122] within tropical dry forest,[111,123] and in undisturbed communities atop elevational gradients.[124,125] Some frugivorous and nectarivorous Neotropical bats that are secondary forest or edge-area specialists may now be more abundant than they were during pre-Columbian times, as they are well adapted for human-modified landscapes. In contrast, gleaning insectivorous, aerial insectivorous, and carnivorous bats prefer well-preserved forests rather than disturbed sites,[120] likely because disturbed habitats do not provide sufficient resources (e.g., food and roosts) for members of these guilds to countermand the increased risk of predation while traversing extensive open habitats to meet minimum energetic or nutrient requirements.[126]

In the Sydney metropolitan area (Australia), bat species richness is lower than in nearby national parks.[127] Species richness is best predicted by forest area and age; however, species composition differs between urban areas and nearby forests. Because suburban areas have many trees that act as corridors for movement between suburban areas, forest remnants, and adjacent national parks, composition of suburban bat assemblages resembles that of forests rather than that of urban areas. This dynamic illustrates the importance of matrix quality (i.e., tree density) on diversity and composition of bats. Indeed, the quality of the matrix is of primary importance in determining interpatch dispersal and patch occupancy by bats.[128] The presence of green spaces (e.g., parks and golf courses) in matrix habitats promotes the use of urban and suburban habitats by bats in Canada[129] and the United Kingdom,[130] suggesting that land-use planning and management of matrix quality to create connected networks of tree habitat that may decrease the vulnerability of some populations to urbanization.

In island biogeography, each island is surrounded by uninhabitable area (e.g., ocean) that represents a barrier to dispersal and provides no resources for terrestrial organisms (i.e., a hard boundary). A study of naturally occurring Amazonian savannahs (forest fragments surrounded by grassy habitats that are adjacent to continuous intact forest) afforded the opportunity to evaluate naturally occurring habitat islands that were surrounded by another terrestrial habitat rather than by water.[131] In this case, bat species composition is similar in all habitat types (grasslands, forest fragments, and continuous forest) and forest fragment size or shape does not affect bat biodiversity.[131] The savannah grasslands provide some resources (insects, fruit, and nectar) for bats and do not represent effective barriers to dispersal (i.e., they are soft boundaries). In contrast, Panamanian bats responded negatively to fragmentation when forest patches were surrounded by water or agriculture, with the degree of negative effect reflecting the quality (from the perspective of bats) of the matrix: continuous forests harbored greater species richness, followed by fragments in agricultural landscapes, with islands having the most depauperate faunas.[132] These effects were guild specific, with gleaning animalivores being most sensitive to fragmentation, and frugivores being least sensitive. The importance of matrix habitats to the populations and communities of bats in forest fragments is consistent with recent work that establishes the value of secondary forest regeneration in human-dominated landscapes.[118,133,134]

Metacommunity structure: a landscape perspective

Few studies have evaluated the effects of landscape structure on bat metacommunities. In human-modified landscapes, the a priori assumption is that metacommunities will be nested, with more heavily modified landscapes harboring faunas that are proper subsets of those from less disturbed landscapes.[135,136] Species should be lost from faunas in a predictable fashion based on the sensitivity of species to habitat loss and fragmentation. Nonetheless, these expected nested structures do not characterize Costa Rican,[55] Amazonian,[137] or Atlantic Forest[138] bat metacommunities at large spatial extents. However, nested structures did manifest in association with landscape modification for Atlantic forest bats at small spatial extents.[139] Phyllostomid bats in Costa Rica exhibit season-specific structure: Gleasonian structure during the dry season and Clementsian structure during the wet season.[55] Distance between forest patches structures metacommunities during the dry season, whereas forest edge density structures metacommunities during the wet season. Rather than the expected nested distributions along a landscape-modification gradient, some species (mostly gleaning animalivores of the subfamily Phyllostominae) occurred primarily in less modified, highly forested landscapes, whereas other species (mostly frugivores and nectarivores of the Glossophaginae and Stenodermatinae) occurred primarily in highly modified landscapes dominated by agricultural land covers.[55]

