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ON THE BIOGEOGRAPHY OF HABITAT ISLANDS: THE IMPORTANCE OF MATRIX EFFECTS, NONCORE SPECIES, AND SOURCE-SINK DYNAMICS

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ABSTRACT

Habitat islands can be defined as distinct patches of habitat surrounded by less contrasting matrix types. In contrast to true island biogeography (traditionally the study of islands surrounded by water), there have been less efforts to synthesize the myriad habitat island biogeography studies that have been published, particularly syntheses that cover the full range of habitat island types. By building on previous work, I aim to provide a review of habitat island biogeography in order to provide a blueprint for future research on habitat islands, including both naturally and anthropogenically fragmented systems. The review is organized into three main parts. First, the differences between habitat and true islands are summarized. Second, the main theoretical frameworks currently used to analyze habitat island systems are reviewed. Third, the findings of habitat island studies focused on various biological patterns are synthesized. Drawing on this synthesis, I put forward two main points regarding improving our understanding of habitat island biogeography: first, increasing the integration of matrix properties (including matrix variation across space and time) into habitat island biogeographic models and, second, testing for, and understanding the implications of, the potential prevalence of mass effects and source-sink dynamics in habitat island systems.

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Introduction

THE natural world is inherently patchy (Tilman and Kareiva 1997; Haila 2002), and many systems can be viewed as consisting of islands at some scale (MacArthur and Wilson 1967; Begon et al. 1990; Whittaker and Fernández-Palacios 2007). One of the major aims of island biogeography is identifying the factors that drive species diversity and species distributions in different types of islands. Until the 1960s, island biogeography had been primarily focused on islands surrounded by a matrix (i.e., the habitat(s) surrounding islands) of water (e.g., oceanic islands, continental shelf islands). These islands have often been called "true islands" (Whittaker and Fernández-Palacios 2007:10). Here, I use an expanded definition of true islands: cases where there is a maximal contrast between island habitat and matrix habitat (i.e., where the matrix is comprised of a habitat type(s) that cannot be colonized by any core island species; see Box 1). This definition includes island surrounded by water, but also systems such as lakes surrounded by a matrix of land. During the 1970s and 1980s, the effects of anthropogenic habitat loss (particularly tropical deforestation) and habitat fragmentation became apparent and, due to the observation that habitat loss tended to create isolated patches of natural habitat surrounded by contrasting land use, first articulated by Preston (1962), researchers began to apply island biogeography theory to the study of what we now call habitat islands, both from a theoretical and an applied perspective (e.g., Vuilleumier 1970; Diamond 1975a; Wilson and Willis 1975; Brown and Dinsmore 1988; the idea was also discussed earlier in MacArthur and Wilson 1967). From this work, the concept of a habitat island emerged, and the subfield of island biogeography focused on the study of habitat islands diverged from its true island counterpart (Harris 1984; Whittaker et al. 2005; Triantis and Bhagwat 2011; Matthews 2015). Here, I define habitat islands as cases where there is a nonmaximal (but also nonnegligible) contrast between island habitat and matrix habitat, meaning some core island species may be able to survive in the matrix (see Box 1 for further discussion). The nonnegligible clarification is important as it highlights that not all systems can or should be viewed as habitat islands.

The study of the process and effects of anthropogenic forest fragmentation is still the largest area of habitat island research (Laurance et al. 1998; Lindenmayer and Fischer 2006). However, the full domain of habitat island research is much broader. That is, forest fragmentation research is part of habitat island biogeography, but habitat island biogeography is not synonymous with forest fragmentation research. Although habitat island biogeography has grown as a discipline, it has done so in somewhat of a haphazard way, often entangled with other research fields, and as of yet there have been few efforts to synthesize, in a biogeographical context, the myriad habitat island studies that have been published, particularly syntheses that cover the full range of habitat island types. By building on previous work (e.g., Haila 2002; Watson 2002; Laurance 2008; Mendenhall et al. 2014a; Itescu 2019), the present study aims to provide such a synthesis.

The remainder of the review is organized into three main parts. First, it is now well known that habitat islands differ from true islands in many ways (Watling and Donnelly 2006; Laurance 2008; Itescu 2019), and I briefly summarize these differences. Second, I review the main theoretical frameworks currently used to analyze habitat island systems in order to draw out generalities. Third, I synthesize the findings of habitat island studies focused on various biogeographic and ecological patterns (e.g., species–area relationships and species abundance distributions), with the aim of identifying any general patterns. Drawing on this synthesis, I conclude with two main points regarding improving our understanding of habitat island biogeography: first, increasing the integration of matrix properties (including matrix variation across space and time) into habitat island biogeographic models and, second, placing a greater emphasis on testing for the prevalence of source-sink and mass-effects dynamics, both common concepts in metacommunity ecology (Leibold and Chase 2018). Source-sink

BOX 1

What is a habitat island?

Figure 1 provides examples of several (mostly habitat) island types discussed in this box. In the present review, I follow previous researchers in distinguishing between true and habitat islands on the basis of matrix type. However, rather than using an aquatic matrix as the distinguishing feature, I use matrix contrast. I define as a true island cases where there is a maximal contrast between island and matrix; that is, where the matrix is comprised of a habitat type(s) that cannot be colonized by any core island species, such as water to terrestrial species and land to aquatic species (Warren et al. 2015). This definition enables lakes (in the context of taxonomic groups consigned to aquatic habitat, such as fish) to be classified as true islands (Figure 1f). Although lakes have sometimes been viewed as habitat islands (e.g., Browne 1981), I would not classify these as such on the basis that the matrix habitat (land) provides the same contrast as, for example, the sea does to oceanic islands. This aligns with MacArthur and Wilson's argument that habitat islands are distinct from true islands as the space separating the former is "not barren of competitors" (MacArthur and Wilson 1967:114).

It follows then that habitat islands are defined as cases where there is a nonmaximal (but also nonnegligible) contrast between island and matrix, and thus some habitat island species are able to colonize or inhabit the matrix habitat and vice versa. In line with previous true island definitions, previous work has often defined habitat islands simply as islands surrounded by a nonaquatic matrix. However, that definition ignores the myriad systems in the marine and freshwater realms—such as hydrothermal vents, seamounts, and coral reefs—that have been considered as habitat islands (Whittaker and Fernández-Palacios 2007; Dawson 2016; Itescu 2019); in such systems, the use of an aquatic/nonaquatic matrix as a distinguishing factor clearly breaks down. As an aside, further work is clearly needed on the habitat island concept in marine and freshwater systems (e.g., Holland and Jain 1981; Itescu 2019). Dawson (2016) has made a good start in this regard.

Although the above definitions of true and habitat islands are sufficient for the present work, I acknowledge that in reality the situation is not so simple. First, there is an argument for using ecology rather than geography for classifying islands, such that islands are classified based on the focal taxon under study (discussed further below). That is, the same island could be classified differently depending on the focal taxon. Second, these definitions ignore the dominant assembly processes structuring habitat island biota. For example, it has been argued that small forest fragments created by the flooding of landscapes (Figure 1d) following dam construction (Matthews 2015) and even some continental shelf archipelagos (Gibson et al. 2017) are more similar to habitat islands as defined above than they are to the oceanic Galápagos Islands. This is because the dominant assembly processes in the first two cases are the same (i.e., they are both immigration-dominated systems with little speciation; see Whittaker et al. 2017). However, speciation has been observed in certain naturally fragmented habitat island systems (Rosenzweig 1995; Porembski 2009).

Third, the distinction between habitat islands and true islands is often simply a matter of scale and perception. For example, a number of studies are framed as analyses of diversity patterns in habitat islands (e.g., Matthews et al. 2014a examined patterns in the abundance of arthropods in forest fragments on the Azores), where the habitat islands are located within true island archipelagos (Figure 1e) that are commonly used as units of study in true island biogeography studies (e.g., the same arthropod dataset has been used in true island studies; e.g., Triantis et al. 2012). In fact, due to the large-scale habitat loss that has taken place on many oceanic islands (Whittaker et al. 2017) and the resultant patchiness of the remaining habitat, it is likely that many recent true island species checklists can more accurately be described as habitat island checklists. The implications of this, for both true island and habitat island research, are not well known.

Fourth, delineating a habitat island is not always straightforward, that is, defining and measuring what is "habitat" (and what are matrix land uses/habitats) is not always a nontrivial task. As such, in some situations the binary distinction between habitat and matrix habitat breaks down, and there is likely a continuum of habitat types for which species have varying tolerances (Frishkoff et al. 2019). This is particularly true in systems where there is a clear gradient of habitat types; for example, a patch of virgin rainforest may be surrounded by secondary regrowth forest that is in turn surrounded by agricultural land. Delineating the island and the matrix habitat(s) in this example can be tricky and to some extent will be dependent on the taxon under study, and may even vary across species within a taxon. For example, some bird species may avoid leaving the area of virgin forest, whereas other species may happily forage in the secondary forest and perhaps even agricultural land (Şekercioğlu et al. 2002). Even in landscapes with a clear distinction between the habitat of interest and the matrix habitat, many patches are often connected by features such as treelines, hedgerows, and thin linear strips of habitat.

For the purposes of this review, I will put the above four concerns to one side and utilize a conceptual model that is based on a dichotomy between island habitat and matrix habitat(s), but importantly not a model where the matrix is uninhabitable to all species. Then, and using the above "habitat island" definition as a guide, we can see that the term habitat island has been used to refer to a diverse variety of different isolated systems, varying substantially in spatial and temporal scale, and including natural isolates (Figure 1b) and those isolates created by anthropogenic activities (Figure 1a). Systems previously classed as habitat islands include forest fragments (Laurance et al. 2002; Figure 1a), meadows, montane wetlands (Peintinger et al. 2003), mountaintop sky islands (Brown 1971; Figure 1b), cliff faces, caves (Culver 1970; Figure 1c), inselbergs (Porembski 2009), city parks, lava flows, sand dunes, and tree-fall gaps (Watson 2002; Itescu 2019). Even individual plants or colonies of plants have been viewed as habitat islands (e.g., colonies of common rock-rose *Helianthemum chamaecistus* in the U.K.; Davis and Jones 1986), and there is a growing literature on the idea of individual trees as habitat islands (e.g., Southwood and Kennedy 1983; Matthews et al. 2017a; Patiño et al. 2018).

Several attempts have been made at bringing together this diverse range of island types, along with true islands, into a single classification system. Watson (2002, 2009) proposed an island classification framework that was based on three system attributes: matrix contrast, origin, and age. Matrix contrast was dichotomized as low contrast (e.g., native forest patches surrounded by plantation forest) or high contrast (e.g., islands surrounded by water). Origin was split into "de novo" islands that emerge as new features (e.g., oceanic islands, caves) and start life with no species, and "fragment" islands that become isolated from larger areas and start life with a full complement of species (e.g., anthropogenically fragmented patches, continental shelf islands). Finally, age distinguished between young and old patches. Thus, Watson's framework does not distinguish between true and habitat islands explicitly. Watson (2002) argued that biogeographical patterns should only be compared within island groups based on these three attributes (e.g., young, low-contrast, fragment islands). It has since been argued that both contrast and age should be classified according to characteristics of the focal taxon (i.e., age and patch persistence in relation to the generation time of the focal taxon, and contrast and matrix permeability in terms of the taxon's dispersal ability; Figure 1c) rather than purely in relation to the islands themselves (Shepherd and Brantley 2005). More recently, Itescu (2019) provided a classification framework for habitat islands (termed "island-like systems"), which separated them into 12 coarse groups, such as freshwater island-like systems, human-generated island-like systems, and subterranean island-like systems.

