Title: Island Biogeography: taking the long view of nature's laboratories

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One Sentence Summary: Island biogeographical processes respond to the geodynamics of

remote islands, producing predictable diversity patterns.

Summary:

BACKGROUND: Ever since Darwin, natural scientists have turned to islands for inspiration and for model systems. For the last half century, they have done so largely within the paradigm established by Robert H. MacArthur and Edward O. Wilson's *Theory of Island Biogeography,* which provided a quantitative, dynamic framework, based upon assumptions of geographically predictable patterns of immigration, extinction and speciation. While this approach has proven productive, its application to remote archipelagos and evolutionary timescales has been hampered by a rather static view of islands themselves, despite mounting evidence of their dynamism as platforms. We review recent progress in integrating the largely ecological thinking of their theory with insights on the longer-term dynamics of both the islands and their biotas.

ADVANCES: Classification and analysis of marine islands by their geophysical dynamics, and of their species by how they colonized, provides a step towards a more nuanced biogeography out of which new insights are already emerging. This perspective is exemplified by the general dynamic model of oceanic island biogeography, which predicts how immigration, speciation and extinction respond to the typical life-cycle of hotspot islands, with phases of emergence, development and submergence. The model successfully predicts such emergent patterns as the occurrence of peak diversification on youthful, expanding islands with maximum vacant niche space. Diversity patterns analysed for large numbers of data sets have confirmed the significance of in situ evolutionary dynamics on remote archipelagos, which typically possess steep island species–area relationships, especially for endemic taxa. We may infer that variations in propagule flow amongst islands within archipelagos are important in modulating these emergent diversity patterns. There is, for example, good support for an 'island progression rule' in which older land masses donate colonists to younger islands (consistent with the generalization of islands as 'sinks'), but there is also increasing evidence of 'reverse colonization', including from

islands to continental regions. Advances are also being made in linking such island biogeographical models with the classic traits and syndromes of insular species, although this first demands that previous generalizations are rigorously re-examined using expanded datasets and modern techniques of analysis. A classic insular syndrome is the loss of dispersability of formerly dispersive species following island colonization, for which there is now good evidence for several taxa, including many genera of land birds. Yet, paradoxically, and perhaps controversially, it has also been inferred that many species of plants lacking specialized dispersal adaptations can colonize quite remote islands, often by non-standard means of transport. Unfortunately, island evolutionary syndromes, such as loss of flight in birds, frequently pre-dispose species to heightened extinction risk when islands are colonized and transformed by humans, as we also document.

OUTLOOK: Developments in theory and in analytical and modelling capabilities within biological and Earth system science, and the pooling of large numbers of data sets, enhancing statistical power, collectively hold the promise of a new synthesis in island biogeography. This synthesis will need to accommodate evidence of the long-term dynamics of remote island systems, whereby some lineages persist far longer than any particular island platform, while others founder as their sole island home sinks under the waves. The promise is of a biogeography in the tradition of the MacArthur–Wilson theory, generating and testing predictive models, but extended to accommodate a more sophisticated suite of insular geological and environmental dynamics, combined with a fuller understanding of patterns and processes of gene flow within and between archipelagos.

Abstract: Islands provide classic model biological systems. We review how growing appreciation of geo-environmental dynamics of marine islands has led to advances in island biogeographic theory accommodating both evolutionary and ecological phenomena. Recognition of distinct island geodynamics permits general models to be developed and modified to account for patterns of diversity, diversification, lineage development and trait evolution within and across island archipelagos. Emergent patterns of diversity include predictable variation in island species–area relationships, progression rule colonization from older to younger land masses, and syndromes including loss of dispersability and secondary woodiness in herbaceous plant lineages. Further developments in earth system science, molecular biology and trait data for islands hold continued promise for unlocking many of the unresolved questions in evolutionary biology and biogeography.

