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The unifying, fundamental principles of biogeography: understanding *Island Life**

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Abstract. I describe the set of fundamental principles of biogeography that can serve as an integrative, conceptual framework for unifying and advancing our abilities to explain the geography of life – generally. I assert that patterns of variation of biotas among regions and across geographic gradients result from the very regular patterns of variation in environmental conditions across the geographic template. This happens through the influence of that variation on the fundamental biogeographic processes (immigration, extinction and evolution), the influence of those fundamental processes on each other, and ecological feedback in the form of interspecific interactions, which influence the fundamental capacities of other species to immigrate, survive and evolve. I then summarize principal patterns and current theory in island biogeography within the context of the fundamental, unifying principles and show how they can inform a more integrative, conceptual framework for explaining a genuinely comprehensive set of ecological and evolutionary phenomena for insular biotas.

Keywords. Biogeography, ecology, evolution, extinction, immigration, island syndrome, islands

Introduction

Among the most intriguing and insightful patterns in diversity and geography of nature are those exhibited by insular biotas (Hooker 1866, Wallace 1880, Carlquist 1974, Whittaker and Fernández-Palacios 2007, Gillespie and Clague 2009, Lomolino et al. 2010). Although island biogeography is sometimes narrowly interpreted as primarily focused on patterns in species richness, it encompasses a much broader and marvelous variety of phenomena. This includes species whose populations exhibit niches that expand and densities that increase far beyond those of their mainland conspecifics. It includes the evolutionary marvels and perils of island life, such as tree-sized stature and secondary woodiness in descendants of herbaceous plants, highly atypical and super-generalist pollinators and seed dispersers that take over the services of their many absent competitors (sometimes from entirely different taxonomic classes), flightless insects and birds, giant rodents and dwarfed elephants, and many hundreds of other insular endemics that became so ecologically naïve as to perish under what Darwin described as “the strangers craft of power” (i.e., the often devastating effects of non-native species, includ-

ing humans; Darwin 1860, Chapter 17, *Galapagos Archipelago*). See Table 1 for definition of glossary terms, set in blue type (including ecological naïveté, which explains the usage of the word ‘naïve’ herein). Understandably, these insular phenomena have captivated biogeographers, ecologists and evolutionary biologists throughout the history of these disciplines, and have generated a great wealth of causal explanations – often with a number of alternative and fundamentally distinct hypotheses for each pattern.

This body of theory has grown to become a burgeoning collection of what may appear to many as disarticulated, if not idiosyncratic, explanations, reminiscent of Lawton’s (1999) lament over the “mess” of theory in community ecology (but see Vellend 2010 for an important conceptual synthesis of community ecology; see also Lomolino and Brown 2009, Scheiner 2010). Yet it is likely that the marvels and perils of island life may all ultimately derive from some very general ecological and evolutionary processes and how features of insular environments influence those processes. One of the most promising approaches to unifying island biogeography theory and providing some truly transformative insights into the geog-

*The reference here to *Island Life* is an homage to one of Alfred Russel Wallace’s seminal contributions on insular faunas and floras (Wallace, 1880).

raphy of nature, in general, is a genuinely integrative approach – one based on four fundamental principles of biogeography. Each of these principles was evident early in the historical development of the discipline, but seldom if ever have they all been utilized to gain a genuinely holistic understanding of ‘island life’ (sensu Wallace 1880). Because these principles address processes and phenomena that are interrelated, theory based on anything less than the full complement of these four principles is liable to provide an incomplete and possibly misleading explanation for the geography of nature.

My first purpose here is, thus, to describe the set of fundamental principles that can serve as an integrative, conceptual framework for unifying and advancing biogeography. After providing a detailed description of the fundamental biogeographic principles and their integral processes, I then describe the interdependence among those processes, how they are influenced by interspecific interactions, and how they are likely to vary among functionally distinct biotas. I then summarize the principal set of patterns and current theory in island biogeography within the context of the fundamental, unifying principles to show how they can inform a more integrative, conceptual framework for explaining a genuinely comprehensive set of ecological and evolutionary phenomena for insular biotas.

The fundamental, unifying principles of biogeography

General statement: Patterns of variation of biotas among regions and across geographic gradients result from the very regular patterns of variation in environmental conditions across the geographic template, the influence of that variation on the fundamental biogeographic processes (immigration, extinction and evolution), the influence of those fundamental processes on each other, and system feedback in the form of ecological interactions, which influence the fundamental capacities of other species to immigrate, survive and evolve. It thus follows that integral to a comprehensive understanding of the geography of nature are four unifying principles, describing 1)

the nature of the geographic template, 2) the fundamental processes influencing all biogeographic patterns, 3) the interdependence among those processes, and 4) how they are influenced by interspecific interactions (i.e., ecological feedback). Below I explain each of these fundamental principles and present an integrative, conceptual model describing their influence on patterns in the geography of nature (Figure 1).

1. The geographic template: Environmental factors vary in a highly non-random manner across the globe and over time, with the characteristics of local environments tending to be more similar for those that are closer in space and in time (Tobler’s first law of geography; Tobler 1970; see glossary entries for spatial and temporal autocorrelation). In addition, most environmental conditions exhibit very regular patterns of variation and covariation along geographic gradients – patterns that combine to form the template and foundations for all patterns in the geography of nature. Also requisite to a comprehensive understanding of biogeography is the knowledge that, just as species and lineages have histories, so do places. Thus, the physiographic and environmental characteristics of place (from local environments and ecosystems to entire ocean basins and continents) are, barring cataclysmic events, assumed to undergo very regular and predictable progressions over their historical development, with the characteristics and dynamics of each time period strongly influencing those of the next. Examples include the dynamics of mountains from early uplift to the final stages of erosion, the expansion and retreat of ecosystems in the higher latitudes with the climatic cycles of the Pleistocene, and the geological ontogeny of oceanic islands from when they first emerge to their geological maturation and eventual submergence beneath the ocean’s surface (see Whittaker et al. 2007, 2008, 2010).
2. Fundamental biogeographic processes: Despite the tremendous diversity in physical and biological processes influencing living organisms, their ultimate influence on the geography of

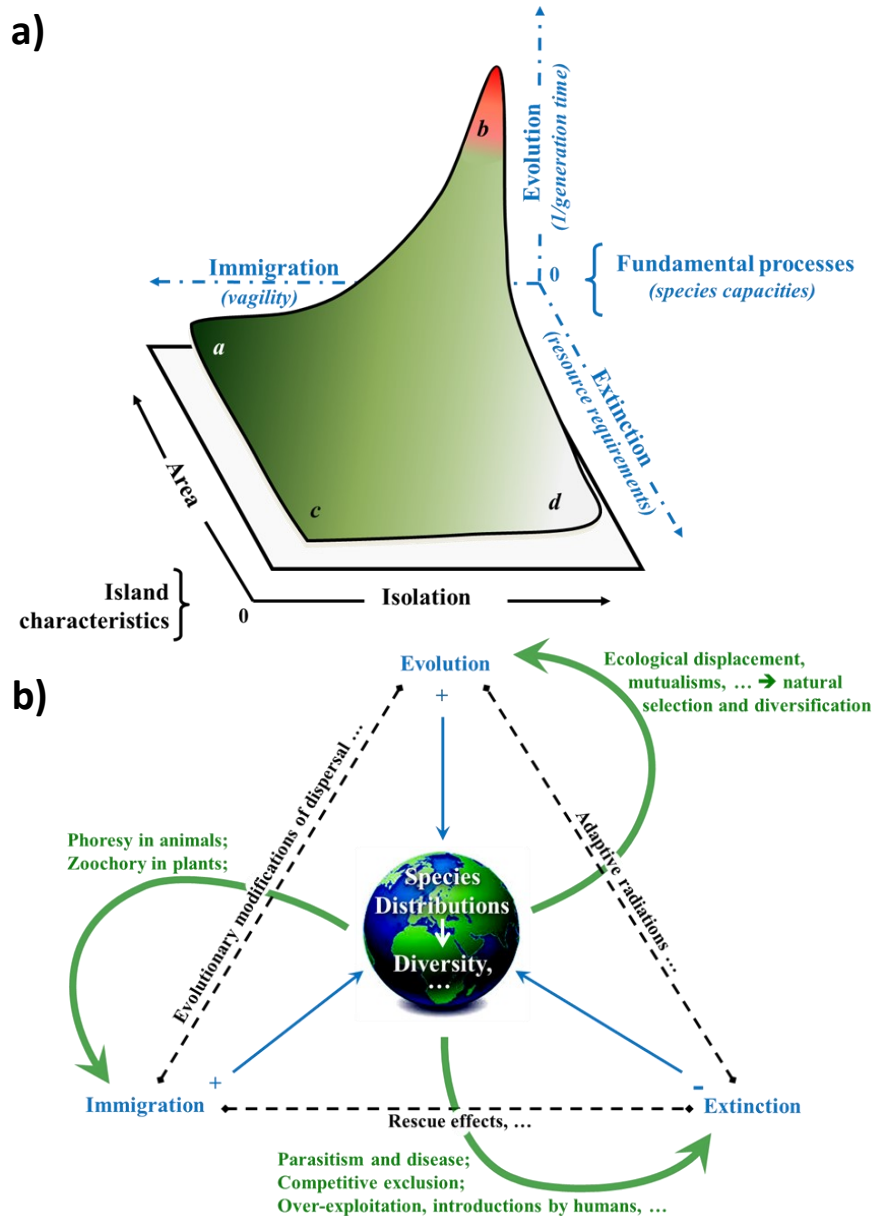


Figure 1. (a) A tripartite (three process) model of island biogeography illustrating the influence of the principal physiographic properties of islands (area and isolation, in black) on the three fundamental biogeographic processes – immigration, extinction and evolution (in blue; fundamental traits or capacities of the species in parentheses). Immigration rates should increase with proximity to a source region and, equivalently, with immigration powers of the focal species. Extinction rates should decrease as island area increases, or increase with increasing resource requirements of the focal species. Evolution (in situ speciation and phylogenesis – sensu Heaney 2000) should be most important where extinction and immigration are lowest and, therefore, increase with island area and isolation, but decrease with generation time and other traits associated with slowly evolving species. Green shading indicates the relative levels of species richness, red indicates areas of high endemism. Community characteristics of islands within the four labelled regions of the shaded surface should be as follows: a) moderate to relatively high richness, low endemism and low species turnover; b) moderate to relatively high richness, high endemism and low turnover; c) moderate to low richness, low endemism and high turnover; and d) depauperate islands. Not shown here are target area effects, rescue effects or the effects of a third principal property of islands, age, which influences the accumulation of species (through immigration and in situ speciation) and also influences island area throughout the geological development of islands (see Figure 5; see also descriptions of the general dynamic model of Whittaker et al. 2008).

(b) A general, conceptual model of the fundamental processes (blue type and arrows) affecting distributions and, in turn, the composition and diversity of regional to global biotas (plus and minus signs signify the qualitative effects on diversity); interdependence of those processes (black type and dashed lines); and ecological feedback in the form of interspecific interactions which influence the capacities of other species to immigrate, survive and evolve (green type and curved green arrows).

nature is through their effects on the abilities of species to expand their ranges by immigration, to establish and maintain populations within their range (or suffer extinction), and to evolve and diversify over time (Figure 1b). Species' distributions, in turn, overlap to create derivative patterns in community structure, including differences in species composition among regions (Buffon's Law; beta diversity), patterns in endemism, disharmony, community similarity, convergence and nestedness among communities, and gradients in species richness over space and time. The very general nature of this geographic variation among populations, species and entire biotas derives from two sets of properties: (1) the very general and pervasive patterns of environmental variation across the geographic template, discussed above, and (2) the equally consistent influences of the characteristics of place on the fundamental biogeographic processes. The nature and influence of each of the fundamental processes varies, not just with the characteristics of place, but also with the traits of the species and taxa. Therefore, the fundamental capacities of species to immigrate to and survive and evolve in particular types of systems are also likely to exhibit predictable patterns of variation with the fundamental properties of organisms (e.g., with their growth forms, baupläne, body sizes, generation times, metabolic rates or principal biochemical pathways). They are also likely to exhibit predictable patterns of covariation.