Although the broad definition of habitat island used here is applicable for the aim of this review, it includes habitat island types that span multiple categories in the aforementioned frameworks of Watson (2002), Shepherd and Brantley (2005), and Itescu (2019). As such, it is recommended that future comparative habitat island studies consider all of the classification criteria outlined in those studies (e.g., age, origin) as a preliminary step. The classification framework adopted by a given study should reflect both the taxon and system under study, and the ecological questions being asked.

dynamics describe the situation where individuals from source habitats (i.e., habitats where the species has a positive population growth rate) continuously emigrate into sink habitats (i.e., habitats where the species has a negative population growth rate), such that sink populations can theoretically survive indefinitely (Pulliam 1988). The mass-effects concept is very similar, describing a directional flow of individuals (of a given species) from successful core habitats (where the number of individuals is high) to unfavorable habitats (where the number of individuals is low) where they would be unable to maintain a population in the absence of constant immigration of conspecific individuals (Shmida and Wilson 1985; Leibold et al. 2004). The difference between source-sink dynamics and mass effects being that the abundance of a species in its sink habitat can theoretically be greater than in its source habitat.

It is important to stress that the present study is not a review of the effects of habitat fragmentation (see Fahrig 2003; Ewers and Didham 2006; Lindenmayer and Fischer 2006; Haddad et al. 2015), nor is it claiming to be the first study identifying differences between true and habitat islands (e.g., Preston

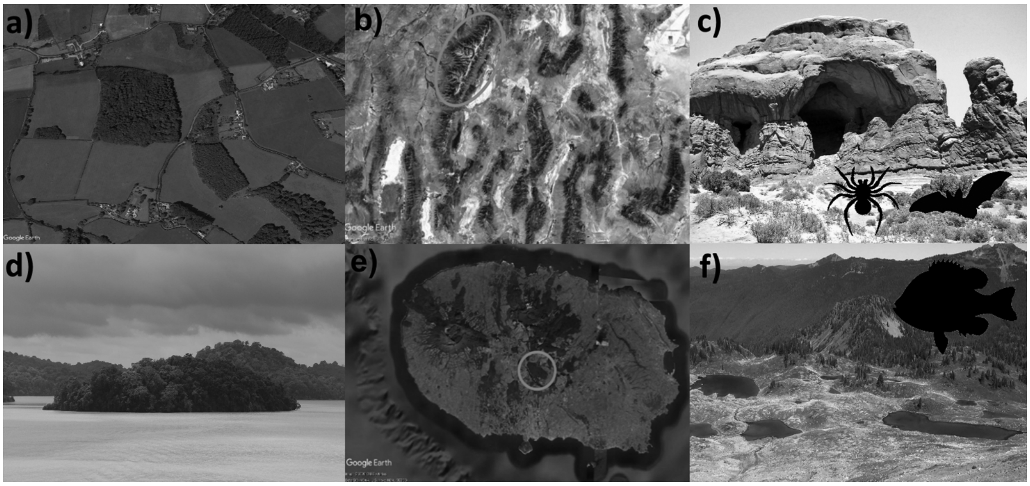

Figure 1. A Selection of Isolate Types

Habitat islands can (a) be created through anthropogenic activities (e.g., forest fragments embedded within an agricultural matrix) or (b) represent naturally isolated systems (e.g., forested "sky island" mountaintops surrounded by an arid matrix; an exemplar sky island is highlighted with a circle in the picture). (c) The same matrix surrounding a habitat island (e.g., shrubland surrounding a cave) can be considered impermeable/high contrast for a particular taxon (e.g., a cave-adapted spider), but permeable/low contrast for another (e.g., a highly mobile bat species). (d) Distinguishing between habitat islands and true islands is not always straightforward; for example, it has been argued that forest fragments created through the creation of reservoirs are more similar to forest fragments embedded in nonaquatic matrices than they are, for example, to islands in the sea. (e) Often, the only natural habitat remaining on true islands (here, Terceira in the Azores) is in the form of habitat islands (an exemplar native forest fragment highlighted with a circle in the picture); it is not always clear whether ecological samples collected in these habitat patches represent true or habitat island datasets. (f) Aquatic systems (e.g., coral reefs, hydrothermal vents) are often considered as habitat island systems, but some (e.g., lakes, from the perspective of aquatic taxa such as fish) are arguably true islands due to the maximal contrast between island and matrix. Credits for images: (a) Google Earth imagery; (b) Google Earth imagery; (c) photograph by Don Graham of flickr.com (CC BY-SA 2.0 license); (d) photograph by Joe Ross of flickr.com (CC BY-SA 2.0 license); (e) Google Earth imagery; (f) photograph by Brian Michelsen of flickr.com (CC BY 2.0 license). Credits for animal vectors: fish by C. Camilo Julián-Caballero of phylopic.org (CC BY 3.0 license); spider and bat by uncredited of phylopic.org (CC0 1.0 license). See the online edition for a color version of this figure.

1962; Brown and Dinsmore 1988; Watling and Donnelly 2006). In addition, many of the ideas discussed are central components of the different frameworks used to study different types of habitat islands (e.g., countryside biogeography), and thus the present review is not proposing an alternative framework for habitat island research or a new classification framework for habitat islands (see Watson 2002; Itescu 2019). Rather, the aim here is to provide a review of habitat island biogeography, drawing on studies across the different frameworks, in order to try and summarize these different ideas and provide a blueprint for future research on habitat islands, including both naturally and anthropogenically fragmented systems. Ultimately, it is hoped that the present review will, echoing Watson (2002), ensure that habitat island biogeography theory has the same predictive capacities as true island biogeography (the latter is comprehensively reviewed in Whittaker and Fernández-Palacios 2007 and Whittaker et al. 2017).

Differences Between True Islands and Habitat Islands: The "Matrix Matters"

Arguably, the main differences between true and habitat islands can be viewed through the concept of the matrix surrounding the islands. The matrix type in true island systems is a constant in the sense that it always has maximal contrast, while the contrast/permeability of the matrix surrounding habitat islands varies between systems, which in turn drives variation in structural and functional landscape connectivity, the total resource pool, and overall ecosystem functioning (Gascon et al. 1999; Daily et al. 2003; Bender and Fahrig 2005; Debinski 2006; Watling et al. 2011; Evans et al. 2017; Frishkoff et al. 2019). Thus, characteristics of the matrix determine habitat island diversity patterns in ways that cannot be derived from classical true island theories, such as the Equilibrium Theory of Biogeography (ETIB), which are built on the idea of a constant inhospitable matrix (Laurance 2008), at least over ecological time scales (e.g., the marine barrier between true islands in certain archipelagos is known to have receded due to past sea-level reduction during glacial cycles; Fernández-Palacios et al. 2016). Generally speaking, the more similar the matrix habitat is to the habitat island, the less isolated the islands are (Ricketts 2001), although this is not true for all taxa (e.g., Gascon et al. 1999; Şekercioğlu et al. 2002). Even if one were to assume that the matrix surrounding a set of habitat islands was barren and contained few resources, it would still likely be an easier landscape to disperse across relative to a maximal contrast matrix, all else being equal (Vuilleumier 1970; but see Brown 1971). Many habitat island taxa (but again, not all) can also utilize resources in low-contrast matrices (an idea related to landscape complementation), which increases the "effective area" of a given habitat island (Brotons et al. 2003; Cook et al. 2004; Driscoll et al. 2013; Mendenhall et al. 2014b), and which in turn affects biogeographic patterns such as the species–area relationship (SAR; Matthews et al. 2016) and nestedness (Watling and Donnelly 2006), both of which are discussed below. The matrix can also transfer resources into islands themselves, acting to increase the resource base within habitat islands.

Given the above it is clear that, in habitat island systems, the role of the classic true island biogeographic variables of area and isolation are, for a given species, modulated by matrix type (e.g., Watson et al. 2005): increasing matrix permeability (i.e., reducing matrix contrast) increases effective habitat island area (Prugh et al. 2008) and reduces habitat island isolation and thus increases interisland dispersal and rescue effects (cf. Brown and Kodric-Brown 1977). In particular, if matrix permeability is high, rescue effects will likely be a dominant process driving diversity dynamics in habitat islands (Leibold et al. 2004). Changes in matrix permeability through time, and thus in connectivity and effective area through time, are also important considerations.

The matrix also underpins other biotic and abiotic differences between true and habitat islands, such as edge effects, which are arguably more pronounced in habitat islands, and the prevalence of external disturbance agents such as hunting (e.g., Benchimol and Peres 2013), fire (Driscoll et al. 2013), and hostile and invasive species that can penetrate into habitat islands from the matrix. Edge effects in habitat islands, particularly forest fragments, are well documented and include factors such as changes in microclimatic conditions, elevated litter fall, and increased invasion of an island by matrix generalist species (for reviews see Laurance et al. 2002; Ries et al. 2004; Pfeifer et al. 2017). The exact set of edge effects depends on the type of habitat island and, more specifically, on island size, the predominant habitat type, structural complexity, matrix permeability and, in certain systems, the speed of edge evolution (i.e., how quickly edge habitats develop and seal; Laurance et al. 2002). It should be noted that, although edge effects are generally studied in the context of habitat islands, there are still edge-related concepts in true island biogeography. For example, Anderson and Wait (2001) provide a discussion of how allochthonous resource subsidies to true islands from the adjacent water are predicted to vary with island size and the area:edge ratio. The biota of smaller true islands (with low area:edge ratios) have also been argued to be more at risk from disturbances such as hurricanes than larger islands (Whittaker and Fernández-Palacios 2007).

The presence of edge effects in habitat islands also indicates a larger role for island shape than assumed by true island theory (Laurance 2008). Studies of anthropogenic habitat fragments have shown that irregular/complex shaped fragments result in lower population sizes of core habitat species due to the higher perimeter-to-area ratio and thus reduced proportion of core habitat and elevated edge effects (e.g., Ewers and Didham 2007). Fragment shape can also affect immigration (less circular shapes having higher immigration) and emigration rates (more complex shapes having reduced emigration rates), in turn affecting metapopulation processes in fragmented landscapes (Ewers and Didham 2006).