Main Text:

Islands as natural laboratories

While there are many types of insular system, including lakes, caves, seamounts, forest habitat islands and sky islands (*1*), our focus here is mostly on marine islands: systems of immense biogeographical interest. Marine islands are great natural laboratories, providing innumerable replicated 'experiments' in the factors controlling the distribution, character, and diversity of species. They also contribute disproportionately to global biodiversity and to the contemporary extinction crisis (*2–5*). Comprising just 3.5% of Earth's land area, islands contribute 15–20% of terrestrial species and 27% of human languages. Spectacular insular radiations include some 154

species of *Anolis* lizard in the Caribbean, an estimated 1000 species of drosophilid flies and >50 species of honeycreeper on Hawaii, and plant genera such as *Aeonium*, *Sonchus* and *Echium* (29–55 species) in Macaronesia (*2, 5–7*). Equally strikingly, more than 60% of the documented terrestrial species extinctions since 1500 CE have been island endemics (2, *3, 8, 9*) (Fig. 1).

Here we reflect on recent advances in understanding these systems, 50 years on from the landmark publication of Robert MacArthur and Edward O. Wilson's *Theory of Island Biogeography* (*10*). First outlined in the journal *Evolution* in 1963 (*11*), their theory was developed only a decade after the discovery of the DNA double helix and contemporaneously with the tectonic shift in Earth Sciences initiated by confirmation of sea-floor spreading. They took a deliberate step away from ad hoc historical narrative towards a predictive, quantitative biogeography, developing a body of theory that continues to inspire (*12–14*). The theory was built around a simple neutral model, easily demonstrated graphically, arguing that the universal processes of island biology – immigration to and extinction from each island – were perpetually operative, varying straightforwardly and predictably in relation to the fundamental geographical properties of isolation and island size, respectively (Fig. 2A).

The 1967 monograph (*10*) inspired numerous studies testing the assumptions, predictions and practical application of their model, in the process generating large numbers of datasets describing the diversity of island biotas. Intriguingly, despite the book's opening observation that islands provide '…the necessary replications in natural "experiments" by which evolutionary hypotheses can be tested…' (*10* p. 3), the theory has fared poorly in application to remote islands and has been criticised, perhaps harshly, for ignoring evolution (*15–17*). Although largely presenting an ecological theory, the monograph developed an evolutionary–ecological argument spanning near-time population processes up to emergent evolutionary processes on remote

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islands. It also discussed the trait shifts indicative of adaptation to island living and the significance of cladogenesis, leading in the fullness of time to a predicted evolutionarily-adjusted equilibrium diversity pattern (Fig. 2B,C). But little attention was paid to the geo-environmental dynamics of islands.

Since the monograph was published, further advances, especially in evolutionary biology and Earth system science, have revolutionized understanding of the dynamics of remote island systems. It has become increasingly evident that the islands themselves are dynamic, changing in size, configuration and isolation through geological and climatic change processes. Advances in theory, computer power, data availability and simulation modelling are increasingly enabling exploration of these dynamics (*18–20*). At issue is the extent to which island biodynamics keep pace with environmental dynamics, reaching meaningful dynamic equilibria, or are better considered dynamic non-equilibrium systems (*15, 19–24*). For example, Valente et al. (*19*, *25*) incorporate likelihood-based phylogenetic birth-death models alongside MacArthur–Wilson dynamics to model island avifaunas of the Galápagos and Macaronesia, drawing the conclusion that whereas the Galápagos finch clade and in general the Macaronesian avifaunas may have reached equilibrium richness prior to human interference, overall avian richness of the Galápagos remains non-equilibrial.

Island geodynamics drive biological dynamics

Islands are typically framed in modern island theory as subject to colonization from mainland species pools (*2, 10*) (Fig. 2A). Yet, stretching back to the 19th Century, there has been argument about the relative importance of long-distance dispersal, which Charles Darwin and Alfred Russel Wallace (*26*) favored, and what is now termed vicariance, the break-up of widespread distributions. In Darwin's day, vicariance thinking took the form of extensionism, the idea of the

widespread foundering of former land connections (*27*). In the 20th Century, Wegener's continental drift and, subsequently, plate tectonic theory, provided an alternative vicariance explanation for the presence of relatively undispersive species on remote land masses: they had persisted following separation by barrier formation (*28, 29*). While dispersalism is currently in the ascendancy (e.g. *30–33*), a complete theory of island biogeography must accommodate the evidence for vicariance processes linked to island submergence/emergence (sometimes repeatedly via subsidence and uplift), subduction, sea-floor spreading and shifting positions of long-lived island terranes (*28, 29, 31, 34*). This highlights the need for a more refined classification of island types than the traditional split (*2*) into oceanic, continental fragment and continental-shelf.