3. Interdependence between processes: The fundamental biogeographic processes often interact with each other to influence species' distributions and derivative patterns in community structure among regions and communities, and along geographic gradients (Figure 1b). For example, one of the premises of metapopulation theory is that population persistence (or its converse, extinction) is influenced by immigration such that populations that frequently receive immigrants may be 'rescued' before their numbers dwindle below some critical extinction threshold (i.e., the rescue effect of Brown

and Kodric-Brown 1977; see also Gilpin and Soulé 1986, Hanski and Gaggiotti 2008). Moreover, most (if not all) traits that influence the capacities of species to survive in, or immigrate to, particular regions are strongly influenced by natural selection and, thus, by evolution. Some of the most remarkable examples include adaptive radiations (which increase likelihood of survival, i.e., reduce extinction probabilities) and the evolution of flight in some lineages and, conversely, the loss of flight and other mechanisms for dispersal and immigration in others (in particular, those inhabiting isolated, species-poor and ecologically disharmonic islands; see discussions on these phenomena in Whittaker and Fernández-Palacios 2007, Gillespie and Clague 2009, Lomolino et al. 2010).

4. Species' interactions and ecological feedback: Most, if not all, natural systems are influenced by feedback, where the dynamics in the properties being modeled influence the fundamental processes driving the system. In biogeography, the 'properties' we are modeling are distributions of species, and we know species interact with each other to either enhance or inhibit the fundamental capacities of others (Figure 1b, green curved arrows and type). For example, the abilities of many species to immigrate to islands and other isolated ecosystems is often dependent on interspecific interactions, in particular phoresy (small animals being dispersed by larger ones) and zoochory (animals carrying plants). Furthermore, species' interactions are integral to natural selection, thus driving diversification in nearly all traits influencing a species' capacities for immigration, survival and evolution (see Pfennig and Pfennig 2012). Thus, adaptive radiation can well be viewed as a process of positive, autocatalytic feedback, with each increase in diversity intensifying ecological displacement and, thus, promoting further diversification of descendent lineages. Perhaps paradoxically, the strongest evidence for the fundamental importance of ecological feedback comes from systems where it is least important. That is, species-poor systems such as those of verte-

brates on many isolated and highly disharmonic ('unbalanced') islands can serve as natural controls for the effects of ecological interactions. In such species-poor systems, the few endemics often lose or wane in those traits that allowed their mainland ancestors to survive in the face of intense ecological interactions – they lose or become highly diminished in their powers to disperse and they become ecologically naïve (losing the spines, chemicals, and suite of behaviors required to detect, avoid or ward off mainland competitors and predators; see Gillespie and Clague 2007, Whittaker and Fernández-Palacios 2007, Lomolino et al. 2010).

Not only should theories in biogeography be based on these four unifying principles and their associated, conceptual models such as that of Figure 1b, but they should be contextual with regard to both the history of place and the history of species. Given the importance of ecological feedback, as discussed above, the dynamics and effects of the fundamental biogeographic processes depend on which species are and were present in the focal system. For this reason and, equally important, because we are interested in understanding a broad diversity of patterns including those in species composition, an implicit but essential tenet of the unifying, fundamental principles is that species be treated as non-equivalent (cf., Hubbell's [2001, 2010] neutral model of biodiversity). This requisite feature for advancing biogeography theory – that it be species-based – not only enhances the inferential power of this body of theory (in particular, its ability to explain patterns in species composition and the evolutionary marvels of island life), but it also identifies some especially insightful yet largely overlooked lines of research on patterns of variation and covariation in the fundamental capacities of species.

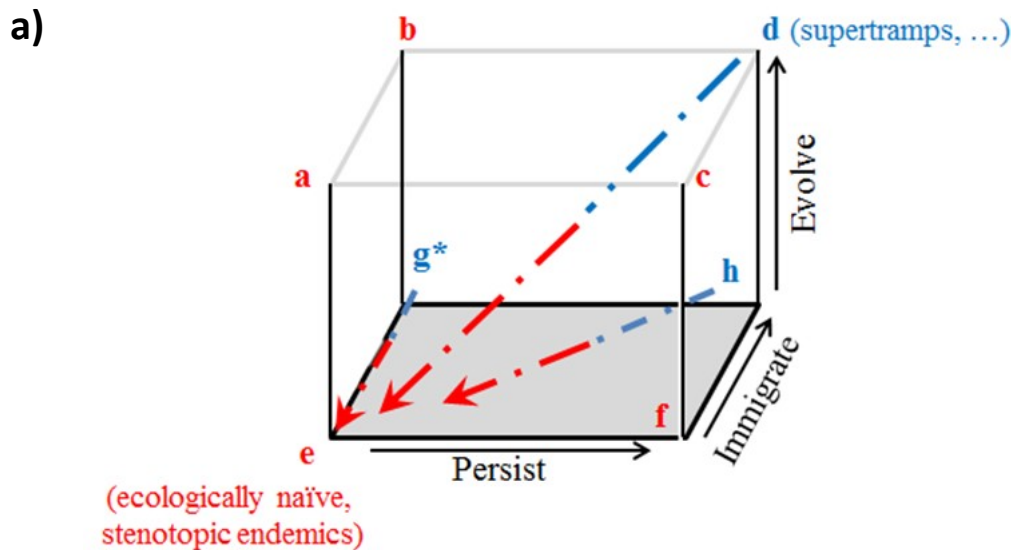
Covariation and evolutionary dynamics in fundamental capacities of insular biotas

In addition to its assertion that the fundamental biogeographic processes and capacities of species are influenced by ecological interactions, Principle 4 also implies that knowledge of the abilities of

one species to dominate others in ecological interactions (as a superior competitor, a predator or a parasite) is also integral to a unifying theory of biogeography. Here I utilize the fundamental principles of biogeography and the conceptual model of Figure 1b to explore likely patterns of covariation in the fundamental capacities of species assemblages and the expected dynamics in these capacities over the evolutionary history of insular lineages (i.e., from founding of insular populations through subsequent changes such as those described in Wilson's [1959, 1961] taxon cycles of insular biotas).

Species with limited immigration abilities are, in the absence of human intervention, unlikely to inhabit isolated, oceanic islands (species types **a**, **c**, **e** and **f** of Figure 2). In addition, under the reasonable scenario that the ability to evolve on isolated islands requires relatively long persistence on those islands, marked propensity for evolution but limited capacity to persist on oceanic islands is an unlikely combination; species type **b**). On the other hand, species that combine high capacities for immigration with relatively low resource requirements and propensities for rapid evolution in isolation (species type **d**), may be characteristic of isolated, oceanic islands (this includes Diamond's [1974, 1975] supertramps – powerful dispersers but poor competitors). Very large and resource-intensive vertebrates with high immigration capacities, such as elephants and tortoises, may also colonize and persist on isolated islands if those islands are also relatively large (species type **g**).

The model of Figure 2 provides a means of conceptualizing likely transformations in fundamental capacities of insular biotas during the taxon cycle (Wilson 1959, 1961). For example, the progression of fundamental capacities following initial colonization of isolated islands by the more powerful immigrants (species types **d**, **g** and **h**) is likely to be one of convergence on the highly stenotopic and dispersal-limited endemics characteristic of the final stages of Wilson's taxon cycle (represented by dashed arrows converging on covariation type **e** in Figure 2). These late taxon cycle species include some of the true marvels of evolu-



* Occurrence of forms with this combination of fundamental capacities [*g*] on isolated islands requires very large (high carrying capacity) islands.

b)

| | Fundamental Capacity to | | | |
|----------|-------------------------|---------|-----------|--|
| | Evolve | Persist | Immigrate | |
| <i>a</i> | + | - | - | - unlikely covariation; unlikely colonists |
| <i>b</i> | + | - | + | - unlikely covariation |
| <i>c</i> | + | + | - | - unlikely colonists |
| <i>d</i> | + | + | + | - Diamond's 'supertramps'; microsnails; ferns; rafting rodents, ... |
| <i>e</i> | - | - | - | - persistence tenuous; endemics near end of taxon cycle; e.g., moas and dwarfed elephants |
| <i>f</i> | - | + | - | - unlikely colonist |
| <i>g</i> | - | - | + | - unlikely persistence, except on very large, predator free islands; elephants, tortoises, ... |
| <i>h</i> | - | + | + | - colonization by slowly evolving species |

Figure 2. A hypothetical set of patterns of covariation and transitions in fundamental biogeographic capacities of species inhabiting isolated, oceanic islands. **(a)** Solid black arrows along axes indicate increasing capacities of species to immigrate to, persist and evolve on islands; red letters indicate combinations of fundamental capacities unlikely to be observed for the biota of isolated islands; while dashed lines from *d*, *g* and *h* indicate likely ecological and evolutionary transformations toward the latter stages of the taxon cycle. Not explicitly included here is ecological feedback in the form of ability of one species to dominate another in interspecific interactions, but the general trend during the taxon cycle and island syndrome should be toward specialization (stenotopy) and ecological naiveté.

(b) Matrix of potential patterns of covariation in fundamental biogeographic capacities of species inhabiting isolated, oceanic islands. Plus and minus signs indicate relatively high or low capacities relative to most other species, respectively. Patterns deemed unlikely or tenuous for biotas of isolated islands are in red type (boxes indicating unlikely patterns of covariation in capacities to evolve and persist on islands). For example, categories *a* and *b* includes species with relatively high potential for evolution, but low capacities for persisting on isolated islands (deemed unlikely here because evolution requires persistence). Dot-dashed arrows indicate that the biotas of isolated islands (e.g., *d* – supertramps of relatively small, isolated islands, and *g* – elephants and other large vertebrates restricted to very large, isolated islands) may undergo evolutionary and ecological transformations toward assemblages characterized by more tenuous persistence, especially following colonization by humans and their commensals (species type *e* – representing those in the latter stages of the taxon cycle).

tion in geographic isolation – giant rodents and insectivores, flightless birds, dwarfed elephants, tree-sized ‘sunflowers’ and other woody descendants of herbaceous plants, and many other highly transformed but often ecologically naïve animals and plants. Not explicitly included in the conceptual model of Figure 2 are anticipated trends in the ability for one species to dominate and displace another. As implied above, however, the predicted general trend during the taxon cycle is one toward reduced ability to dominate other species in ecological interactions.

A key heuristic value of this exercise is that it identifies some potentially insightful, yet largely (if not totally) overlooked, lines of research – those focusing on patterns of covariation in the fundamental capacities of species to immigrate to and persist, evolve and ecologically dominate other species on islands. In the next section I illustrate how the fundamental principles of biogeography and the conceptual model of Figure 1b can serve to unify explanations for a broad diversity of ecological and evolutionary phenomena on islands, from density compensation and niche dynamics of particular species, and patterns in diversity and species composition among insular communities, to the evolutionary marvels and perils of island life.