The role of source-sink dynamics and mass effects (Shmida and Wilson 1985; Pulliam 1988) is also more pronounced in habitat versus true islands. This is due to the often overlooked fact that, in habitat island systems, the matrix is both the surrounding land use and a source pool of species (Itescu 2019). Due to the presence of nonmaximal contrast habitat adjacent to habitat islands, there are often large mass effects and thus a constant supply of matrix specialist and generalist individuals permeating into habitat islands where, unless immigration rates are so high that extinctions never occur, they cannot maintain populations and so frequently undergo local extinction and recolonization (Matthews et al. 2014b, 2019a). Although equivalent processes do occur to some extent in some true island systems, the presence of a maximal contrast matrix means they occur at a reduced level. The effects of such ephemeral dynamics on biogeographic patterns in habitat islands are beginning to be realized (e.g., Borges et al. 2008; Magura et al. 2008; Bueno et al. 2018; but see Kunin 1998). For example, Matthews et al. (2019a) have recently shown that a prediction of the theory of island biogeography for exotic species (Burns 2015)—that exotic species have a greater rate of turnover than native species—holds in habitat island systems. However, rather than the patterns being driven by island area and isolation as in true islands (Burns 2015), in their study system of forest fragments on the Azores, the greater turnover of nonnative species was seemingly driven by source-sink dynamics and/or mass effects (the nonnative species being more adapted to the anthropogenic source habitats surrounding the habitat islands, and present in the sink forest fragments in very low numbers on average, thus being at greater risk of extinction).

One thing to note is that the above discussion of matrices has been based on the idea of a matrix as a (nonmaximal) contrasting land use to the habitat island itself (e.g., a matrix of cropland surrounding forest fragments). However, the matrix concept can be extended to any difference in conditions in the space outside a habitat island that affects a habitat island species' ability to survive and/or disperse (e.g., light for cave-adapted species; Itescu 2019).

Theoretical Frameworks Used in Habitat Island Research

Habitat island biogeography was first studied using the ETIB as a theoretical framework (e.g., Brown 1971; Diamond 1976; Burgess and Sharpe 1981; Brown and Dinsmore 1988; see Haila 2002 for a review) whereby the number of species in a given habitat island was predicted to be an increasing function of island area (larger islands have lower extinction rates) and a decreasing function of isolation from the "mainland" (more isolated islands have lower colonization rates; MacArthur and Wilson 1963, 1967). The ETIB is neutral in regards to species identity (MacArthur and Wilson 1967), and thus all species are considered to respond to patchy landscapes in the same manner. During the 1970s, a particular focus was on using the ETIB to generate conservation and protected area guidelines for use in fragmented landscapes (e.g., Diamond 1975a; Wilson and Willis 1975; but see Simberloff and Adele 1976).

Although some of the basic tenets of the ETIB were found to hold in habitat islands, success of the theory as a whole was limited (e.g., Brown 1971; Brown and Dinsmore 1988), but it has been argued that part of this failure is due to workers selecting the wrong types of true islands as models for understanding habitat islands (Triantis and Bhagwat 2011). In particular, it has been argued that we should be using relatively small and nonisolated islands, such as islands in lakes or small nearshore islands, rather than large isolated oceanic islands as models. Nonetheless, application of the ETIB in habitat island research was superseded in the 1980s and 1990s by metapopulation ecology; a body of theory focused on individual species within a spatially structured set of subpopulations (patches) that are connected through interpatch dispersal (Levins 1969; Hanski 1999). Variation in patch size and isolation underpin the extinction and colonization rate among patches (Opdam 1991; Hanski 1994). Precisely how extinction and colonization rates are linked to patch variables depends on the metapopulation model employed (Hanski 1999). Thus, the binary concept of hospitable island habitat and inhospitable matrix habitat, along with primary roles for extinction and colonization, is still ingrained within metapopulation theory, but there is a greater focus on the spatial dynamics of populations (Hanski 1994, 1999). Thus, it does not necessarily represent a full paradigm shift, but simply a greater focus on how a set of habitat islands form an interconnected network of patches linked by dispersal: it created a link between habitat geometry and population dynamics (Harrison and Bruna 1999). The theory of source-sink dynamics (Pulliam 1988) can be seen as being linked to ideas within metapopulation theory.

Metapopulation theory has found much success in the habitat island literature; although it has been argued that it only really applies to species with strong habitat specificity and is thus not applicable in all real-world contexts (Hanski 1999; Driscoll 2005). It also largely ignores properties of the matrix. This considerably simplifies the modeling of patch diversity, but at the expense of important realism in many cases (Hanski 1994; Ricketts 2001; Prugh et al. 2008). The increasing recognition of the importance of the matrix led to the development of new theory in the 1990s and 2000s, generally focused on anthropogenically fragmented landscapes, such as the matrix tolerance model (focused on the ability of species to use the matrix habitat; Gascon et al. 1999), the matrix quality model (see Pulsford et al. 2017), the patch-corridor-matrix mosaic model (Forman 1995), and the landscape variegation model (McIntyre and Hobbs 1999). These different models can be placed on a spectrum of complexity and independence/interdependence of species responses to fragmented landscapes. The ETIB, with its binary view of habitat-nonhabitat and assumption of species-level neutrality, is at one end of this spectrum, the patch-corridor-matrix mosaic model and landscape variegation model are toward the center, and continuum theory is at the other end of the spectrum. Continuum theory, and its related variants such as continua-Umwelt (Manning et al. 2004), is based on the idea that habitat islands (again, the focus has generally been on anthropogenically fragmented landscapes) are defined from a human perspective, and that individual species may perceive and experience the landscape differently (Wiens and Milne 1989; McIntyre and Hobbs 1999; Fischer and Lindenmayer 2006; Lindenmayer and Fischer 2007; Pulsford et al. 2017). Such considerations are less important in true islands as the water (or land to aquatic true islands) is inhospitable to the majority of island taxa (Lindenmayer and Fischer 2007). Continuum theory is an individualist concept whereby the landscape is conceptualized as a set of species-specific habitat gradients (Manning et al. 2004; Fischer and Lindenmayer 2006). Species are distributed across these habitat gradients in accordance with their individual requirements, and these requirements may vary with landscape context (Villard and Metzger 2014). The continuum model thus requires substantially more data than simple ETIB and metapopulations-type models (Fischer and Lindenmayer 2006).

Clearly, if the continuum model is true in all cases, attempting to identify any generalities in habitat island biogeography will be difficult. Indeed, a recent study of frogs and reptiles in an agricultural landscape in Australia found that responses of many of the species studied agreed with the continuum model, with species-specific responses to different observed environmental gradients (Pulsford et al. 2017). However, other studies have rejected the application of strict individualistic models that predict species responses to patchy landscapes, instead arguing that there is a degree of interdependence in how species respond to fragmentation (e.g., Didham et al. 2012). Going forward then, the decision of whether to use an island-matrix model or a continuum model is clearly an important consideration. In certain cases, it may be more appropriate to view the landscape as a mosaic of habitat types without any one representing an "island," and where species respond to the landscape in an individualist manner, particularly in landscapes where habitat cover is sparse and scattered in such a way as to make delineation of a habitat island impractical (McIntyre and Hobbs 1999). However, in others the concept of a habitat island will still be applicable, as long as factors such as matrix and edge effects are accounted for. The important thing then is to ensure the most appropriate framework is applied in a given context, which will depend on both the system and taxon under study.

Another recent theory that implicitly argues that the habitat island concept is obsolete is the "habitat amount hypothesis" (Fahrig 2013). This theory challenges the idea that habitat islands are natural units of ecological measurement in patchy landscapes, and instead argues that the species richness of a given sample site (species density) within an area of habitat is a function of the amount of habitat in the local landscape; an equal-sized site will contain more species if situated in a local landscape with greater amounts of suitable habitat than a local landscape with a smaller amount of suitable habitat (Fahrig 2013). Island area will only affect species richness in sites through its contribution to habitat amount. Tests of the habitat amount hypothesis are ongoing, and results are mixed thus far (e.g., Haddad et al. 2017; Melo et al. 2017; Merckx et al. 2019; Watling et al. 2020). One drawback of the theory is its omission of matrix effects, acknowledged by Fahrig (2013), which are known to be important in many habitat island systems (e.g., Brotons et al. 2003). A second consideration is that it is not always straightforward to delineate the local landscape in practice; the size of the local landscape also likely varies as a function of the taxon and habitat type under study, as well as the properties of the surrounding matrix. Estimating the size of the local landscape empirically is thus recommended (Watling et al. 2020). The habitat amount hypothesis has largely been discussed in the context of anthropogenic forest habitat island systems, and its applicability to habitat islands more generally is unknown.

In regard to anthropogenically fragmented systems, an important framework for the study of habitat islands is countryside biogeography. Countryside biogeography has developed over the last 25 years and has been widely used to study the diversity and abundance of species in (primarily) terrestrial fragmented forest systems (Daily 1997; Daily et al. 2003; Mendenhall et al. 2014a; Frishkoff et al. 2019). It incorporates many of the key processes of ETIB, such as colonization and extinction dynamics, but is also based on the idea that a large amount of natural terrestrial habitat at the global scale is currently embedded within a matrix of human-made habitats, such as pastureland and plantation forest (Daily et al. 2003). This human-made habitat provides resources that many species can utilize (Mendenhall et al. 2014b) and thus "countryside" landscapes can support a larger number of species and have lower community-level extinction rates than true island archipelagos (Daily et al. 2003; Wolfe et al. 2015). It does not ignore the importance of natural habitat or the fact that certain species are full habitat specialists (i.e., they do not use any resources in the wider landscape). Rather, it simply recognizes that, in many places, what is left of natural habitat on its own is unable to support a full complement of species, and thus in such cases the fate of many species depends on the hospitality of the wider countryside ecosystem (Mendenhall et al. 2014a). Importantly, the countryside biogeography framework thus highlights how the species diversity within natural habitat can often be sustained through increasing the hospitability of the surrounding habitat in the wider landscape (Mendenhall et al. 2014a,b). However, it is important to remember that the raw number of species is not the only measure of landscape health, and workers focused on maintaining species diversity in countryside landscapes should also take into account factors such as changes to species interactions, which may result in delayed extinctions at a later stage.

Tests of the countryside biogeography concept have mainly been undertaken in (neo) tropical agricultural landscapes and have generally found that countryside biogeography provides a better predictive framework than ETIB (e.g., Daily et al. 2003; Mendenhall et al. 2014a,b; Wolfe et al. 2015). Although countryside biogeography studies emphasize the importance of the matrix, they often do not divide systems into island and matrix; rather, they regularly view (anthropogenic) landscapes as a mosaic of different habitat types (e.g., farmland, forest, individual trees, riparian strips), with species have varying tolerances to each (Frishkoff et al. 2019). Thus, it can represent a slightly contrasting viewpoint to those frameworks where the habitat islands themselves are the units of interest. Linked to this point, a recent study has argued that countryside biogeography and the habitat amount hypothesis are complementary frameworks, with the former being more effective at explaining how regional richness changes with habitat area (i.e., beta and gamma diversity), and the latter being more effective at explaining the diversity of individual habitat types (i.e., alpha diversity; Merckx et al. 2019). More work is needed to explore this interesting hypothesis.