Recently, Jason Ali (*35*) proposed just such a framework of major geophysical settings: continental, island arc, composite terrane, mantle-plume hotspot, and 'other minor types'. Alongside which, he proposed classifying island life-forms based on how an organism's ancestors are thought to have colonized the island in question: recent land-bridge, recent ice-sheet, overwater-dispersed and deep-time vicariant. Recent land-bridge colonization typically refers to species that were able to cross dry land during periods of lowered sea-level, recent ice-sheet to high-latitude systems where the past extension of sea-ice allowed over-ice colonization. Globally, many continental-shelf islands derived most of their contemporary biota from larger mainland areas during Quaternary sea-level minima of as much as 134 m below present (*36*). Even true oceanic islands were greatly reduced in isolation at those times by the emergence of present-day seamounts as islands. While the majority of New Zealand's biota appears to owe its origins to dispersal, recent work has identified Zeelandia as a largely drowned continent, including present-day New Zealand and New Caledonia (*37*). The heated vicariance–dispersalist

arguments, so often focused on island systems with continental underpinnings (e.g. New Caledonia, New Zealand, Madagascar), but including even mantle-plume hotspot systems (cf. *28, 29, 38*) may thus be superseded by recognizing that an island can host multiple colonizer types (*35, 39*). Given all these processes and sufficient time, we can envisage particular lineages becoming distributed across a set of now far-flung islands by a combination of relatively modest dispersal prowess and excellent persistence. In perhaps many cases, the distances crossed, while substantial, were less impressive than might appear from a contemporary map (*31, 38*).

Situations such as Zeelandia are geographically limited, however, and oceans are mostly floored with oceanic crust, created at mid-oceanic ridges. As this crust cools and becomes denser, the plate and islands formed upon it subside for up to 70 million years, sinking as much as 2 km (*35*). This again is a generality. For example, it has recently been shown that the oldest Azorean island, Santa Maria, which first emerged 6 million years ago, initially subsided to form a guyot (a submerged island), before re-emerging during the last 3.5 million years (*40*). These findings have greatly shortened the timeframe of colonization and evolution in the Azores. Since final emergence, the Azores have remained remote, gathering their biota by dispersal from distant islands, and Old and New World mainland, across very substantial stretches of open ocean (*41*). Such findings reaffirm a role for long-distance dispersal within island biogeography (*30–33*).

Another category we might add to Ali's (*35*) typology is sub-surface seamounts (*42*). Estimates of their number vary from 8000 to 100,000 of >1km height (*43*) and just a fraction, perhaps <5%, have been directly sampled scientifically (*44*). Many seamounts and oceanic islands have a common origin and form part of the same mantle-plume hotspot systems (Fig. 3A). To simplify, as the plate moves over the hotspot, a sequence of islands is produced, each of

which erodes and subsides as it is carried away from the hotspot. Within the North Atlantic, Macaronesia has featured substantial islands for some 40–60 million years, although the oldest contemporary islands (e.g. Selvagem Grande) are half this age (*38*). The Hawaiian hotspot has been producing islands even longer but the oldest high island dates to only 5.1 million years, all older islands having subsided to become atolls, or seamounts (*2*).

Hotspot islands thus typically shrink and submerge after a few million years. At some point, the tendency to gain species through occasional immigration and cladogenesis is countered by an increasing rate of species extinction: diversification slows and is reversed. Ultimately any single-island endemic species failing to migrate to another island become globally extinct.

These coupled geodynamic and biological process regimes are the basis of the general dynamic model (GDM) of oceanic island biogeography (*21*) (Fig. 3B), which has had some success in predicting patterns of insular diversity across archipelagos (*24, 45*). Of course, it takes time for island colonists to evolve into distinct species and whereas some lineages respond to the availability of comparatively unexploited terrain on young islands by diversifying at extremely fast rates (*46*), to peak on intermediate-aged islands (*47, 48*), others may be slowly increasing in species richness even on old, foundering islands (*49*). It remains a challenge to determine which traits best explain the greatly varying rates of divergence exhibited by different colonizing lineages (*31, 45–48*).