Applications of the fundamental, unifying principles: Islands

The island syndrome, taxon cycles and the island rule

The island syndrome (*sensu lato*) includes the suite of demographic, behavioral, life-history, morphological and ecological characteristics that distinguish the biotas of isolated, oceanic islands from their mainland ancestors (see Adler and Levins 1994; see also the terms in glossary of Table 1 marked with asterisks). For example, insular populations of small mammals, birds and other vertebrates often exhibit ecological release (occurring at abnormally high numbers and in an expanded range of habitats), reduced reproductive output, reduced aggressiveness, increased tameness and ecological naïveté, and increased body size, sur-

vival, and lifespan in comparison to their mainland ancestors (Crowell 1962; see Whittaker and Fernández-Palacios 2007). Insular populations of large vertebrates often exhibit trends that differ in some respects from those of small species (e.g., their body sizes tend to decrease, with perhaps concomitant increases in population densities and reproductive potential), while exhibiting a similar trend toward ecological naïveté and heightened vulnerability to extinctions – especially those at the hands of non-native species, including humans and their commensals. In his classic works on these and related insular phenomena, E. O. Wilson’s theory of taxon cycles (Wilson 1959, 1961) presented a largely phenomenological model that described these ecological and evolutionary shifts of insular lineages as a series of responses to the ecological opportunities and pressures following colonization of an initially species-poor island. This involves release in densities and habitats in the early stages, and penetration of and specialization for interior habitats in the later stages, ultimately culminating in extinction of the now stenotopic and ecologically naïve population as it is replaced by new colonists (see Ricklefs and Cox 1972, 1978, Ricklefs and Bermingham 2002, Losos and Ricklefs 2009, Ricklefs 2005, Rosindell and Phillimore 2011).

In an analogous fashion, evolutionary shifts in body size noted above may be part of a remarkable trend exhibited by a variety of insular vertebrates, which again may be largely driven by ecological interactions. This phenomenon, labeled the island rule by Van Valen (1973), describes a graded trend for insular vertebrates from gigantism in small species to dwarfism in the large species (Figure 3; Heaney 1978, Lomolino 1985, Jianu and Weishampel 1999, Clegg and Owens 2002, Meiri et al. 2004, Meiri 2007, Clegg 2010, Lomolino et al. 2011, 2013). The trend is referred to as “graded” because the degree of deviation from body size of mainland forms is most pronounced in species of most extreme ancestral size. Insular proboscideans are known to have dwarfed to less than 5% of the mass of their mainland ancestors, while insular rodents and insectivores often increased over an order of magnitude in body mass.

Table 1. Glossary. * indicates phenomena that comprise the island syndrome, *sensu lato*.

Adaptive radiation – evolutionary divergence from a single ancestral species into a variety of different forms and ecological niches.

Bauplan (pl. **baupläne**) – the body plan or ‘blueprint’ of the design of an organism; how it is structured including characteristics such as symmetry, number of body segments and relative sizes of limbs and other appendages.

Beta (β) diversity – a measure that describes the dissimilarity in species composition between communities or assemblages.

Biogeography – the science that describes and develops causal explanations for all patterns in spatial variation of biological diversity.

Buffon’s law – a fundamental pattern of biogeography, credited to Georges-Louis Leclerc Comte de Buffon (1707–1778) who observed that different regions, even those with similar environmental conditions, are inhabited by different assemblages of species.

Checkerboard distributions* – the tendency for ecologically similar species (e.g., close competitors) to exhibit exclusive or non-overlapping distributions on islands (see Diamond 1975).

Community convergence – the tendency for some isolated communities to become more similar over time with respect to the appearances or functional characteristics of their component species.

Community nestedness – an archipelago- or regional-level pattern, where the species found in less diverse communities form proper subsets of (i.e., are also found within) communities with more species.

Community similarity – various measures of the degree to which different ecological communities share the same species.

Density compensation* – the tendency for the population of a species inhabiting a low diversity (species-poor) island to approximate the combined population densities of similar species from the mainland.

Derivative patterns in community structure – patterns in the characteristics of local to regional biotas that derive from patterns of overlap in the geographic ranges of particular species, including patterns in species diversity and distinctiveness or similarity among ecological communities.

Disharmonic/unbalanced biotas – assemblages of species that are very limited in diversity and/or highly biased in composition (dominated by just a few taxa or functional groups) in comparison to those from the mainland or source biota.

Ecological displacement – interactions among species that tend to result in a segregation of their realized niches toward different habitats or different functional characteristics.

Ecological naiveté* – the tendency for long-term inhabitants of low diversity and disharmonic (unbalanced) islands to lose their capacities for detecting, avoiding or otherwise coping with competitors, predators and parasites from the mainland or otherwise more-balanced and species-rich assemblages (i.e., species at least initially absent from these islands).

Ecological release* – the tendency for populations of species inhabiting low diversity communities to exhibit a relatively broad niche in comparison to that of their populations from the mainland or other high diversity communities.

Endemicity* – a measure of the number or proportion of species from a particular island or region that are endemic to (occur nowhere else but) that area.

Flightlessness (loss of dispersibility)* – the tendency among birds, insects and other flighted organisms to lose their powers of flight after evolving on isolated, species-poor and ecologically disharmonic islands.

Fundamental capacities of species – the abilities of species to immigrate (disperse to), and maintain populations and evolve on islands.

Fundamental versus realized niche – the total range of environmental conditions in which a species can survive (or functions and behaviors it can perform), versus those that it actually occupies (or performs).

Fundamental versus realized range – the geographic distributions that a particular species may achieve based solely on its physiological and abiotic tolerances, versus the more-restricted distributions that result from barriers to dispersal and from ecological interactions among species.

General dynamic model (GDM) of oceanic island biogeography – a conceptual and graphical model describing the sequential and highly regular changes in physiographic characteristics of islands which, in turn, affect the fundamental process of biogeography (immigration, extinction and evolution) and, in turn, influence biological diversity during the geologic development an oceanic island from emergence to its geological maturation and ultimate submergence beneath the surface.

Geographic gradients – patterns of variation in characteristics such as those of species, communities, or environments along geographic clines including those of latitude, elevation, depth, isolation and area.

(cont.)

Table 1. (cont.) * indicates phenomena that comprise the island syndrome, *sensu lato*.

Geographic template – the highly non-random, spatial variation in environmental conditions that forms the foundation for all biogeographic patterns.

History of place – the past environmental and ecological conditions, configurations and locations of landmasses or oceanic basins and other bodies of water.

History of species – the environmental and ecological conditions experienced by the ancestors of a particular species or taxon during its evolutionary development.

Insular distribution function (IDF) – a line or curve on a graph that identifies those combinations of island isolation and area above where (i.e., less isolated and larger islands) the immigration rate for a particular species exceeds its extinction rate.

Island rule* – a graded trend in insular vertebrates from gigantism in the smaller species to dwarfism in the larger species.

Island syndrome* – the suite of demographic, behavioral, life history, morphological and ecological characteristics that distinguish the biotas of isolated, oceanic islands from their mainland ancestors.

Metapopulation – a set of local populations of a particular species that are linked by dispersal among those populations.

Nestedness (see **Community nestedness**)

Phoresy – the phenomenon where relatively small organisms depend on larger ones for their dispersal.

Physiographic – referring to the physical features of islands or other areas, including their size, shape, isolation, elevation (depth) and topographic variation.

Predator-mediated coexistence – coexistence of two otherwise intense competitors which results from a predator that maintains their populations below the levels where one would exclude the other.

Realized niche (see **Fundamental versus realized niche**).

Realized range (see **Fundamental versus realized range**).

Spatial and temporal autocorrelation – the tendency for entities (e.g., environments, species, or biological communities) that are closer in space and time to be more similar than those that are further isolated or more disparate in time periods.

Species composition – the particular species, or types of species that co-occur in a given site, community or region.

Species richness – the number of species inhabiting a particular site, community or region.

Species-based models – those based on the assertion that species are not equivalent and that many of the patterns in variation among communities results from regular patterns in the differences among species.

Super-generalist – a tendency for some species of very isolated, species-poor and disharmonic islands to increase their abilities to interact with an otherwise inordinate number of symbionts (e.g., as generalist pollinators or dispersers).

Supertramps – species that are relatively common on small and isolated, oceanic islands but absent from those with more diverse communities, presumably because they combine strong abilities for dispersal and colonization with limited abilities to compete or otherwise coexist with ecologically similar species.

Sweepstakes immigration (colonization) – the highly unlikely colonization of a relatively isolated island that, if successful, results in the founding of a population with ample opportunities for ecological expansion and evolutionary development.

Taxon cycle* – the predicted, progressive ecological and evolutionary changes in the descendants of founding populations from their colonization of beachfront habitats, subsequent expansion into interior habitats, specialization, and niche contraction, to their ultimate extinction and replacement by subsequent waves of colonists and their descendants.

Tobler's first law of geography (spatial autocorrelation) – originally described by Tobler (1970: 236) in the observation that “Everything is related to everything else, but near things are more related than distant things.” In modern terms, this describes positive, spatial autocorrelation or the very general tendency for the environmental or biological characteristics of sites to decrease in similarity as distance between those sites increases.

Trophic cascades – a phenomenon where changes at one trophic level (e.g., in the abundance of a species) result in changes (often alternating between positive and negative effects) in populations occupying other trophic levels throughout an ecosystem (see Carpenter et al. 1985).

Waif biota – the individuals or propagules (seeds and other stages of the life cycle that can reproduce) of species that are carried passively by water or air currents to distant places.

Woodiness* (secondary) – the evolutionary development of increased cellulose content and tree-stature in descendants of herbaceous plants after they colonize isolated and disharmonic (marked by a paucity of tree species) islands.

Zoochory – the transport of plant propagules (seeds and other stages of the life cycle that can reproduce) by animals.

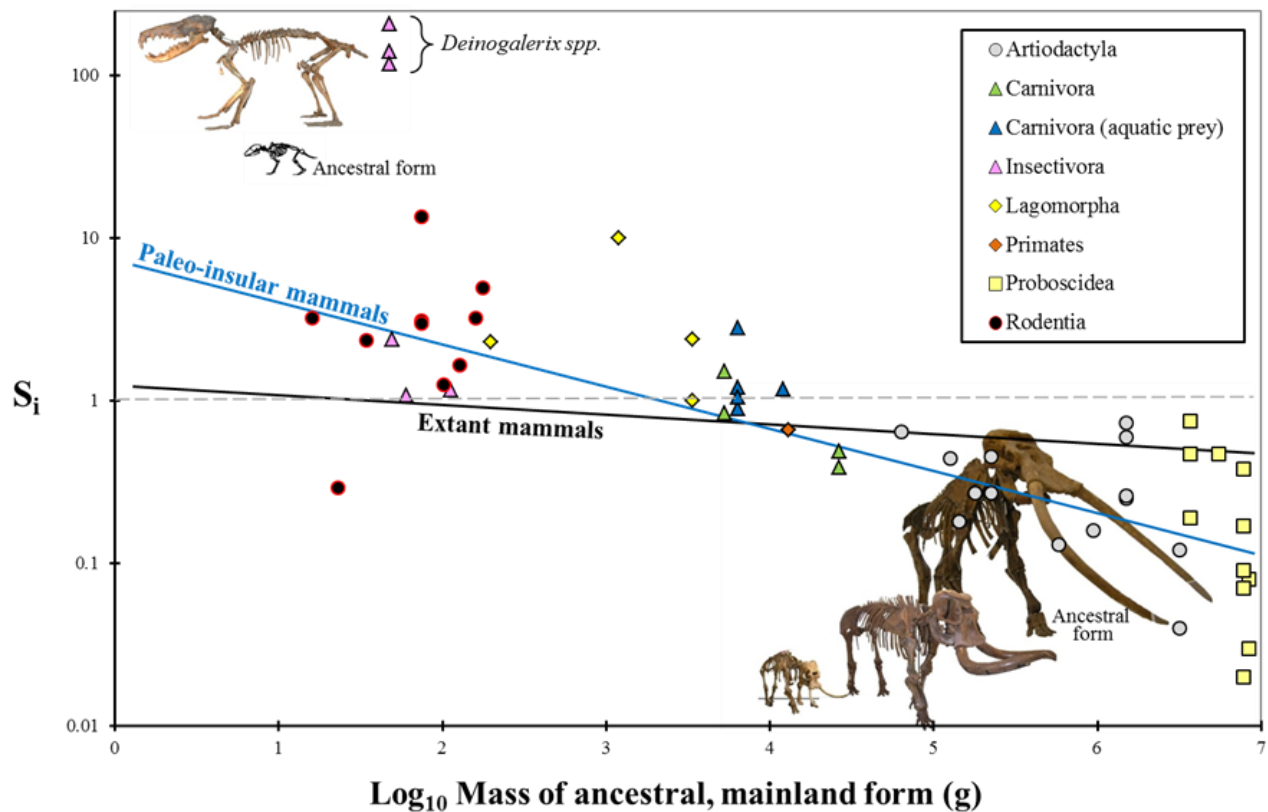


Figure 3. The island rule describes a graded trend from gigantism in otherwise small species of mammals and other vertebrates to dwarfism in larger species. S_i is a measure of insular body size expressed as a proportion of body mass of the ancestral, mainland relative. Illustrations at the two extremes of this trend are those for the extinct ‘moonrat’ (Erinaceomorpha) – *Deinogalerix koenigswaldi* from the paleo-island of Gargano ($S_i > 100$), and for the extinct proboscideans – *Palaeoloxodon antiquus* (mainland ancestor), and paleo-insular species *P. mnaidriensis* and *P. falconeri* (from Sicily; $S_i = 0.17$ and 0.02 , respectively). Illustrations of skeletons by Georgios Lyras. (See Lomolino et al. 2011 and 2013; van der Geer et al. 2010; van der Geer et al. 2013.)