Much has also been gained by studying habitat islands through the lens of metacommunity theory (Leibold et al. 2004; Holyoak et al. 2005; Leibold and Chase 2018). Building on ideas in metapopulation ecology, a metacommunity can be defined as a set of local communities that are linked through the dispersal of multiple interacting species (Leibold et al. 2004). Metacommunity research is wide ranging, but key research questions include how metacommunities are structured (e.g., along gradients; Leibold and Mikkelson 2002), and what models best describe metacommunity dynamics. Traditionally, four theoretical models/archetypes have been used for studying metacommunities: neutral theory (i.e., the idea that species are functionally equivalent), species sorting (i.e., niche-/selection-based factors), mass effects, and patch dynamics (e.g., competition–colonization tradeoffs; Leibold et al. 2004; Holyoak et al. 2005). However, there has been increasing recognition that these four are not alternative mutually exclusive hypotheses, but rather represent a set of mechanisms that interact (to different degrees in different communities) to determine community assembly and species composition (Leibold and Chase 2018). Many of the ideas in metacommunity ecology (e.g., the strong focus on dispersal) are relevant to habitat island research (indeed it could be argued that habitat island research simply represents a subset of metacommunity research), but metacommunity theory also applies to nondiscrete patches and sample areas with diffuse barriers. In the context of habitat islands, metacommunity theory that distinguishes between core habitat (here, the habitat island itself) and matrix habitat will be most applicable (as depicted in Figure 1.4a in Leibold and Chase 2018:12). There is also less discussion of matrix characteristics in metacommunity theory than in some of the other aforementioned frameworks used for studying habitat islands and, whereas metacommunity research tends to be more focused on species interactions and population biology (Leibold and Chase 2018), the biogeographical study of habitat islands is generally more focused on emergent statistical and ecological patterns.

A final interesting potential framework for studying habitat islands is the “terrageny” framework of Ewers et al. (2013). Within this framework, habitat fragments are treated like tips in a phylogeny and the internal nodes represent fragmentation events; this allows the ancestry of fragments to be explicitly modeled using common phylogenetic metrics and provides information on how continuous habitat in the past was broken up into smaller pieces. The approach provides a number of predictions, such as the locations of locally endemic species and the proportion of shared species in any two fragments, which can be tested using empirical data (Ewers et al. 2013). It is thus arguably a more useful null model than the ETIB in habitat island systems where it applies (i.e., where isolated habitat islands were once connected and where the age of division is known), but as of yet there are few empirical tests of the approach. The approach also clearly illustrates the importance of considering landscape history when attempting to predict current species diversity patterns (see also Kuussaari et al. 2009). Ewers et al. (2013) applied the framework to anthropogenically fragmented landscapes. However, as many habitat island systems (e.g., mountaintop sky islands) have complex historical spatial relationships, such as changes in isolation and connectivity through time, the terrageny framework may be applicable to a wider range of habitat island systems than has currently been explored. Further research is needed to better understand the implications of this observation.

Identifying Generalities in Biogeographic Patterns in Habitat Islands

Workers have been studying individual habitat island systems for decades (e.g., Brown 1971; Laurance et al. 2002) and a large number of published datasets exist, with recent work focused on bringing these datasets together in macroecological syntheses (e.g., Watling and Donnelly 2006; Matthews et al. 2016). As Whittaker et al. note, "numerous habitat island data sets have been collected, and so what is needed is not necessarily new field efforts, but more concerted efforts in analysis and synthesis, to tease out the scale sensitivity of habitat island data sets, particularly, the form of their [species–area relationships] . . . , and their compositional structure" (Whittaker et al. 2005:13).

Below I review research on four core diversity patterns (that have been commonly studied in true island biogeography) in habitat islands: diversity–area relationships, incidence functions, island composition patterns (e.g., nestedness), and relative abundance patterns. This is by no means a comprehensive list, and habitat island studies have focused on numerous other diversity patterns, such as species body-size distributions, interaction networks, and the species–isolation relationship (e.g., Brown and Kodric-Brown 1977; Hanski 1999; Terborgh et al. 2001; Itescu 2019).

It should also be noted that many of these patterns have been studied under the different habitat island frameworks outlined above (e.g., all four have been studied under the countryside biogeography banner), and where relevant I highlight how a particular framework has advanced our understanding of a specific pattern in the context of habitat islands. However, this section is not meant to provide a comprehensive review of each pattern; indeed, each could form the basis of a dedicated review in its own right. Rather the aim is simply to identify general patterns that hold across habitat island systems, or that vary systematically as a function of some system property (e.g., matrix type), in order to develop habitat island biogeography into a more predictive discipline. It is also hoped that this effort will help future researchers better understand how theories and models derived in the context of true islands can be adapted for habitat islands. Work on this latter issue will help answer one of Patiño et al.'s 50 fundamental questions in island biology: "How applicable are island biogeographical theories derived from . . . [true] islands to other forms of insular system, such as sky islands and seamounts?" (Patiño et al. 2017:969).

DIVERSITY–AREA RELATIONSHIPS

The island species–area relationship (ISAR) describes how the number of species increases with island area and is a near universal pattern in island biogeography (Rosenzweig 1995; Triantis et al. 2012; Matthews et al. 2021). It is perhaps the most well-studied pattern in habitat islands. The power model is the most commonly used ISAR model in habitat island studies, as in ISAR research more generally. The power model is given by the function $S = c^{*}A^{z}$, where S and A are species richness and (island) area respectively, and c and z are fitted parameters (Triantis et al. 2012). In log-log space the model is linearized; here, $\log(c)$ is the intercept and z is the slope of the line. Comparative analyses of z-values have found z is, on average, lower for habitat islands relative to true islands (Watling and Donnelly 2006; Matthews et al. 2016). These lower slopes are likely due to matrix effects. As outlined above, as many species are able to utilize resources in the matrix, island area has less of an effect on richness in habitat islands than true islands. Based on this argument, it follows that *z* should be linked to matrix type and by extension matrix permeability, and this indeed seems to be the case. Freeman et al. (2018) found that ISARs for birds in South African coastal forest fragments were steeper in fragments surrounded by anthropogenic matrices (e.g., urban land uses) than in lower contrast natural matrices (e.g., grasslands). Matthews et al. (2016) showed that *z* increased from fragments surrounded by agriculture to mountaintop sky islands to fragments surrounded by urban land use; the latter category had *z*-values more similar to true islands, which highlights the lack of connectivity in urban landscapes. Prugh et al. (2008) found that sensitivity to island area was higher in human matrices than in matrices that are more natural. Farneda et al. (2020) found that *z* was larger for bat ISARs in a true island system in Panama, than a forest fragment system in the Amazon. A recent synthetic analysis of 123 habitat fragment studies by Chase et al. (2020) found that the relationship between standardized species richness and fragment size was steeper for harsher matrices (e.g., urban areas).

Although the aforementioned findings imply matrix effects are important in driving variation in *z*, it is possible that some of the processes researchers often associate with the matrix actually directly impact island richness; in this case, matrix permeability would simply be associated with ISAR slope rather than being the driver. Nonetheless, the findings of the aforementioned studies are important as the ISAR is widely used in conservation studies to predict, for example, the number of species to be lost following habitat destruction (see Fattorini et al. 2021). However, many such studies use *z*-values taken from the true island literature (see Fattorini et al. 2021) that likely leads to inaccurate extinction predictions and can in turn result in lower public confidence in conservation work (Mendenhall et al. 2014a). Indeed, studies that have adapted commonly used ISAR models to incorporate matrix effects, differential tolerances of species to different habitat types, and other habitat island specific factors, including many countryside biogeography studies (e.g., Pereira and Daily 2006; Proença and Pereira 2013; Merckx et al. 2019), have generally found improved fits. A number of such models have been proposed and these are summarized in Table 1. More work is needed to test and compare these various models.

Other SAR models and approaches (that are not included in Table 1 due to their different focus) have been proposed in the habitat fragmentation literature to predict the number of species that will be lost through habitat destruction. For example, the species–fragmented area relationship model is an extension of the power SAR model that incorporates the effects of the fragmentation of habitat as well as changes in habitat area, and is useful for predicting richness at the landscape level (Hanski et al. 2013). More recently, Chisholm et al. (2018) introduced the “Preston function.” Based on a spatially explicit non zero-sum neutral model, the Preston function is the SAR for contiguous circular sample areas taken from an infinite world, and has many applications in fragmentation research (Chisholm et al. 2018; Rosindell and Chisholm 2021). Other fragmented SAR approaches are discussed in Rosindell and Chisholm (2021).

Table 1 also does not cover threshold models, that is, those that include a threshold in the ISAR, such that below a certain habitat island area the rate of decline in richness changes. This is not to be confused with landscape habitat amount thresholds. Thresholds in the ISAR have been found for some habitat island datasets (e.g., Matthews et al. 2014c; Wang et al. 2018); however, the identification of thresholds, for example, by using piecewise regression models, is sensitive to the use of log-transformation, which is common in ISAR studies (Matthews et al. 2014c). Recent work has proposed a number of additional threshold ISAR models (e.g., with two thresholds; Gao et al. 2019), and open-source software is now available for fitting a range of threshold models to ISAR data (Matthews and Rigal 2021). Future tests of these models using additional habitat island datasets will likely be revealing.

The form of the ISAR in habitat islands (particularly anthropogenically fragmented systems) may be affected by many other factors,

TABLE 1

The various proposed species–area relationship (SAR) models that account for matrix and/or habitat effects

Model Name	Description	References
Multihabitat SAR	A model of species richness in multihabitat landscapes that simply combines the SAR curves (e.g., power or logarithmic curves) of individual habitats.	Tjørve (2002)
The choros model	An extension of the power SAR model in which the island area term is replaced with the term K, where K is equal to island area * the number of habitats within an island.	Triantis et al. (2003); Proença and Pereira (2013)
Countryside SAR	An extension of the power SAR model that accounts for the presence of multiple habitats in the surrounding matrix and for differential use of these habitats by species. The approach has subsequently been extended to include underlying functions other than the power function (e.g., the negative exponential).	Pereira and Daily (2006); Proença and Pereira (2013); Martins and Pereira (2017)
Matrix-calibrated SAR	Based on the power SAR model but partitions the *z*-value into two parts: a constant and a part that measures the sensitivity of a taxon to the matrix habitat.	Koh and Ghazoul (2010)
Matrix- and edge-effect-calibrated SAR	An extension of the matrix-calibrated SAR that also includes edge effects (i.e., the effective area of islands after accounting for edge habitat).	Koh et al. (2010)
Two-habitat SAR	A landscape-level model developed in the context of birds in natural and open/human habitat. Based on the idea that land-use change often creates new open habitats that can support a different subset of species. Total landscape richness is modeled as the sum of the natural habitat and human habitat SARs. Empirical tests of the model have revealed a peaked relationship between bird richness and the proportion of natural habitat in a landscape.	Desrochers et al. (2011)
Lost-habitat SAR	A structurally similar model to the two-habitat SAR model but includes a third habitat category (lost habitat) that accounts for the fact that in some cases natural habitat is converted into land uses that support no unique species (e.g., urban buildings).	De Camargo and Currie (2015)

Several of these models are focused on richness at the landscape scale (i.e., across multiple habitats) rather than simply in a set of habitat islands, but are included here due to their inclusion of matrix-type effects.

including time since patch isolation (Bueno et al. 2020), human disturbance (e.g., hunting; Benchimol and Peres 2013), and the presence of noncore species, such as habitat generalists, invasive species, matrix specialists, and vagrants (see Box 2), which may result in flatter, or even negative, ISAR slopes (Cook et al. 2002; Lövei et al. 2006; Matthews et al. 2014b). This latter point is an extension of the argument of MacArthur and Wilson (1967; see also Connor and McCoy 1979) that nonisolated continental areas will have lower SAR slopes than true islands due to the presence of "transient" species. SAR models that account for differential habitat use by different species (e.g., the countryside SAR; Table 1) will be useful tools in understanding how noncore species affect ISAR form.