The hotspot island ontogenetic model underpinning the GDM (above, Fig. 3A,B) is highly simplified but the reasoning can be extended to differing geophysical contexts (*20, 24*) (Fig. 3C). More realism can be added at the expense of generality, by incorporating Quaternary (or earlier) sea-level changes (*22, 23, 36*). Dealing with such complexities requires combinations of empirical and simulation methods drawing on a range of disciplinary areas (*19, 20, 24*). As we

gain increased resolution on the various distinct forms of insular geodynamics, more sophisticated theories will be enabled, describing the varied roles of islands as generators of diversity, culs-de-sac, refugia and stepping stones (e.g. *30– 32, 39, 41, 50*). Extending such thinking to various forms of habitat islands provides further challenges, focused on identification of environmental change processes common to and impacting upon the systems in question, and how these processes may interact with shorter term ecological dynamics (*2, 9, 51*).

Remote archipelagos and island species–area relationships

The increase in species richness with area is one of the few law-like regularities in ecology (*52, 53*). Island area holds a central role in the theories outlined above, acting as a proxy for space and resource availability, constraining resulting species richness patterns (Figs 2, 3). That island species–area relationships (ISARs) are steeper than sampling curves for non-isolated areas was a key observation leading to the MacArthur–Wilson theory (*10*) and its application in predicting species losses following habitat fragmentation (*2, 51, 52*). In practice, the use of island theory in this way has proven controversial, due in part to the mixing of different forms of species–area relationship (*53–55*). For example, it has been shown that nested sampling curves, whereby smaller sample areas are nested within large, are typically triphasic in logarithmic space, characterized by steeper increases in species richness at both small and large spatial scales (*53, 56*). However, ISARS are not nested, but comprise data series of paired values of richness and area for each island (*55*). Here, we therefore focus on synthesis of results from ISAR meta-analyses of several hundred datasets, based on the application of the log-transformed power model: $\log(S) = \log(c) + z * \log(A)$, wherein $\log(c)$ represents a crude 'biotic richness' constant, z represents the slope of the relationship, S is species richness and A is island area (*57, 58*). The logic for doing so is that the power model has been shown to be the best general model for the

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ISAR, providing significant fits for a large majority of data sets (*57, 58*) and having the added virtue of simplicity of representation (*52, 58*).

In general, ISAR slope (z) increases from habitat, to continental-shelf, to oceanic islands (Fig 4A). The shallowest slopes and higher intercepts characterize systems with minimal isolation, in which island-extirpation events are typically rapidly reversed by recolonization ('rescue effects'), thus maintaining relatively high richness on small islands. By contrast, remote oceanic islands receive such low rates of immigration that colonizing lineages can diversify in isolation. In these systems, the smallest islands have low species richness because their small, unreliable resource bases cannot sustain marginal populations of small size or permit the origin and persistence of new-formed endemics. Hence the ISARs are characterized by high z and low log(c) values, a pattern that is especially pronounced for the endemic species sub-set (Fig. 4B).

Encouragingly, these recent studies support the idea that we can link pattern to process through the analysis of ISAR form. In general, steeper slopes (higher z) imply the increasing relevance of evolutionary as opposed to ecological dynamics. Remote archipelagos typically generate a high proportion of their own species by in situ speciation, with some lineages also producing distinct species on/within each island. This makes the archipelagos more akin to true biotic provinces (sensu *52*), than is the case for each constituent island. This reasoning is supported by analyses showing that for oceanic archipelagos, inter-Archipelago Species–Area Relationships (ASARs) are systematically steeper than the constituent ISARs (*57–60*) (Fig. 4C). There is a caveat: ISAR slopes for remote archipelagos can sometimes be much lower than suggested in Fig. 4A. Three linked factors may explain this: first, a high proportion of colonists of remote islands are derived from another island in (or near) the same archipelago, not from the mainland; second, archipelago area may therefore be the principal determinant of the size of the

species pool supported and of the degree of endemism; and third, the pattern of isolation amongst islands within the archipelago may further modulate ISAR form (Fig. 4C).