Because body mass strongly influences nearly all physiological and ecological traits in vertebrates, the island rule may be causally related to the island syndrome and possibly taxon cycles as well. That is, body size evolution is likely to strongly influence the other fundamental capacities of species – to immigrate to and persist and evolve on islands and, thus, may ultimately explain why these fundamental capacities exhibit particular patterns of covariation and not others. For example, larger vertebrates are predicted to be relatively powerful immigrants (strong, active dispersers), but should be more limited than smaller species in their capacities for persisting on islands (because they require more energy to survive), and for evolving on islands (because they have relatively long generation times).

Among the other marvels of island life are reversals in immigration powers of plants and ani-

mals that have been long-established on isolated and ecologically disharmonic islands; in particular, those lacking ground-dwelling mammals (Carlquist 1974, Whittaker and Fernández-Palacios 2007, Lomolino et al. 2010). Many hundreds of species of insects and birds – descendants of long-distance colonists of isolated oceanic islands – have either greatly reduced wings or have totally lost the power of flight. In an analogous fashion, many species of plants – again derived from those of long-distance immigrations, have lost or are greatly reduced in those structures that served to enhance their ancestors’ abilities to disperse by wind, by water currents, or in the fur, feathers or guts of animals. Again, all of the phenomena discussed above form an intriguing mosaic of patterns that often culminate in genuinely remarkable transformations, these often associated with heightened vulnerability and susceptibility to ex-

tinctions – including reductions in the ability to escape extinctions by colonizing other islands.

In the next section, I address the potential causal explanations for the island syndrome and the ecological and evolutionary marvels of island life in more detail, again within the context of the fundamental principles of biogeography. These, along with a variety of other phenomena exhibited by insular populations and communities, are contextual in that they are patterns that become emergent at particular spatial and temporal scales, but not others (Figures 4 and 5). That is, some of these insular phenomena (e.g., density release and habitat expansion) represent more local and short-term or relatively rapid responses to the nature of insular environments and the forces operating over those scales, while others (e.g., island rule patterns and development of insular hotspots of endemism) result from evolutionary responses over broader spatial and longer temporal scales.

Ecological Release, Ecological Displacement and the Ecology of Evolution

The ecological shifts and evolutionary transformations of species inhabiting ecologically simplified, isolated islands discussed above serve as compelling evidence for the central role of species’ interactions in driving both the ecological and evolutionary dynamics of species-rich (i.e., mainland) assemblages. In the latter systems, intense and diverse interspecific interactions put a premium on diversification: in ecological time (within just a few generations) driving segregation of niches by shifting, specializing and reducing the realized niches of populations to a small subset of their fundamental niches; in evolutionary time driving adaptive radiations and diversification of fundamental niches among evolving lineages.

On isolated islands, these selective pressures and resultant ecological and evolutionary dynamics are often reversed in response to ecological release and ecological displacement: re-

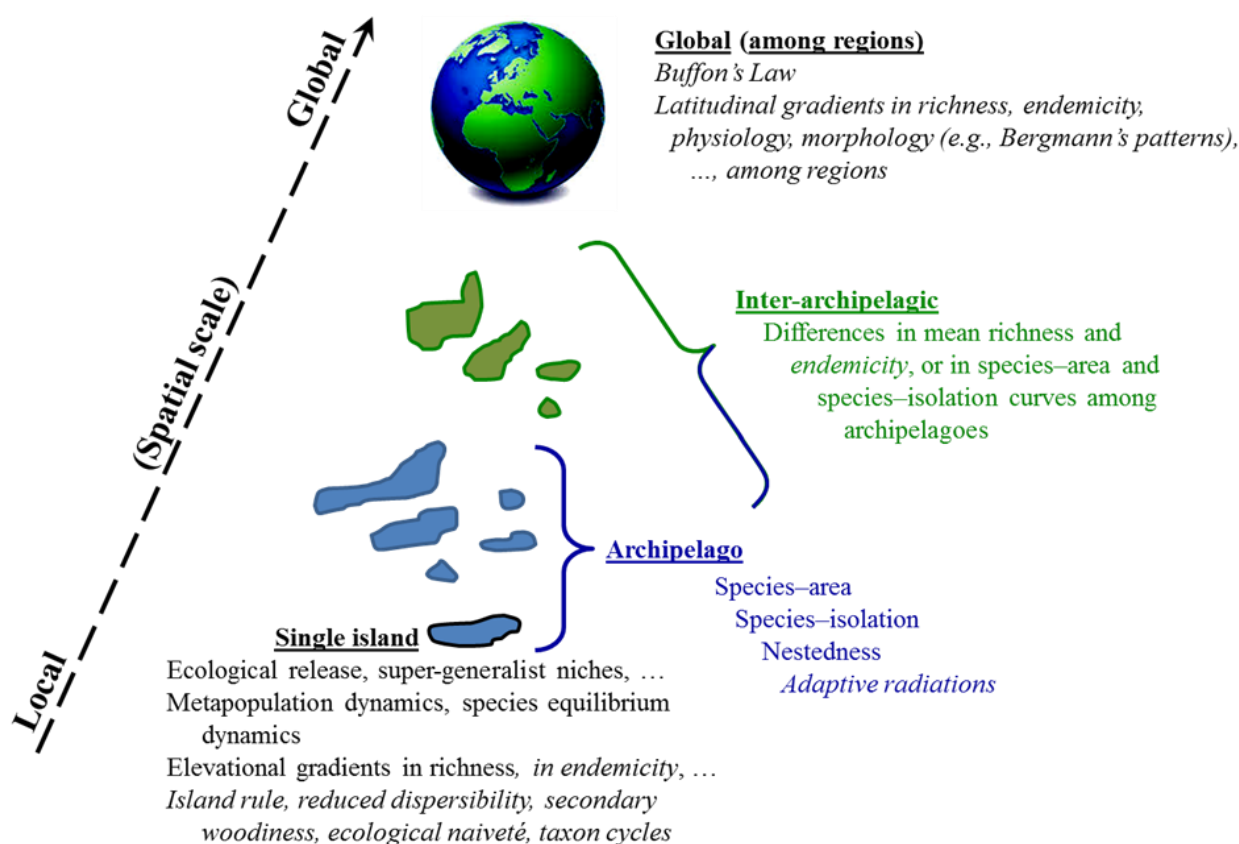


Figure 4. A spatial hierarchy of biogeographic patterns exhibited by insular and continental (oceanic) biotas. Normal and italicized font indicate patterns arising over relatively limited (within generations) to more extensive (evolutionary) time periods, respectively. See Glossary (Table 1) for a description of biogeographic patterns listed here.

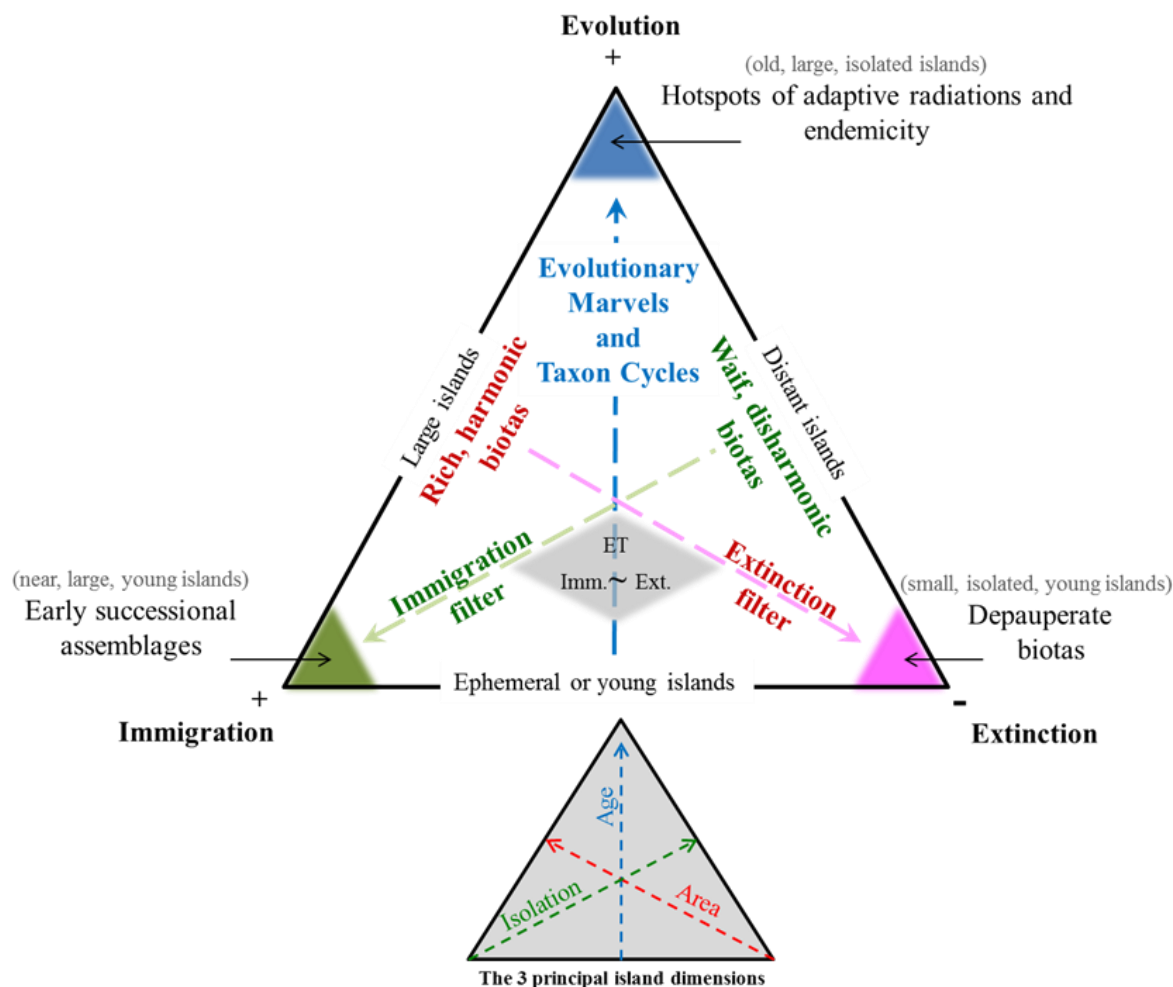


Figure 5. Conceptual, phenomenological model describing conditions promoting various insular phenomena across the three principal island dimensions of area, isolation and age. Each of these strongly influences the fundamental processes of extinction, immigration and accumulation of species by evolution, respectively. The rates and relative influence of each of the fundamental processes are highest at their respective vertices (darkened corners in the figure), immigration decreasing with isolation, extinction decreasing with area, and evolution increasing with age. Plus and minus symbols indicate the qualitative influence of each process on biological diversity. ET refers to the conceptual space where community dynamics are consistent with those predicted by the Equilibrium Theory of MacArthur and Wilson (1967), where richness and community turnover result from a hypothesized balance of immigration and extinctions among relatively equivalent species and in the absence of significant, in situ evolution. [Note that a limitation of triangular conceptual models such as this is that certain combinations of principal variables are not included – e.g., biotas of islands that are Near and Old, Old and Small, or Small and Near].

lease especially from non-volant mammals which tend to dominate species-rich (mainland) communities, and displacement from conspecifics and the highly disharmonic biota of long-distance dispersal, which often includes a diverse assemblage of birds, insects and pioneering plants. In terms of the conceptual construct of the model of Figure 1b, the ecological and evolutionary phenomena that constitute the island syndrome derive primarily from the attenuation or highly altered nature of ecological feedback (green arrows in Figure 1b) and, by default, from the increased influence of

intraspecific interactions. Again, the result is that populations of the few winners of sweepstakes colonization increase in numbers (density compensation) and expand across a broader range of habitats and trophic strategies (habitat and niche shifts and expansions) to more fully occupy and even expand the fundamental niches of these species.