Species richness is only one measure of diversity and a number of recent studies have explored functional diversity (FDAR) and phylogenetic diversity–area relationships (PDAR; see Mazel and Thuiller 2021). It has been argued that the study of diversity–area relationships (DARs) in tandem can provide more in-depth insight into the mechanisms of community assembly than is possible from purely analyzing the SAR (Wang et al. 2013). The difference between FDARs and PDARs for a given system will depend on the phylogenetic signal in the analyzed traits. FDARs have been studied on true islands (Whittaker et al. 2014),

BOX 2

Habitat islands and the role of noncore species

A primary characteristic of many habitat island systems is the presence of what I have termed here "noncore" species. As with my definition of habitat island, this definition of noncore is purposefully broad and is simply used as a catch-all term to group together a range of different types of species. In an anthropogenically fragmented habitat island, noncore species can be roughly conceptualized as those species found within the island but not within a sample area the same size as the island located in the central part of nearby continuous forest. However, this conceptualization does not necessarily extend to naturally fragmented habitat islands. Regardless, in both types of habitat island, noncore species will often include some or all of tourist species (species that are present in low abundance in a focal habitat but are found in much higher abundance in an adjacent habitat; Ribeiro and Borges 2010), nonnative species (a species permanently living outside of its native distributional range), sink species (species present in a focal habitat, whereby their death rate, in the focal habitat, exceeds their birth rate; Pulliam 1988), vagrants and accidentals (individuals found outside their normal range and/or habitat; Grinnell 1922), matrix specialists (species that are associated with habitats, such as farmland, surrounding a focal habitat; Cook et al. 2002), transient species (species that occur infrequently in a focal habitat and do not maintain viable local populations; Snell Taylor et al. 2018), and habitat generalists (species that are able to persist and utilize resources in both the focal habitat and the surrounding matrix; Brotons et al. 2003). These different groups are clearly not mutually exclusive.

Although many or all of these types of species are also found in true islands (see Whittaker and Fernández-Palacios 2007), the prevalence of most is presumed to be higher in habitat islands. That is, the ratio of many of these types of species to core species is expected to be higher in habitat islands (and greater in smaller compared to larger habitat islands; Matthews et al. 2014b). This is primarily due to the effects of the surrounding matrix: species that are adapted to matrix habitats can "spill over" into habitat islands due to mass effects, and edge effects at the boundary of the island and matrix can cause disturbances that allow many of these types of species to thrive (Cook et al. 2002; Driscoll et al. 2013). High rates of within-island disturbance in many habitat island systems (particularly anthropogenic habitat islands) can also result in favorable conditions for many of these types of species.

As well as resulting in direct impacts to habitat island communities, for example, through changes to species interaction networks, the presence of noncore species will likely influence many patterns that we study as biogeographers and ecologists (Snell Taylor et al. 2018). For example, the presence of habitat generalists, matrix specialists, nonnative species, and tourists in habitat island systems, and in particular the higher proportion of these species in smaller islands, has been argued (and shown) to lower ISAR slopes (e.g., Martin 1981; Magura et al. 2008; Matthews et al. 2014b; Freeman et al. 2018). This lowering of ISAR slope (in anthropogenically fragmented systems) may sometimes lead to the interpretation that anthropogenic habitat fragmentation has positive effects on diversity (see Watson 2002). The fact that many of these types of species (e.g., tourists, transients) will be present in habitat islands in low abundance (and thus increasing the proportion of rare species) will also influence relative abundance patterns, such as the species abundance distribution (Magurran and Henderson 2003; Labra et al. 2005; Matthews and Whittaker 2015; Snell Taylor et al. 2018). As the persistence of many of these groups of species is likely to be primarily driven by stochastic factors, in comparison to the deterministic process that are likely to have a greater role in driving the distribution of core species (Magurran and Henderson 2003; Snell Taylor et al. 2018), examination of the processes driving species distributions in habitat island systems is also likely to be influenced by including these species in analyses. If noncore species distributions are governed by different processes to core species (e.g., if their probability of occurrence is unrelated or negatively related to island area), their presence in habitat island assemblages will also affect composition patterns, such as nestedness and beta-diversity (Fischer and Lindenmayer 2005a; Wethered and Lawes 2005; Matthews et al. 2019a; Freeman et al. 2018).

As well as being of theoretical interest, the issue of noncore species influencing biogeographical patterns is also of applied relevance. For example, the ISAR (and in particular the *z*-value) is often used in conservation studies of anthropogenically fragmented systems, such as for strategic conservation planning and extinction predictions (Fattorini et al. 2021). In these types of evaluations, if, for example, the observed *z*-value for a set of forest fragments in an agricultural matrix is relatively low, it may be assumed that habitat loss has only had a minimal effect in this system. However, a focus on this value alone would obscure any extirpation of forest specialists if these species have been replaced by noncore species (e.g., matrix species, habitat generalists; see Banks-Leite et al. 2012). That is, a focus on total species richness may mask the decline of habitat specialists, which are generally the species of most conservation concern (Banks-Leite et al. 2012; Matthews et al. 2014b).

One important consideration in analyses of habitat island data is whether noncore species are something to be controlled (e.g., removed from the dataset), or if in fact they actually represent a key component of the habitat island biota (e.g., via compensatory dynamics; Morante-Filho et al. 2018) that should be explicitly accounted for. It is likely that there may be different answers to this question for the different types of noncore species, and the type of habitat island, in a given study. And then, how are these species to be defined? In some cases, detailed ecological evaluations of the species in both the focal habitat and the surrounding land uses can allow accurate species classification. For example, as has been done for arthropods in native forest fragments embedded in matrices of secondary forest and agricultural land in the Azores, where species in the forests have been classified as native-nonnative (to the Azores), tourist-nontourist, and forest specialist-habitat generalist (Borges et al. 2008; Ribeiro and Borges 2010). Another possibility is to use the frequency a species is recorded in a temporal sequence of samples to classify it as, for example, transient (e.g., transient if in less than 33% of samples; Snell Taylor et al. 2018). Both of these approaches require relatively substantial amounts of data. The latter approach also suffers from the issue that low temporal occupancy and stochastic occurrences may indicate the presence of transient species, but they may also arise from other dynamic processes acting in habitat islands (e.g., biotic interactions, responses to changing environments, historical contingency).

An alternative approach to simply identifying and removing noncore species is to use empirical mechanistic and dynamic hierarchical models (e.g., Snell Taylor et al. 2020; see Lasky et al. 2017 for an island biogeography example) to directly model the dynamics of core and noncore species separately. These types of models can also include additional types of data as covariates (e.g., trait and phylogeny data, sampling information, and species interaction data). Thus, the use of such models may allow the study of core and noncore species in habitat islands to go beyond simply explaining species diversity patterns to providing a more quantitative insight into the mechanistic drivers of community structure in habitat islands. At the very least, it is clear that going forward there needs to be a greater consideration of the roles of noncore species in habitat island dynamics, and their effects on our understanding of habitat island biogeography.

and both FDARs and PDARs have been studied along land-use change gradients (e.g., Bregman et al. 2016) and at broad spatial (e.g., continental) scales (Mazel and Thuiller 2021). However, the analysis of FDARs and PDARs in habitat islands *sensu stricto* has been limited, although work has shown that habitat island area is an important driver of the functional and phylogenetic diversity of frugivorous and insectivorous birds in Amazonian forest fragments (Bregman et al. 2015).

In regard to whether different DARs are concordant or not, results are equivocal. For example, several studies have shown that the three main types of DAR (SAR, FDAR, and PDAR) can show discordant patterns (e.g., Mazel and Thuiller 2021). In contrast, a recent study of island DARs (ISARs, IFDARs, and IPDARs) of birds in three habitat island systems in Brazil found that, when species richness was accounted for, the IFDARs and IPDARs were relatively flat and had similar form (i.e., the same models provided the best fits to all three DARs; Dias et al. 2020). Thus, species richness is the primary driver of IFDARs and IPDARs, at least in these systems. However, the authors do show that the three island DARs are not entirely concordant, as species richness was found to increase at a faster rate (i.e., larger *z*-value) than both functional and phylogenetic diversity, implying an increasing number of functionally and phylogenetically redundant species with increasing area (Dias et al. 2020; see also Farneda et al. 2020 for a similar example in a countryside biogeography context). This finding has important conservation implications, as it implies that certain ecological functions may be maintained in fragmented landscapes even as species richness is reduced (Farneda et al. 2020).

To illustrate how the analysis of DARs in habitat island research can be revealing, I selected three datasets used in previous work that sampled birds in forest habitat islands (in France, Madagascar, and the U.S.) embedded within anthropogenic matrices. The original datasets all contained one island that was much larger than the rest. These were excluded (prior to model fitting) to increase the readability of the resultant plots. For each dataset, I fitted 20 models to the ISAR data (i.e., area and species richness values), including the power model, using functions in the "sars" R package (Matthews et al. 2019b). The power model was focused on in particular as it is by far the most widely used ISAR model (Triantis et al. 2012), and the *z*-value can easily be interpreted (in arithmetic space) as the rate at which the increase in diversity with area decelerates. A multimodel averaged curve was also fitted using the AIC_c weights from the different individual model fits (see Matthews et al. 2019b). Within the model-fitting functions, the "grid_start" argument was set to "partial," and no model residual checks were implemented. To calculate phylogenetic diversity, for each dataset I first took 1000 trees from Jetz et al. (2012) and pruned them such that they only contained those species present in the dataset, using the "ape" R package (Paradis et al. 2004). I then used the TreeAnnotator program (v1.10.4; Drummond and Rambaut 2007) to create a maximum clade credibility tree (node heights = median heights) for that dataset. The phylogenetic diversity (PD) of each habitat island in each dataset was calculated using this maximum clade credibility tree and the PD metric (Faith 1992). As PD increases with increasing richness, I used a null model to calculate PD standardized effect size (i.e., *z*-score) values (PD.SES). The null model (999 iterations, "phylogeny pool" in the "picante" R package; Kembel et al. 2010) randomizes the community matrix by selecting species from the pool of species occurring in the distance matrix with equal probability. For each dataset, the SES values were put on a positive scale by shifting all values by the same amount to ensure that the lowest SES value was one. This was done to aid model convergence, as some models had issues with negative response values (see also Dias et al. 2020). The 20 ISAR models (and the multimodel averaged curve) were then fitted to the IPDAR data (i.e., area and PD values) and the shifted IPDAR.SES data (i.e., area and PD.SES values).