Numerous other factors influence insular diversity (e.g. traits of the taxon, contemporary climate, elevational range, Quaternary climatic and sea-level change, anthropogenic impact) (*4, 12, 23, 26, 50, 61*) and hence within each class of island system, much variation exists in the form and explanatory power of the ISAR. Yet by collating and analysing multiple data-sets within a comparative framework, we are increasingly able to distinguish the general from the specific (*57–61*). Further work is needed to test these propositions and develop a more complete species–area theory linking pattern to process (e.g. *12, 53, 56*).

Sinks and sources

Islands have traditionally been viewed as backwaters, or culs-de-sac, where lineages diversify for a while, becoming ever more insular and localized, but from which they rarely escape to recolonize continents. This idea was captured in the taxon cycle model, originally formulated for Ponerine ants (*10, 62*) (Fig. 5A) and recently re-affirmed for Pacific ants by new phylogenetic and distributional analyses (*63*). In taxon cycles, early colonists are pushed deeper into island interiors by later, more competitive colonists, continuing a pattern of movement from mainland source regions into the oceanic realm.

The general tendency of movement from mainland to island systems is repeated within hotspot archipelagos, as an island progression rule, of colonization from older to younger islands, with subsequent evolutionary divergence (Fig. 3A). This appears common, especially for taxa colonizing remote archipelagos contemporaneous with, or before the emergence of the oldest current island (*24, 33, 39, 64*). The occurrence of endemics older than the island, detected in a number of lineages and archipelagos, is consistent with the long-term operation of the dynamics

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inferred in Fig. 3A,B, and in cases may indicate very long-term persistence of insular lineages across a network of islands (cf. *28, 29, 31*).

While the classic view of islands as sinks (Figs 2, 5A) remains relevant for many lineages, increasingly, the ubiquity of that model has been challenged by phylogenies that indicate cases of back-colonization within archipelagos and from islands to mainlands, as well as island-hopping across extensive ocean basins (*7, 30–33, 41*) (Fig. 5B). Genetic analyses of Macaronesian bryophytes, for example, support de novo foundation of continental populations from insular ancestors, indicating that the islands of Macaronesia have provided stepping-stones for transoceanic movement linked to long-term westerly atmospheric circulation (*41*). Even more startling is the claim, again from molecular phylogenetic studies, that the uplift and formation of the Wallacean archipelago triggered the global radiation and expansion of all songbirds (the Oscines, constituting approximately half of the word's 10,000 bird species (*65*)), which originated in the region of present-day Australia or New Guinea and expanded in multiple directions along the arc of islands then postulated to have emerged between the Australian, Pacific and Asiatic plates (*65, 66*) (Fig. 5B).

Island Syndromes

Larger remote islands typically feature high proportions of endemic species and sometimes feature relictual or palaeo-endemic species (differing only slightly from extinct mainland ancestors): examples include several Macaronesian laurel forest trees (*28, 38*). Yet most oceanic island endemics have evolved into neo-endemic forms in situ. They have done so not through a single mechanism but through the operation of a rich variety of evolutionary processes (*33, 67, 68*), despite which, it appears possible to identify particular traits and syndromes, on which island forms repeatedly converge. Commonly discussed examples include a tendency towards

flightlessness and loss of dispersal powers, naïveté towards predators, diminished clutch size in birds, woodiness in typically herbaceous plants, and body size changes (*67, 69*).

Although these examples are fascinating and intuitively appealing, systematic efforts are needed to determine that the proposed syndromes are indeed robust phenomena (cf. *69, 70*) and having done so to understand their causation. Progress is being made. The rapidly increasing availability of large trait databases and of molecular phylogenies has greatly advanced our understanding of these varied patterns of insular evolution, both across large clades of species and at sub-specific level, often revealing patterns of repeated convergent trait evolution across multiple lineages on multiple islands (*31, 47, 67, 71–75*).