Over longer time periods, capacities for immigration and survival may be transformed as species evolve, often producing island endemics that are limited, at least in comparison to their main-

land ancestors, in their abilities to avoid mammalian competitors and predators by dispersal, or by use of chemical, behavioral or morphological defenses. Thus, ecological release and displacement in species-poor and disharmonic insular communities (over many generations) combine to produce the evolutionary marvels of island life, including insular endemics of bizarre baupläne and the oxymora of island life – ‘giant shrews’ and ‘pygmy mammoths’. In the case of such transformations in body size, while a combination of island factors may contribute to the island rule, it may be most readily explained as driven by a reversal in the ecological selection pressures. On the mainland, natural selection in response to intense ecological pressures may drive diversification in body size – some species of mammals and other vertebrates becoming smaller and thus avoiding competition or predation (smaller size allowing them to become more specialized for different diets, or to avoid predation by utilizing small refugia not available to larger species), other species becoming larger and consequently better able to dominate competitors in interference competition, and to avoid predators by outgrowing them.

Thus, on islands and in the absence of such ecological pressures from mammalian competitors and predators (but with persistent if not increased competition from insular birds, reptiles and possibly invertebrates as well), the trend in mammals and perhaps some other vertebrates is often toward convergence on intermediate body size. Not only does this scenario of release and displacement explain the island rule, but it also provides an explanation for the equally striking phenomenon of super-normal size observed in numerous lineages of insular birds. The giant flightless dodos and solitaires of the Mascarene Islands (Indian Ocean) and the nine to 15 species of moas of New Zealand, which ranged up to 3 m tall and over 200 kg (Worthy and Holdaway 2002, see also Allentoft et al. 2014), are all quite difficult to explain based on ecological release (from mammals) alone. Although these islands lacked native mammals, the ancestors of these bizarre birds did have to compete with a diverse assemblage of other birds. New Zealand, for example, included

well over 200 species of relatively small avian competitors at the time moas were evolving, and predatory birds as well, including Haast eagle (*Harpagornis moorei*), which may have become locked in an evolutionary escalation of body size with the moas (see Worthy and Holdaway 2002, Davies 2003). These birds were converging, not on the intermediate size of avian assemblages, but on the size (and diet) of large mammalian herbivores that were absent from New Zealand until introduced to the islands long after the moas went extinct. Again, the salient lesson here is that the evolutionary marvels of island life may be as strongly influenced by ecological displacement from the highly disharmonic assemblage of insular communities as by ecological release and the ecological simplicity of those islands.

Finally, under the requisite conditions for prolonged adaptive radiations (i.e., very large and isolated islands colonized by a lineage with high propensity for evolutionary diversification) ecological diversity and, therefore, ecological feedback should continue to increase over evolutionary time. Thus, many insular biotas have been transformed from species-poor and highly disharmonic assemblages, to diverse and (at least ecologically if not taxonomically) more balanced ones, often rivaling those of even the diverse mainland biotas. Notable exemplars of this phenomenon include the honeycreepers, ferns and drosophilids of Hawaii, the cichlids of Africa’s Rift Valley lakes, and the lemurs of Madagascar (see Poux et al. 2005, Mittermeier et al. 2006, Gabrutt 2007).

Gradients in Insular Community Structure (Richness and Composition) among Islands

Species richness gradients

Gradients in insular communities are often very general, at least in a qualitative sense; e.g., species richness increases with island area and decreases with isolation. These and other gradients in insular community structure, however, may not be simple linear functions of the principal dimensions of islands – area, isolation and age (see Figures 6 and 7). Such non-linear or otherwise complex relationships in species richness and composition along geographic gradients are expected for

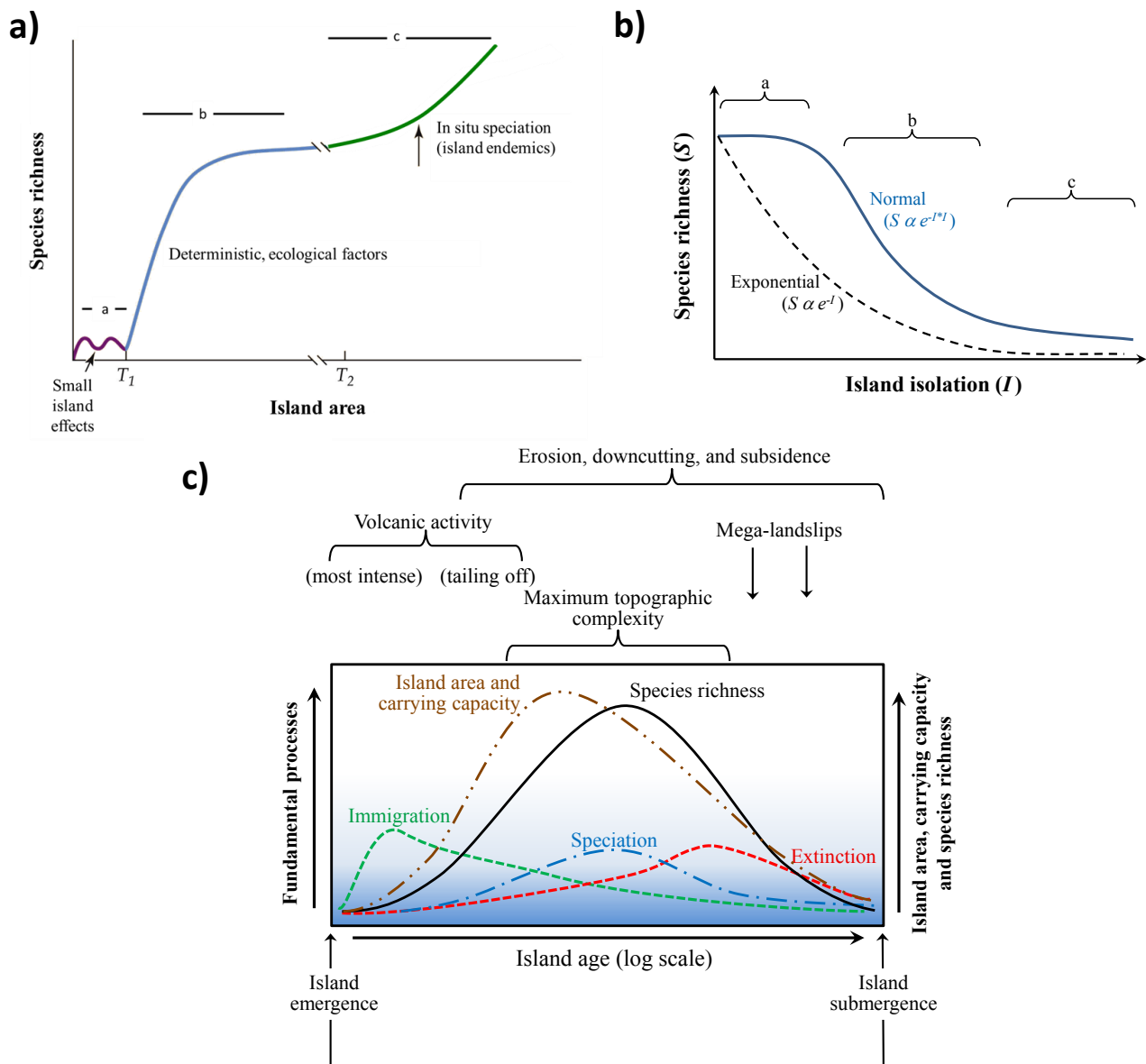


Figure 6. Insular species richness over gradients of area, isolation and island age.

(a) Although typically illustrated as a log-normal response curve (as in the intermediate section, *b*, of the curve, in blue), the species–area curve may be substantially more complex, exhibiting non-linearity and threshold responses (the latter reflecting phase changes from regions *a* through *c*, where the principal forces driving insular community structure grade from one set of processes to another) (Modified from Lomolino et al. 2010).

(b) Although less general and not as well studied as the species–area relationship, the species–isolation relationship likely takes one of two forms, i.e., that of a negative exponential (with a constant proportion of potential immigrants ‘dropping out’ as isolation increases) or a normal curve (where immigration abilities are assumed to be normally or log-normally distributed, and immigration rates remain relatively high until isolation exceeds a distance approximating the dispersal abilities of the most limited immigrants in the focal taxon). A key distinction between these graphical models is the bracketed range in isolation for near islands (region *a*) where the normal curve predicts that isolation should have little influence on species richness until the degree of isolation exceeds that of the most limited immigrant in the pool of species considered. Region *c* also identifies another region (the very isolated islands) where the effects of isolation on species richness may be difficult to detect. The graphical models illustrated here do not include the potential effects of in situ speciation on isolated (and large) islands which, if significant, would result in a rise in species richness for the more isolated islands (see Patiño et al. 2015).

(c) The general dynamic model of island biogeography (Whittaker et al. 2007, 2008, 2010) describes the geological ontogeny and biotic dynamics of volcanic, oceanic islands from their emergence to their geological maturation and ultimate submergence beneath the ocean’s surface (graph modified from Whittaker et al. 2008). The curves in this graph illustrate how the fundamental biogeographic processes and the principal characteristics of islands should change (and, in turn, influence species richness) during the ontogeny of a volcanic, oceanic island.