The model fits for each dataset are plotted in Figure 2. It can be seen that the ISAR and IPDAR are relatively similar in all three cases, which is to be expected as richness and PD tend to be positively correlated. Nonetheless, the *z*-value of the power model was always higher in the ISAR compared to the IPDAR, indicating a greater rate of increase of richness with area than PD. After accounting for richness using a null model, there is an apparent lack of relationship between area and PD.SES for the French and U.S. datasets (Figures 2c, 2f), indicating that richness is the primary driver of the IPDAR in these systems, which is a similar finding to Dias et al. (2020). Interestingly, for the Madagascan dataset, the IPDAR.SES closely resembles the IPDAR (and the *z*-value of the power IPDAR.SES model is higher than the equivalent IPDAR model). Thus, in this case phylogenetic diversity increases with area even after accounting for richness. The reason for this finding is unknown, although Madagascan forests are known to contain high numbers of evolutionary unique (i.e., endemic to Madagascar) species across a broad range of lineages. If these endemics were restricted to the larger habitat islands, while the smaller islands contained primarily closely related nonendemic (and possibly noncore) generalists, this could explain these patterns. Regardless of the causes of these patterns, these examples highlight that datasets with similar ISARs can exhibit different relationships between area and PD (when richness has been accounted for). It is clear then that more research on PDARs (and FDARs) in habitat islands is sorely required.

Finally, in addition to the increasing research effort on DARs, and occurring in parallel with the increasing focus in ecology on the temporal dimension of biodiversity patterns more generally, there is growing interest in both the species–time relationship (STR)—the pattern describing how the richness of a site increases as the site is observed for longer time periods—and the species–time–area relationship (STAR; Adler et al. 2005; Song et al. 2018)—the interaction between the SAR and the STR. An evaluation of multiple STRs, including some habitat island systems, found them to be relatively consistent across systems and taxa, and best fit by power and logarithmic models, similar

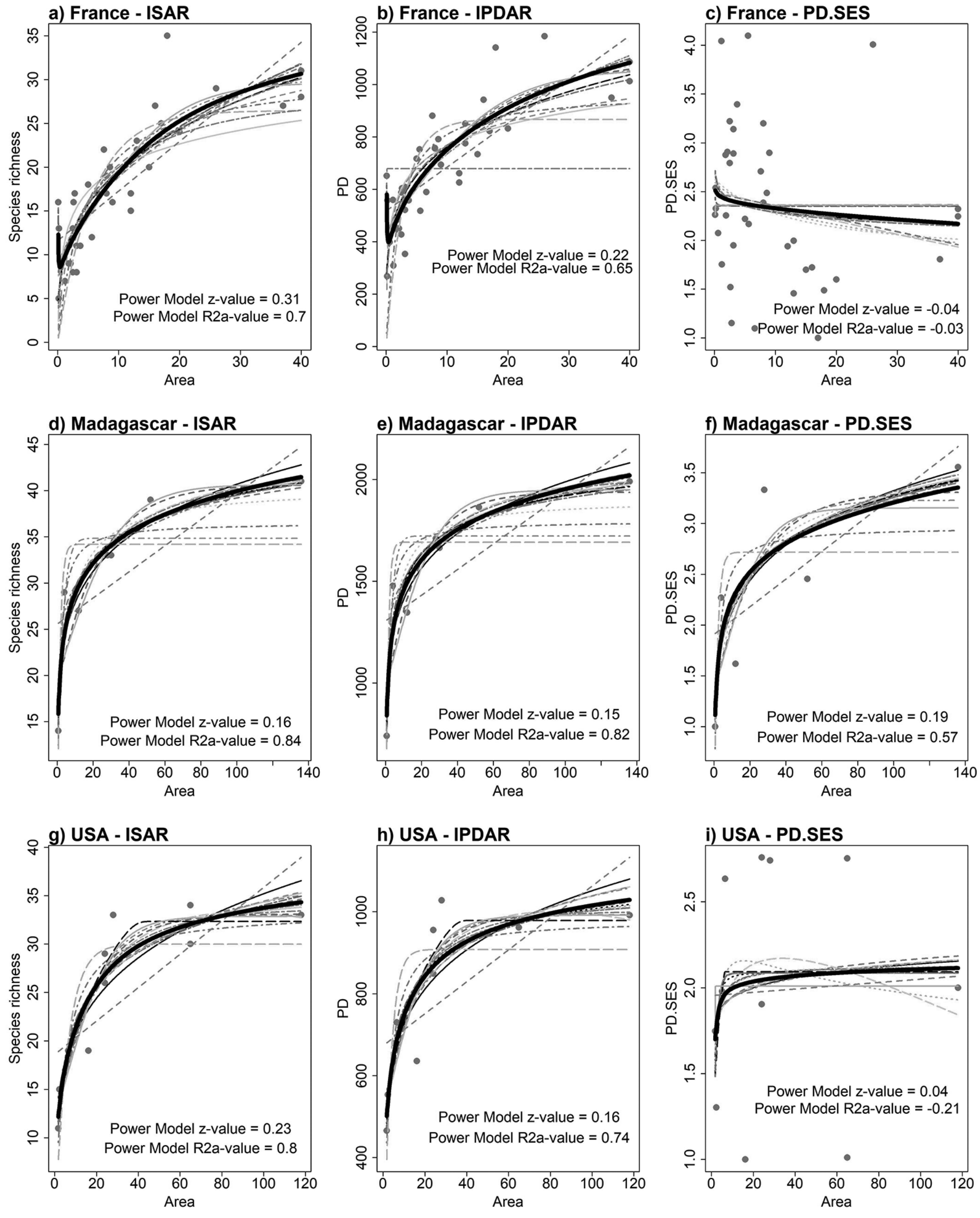

Figure 2. Diversity–Area Relationships for Three Avian Habitat Island Datasets

The three datasets are: France (39 islands, 60 species), Madagascar (7 islands, 47 species), and the United States (11 islands, 44 species). In each case, 20 SAR models were fitted (thinner lines) to ISAR (a, d, g), IPDAR (b, e, h), and IPDAR.SES (c, f, i) data (see the main text for definitions of these SAR types and variable names). The 20 models and model-fitting procedure are detailed in Matthews et al. (2019b). In each plot, a multimodel averaged curve was constructed using AIC$_c$ weights (thick line). The *z*-value and adjusted-R$_2$ of the power model fit are provided in each. See the online edition for a color version of this figure.

to SARs (White et al. 2006). However, the STRs analyzed by White et al. were constructed using a temporal sliding window approach and are thus more akin to nested SARs than ISARs. Going forward then, analyses of nonnested STRs in habitat islands, as well as further evaluations of how area and time interact to determine habitat island diversity (as has been done in some relaxation and extinction debt studies; e.g., Gibson et al. 2013), could represent fruitful avenues for future research.

INCIDENCE FUNCTIONS

Incidence function models predict spatial patterns of occupancy for single species, as a function of particular site or landscape characteristics (MacKenzie et al. 2006; Rueda et al. 2013); they are thus akin to simple species distribution models. The incidence function concept was introduced by Jared Diamond in his work on the distribution of birds in New Guinea (e.g., Diamond 1975b), and the concept has been employed in several habitat island studies since. Ilkka Hanski (e.g., Hanski 1992, 1994, 2010) took Diamond's incidence function model and adapted it for modeling metapopulation dynamics. Most of Hanski's metapopulation models can be used to calculate the probability of occupancy and the fraction of patches in a metapopulation predicted to be occupied through defining an explicit function linking extinction and colonization rates to patch area and isolation. However, although Hanski's incidence function work focused on both area and isolation, the majority of habitat island incidence function studies simply relate species occupancy to patch/island area (e.g., Watson et al. 2005) or isolation (e.g., Cottee-Jones et al. 2015) individually using, for example, a logistic regression model.

Although not a universal observation, when constructed using a logistic regression model/binomial generalized linear model, the incidence function of most species is characterized by a squashed S-shaped curve. Thus, the steepest change in the probability of occurrence occurs in the lower-middle part of the area gradient. Although the response variable represents a binomial outcome (i.e., a species is either present or absent), the regression returns a probability, which can be interpreted as the probability that a species is present on an island of a given size.

Incidence function models have been argued to represent useful conservation tools, and can be used in a number of conservation applications, including protected area design, endangered species action plans, and assessing the extinction risk of individual species (Hanski 1994; Araújo and Williams 2000; Hu et al. 2012). The general protocol employed when using incidence function models in conservation-focused studies has been to select a specific probability of presence value as the value of interest. Various values have been used ranging from 30% to 60% (van Dorp and Opdam 1987; McCoy and Mushinsky 2007; Rueda et al. 2013). However, perhaps the most commonly used probability value is 50% (0.5; e.g., Watson et al. 2005; Hanski 2010). Hanski (2010) refers to the 50% probability level as the "Critical Island Area."

The real utility of incidence functions in habitat island systems rests on the assumption that a given species' incidence function does not vary to any substantial extent across space and time (MacKenzie et al. 2006). For example, it would be no use designing a protected area network in Location B based on the results of an incidence function study of a species in Location A, if it was found that the incidence function of the same species was substantially different in Location B. A number of habitat island studies have attempted to test this stability assumption, at least implicitly, with generally negative results. For example, Watson et al. (2005) compared the incidence functions of bird species in forest fragments distributed across three matrix types in Australia: urban, peri-urban, and agricultural. Their study found that the form of the incidence functions and the Critical Island Areas varied considerably for individual species across the three matrices. For example, the brown treecreeper (*Climacteris picumnus*) had Critical Island Area values of 40 ha, 320 ha, and 410 ha in the agricultural, urban, and peri-urban landscapes, respectively. This study provides further evidence supporting the argument that matrix properties are key considerations in habitat island research. More recently, it was shown that Atlantic Forest bird species are more sensitive to forest area loss at their range edge, again implying that the effect of area on species occupancy varies spatially (Orme et al. 2019). An illustrative hypothetical example of spatial variation in habitat island incidence functions for a given species as a function of matrix type is given in Figure 3. It can be seen that, in this simulated example, the Critical Island Area varies with matrix type (increasing with decreasing matrix permeability from the point of view of the forest specialist species; Figure 3). Thus, care would need to be taken in using these curves to inform area-based conservation applications. However, as outlined above, incidence function models can include predictor variables other than area, and thus the utility of incidence functions in habitat island research could potentially be improved by including some measure of matrix permeability as an additional covariate.