One good example is the occurrence of insular woodiness in otherwise herbaceous lineages, where it has been clearly established that the general pattern is for the insular woodiness to be secondary, evolving from herbaceous ancestors (*73*). Another is flightlessness in birds, which is generally associated with ground nesting and is exemplified by birds such as the solitaire (Fig. 1A). Statistical testing had previously suggested it to be a feature of relatively small numbers of higher taxa, most notably rails (Rallidae) (*74*). However, it has recently been established from studies of several hundred populations that even in actively volant species there have been changes in flight muscles and hind limbs consistent with a broad trend towards insular flightlessness, repeated in four orders, nine families and numerous genera of land birds (*75*). This trend manifests in a shift in investment from forelimbs to hindlimbs and appears to be a direct response to reduced predation pressure in the absence of terrestrial mammals and specialist bird-hunting avian predators. Unfortunately, the syndrome of traits of which this is the most striking manifestation has also left these island forms especially vulnerable to introduced vertebrate predators, and many have become extinct or are threatened with extinction (*76, 77*) (Fig. 1).

The role played by chance long-distance dispersal has remained at the heart of debate in island biogeography since the 19th Century, hence evolutionary syndromes connected with dispersal, such as flight loss, are of abiding interest. Whereas Darwinian interpretations emphasize adaptive features that enable colonization of distant oceanic islands, and then the subsequent loss of dispersiveness (e.g. *46, 75*), Darwin's contemporary Joseph Hooker argued that the existence of a set of plant species lacking such traits on the Southern Ocean islands supported extensionism. Ever since, island biologists have focused on dispersal adaptations and have continued to debate the explanatory power of long-distance dispersal (*26–33*).

Intriguingly, recent work has emphasized the importance of non-standard dispersal, i.e. dispersal seemingly unconnected with diaspore specialization (*78, 79*). Viable seeds of dozens of plant species eaten by Canarian island lizards (*Gallotia atlantica*) have been found in pellets of predatory birds, capable of inter-island movements (*79*), while 63% of the Azorean native flora (most of which are not endemic) have unspecialized diaspores (*80*). Similarly, the survival of snails and beetles swallowed by birds allows for their movement between islands (*81*), while even exceptional geophysical events, including volcano flank collapses, have been invoked as potentially explaining particular colonization events (*82*). Comparative analysis of the Galápagos flora rather remarkably suggests that the availability of suitable habitat on the islands provides a more general explanation of species assembly than dispersal limitation (*83*). Hence, although the poor dispersability of many island species has been shown to be a consequence of the post-colonization loss of dispersal capacity (*2, 75*), it also appears that at least for plants and invertebrates, many species lacking evident long-distance dispersal adaptations can reach quite remote archipelagos (*81, 83–85*).

The re-affirmation that islands are stocked by colonists possessing a wide range of intrinsic dispersal capabilities prompts reflection. MacArthur and Wilson (*10*) argued that it was towards the extreme edge of a taxon's dispersal capacity that the few lineages arriving had best opportunity for diversification. But most colonist lineages fail to diversity, the colonizing event resulting in a single native (sometimes endemic) species. Those undergoing cladogenesis are species able to spread from initial points of landfall, yet also able to attain reproductive isolation within/between islands: they then have to diversify swiftly within quite small areas. Peak diversity is thus expected to be concentrated in clades of fast generation times, small body sizes and intermediate dispersability (cf. *33, 46, 47, 64, 86*).

Concluding Remarks

Fifty years on from the landmark *Theory of Island Biogeography* (*10*), the subject is in a vigorous period of development (*13, 14, 87*). Several additional themes would warrant separate review: the legacies of Quaternary environmental change, the unexploited potential of islands as model Anthropocene systems, and the multi-level analysis of archipelagic processes are just three broad examples (*12, 22, 88, 89*). The impacts of Quaternary environmental change are complex, involving repeated cycles of varying amplitude of climate, and sea-level change, generating changes in current systems, isolation and connectivity on multiple scales (*22, 23, 50*). We are only beginning to tease out how these change processes impacted on remote island systems, and for many systems to distinguish the impact of human colonization from natural change drivers (*77*). The analysis of habitat fragmentation through the lens of island theory has played an important role within conservation biology, as discussed above, but arguably the opportunities for using anthropogenically modified or created systems remain under-exploited (*12*). For example, just one dam in China, built in 1959, created the Thousand Island Lake