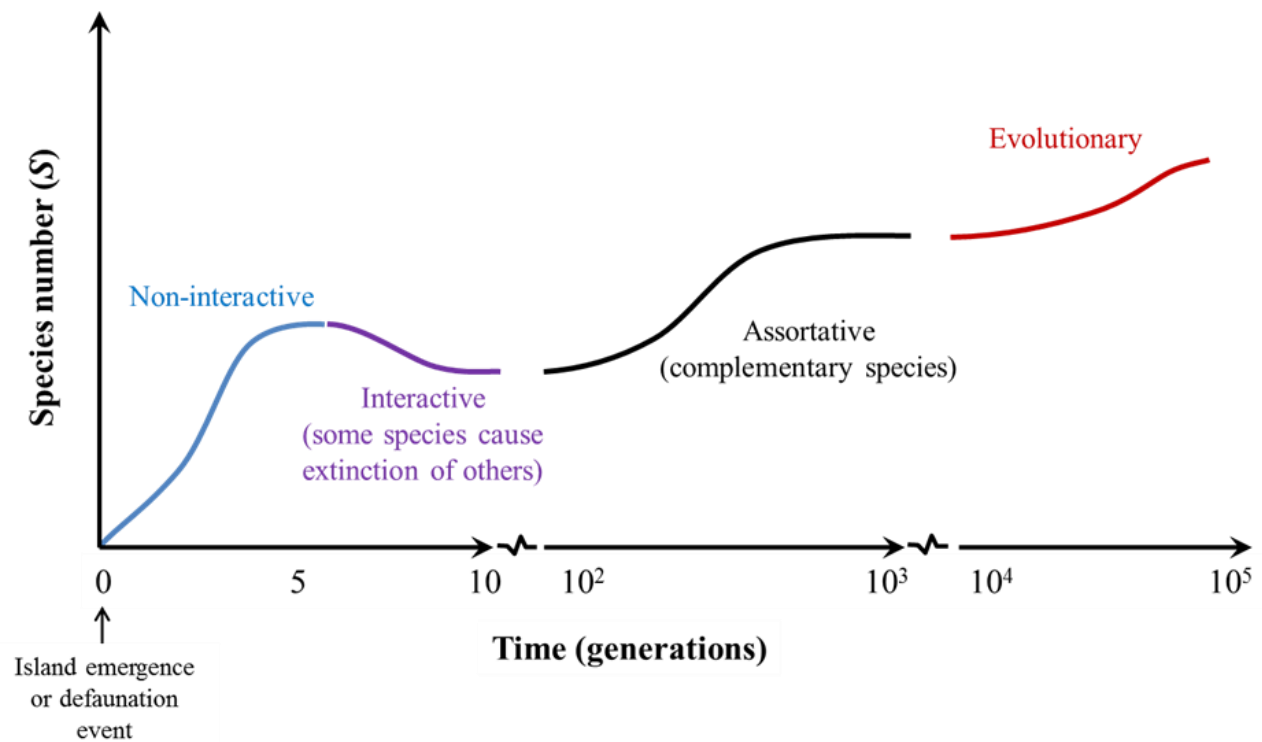


Figure 7. A hypothetical model illustrating how insular biotas may undergo a progression through multiple equilibria and community dynamics as they accumulate species, including non-interactive, interactive (where competition, predation and other ecological interactions reduce species number), assortative (where mutualisms and other complementary interactions increase species number), and evolutionary equilibria (where species number either equilibrates at a higher diversity or continues to rise as a result of the combined effects of speciation and immigration on the one hand, and extinction on the other). (Modified after Simberloff and Wilson 1969, 1970; Wilson 1969.)

at least four reasons, including the nature of the geographic template, scale-dependence of fundamental biogeographic processes, non-equivalence of species, and ecological feedback from species' interactions.

1) Multifactorial nature of the geographic template: Insular community structure is likely influenced by a combination of the fundamental processes, and each of these in turn may be influenced by more than one principal dimension of islands (isolation, age and area). For example, diversification of insular biotas should be a function of geographic isolation (promoting diversification by limiting gene flow), island age (i.e., the time available for accumulating species) and island area (influencing both the likelihood of in situ barriers to gene flow in the form of large rivers, mountains and other topographic barriers, while also influencing carrying capacity of insular ecosystems and persistence of lineages, thus allowing more time to accumulate species

by in situ evolution). The general dynamic model of Whittaker and his colleagues (Figure 6c; Whittaker et al. 2007, 2008 and 2010) provides an insightful illustration of how the first principle of biogeography can be applied to develop an integrative understanding of the dynamics in the geographic template and their effects on the fundamental biogeographic processes during the ontogeny of an island (see also Heaney 2000, Stuessy 2007).

2) Multiple effects and scale-dependence: Even if we were somehow able to hold all but one of the three principal island dimensions constant, non-linear response curves may still emerge because the remaining variable may influence more than one fundamental process. For example, as noted above, island area should influence both the processes of extinction (persistence) and evolution (species diversification) – larger islands increasing the likelihood that populations will persist long enough to evolve, while also increasing the opportunities

for in situ speciation because larger islands are more likely to include internal barriers to gene flow. Island area may also influence the third fundamental processes – immigration, because larger islands are bigger ‘targets’ for potential colonists (see Buckley and Knedlhans 1986, Lomolino 1990).

One emergent result of this complex nature of influence of the principal island dimensions is scale-dependence. Biogeographic gradients such as those in species diversity may often include phase shifts along the gradients of island area, isolation or age, marking changes in the nature of driving forces. Take for example the species–area relationship. Within an archipelago and spanning only a limited range in island area, this function (in arithmetic, not log-transformed space) is well-approximated by a positive curvilinear relationship with an attenuating slope (blue trend line of Figure 6a). However, when studied over a broader span of area, including very small and very large islands (those either overlooked in biogeographic surveys because they are ecologically uninteresting or those too difficult to adequately survey completely because they are so large, respectively), a more complex relationship may emerge (Figure 6a; Lomolino 2000b, Lomolino and Weiser 2001, Triantis et al. 2006, Gentile and Argano 2005, Triantis and Sfenthourakis 2012, Triantis et al. 2012, Whittaker and Triantis 2012). Very small islands are often characterized by highly unpredictable habitat and environmental conditions (they are poor geographic sampling units), and by frequent but highly unpredictable extinctions. As a result, species richness may appear independent of island area until some critical minimum size is reached. This phase shift may correspond to areas that are now sufficiently large to include representative samples of principal habitats, or those that are large enough to provide adequate refugia against storms, floods or other sources of catastrophic extinctions on much smaller islands. Another phase change, marking a second shift in underlying processes driving the species–area relationship is predicted

to occur when islands are large enough to accumulate species by in situ speciation (region c of Figure 6a –see Lomolino 2000a,b, Kisel and Barraclough 2010, Matthews et al. 2014, Patiño et al. 2014, Whittaker et al. 2014). Given the presumed non-equivalence of species in their capacities to colonize and survive and evolve on islands, these phase shifts should be gradual rather than step-function responses.

- 3) Non-equivalence of species: An alternative reason for predicting complex responses to one or more of the principal biogeographic dimensions of islands is that species are not equivalent in their capacities to immigrate to, and survive or evolve on, islands (cf., Hubbell’s [2001, 2010] neutral theory of biodiversity). If, for example, under the likely scenario that immigration abilities of animals are correlated with their body size and, thus, are normally or log-normally distributed, their species–isolation relationships should approximate a sigmoidal function (Figure 6b). While this or qualitatively similar patterns may be expected to hold for the other fundamental biogeographic capacities of species (i.e., to survive and evolve on islands), we simply have not done the necessary research to assess the nature of these fundamentally important patterns (i.e., patterns of variation and covariation in fundamental capacities of species over gradients of isolation, area or age).
- 4) Ecological feedback and species’ interactions: Finally, as emphasized in Figure 1b, all patterns in insular community structure may be strongly influenced by interspecific interactions. Thus, as species accumulate on islands of increasing area or age, or on those of decreasing isolation, interspecific interactions become increasingly more important. The influence of such ecological feedback is, however, likely to be even more complicated than this, as it may vary depending on which fundamental process (immigration, extinction or evolution) dominates this phase of the species–area, species–age or species–isolation response curve. For example, on near and very young islands that are strongly influenced by immigration, species

accumulation curves may accelerate following establishment of early colonists that can then serve as facultative mutualists or those that modify environments to favor establishment of others. Alternatively, on isolated and very large islands where in situ evolution becomes prominent, ecological interactions (including pollination and seed dispersal systems, trophic cascades, predator-mediated coexistence and a diversity of obligatory mutualisms) may contribute to diversification and an increase in the slope of the species–area curve (see Figure 7). Indeed, the notion that evolutionary diversification is often accelerated by (if not driven by) interspecific competition and other forms of ecological feedback, has been a common theme since the earliest articulations of biogeography (see Pfennig and Pfennig 2012).

Community nestedness

One of the most general patterns in insular community structure across entire archipelagoes, one rivaling the generality of the species–area relationship, is community nestedness. When comparing species composition among islands, many, if not most, archipelagoes and taxa exhibit a pattern whereby species inhabiting less diverse islands constitute proper subsets of those inhabiting richer islands (Figure 8). Nestedness, along with its putative causal forces, may be explored by searching for nested patterns in species composition when islands are ordered, not just by species richness but by the principal dimensions of islands – area, isolation and age. Thus, a comprehensive explanation for nestedness and deviations from perfect nestedness should be based on the unifying principles of biogeography.

a) The geographic template: The observed, orderly sequence of species composition across islands and other isolated systems likely derives from species-selective immigration filters and species-selective extinction (functions of two principal geographic dimensions – island isolation and area, respectively; Figure 5). On the other hand, deviations from perfect nestedness may be driven, at least in part, by evolution of insular endemics (which, since they occur on no other islands, cause departures from per-

fect nestedness). Thus, we might expect higher nestedness for archipelagoes that span a broad range in isolation and area, but lack islands that are large, isolated and old enough to have accumulated endemic species.

b) Fundamental capacities of non-equivalent species: Nestedness requires not just non-random variation of physiographic and environmental conditions across the archipelago, but also that the species present differ in the traits affecting their fundamental capacities. That is, this and other non-random patterns in species composition imply, if not require, non-equivalence of the species; otherwise there would be no differences for immigration and extinction filters to act on. Models that assume otherwise – i.e., equivalence of species, such as MacArthur and Wilson's (1963, 1967) equilibrium model and Hubbell's (2001, 2010) neutral theory, provide intriguing explanations for patterns in diversity, but they cannot explicitly address nestedness or other patterns in community structure among islands – those where species exhibit differences in their distributions owing to differences in their fundamental capacities to respond to environmental variation across the geographic template.

c) Interdependence (covariation) among fundamental capacities: As discussed earlier, fundamental biogeographic capacities are likely to covary among species (Figure 2), and the nature of that covariation will either reinforce or create deviations from perfect nestedness. To illustrate this, it is helpful to introduce the Insular Distribution Function (IDF), which is a line or curve that describes the likely occurrence of populations of a focal species as a function of island area and isolation (these variables being correlates of the likelihood of population persistence and of immigration, respectively; Figure 9). Patterns in nestedness across an archipelago (and species richness as well) can then be illustrated by overlaying IDFs for different species onto the same graph for an archipelago (Figure 9a). Deviations from perfect nestedness are indicated when IDFs intersect, this occurring when the slope of the IDF (an inverse measure