The distributions of phyllostomid bats in a fragmented landscape in southern Amazonia were not coherent; the preponderance of species did not respond to the same environmental gradient. Such random structure also occurs for carnivorous phyllostomids, whereas herbivorous phyllostomids (frugivores and nectarivores) exhibit quasi-Clementsian structure.[137] Importantly, this fragmented landscape is just south of and adjacent to intact, continuous Amazonian forest, which likely harbors source populations for all of the 44 species captured in forest fragments. The herbivorous species can be categorized into three groups based on their responses to open habitats and forest fragment sizes: (1) species that prefer large fragments and landscapes near the intact continuous forest (e.g., *Chiroderma trinitatum*, *Vampyressa pusilla*, and *Platyrrhinus brachycephalus*); (2) species that prefer small forest fragments with an abundance of forest edges and secondary forest (e.g., *Artibeus concolor*, *A. anderseni*, *A. glauca*, *Lichonycteris obscura*, and *Platyrrhinus lineatus*) that produce an abundance of fruit and flowers on which these bats feed, and (3) species that are ubiquitous (e.g., *A. lituratus*, *A. planirostris*, *Carollia perspicillata*, and *Rhinophylla pumilio*) and use all forest fragments regardless of size or location.[137] In addition to differences in size, forest fragments in this landscape also differ in plant species composition and physical forest structure, and responses by bats to this variation in forest physiognomy are species and feeding class specific.[140] Gleaning animalivores are particularly sensitive to vertical forest structure, as they require an open stratum between the understory and canopy to forage effectively.[141] These multidimensional and feeding class-specific responses of bats to a fragmented landscape likely account for the lack of coherence for all phyllostomids and all carnivorous bats. This demonstrates that even random metacommunity structure may arise from ecological responses and is worth further investigation as autecological knowledge is paramount for understanding the species- or functional group-specific responses within a metacommunity.

Less than 10% of the original extent of Atlantic Forest remains,[142] creating human-dominated, highly modified landscapes. In a study at both large extent and focus, phyllostomid bats of Atlantic Forest exhibited a quasi-Clementsian structure that was associated with spatially structured environmental variation, as well as with habitat loss associated with human activities.[138] However, structure was feeding class specific: herbivores and carnivores exhibited Clementsian and nested structures, respectively. Nonetheless, spatially structured environmental variation was the driving force behind each of these structures, rather than habitat loss or fragmentation, showing that the same process can give rise to different metacommunity structures in the same system. In contrast, nested (phyllostomid bats) and quasi-nested (animalivorous bats) structures occur at small spatial scales (small extent and focus) in fragmented landscapes of Atlantic Forest.[139] For both groups of bats, species found in smaller fragments represented a subset of species occurring in larger fragments or in continuous forest, and metacommunity structure reflected a combination of disturbance tolerance and interfragment dispersal ability.[139] This combination of studies shows how different structures and different structuring mechanisms can occur at different spatial scales in the same biome.

Environmental and spatial drivers of bat species composition

A comprehensive and novel study evaluated the effects of landscape and spatial characteristics on taxonomic, functional, and phylogenetic composition and dispersion of Costa Rican bats.[38] In these contexts, composition characterizes the central position of a community within functional or phylogenetic space based on the averages of species functional or phylogenetic characteristics, similar to a community-weighted mean. Dispersion measures the distribution of species in a community with respect to functional or phylogenetic characteristics, and is conceptually similar to a variety of dispersion metrics that measure functional diversity, such as Rao's quadratic entropy.[143] Almost 40% of the variation in taxonomic composition among communities was explained by landscape structure (composition and configuration of habitat patches in landscapes) and the spatial arrangement of those sites, with the former having the larger effects. This result is consistent with the mass effects mechanistic model.[3] In contrast, neither landscape nor spatial characteristics explained variation in functional or phylogenetic composition, with Costa Rican bat communities differing little in either regard.[38] However, nearly all (~95%) of the variation in functional or phylogenetic dispersion (i.e., the amount of functional or phylogenetic space occupied by a community) among sites was related to spatially structured landscape composition, once again consistent with mass effects. This spatially structured effect likely arises because humans generally use space by creating a gradient spanning urban to suburban to rural to natural habitats. Interestingly, functional and phylogenetic dispersion is associated with this habitat heterogeneity gradient, with greater dispersion associated with increasing habitat heterogeneity (forest, cropland, pasture, bare ground, impermeable surfaces, and water) leading to increased dispersion.[38] This effect on dispersion is consistent with the typically observed increase of bat biodiversity at intermediate levels of habitat loss and fragmentation.[108,111,119,121–123]