To take a temporal incidence function example, Hinsley et al. (1995, 1996) observed that the incidence functions of certain bird species in U.K. forest islands varied across years (i.e., the same habitat islands sampled in different years), due partly to changes in weather/climatic conditions across the years (e.g., harsh winters).

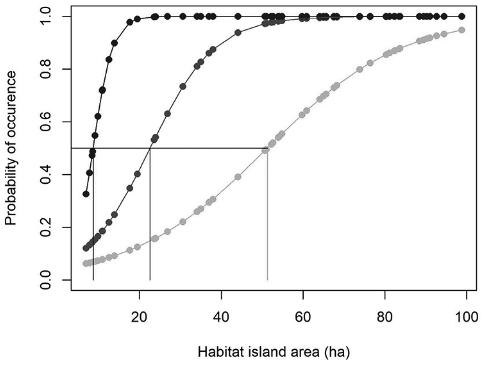

Figure 3. Incidence Functions for a Hypothetical Forest Specialist Species in Forest Fragments Embedded Within Three Different Matrix Types

The three different matrix types are secondary forest (top curve), low-intensity agriculture (middle curve), and urban land uses (bottom curve). Fifty fragments were used. The Critical Island Area value (i.e., 50% occupancy probability) is highlighted for each curve with a vertical line (top curve = 9 ha, middle curve = 23 ha, bottom curve = 51 ha). The data were simulated by varying the intercept and slope parameters of a binomial generalized linear regression model. See the online edition for a color version of this figure.

COMPOSITION PATTERNS

Evaluation of compositional patterns (i.e., species composition on islands) has been a major focus of island biogeography (Whittaker and Fernández-Palacios 2007). One primary compositional pattern of interest is that of nestedness. Assemblages are nested when the species found in species-poor sites represent subsets of those species found in species-rich sites (Patterson and Atmar 1986). Various mechanisms have been proposed to explain nestedness in island systems, including area-dependent extinction, isolation-dependent colonization, and nested habitats (Ulrich et al. 2009; Matthews et al. 2015a). Nestedness is an important consideration in conservation biogeography and protected area design (Fischer and Lindenmayer 2005a,b); perfect nestedness would mean all species in a habitat island system could be protected by simply designating the largest island as a protected area. However, it is important to remember that perfect nestedness (i.e., the largest island contains all species in a set of islands) and significant nestedness (i.e., systems significantly more nested than expected by chance) are different concepts (Fischer and Lindenmayer 2005a). Even if a system is significantly nested, it may still need a large number of islands to be included in a set of protected areas to cover all species (Fischer and Lindenmayer 2005a; Matthews et al. 2015a).

Although the majority of nestedness studies have been undertaken in true island systems (e.g., Dennis et al. 2012; see Whittaker and Fernández-Palacios 2007 for a review), nestedness has been found in a variety of habitat island systems, such as bird communities in: Afromontane forest patches embedded within grasslands in South Africa (Wethered and Lawes 2005); urban forests in China (Wang et al. 2013); and Australian forest fragments (Fischer and Lindenmayer 2005b). A meta-analysis of nestedness in habitat islands found significant nestedness to be almost universal (Watling and Donnelly 2006), and area-dependent extinction to be the most likely driver. A more recent meta-analysis using a more conservative nestedness metric based on overlap and decreasing fill (NODF; Almeida-Neto et al. 2008) and null model procedure, found significant nestedness only characterized 9% of 97 habitat island systems evaluated (Matthews et al. 2015a). Indeed, there was a greater prevalence (16%) of antinestedness (i.e., systems significantly less nested than expected by chance; Matthews et al. 2015a).

Based on these recent results (Matthews et al. 2015a), it appears that nestedness is not that common a phenomenon in habitat islands; this observation provides support to recent studies that have argued for the importance of small patches and natural features in biodiversity conservation (Fischer and Lindenmayer 2002; Tulloch et al. 2016; Kendal et al. 2017). The lack of nestedness in habitat islands is perhaps not that surprising when we consider the effect of source-sink dynamics and the high prevalence of noncore species in many habitat island systems (see Box 2). The presence of these species, whose distributions are more stochastic in nature due to source-sink dynamics and mass effects, will act to reduce nestedness (e.g., Freeman et al. 2018; see Figure 4 for an example). Put another way, I would predict that, in general, nestedness should be stronger for core species in comparison to noncore species; although that is not to say that I believe that all habitat island systems (when focusing on the core species only) will be significantly and/or highly nested. That being said, a recent study of nestedness in insects in a fragmented forest within a grassland matrix in Brazil found that generalist species actually contributed *more* to the observed nestedness pattern than specialists (Neves et al. 2020). However, this could partly be due to the authors combining two habitats (forest islands and the grassland mosaic) together into a single metacommunity. In this design, it would make sense that the specialist species, which would likely only be found in one of the two, would not contribute as much to nestedness at the combined habitat scale.

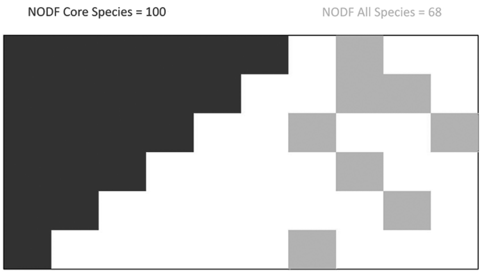

Figure 4. The Theoretical Effect of Noncore Species on Nestedness Patterns

The data here are simulated but can be seen to represent the distribution of species (of a given taxon, columns) in a set of six patches (rows) of natural habitat. The sites are ordered by decreasing area (i.e., the largest patch corresponds to the top row). In this presence-absence matrix, the core species (cells in the solid block on the left, number of species = 6) are perfectly nested by patch area (NODF = 100), while the noncore species (disjointed cells on the right, number of species = 4) are stochastically distributed (i.e., independently of patch area), which acts to reduce the nestedness of the matrix (NODF = 68). The noncore species can be seen as species adapted to the matrix habitat surrounding the patches and are only present in patches in small numbers because of source-sink type dynamics. See the online edition for a color version of this figure.

As with diversity–area relationships and incidence functions, it is likely that matrix effects (e.g., matrix type, contrast, permeability) also influence the prevalence of nestedness (Wethered and Lawes 2005). First, through the influence of the matrix on the supply of noncore species to habitat islands. Second, through the role of the matrix in supplementing resources and habitat. For example, a highly permeable matrix that contains plentiful resources that habitat island species can utilize will likely reduce nestedness by reducing the importance of area-dependent extinction and isolation-dependent colonization. In contrast, a high-contrast matrix may increase nestedness (for core species at least) by increasing the importance of area-dependent extinction. Based on these ideas, we might predict that nestedness will be more prevalent in higher contrast (*sensu* Watson 2002) habitat island systems. Historical factors, such as land-use history and human disturbance regimes (e.g., hunting, forestry) may also act to reduce the nestedness of habitat island systems (Kendal et al. 2017) by reducing the importance of specific variables (e.g., area, isolation) in driving habitat island composition.

As with diversity–area relationships, the study of nestedness in habitat islands has recently been extended to other types of diversity, leading to the evaluation of functional and phylogenetic nestedness. For example, Matthews et al. (2015b) undertook the first comprehensive analysis of functional nestedness using 18 bird-habitat island studies and found that many bird-habitat island communities are significantly functionally nested, although results were sensitive to the choice of null model. More recently, Almeida-Gomes et al. (2019) reported significant functional nestedness of anuran communities in Atlantic Forest fragments. Interestingly, this study found that although all species and habitat specialists were significantly functionally nested, habitat generalists did not exhibit significant functional nestedness (Almeida-Gomes et al. 2019). This finding aligns with the arguments presented above for standard taxonomic nestedness (see also Box 2) that the presence of noncore species (e.g., transients, vagrants, generalists) acts to reduce nestedness in habitat islands.

Other composition patterns of interest in habitat islands include the study of between-island beta-diversity (i.e., differences in the composition of habitat island communities; Anderson et al. 2011), and the degree to which the composition of habitat island and matrix communities differ (i.e., between-habitat beta-diversity; Nowakowski et al. 2018; Frishkoff et al. 2019). One particular hypothesis of interest is that, in anthropogenically fragmented systems, the loss of habitat specialist species and the increase in prevalence of generalist species through time following a fragmentation event will result in increased biotic homogenization (i.e., a reduction in between-habitat beta-diversity).

ABUNDANCE PATTERNS

Although the majority of habitat island biogeography studies have focused on species incidence/presence-absence data, there has been some work done on abundance patterns in habitat islands and, in particular, the species abundance distribution (SAD). The SAD describes how the total number of individuals sampled within a given community is distributed among the sampled species (McGill 2011). In regard to habitat islands and the SAD, most work has focused on SADs in anthropogenically fragmented systems. For example, in a comparative countryside biogeography study of neotropical bats in forest fragments embedded within agricultural land and true islands within a lake, Mendenhall et al. (2014a) found that the forest fragment communities were more even than the true island communities, a finding they attribute to the resources present in the arable matrix (that are not present in the aquatic matrix) that support many species in the fragments. Freeman et al. (2018) also found that bird communities in South African forest fragments were less even in high-contrast anthropogenic matrices compared to low-contrast natural matrices, and that in both cases evenness decreased with increasing habitat island area. Community evenness has also been shown to vary as a function of island area in other studies; for example, a recent study of 123 habitat fragment datasets found that abundance across species is less even in smaller compared to larger fragments (Chase et al. 2020).

Anthropogenic fragmented habitat island systems can be viewed as being in a disturbed state, and thus a theoretical expectation is that SADs will shift from lognormal-like SAD shapes (SADs with relatively few very abundant or very rare species) in the prefragmented habitat to logseries-like SAD shapes (SADs with a high proportion of very rare species) in the disturbed/fragmented habitat islands. This expectation is based on the idea that lognormal SADs characterize undisturbed "equilibrium" communities, while logseries SADs are characteristic of disturbed communities (May 1975; Gray 1979). However, the utility of this simple dichotomy has been questioned (see Matthews and Whittaker 2015), and other authors have in fact argued the opposite, i.e., that SADs shift from logseries to lognormal shapes following disturbance (e.g., Newman et al. 2020).

Few studies have tested the idea that SADs undergo systematic shifts in form following fragmentation events, likely due to a lack of suitable before-and-after relative abundance data in fragmented landscapes. An exception is Mac Nally (2007), who studied the relative abundance of birds in highly fragmented landscapes in Australia, and found little evidence of the systematic changes through time outlined above, although the abundance of some individual species did shift considerably, particularly in the smaller fragments.