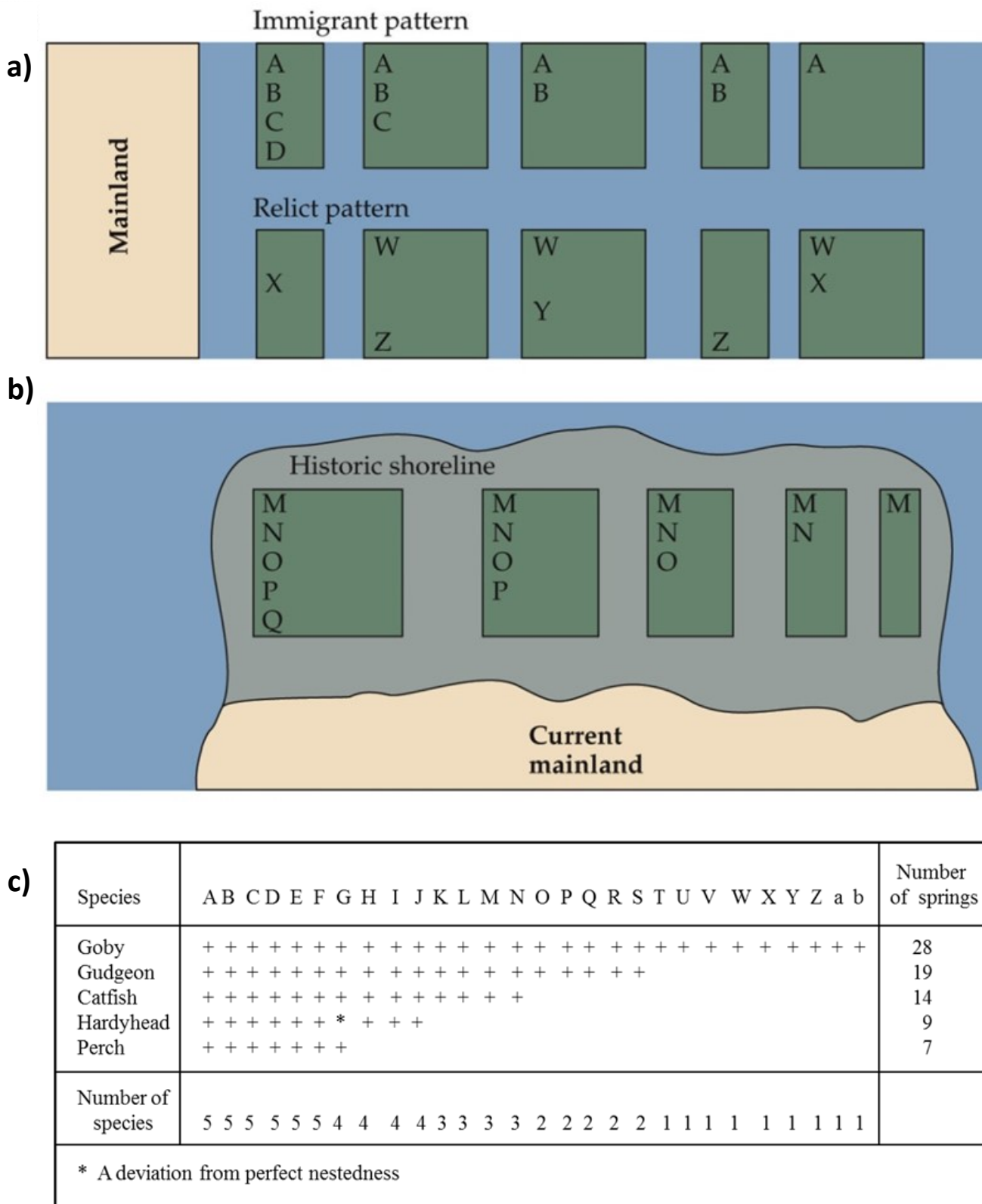


Figure 8. Community nestedness describes a pattern where species composition on less diverse islands constitutes a proper (nested) subset of those on richer islands, and may be generated by processes including **(a)** species-selective immigration (thus being a function of island isolation), and **(b)** species-selective extinction (being a function of island area). **(c)** illustrates the empirical pattern of near-perfect nestedness shown by communities of fish inhabiting 28 isolated springs in the Dalhousie Basin of southern Australia. (A after Darlington 1957; B after Lomolino 1996; C from Brown and Kodric-Brown 1993).

of immigration ability) and its intercept (a direct measure of resource requirements) are negatively correlated among species (Figure 9b). This may often be the case for animals whose principal means of island colonization is by active immigration, because larger body size should confer both greater resource requirements and greater immigration capacities (i.e., IDFs with higher intercepts but lower slopes). In contrast, animals depending primarily on passive immigration (e.g., small mammals rafting on logs or floating with ocean currents) may exhibit just the opposite pattern – larger species requiring more resources to maintain their populations, but also being more limited in their capacities for (passive) immigration (IDFs for larger species having higher intercepts and steeper slopes; Figure 9a).

d) Interspecific interactions and ecological feedback: Interspecific interactions are likely to strongly influence patterns in community nestedness across an archipelago. Whereas obligatory mutualisms may increase nestedness (with pairs of symbionts appearing or dropping out simultaneously), negative interactions such as predation, competition and parasitism may create deviations from perfect nestedness – in this case by excluding species from certain regions of their fundamental range (islands they should inhabit based solely on their immigration capacities and resource requirements). The most extreme, purported cases of such exclusive distributions are checkerboard patterns, where two or more species either never co-occur on the same islands or do so much less frequently than would be expected by chance (Figure 9b).

A Research Agenda for Unifying Biogeography Theory - Islands

The salient point from the above discussion is not that ecological feedback and covariation among fundamental capacities of species make biogeographic patterns so complex that they are rendered inexplicable, but just the opposite. A comprehensive understanding of the marvels of island life is achievable, but only if we expand our re-

search programs to better understand the nature of the geographic template, the way in which this influences the fundamental biogeographic processes, the nature and importance of the interdependence among these processes, and how they are influenced by interspecific interactions.

Similarly, the value of exercises such as that illustrated in Figure 2 and Figures 6–9 is not that they elucidate some universal or invariant patterns of nature. Indeed, we expect there to be many exceptions and particular taxa and lineages that may exhibit quite distinct and initially confounding patterns in their fundamental capacities and emergent biogeographic patterns. Rather, the principal value of these exercises is in identifying seldom studied but very promising lines of future research for biogeography, in general, and island biogeography in particular. These include research assessing:

1. the patterns of covariation in the capacities of species to immigrate to isolated systems, and to persist, evolve, and dominate other species within those communities;
2. the differences in patterns of covariation of fundamental capacities among assemblages from different taxa or functional groups, from different geographic regions, during different stages of the taxon cycle, and along different geographic gradients (e.g., those of latitude, elevation or depth);
3. the nature and rate of evolutionary transformations in *baupläne* (e.g., dwarfism, gigantism, development of secondary woodiness in plants, and loss of flight in birds and insects), in physiological and metabolic pathways, and in ecological functional types (e.g., from super-tramps to ecologically naïve island endemics), and how the rates and directions of these evolutionary transformations may differ among taxa, types of ecosystems, and time periods;
4. the influence of island age and the importance of highly unlikely events (e.g., sweepstakes dispersal, volcanic eruptions, megafloods or cataclysmic storms) that nevertheless may have persistent and fundamentally transformative impacts on isolated biotas (see Grinnell 1922, Darlington 1938, Simpson 1940).

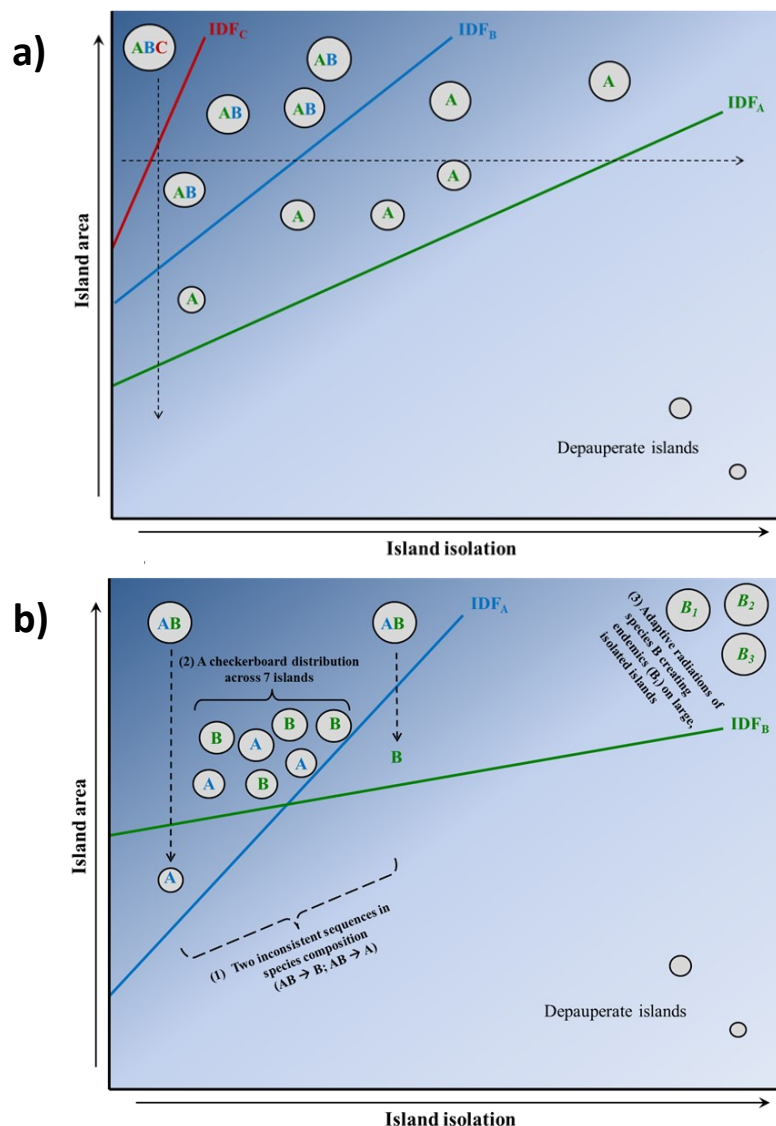


Figure 9. (a) Insular Distribution Functions (IDFs) indicate the combinations of area and isolation where persistence (or conversely, extinction) rates of populations of particular species (here, the hypothetical species A, B and C) equal their rates of immigration to each island. The intercept of these functions should be a direct function of resource requirements, while their slope should be an inverse function of immigration abilities. The fundamental ranges of these species (islands that their populations should inhabit in the absence of significant ecological interactions or catastrophic disturbance) are thus expected to be limited to islands that fall above their respective IDFs in this coordinate space. Modeled here are IDFs under one of a number of alternative scenarios – in this case, that of positive covariation in their intercepts and slopes, which assumes negative covariation in resource requirements and immigration abilities (see Figure 9b for an illustration of IDFs exhibiting negative covariation of IDF intercepts and slopes between species). The emergent pattern, as illustrated by the results of two hypothetical surveys across islands of increasing area or increasing isolation (dashed horizontal and vertical arrows, respectively) is that such biotas should be characterized by highly nested communities, with species composition of less rich communities forming proper subsets of those from more diverse ones (nested sequences describing species composition are consistently from A to AB to ABC) (after Lomolino 1999, 2000c).

(b) Deviations from perfect nestedness of insular communities across an archipelago may be generated if (1) insular distribution functions (IDFs) of two or more species intersect, which occurs when resource requirements and immigration abilities are positively correlated (intercepts and slopes of the IDFs are negatively correlated) among species, (2) where competition or predation may create exclusive, checkerboard distributions of the species within their fundamental ranges, or (3) when islands are sufficiently large, isolated and old (island age not illustrated here) such that descendants of founding species may undergo adaptive radiations, creating endemic species (B_1, B_2, B_3) on different islands. Letters represent islands with at least one of the focal species (A or B). Dashed arrows depict a deviation from perfect nestedness with decreasing island area (from that with both species AB co-occurring on large islands to that on the smaller islands with either A or B being the sole inhabitant depending on isolation of the islands).

Box 1. A summary of recent theories of biogeography and biodiversity of insular biotas.