CONCLUDING REMARKS, FUTURE PROSPECTS, AND CAUTIONS

The study of bats on islands in isolated habitat patches has benefited from perspectives and tools of island biogeography, landscape ecology, macroecology, and metacommunity ecology. Similarly, conceptual development of these disciplines has been enhanced by empirical studies of bats on islands or in patches of terrestrial habitat that are surrounded by a matrix of various types, including native and converted land uses. Moreover, studies of the effects of area on variation in bat biodiversity have evolved considerably beyond considerations of species richness to include abundance-based metrics of taxonomic biodiversity (e.g., species evenness or diversity), as well as considerations of functional or phylogenetic biodiversity. Similarly, area-based factors thought to affect variation in local biodiversity have expanded to include: (1) area of sampling units, (2) area of focal habitat, and (3) area of nonfocal habitats, including both native and anthropogenic land uses. In addition, the spatial configuration of islands or patches of habitat can affect variation in biodiversity at multiple spatial scales. Finally, all considerations of habitat composition or configuration require a multiscale approach to identify the scales at which species or communities respond. To a lesser or greater extent, all of the factors reflect processes related to origination-extinction dynamics or sources-sink dynamics linked to dispersal. Research on bats has documented that patterns and the importance of particular processes may be species, guild, season, or context dependent.

Because landscapes of the future are likely to be characterized by increasing loss and fragmentation of native habitats, expansion of human-modified habitats, and critical changes related to global warming or the increased frequency of extreme events, conservation research, management, and policy need to fully consider perspectives explored in this review. In particular, multiscale and cross-scale perspectives should play an important role in refining ecological understanding.

Cross-scale interactions, such as those initiated by disturbances, modify the biodiversity of landscapes by effecting dynamics in time and space.[144–146] Cross-scale interactions are processes at one spatial or temporal scale that interact with processes at another scale to enhance the likelihood of nonlinear dynamics or thresholds. These interactions modify the relationships between patterns and processes across spatial scales. In essence, fine-scale processes influence dynamics across broad spatial extents or over long time periods, while broad-scale drivers can interact with fine-scale processes to determine system dynamics. Disturbances affect the life history and demographic parameters of species at fine spatial scales by altering the local abiotic, biotic, or structural environment (Figure 6). Moreover, the differences among islands or local patches in environmental characteristics, as well as their spatial configuration, affect the movement of individuals among islands or patches, altering the effective connectedness among sites in a species-specific manner. As secondary succession advances, the biotic, abiotic, and structural characteristics of local sites change as a result of interactions between fine-scale and broad-scale processes. Changes in local environmental characteristics alter the nature and