Perhaps not surprisingly, given the above discussions on diversity–area relationships and nestedness, SADs in habitat islands have also been argued to be affected by the presence of noncore species. For example, Matthews et al. (2017b) showed that, for arthropods in native forest fragments on the Azores, fragment isolation was a primary driver of SAD shape. Increasing isolation resulted in a shift from lognormal-like SAD shapes to logseries-like SAD shapes. One potential explanation for this finding provided by the authors is that the most isolated fragments, which are isolated by matrices of human land uses (e.g., pastureland), have a higher proportion of tourist species adapted to the surrounding anthropogenic land uses. These tourist species will be present in low numbers in a fragment, elevating the number of rare species (Matthews et al. 2017b). To take another example, it has become increasingly apparent that many SADs may in fact be multimodal, that is, characterized by multiple distinct modes (Dornelas and Connolly 2008; Antão et al. 2017). One potential mechanism underpinning multimodal SADs is the amalgamation of multiple different groups of species within samples, such as native and invasive species, specialists and generalists, and core and satellite species (Magurran and Henderson 2003; Labra et al. 2005; Antão et al. 2017). Future work investigating whether the presence of noncore species (e.g., tourists, generalists) in habitat island assemblages is a cause of SAD multimodality is warranted. An example of how the presence of noncore species in a sample could affect the shape, and thus subsequent interpretation, of SADs is provided in Figure 5.

The Weibull distribution has recently been proposed as a SAD model that provides a measure of the proportion of core species in a community (Ulrich et al. 2020), and thus the application of this model in habitat island datasets will likely provide additional insight into the effect of noncore species on habitat island SADs. More generally, further work on SADs in habitat islands (particularly naturally fragmented systems) is sorely needed; in particular, evaluation of how SADs vary across islands within a habitat island system (e.g., as a function of area), and then across systems (e.g., as a function of matrix type).

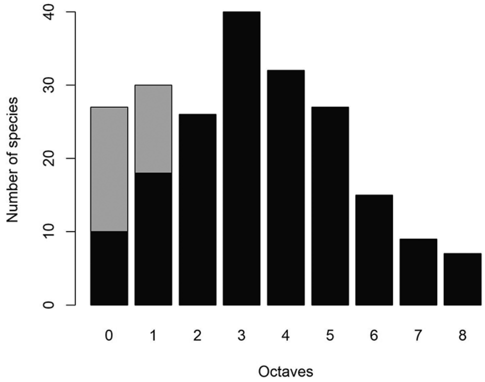

FIGURE 5. THE THEORETICAL EFFECT OF NONCORE SPECIES ON THE SPECIES ABUNDANCE DISTRIBUTION (SAD)

The data here are simulated but can be seen to represent a sample of a given taxon in a patch of natural habitat. In this sample, the core species (darker bars, number of species = 184) roughly follow a classic lognormal SAD, while the noncore species (lighter bars, number of species = 29) are only present in the sample in low numbers and are represented in the first two octaves. The simulated abundance data are binned into octaves: the first octave contains the number of species represented by one individual, the second octave contains the number of species with two to three individuals, and so on.

In addition to the SAD, several habitat island studies have also focused on other types of abundance patterns, such as how the abundance of individual species can differ considerably in smaller compared to larger fragments within the same system. For example, in a study of plant succession dynamics in experimental fragments of different sizes, Collins et al. (2009) observed that for the majority of early successional species analyzed, the decline in abundance through time as succession proceeded was slower in larger compared to smaller fragments, although for some species the opposite pattern emerged. Thus, species did not respond in a consistent manner to habitat insularity in terms of their abundance. More recently, in a study of 123 habitat fragment datasets where species abundance data were available, it was found that, after accounting for sampling effort, the density of individuals was lower in smaller compared to larger fragments (Chase et al. 2020). However, a countryside biogeography study of birds in different habitat types in a landscape in Costa Rica found that the populations of more bird species, particularly insectivores, were decreasing in a large fragment compared to a number of small fragments, likely due to the fact that the most sensitive species have already been lost from the smaller fragments (Şekercioğlu et al. 2019).

Conclusions and Directions for Future Research

As a first step, it is important to consider whether the habitat island concept is still operational, that is, whether the concept of a patch of habitat surrounded by a matrix of contrasting land-use/habitat types is a valid conceptual model. The various proposed frameworks based on continuum models would suggest otherwise. However, reviewing the literature indicates that a large number of authors are still interested in viewing patchy systems in this way. In addition, based on the results of many of the studies that have used this island-matrix model, it does appear that this conceptual model often provides a reasonable representation of habitat islands, as long as the ways in which the matrix acts to control dynamics within the patches themselves is taken into account. That being said, it is important to acknowledge that the habitat island concept is not relevant to all patchy systems. As such, in certain cases it may be more appropriate to adopt a continuum approach (e.g., Pulsford et al. 2017) or to view landscapes as containing a mosaic of different habitat/land-use types (e.g., in a similar way to many countryside biogeography studies) rather than necessarily focusing on one specific habitat/land-use type as the unit of interest.

Going forward then, and based on the material reviewed above, I would argue that there are two main points that future habitat island research (in both natural and anthropogenic systems) should consider. First, the effect of the matrix. The matrix determines habitat island isolation and effective island area, and thus the key island biogeography processes of colonization and extinction, and also acts to determine the severity of many edge effects, which are important processes in many habitat island systems (Laurance 2008). The matrix is the primary distinguishing feature between habitat and true islands. Although the degree of matrix contrast is a constant in true island studies and thus matrix effects can be largely factored out (with the exception of changing water levels and differences in ocean productivity affecting marine subsidies; Anderson and Wait 2001; Fernández-Palacios et al. 2016), it is arguably impossible to fully understand habitat island dynamics, including the key processes of colonization and extinction, without explicit consideration of the matrix. This is not a novel observation and, for example, forms a central component of several landscape theoretical frameworks, such as countryside biogeography and the matrix tolerance and quality models (Frishkoff et al. 2019). However, there is still considerable scope for habitat island research to better account for matrix characteristics and, in particular, the dynamic nature of the matrix in both space and time. In most habitat island systems, the surrounding matrix is not uniform, but exhibits spatial variation (i.e., it comprises a patchwork of multiple habitat types). Studies have started to explore how this spatial variation affects habitat island dynamics (e.g., interisland dispersal, rescue effects, resource provision, disturbance), but further research is warranted. Equally, the dynamic temporal nature of the matrix (i.e., changes to matrix characteristics through time) is also an important consideration that is often overlooked (Driscoll et al. 2013; Wolfe et al. 2015).

One potentially fruitful area of research is adapting true island research frameworks to account for matrix effects. The adaption of common island species–area relationship models to account for factors such as matrix and edge effects (see Table 1) is one example. It has also been shown that species occupancies in habitat islands (i.e., a form of incidence function) can be more accurately modeled using the classic ETIB variables of island area and isolation if matrix permeability is explicitly accounted for in the metric used to characterize island isolation (Brodie and Newmark 2019). This can be achieved with empirical data and/or detailed simulations to construct landscape matrix permeability/resistance surfaces (e.g., Evans et al. 2017) or parameterize graph theoretic approaches and dispersal-based models. Further empirical and simulation work on dispersal between habitat islands as a function of matrix resistance will likely prove rewarding (e.g., Evans et al. 2017; Diniz et al. 2020).

Second, and linked to matrix effects, the effect of noncore species on habitat island diversity dynamics. The extent to which noncore species will alter biodiversity patterns in a given habitat island system will vary according to the habitat island type and the properties of the surrounding matrix (e.g., matrix contrast, human activities within the matrix). A minimum consideration for future habitat island research then is greater acknowledgement that habitat island species assemblages contain these different types of species and consideration of the implications of this on any results. As the extinction and colonization rates of noncore species will often be related to island and landscape characteristics in different ways to core species, coupled with noncore species occupancy patterns being more governed by stochastic processes, failing to account for noncore species in habitat island analyses could affect results. If suitable data are available, it is possible to directly classify core and noncore species (e.g., Borges et al. 2008) and then a decision taken on whether to remove noncore species prior to analysis or to explicitly model the different dynamics of core and noncore species within a single analytical framework (e.g., Ewers and Didham 2007). In regard to the latter, a number of models developed in the field of countryside biogeography (e.g., the countryside SAR; Table 1) account for differential habitat use by different species. There have also been substantial advances made in hierarchical modeling in ecology and biogeography in recent years. The further application of these techniques to habitat island systems, enabling the dynamics of species to be modeled individually, will likely prove rewarding. Species-centric approaches based on the use of continuum models where each species responds individualistically to a gradient in habitat suitability may also be useful in some cases for understanding the dynamics of different types of species in patchy landscapes.

The integration of noncore species dynamics could also be achieved through a greater application of the metacommunity framework to habitat island datasets. Through its central focus on dispersal and explicit consideration of mass effects (e.g., through the mass effects "archetype" of community assembly; see Leibold and Chase 2018), metacommunity theory enables the processes driving core and noncore species to be separated. For example, in terms of dispersal, it is likely that dispersal limitation (i.e., species are not present in islands where the habitat is suitable) and dispersal sufficiency (i.e., most species are present in islands where the habitat is suitable) will be useful concepts for understanding the distributions of core species across a set of habitat islands, whereas dispersal surplus (i.e., leading to source-sink dynamics) will be more useful with respect to noncore species (see Leibold and Chase 2018:7–8). Equally, the mass-effects framework will likely be useful for studying noncore species, whereas perhaps the species-sorting and patch dynamics models will be more applicable to the core species (Leibold et al. 2004). One promising research avenue will be to adapt common metacommunity theoretical approaches to better incorporate spatially and temporally heterogeneous matrix characteristics. Much of the above discussion has focused on studying the role of habitat islands as sink habitat for matrix species; however, the question of to what extent matrix habitats represent sinks to habitat island specialists is also of interest, particularly in cases where the islands represent remaining natural habitat, and the matrix comprises human land uses (Frishkoff et al. 2019).

Another fruitful future research avenue will be to analyze the core species in anthropogenically fragmented habitat islands through the lens of the extinction filter hypothesis. The extinction filter hypothesis predicts that disturbance resilience will be higher for species that have evolved in regions characterized by frequent disturbance (e.g., fires, glaciation) and vice versa (e.g., Balmford 1996). A recent study of 73 forest datasets across the world found strong support for the hypothesis (Betts et al. 2019) in relation to forest fragmentation sensitivity. However, there is scope for extending this work to other anthropogenic habitat island systems (e.g., grassland fragments) and locations. A further hypothesis from the study of Betts et al. (2019) relevant to ideas discussed here is that the proportion of core species within anthropogenic habitat islands (perhaps all habitat island systems?) will be greater in areas that have not experienced broadscale historical disturbances. Repeated glaciation coupled with a longer history of land-use change is predicted to have resulted in lower proportions of core species in anthropogenic habitat islands in places such as Europe and eastern North America. Future tests of this prediction, perhaps using the many habitat island datasets that have already been published, will be revealing.

In summary, by combining a more in-depth analytical and conceptual consideration of matrix properties with a greater focus on the role and analysis of noncore species, the future analysis of habitat island data based on the arguments outlined here will allow us to better understand the assembly processes governing diversity in this broad range of systems.

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