Table A. Descriptions of ten models or theories of island biogeography that have been proposed since 1959.

| | |
|---|---|
| Taxon Cycles (Wilson 1959, 1961) (Ricklefs and Bermingham 2002; Ricklefs 2005) | Following colonization by successive species, their interspecific interactions drive a series of ecological and evolutionary transformations of populations from those adapted to characteristics of the beachfront, to those adapted to characteristics of the interior habitats of the island, ultimately resulting in their extinction and replacement by descendants of more recent colonists. |
| Equilibrium Model of Island Biogeography (MacArthur and Wilson 1963, 1967) | Species richness on a particular island results from a dynamic balance between immigrations and extinctions, with differences among islands resulting from effects of isolation and area on immigration and extinction rates, respectively. Although an earlier version of MacArthur and Wilson's mathematical model included speciation, this was dropped from the model that became paradigmatic for the field during the late 1960s. |
| Assembly Rules (Diamond 1975) | Non-random patterns in species' distributions and co-occurrence among islands results from species-selective immigrations, extinctions and species' interactions. |
| Ecological Model of Body Size Evolution (Lomolino 1985; Lomolino et al. 2011) | Patterns in body size evolution among islands, among species and over time result from immigration abilities, resource requirements, and ecological interactions among species – all of these being strongly influenced by body size. |
| Species-based, Hierarchical Model (Lomolino 1999, 2000) | Patterns in species' distributions, co-distributions and species richness among islands result from non-random variation and covariation in the capacities of species to immigrate, survive, evolve and dominate other species on islands. |
| Model of Dynamic Disequilibrium and Phylogenetic Diversification (Heaney 2000) | Patterns in species richness and endemism among islands result from the balance between immigration (colonization) and phylogenesis (evolutionary diversification), the former varying with isolation and the latter varying with area of the islands and age of the insular biotas. |
| Model of Ontogeny and Anagenic Evolution (Stuessy et al. 2006; Stuessy 2007) | Species diversity and genetic diversity of insular biotas result from anagenesis and cladogenesis, both of these varying with characteristics of the species, and with ecological heterogeneity and age of the islands. |
| Global, Statistical Model of Island Biogeography (Kalmar and Currie 2006) | The variation in richness among islands can be statistically related to contemporary abiotic/environmental variables, especially island area, isolation, climate and habitat characteristics. |
| General Dynamic Model of Island Biogeography (Whittaker et al. 2008; Whittaker et al. 2010) | Patterns in species richness among volcanic, oceanic islands results from the combined influences of immigration, extinction and speciation, each varying in a non-random manner with physical characteristics of the islands which, in turn, change in a predictable manner with age of the islands. |
| Unified, Neutral Model of Island Biogeography (Rosindell and Phillimore 2011) | An individual-based model, derived from Hubbell's Neutral Theory of Biodiversity (2001), where immigration and speciation are functions of island isolation, with cladogenesis exhibiting a threshold response with island area, and anagenesis exhibiting its highest level at intermediate levels of isolation. |

Box 1. (cont) A summary of recent theories of biogeography and biodiversity of insular biotas.

Table B. Summary of features included in some of the principal models of island biogeography within the context of their integral processes and conceptual domains (highlighting and a "+" indicates that this feature was included in the model).

| Theories and models (listed chronologically) | Integral Processes and Mechanisms | | | | Conceptual and Explanatory Domain | | | | | | | | | |
|--|-----------------------------------|------------|--|--|---|-------------------------------------|-------------------------------|--------------|-------------------|---------------------|----------------------------------|----------------------------------|---|---|
| | Fundamental processes included | | Interactions between fundamental processes | Interspecific difference in processes/capacities | Ecological interactions between species | Dynamics of the geographic template | Gradients in species richness | | | The Island Syndrome | | | | |
| | Immigration | Extinction | | | | | Evolution | Species-area | Species-isolation | Species-age | Species composition ^b | Ecological dynamics ^c | Evolutionary transformations ^d | |
| Taxon Cycles (Wilson 1959, 1961) | + | + | + | + | + | | | | | | + | + | + | |
| Equilibrium Model of Island Biogeography (MacArthur and Wilson 1963, 1967) | + | + | (+) ^a | + | | | + | | | | | | | |
| Assembly Rules (Diamond 1975) | + | + | | + | + | | | | | | | + | | |
| Ecological Model of Body Size Evolution (Lomolino 1985; Lomolino et al. 2011) | + | + | + | + | + | | | | | | | | | + |
| Species-based, Hierarchical Model (Lomolino 1999, 2000) | + | + | | + | + | | | | + | | | + | | |
| Model of Dynamic Disequilibrium and Phylogenetic Diversification (Heaney 2000) | + | | + | | | | | | + | + | | + | | |
| Model of Ontogeny and Anagenic Evolution (Stuessy et al., 2006; Stuessy 2007) | | | + | | + | | | | + | + | | | | |
| Global, Statistical Model of Island Biogeography (Kalmar and Currie 2006) | | | | | | | | | | + | | | | |
| General Dynamic Model of Island Biogeography (Whittaker et al 2008; Whittaker et al. 2010) | + | + | + | | | | | | | | | | | |
| Unified, Neutral Model of Island Biogeography (Rosindell and Phillimore 2011) | + | + | + | | | | | | | | | | | + |

^aMacArthur and Wilson's earlier, mathematical version of their model included speciation along with immigration and extinction, but this was dropped from their paradigmatic model which, as a result, became limited to patterns in species-richness within ecological time scales.

^bIncludes endemism (boxes marked as +e), disharmony and other patterns in composition and co-occurrence of species on islands.

^cIncludes niche shifts, ecological release, density compensation and supergeneralist phenomena.

^dIncludes evolutionary modifications in dispersal capacities, body size and bauplan (animals) or growth form (plants).

^eIncludes patterns in endemism.

As illustrated in Box 1, island biogeography theory comprises a collection of theoretical models, most of these developed over the past five or so decades, and varying in the breadth of their conceptual domains and the particular insular phenomena they attempt to explain. While this is not an exhaustive list, and full explanations of each of these models are well beyond the scope of this monograph, the models featured here serve to demonstrate the diversity of approaches, their limitations and, most importantly, the potential for applying the fundamental principles of biogeography to expand the conceptual domain of particular models, to provide a more holistic and integrative understanding of ecological and evolutionary phenomena exhibited by insular biotas.

The first and earliest model featured here is that of Wilson's (1959, 1961) taxon cycles, which is arguably one of the most insightful and inclusive, with emphasis on all three fundamental processes along with interspecific differences and ecological interactions among species – the latter being the principal force driving the ecological and evolutionary dynamics of insular populations on each focal island. On the other hand, although the taxon cycle's conceptual and explanatory domain includes some of the major features of the island syndrome, explanations for patterns in species richness among islands are not an integral part of Wilson's theory (see also Economo and Sarnat 2012, Economo et al. 2015).

The next model featured in Box 1 resulted from the seminal collaboration between Wilson and MacArthur (MacArthur and Wilson 1963, 1967), which produced what was arguably the most influential of all models of island biogeography – the equilibrium model (see Lomolino and Brown 2009, Sax and Gaines 2011). In a real way, the equilibrium model appears to be the converse of Wilson's taxon cycles theory – sacrificing a focus on the biology of species and explaining the biotic dynamics of the island syndrome for the versatility of an elegantly simple model capable of explaining two very general patterns in richness (of hypothetically equivalent species), the species–area and species–isolation relationships. That is, the equilibrium model is distinguished, but also

limited, by its simplifying premise of being species-neutral, largely ignoring both differences among, and interactions between, species (Table B of Box 1). Similarly, although the first articulation of the equilibrium model included evolution (speciation) as one of the fundamental processes contributing to a balance in species numbers, the model in its most familiar graphical form was simplified to focus only on the processes of immigration and extinction. Thus, its conceptual domain is largely limited to explaining patterns in species richness as a function of island area and isolation, and this only under the assumption of a dynamic equilibrium between immigration and extinction.

Diamond's (1975) assembly rules and Lomolino's (1999, 2000c) hierarchical model also fail to explicitly include evolution as a fundamental, biogeographic process but, because they do include differences and interactions between species (i.e., they are species-based rather than species-neutral), their conceptual domains encompass patterns in species composition (and also ecological dynamics in the case of assembly rules; species–area and species–isolation patterns in the case of the hierarchical model; see Figure 9). The ecological model of body size evolution (Lomolino 1985, Lomolino et al. 2011; see Figure 3), although inclusive of all three fundamental biogeographic processes, interactions among those processes, and species differences and species' interactions, is, as its name implies, quite limited in its scope. It is, however, the only model of those listed in Table B of Box 1, other than Wilson's theory of taxon cycles, to explicitly address evolutionary transformations of insular biotas. At the other end of the spectrum in terms of its simplicity is the global statistical model of Kalmar and Currie (2006; see also Kreft et al. 2008), which is not only species-neutral but process-neutral as well; i.e., it provides an empirical, correlative model for predicting patterns in species richness among islands, based on their environmental and physiographic characteristics, but without explicitly addressing any of the fundamental biogeographic processes.

MacArthur and Wilson's equilibrium model was antecedent to Hubbell's (2001, 2010) unified, neutral theory of biodiversity which, in turn, was

the basis of Rosindell and Phillimore's (2011) neutral model of island biogeography (Box 1). Although the latter model accounts for patterns in richness (including that of endemics) over islands varying in area, isolation and age, its ability to explain the ecological and evolutionary dynamics of insular populations and patterns in species composition (other than the relative proportion of endemics in each assemblage) is limited. Heaney's (2000) model of disequilibrium and phylogenetic diversification also addresses patterns in endemism, as well as those of species–area and species–isolation, and it does this without explicitly assuming an equilibrium (between evolution and extinction) or including extinction as a fundamental process (see also Heaney 2007, Heaney et al. 2013).

Only two of the models featured in Box 1 include the dynamics of the geographic template (specifically, the age and geological development of islands) as an integral foundational process, thus extending their conceptual domains to explaining patterns in richness over island age, as well as island area and isolation. In contrast to Stuessy's model of ontogeny and anagenic evolution (Stuessy et al. 2006, Stuessy 2007), which is based on the influence of island age on speciation, the general dynamic model of Whittaker and his colleagues (Whittaker et al. 2007, Whittaker et al. 2008, Whittaker et al. 2010, Borregaard et al. 2016b; see also Steinbauer et al. 2013, Ali and Aitchison 2014, Valente et al. 2014) explicitly includes the temporal dynamics of all three fundamental biogeographic processes, i.e., from the time of island emergence to its geological maturation and eventual submergence beneath the ocean surface (Figure 6c).

Clearly, at least in their current form, none of these models provides a fully integrative theory of the range of ecological and evolutionary phenomena that characterize insular biotas. Consistent with the central assertion of this review, such an integration and synthesis requires that we expand the fundamental premise and conceptual domain of our models to include all three fundamental biogeographic processes (immigration, extinction and evolution), and their associated processes and mechanisms (interactive effects,

species differences, species' interactions and dynamics of the geographic template). Perhaps an entirely new and integrative model will emerge to serve this goal of unifying island theory, but it is at least as likely that this will be achieved through advancing one of the existing models. For example, the species-based, hierarchical model may be advanced by including evolution and the temporal dynamics of islands and insular biotas, or the general dynamic model may be expanded to more explicitly include species' differences, ecological interactions among species, and their ecological and evolutionary consequences. In fact, Robert J. Whittaker and his colleagues are making impressive strides toward these ends (e.g., see Matthews et al. 2014, Whittaker et al. 2014, Parmakelis et al. 2015, Borregaard et al. 2016a,b).

Let us now return to the conceptual model of Figure 1b for a final lesson – not as much on the marvels of island life, but on the perils of evolution in the ecologically simplified and disharmonic communities of isolated, oceanic islands. As noted in the model, immigration of species already residing on the island may rescue their populations from extinction. However, rather than rescuing populations from extinctions as is often the case for natural metapopulations, anthropogenically accelerated immigrations of mainland biotas may have just the opposite effect (Figure 1b, green arrow and text at the bottom of the figure). As humans have demonstrated in all too many unwitting 'experiments' of species introductions, the rate of anthropogenic immigrations far exceeds that of natural immigrations and, more importantly, it far exceeds the abilities of native insular forms to adapt or avoid "the stranger's craft or power" (Darwin 1839: 47) by shifting their ecological niches, by somehow reversing their ecological naiveté, or by regaining their lost powers of dispersal.

Over 135 years since Alfred Russel Wallace published his seminal and holistic treatise on *Island Life*, and some five or so decades after the paradigm shift driven by MacArthur and Wilson's elegant and simplifying equilibrium model, island biogeography appears to be primed for the emergence of a genuinely integrative theory on the

ecological and evolutionary phenomena exhibited by insular biotas. This potential advance in island theory, in turn, may serve as an exemplar for advancing biogeography theory in general – i.e., by integrating and applying the field's fundamental, unifying principles in order to understand and conserve island life.

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