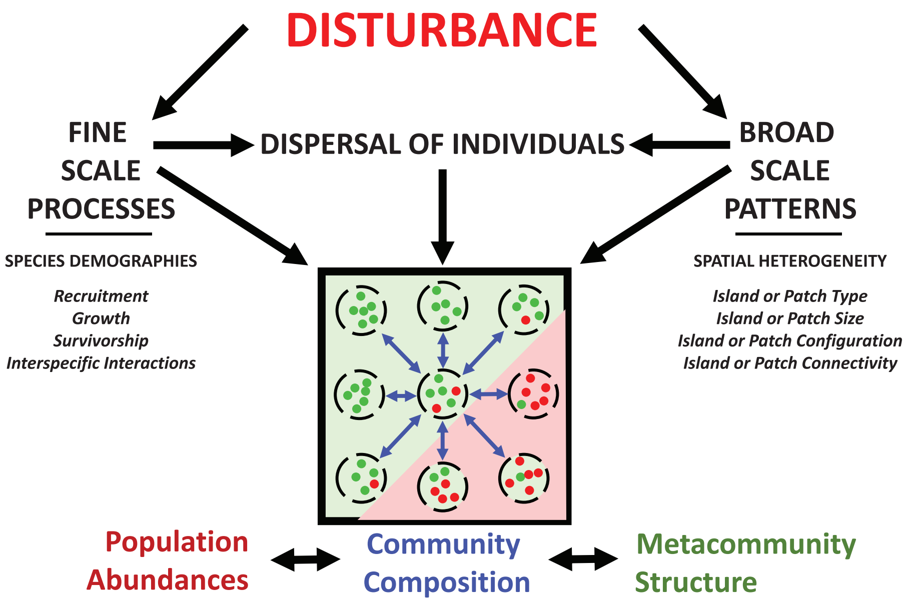

FIGURE 6 A conceptual model illustrating the interactions among environmental factors that affect variation in time and space in a disturbance-mediated system. Disturbances affect fine scale processes that occur within islands or habitat patches (dashed circles), as well as broad scale patterns that emerge in the landscape (light green and red shaded areas in the landscape). Processes at these two spatial scales interact (i.e., cross-scale interactions) to affect the movement of individuals among islands or patches in a species-specific manner (red and green dots). Such movement of individuals among sites (i.e., blue arrows indicate such movements for the central site) is the ecological glue that establishes metacommunity characteristics in concert with additional processes related to spatial and environmental gradients (e.g., neutral processes, species sorting, and mass effects). Over time, these cross-scale interactions catalyze postdisturbance successional changes in population and community characteristics, and the structure of metacommunities

configuration of islands or patches at the broad scale, thereby creating a cascade of cross-scale interactions (Figure 6). Consequently, cross-scale interactions have the potential to significantly mold spatial patterns of abundance, composition, and biodiversity, and will likely do so in complex ways, especially during the Anthropocene.

Because mechanisms at multiple spatial (from local to global) and temporal (from seasonal to geologic) scales operate to mold spatial patterns in species composition, biodiversity, and distribution, understanding these patterns requires a broad perspective that considers ecological and evolutionary mechanisms as well as the admission that some patterns can result from many potential processes. The difficulty in conducting large-scale, replicated experiments to explicitly test mechanisms that may structure communities or metacommunities means that most work in island biogeography, landscape ecology, macroecology, and metacommunity ecology are exercises in pattern matching (i.e., identifying empirical spatial patterns that are consistent with patterns predicted by theory). Consequently, care must be taken to understand alternative explanations that can produce the same or similar patterns, using the preponderance of evidence to identify the most likely causal explanations. This manifests in island biogeography with the confounded nature of elevation, island area, and habitat diversity, all of which can contribute to increasing biodiversity, but the relative contributions of each are difficult (or impossible) to isolate. Similarly, in landscape or metacommunity ecology, the perception of the relative importance of particular environmental characteristics can change when models include different environmental or spatial characteristics or when those characteristics are measured at different spatial scales. In spatial ecology, it is always important to ensure that the response and explanatory variables are measured at the same or appropriate scales and that explanatory mechanisms operate at the scale of measurement. In addition, there are some limitations to available data or methods, especially those that use only incidence data (e.g., analyses based on species richness and EMS), which is a coarse approach to estimate biodiversity or community composition. Historically, taxonomic approaches have dominated studies of biodiversity in spatial ecology; however, as more data on species function and phylogeny become widely available, adding approaches that evaluate patterns of functional or phylogenetic biodiversity may help to distinguish between theories that predict similar taxonomic biodiversity, but distinct patterns of functional or phylogenetic biodiversity on islands,[147,148] in metacommunities,[149,150] or in human-dominated landscapes.[119,151,152]

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