(Xinanjiang River), a system of abundant small islands that has generated highly resolved data on species–area relationships, compositional nestedness, turnover and species extinction (*90, 91*). There is also considerable unexploited model system potential in undertaking systematic monitoring of ongoing dynamics involving native and non-native species in highly altered and conserved ecosystems on oceanic archipelagos, as such systems allow linkage between population level processes, trait biology and emergent diversity patterns (*89,* 92). While much island research is firmly rooted in an archipelagic context and framing, e.g. most ISAR analyses are for discrete archipelagos, it is important to recognize that there are in fact multiple levels of isolation from that of habitat patches within islands, to the island as a whole, to archipelagos and groups of archipelagos. The spatial configuration of these different system elements and their dynamics over time may hold the key to understanding variation in form of ISARs, degrees of endemism, and biogeographical structure, and warrants further research effort (*23, 88, 93*).

We have focused herein on remote islands, systems of rapid recent scientific progress. These advances stem from multi-disciplinary attention to island geodynamics and evolutionary dynamics and how they interplay, offering encouragement that it may prove possible to reconcile perspectives of equilibrium and non-equilibrium, and even perhaps of dispersal and vicariance. Many of the themes discussed are also highlighted within a compilation of fifty key questions in island biology, in which a focus on long-term dynamics, changes in key biogeographical rates through time, and island trait evolution, are well represented (*14*). The combination of increasing application of molecular tools with advances in functional trait biology holds promise for unlocking many of the unresolved questions in longer-term (eco-evolutionary) island biogeography, and of developing models capable of accounting for the emergent patterns of lineage evolution discussed above (*24, 33, 68*). However, it remains something of a race against

time, because of the extraordinary pressures human activities are placing on island systems and

the ongoing loss of insular endemics. As we look to the future, we surely need to increase our

efforts to conserve island ecosystems (*77*).

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Fig. 1: Insular species extinctions since 1500CE. (**A**) Comparison of insular and continental extinctions for birds, plants and invertebrates (data source: *8*). (**B**) Cumulative island endemic extinctions, for those species for which an estimate of date of loss is available (compiled from: *8, 9, 94*). Inset: Rodrigues solitaire (extinct flightless endemic: by Frederick William Frohawk, 1907).

Fig. 2: MacArthur and Wilson's equilibrium theory of island biogeography. (**A**) The core model of how isolation-controlled immigration, *I*, and area-controlled extinction, *E*), respond to species richness (P, mainland species pool; dotted lines indicate combinations of richness and turnover rate for particular combinations of island area and isolation). (**B**) Hypothesized adjustments of initial equilibrium through community and evolutionary processes, leading to (**C**) predicted elevation of the island species–area relationship due to in situ diversification. The possible correspondence between time points in B and C is our addition. (A,C modified from *10*, B modified from *95*).

Fig. 3: The implications of island geodynamics for island biogeographical processes. (**A**) The dynamics of a generalized hotspot archipelago: island emergence, building, erosion and subsidence to become seamounts (guyots), drives phases where in turn immigration, diversification and extinction dominate, generating island progression-rule patterns; and (**B**) trends in key process rates (*I*, immigration, *S*, speciation, *E*, extinction (dashed lines), generating a realized species richness trajectory over time in relation to a hypothetical carrying capacity K,

controlled by the island ontogeny, as formalized in the general dynamic model of oceanic island biogeography (*20*); (C) alternative ontogenies, which can be used to generate alternative biogeographic models (*20, 24, 96*).

Fig. 4: Generalizations about Island Species–Area Relationships (ISARS) based on recent analyses of multiple data-sets (*57–60*). (**A**) As island isolation increases, the ISAR slope (*z*) increases, with intermediate isolation generating the highest rates of species turnover; and (**B**) for remote archipelagos, the endemics subset produce steeper slopes and lower intercepts than non-endemic native species; and (**C**) the slope of the archipelago species–area relationship (ASAR) should generally exceed the slopes of the constituent archipelago ISARs. Points A and B on the ASAR, represent the archipelago diversity for archipelagos A and B, respectively.

Fig. 5: Contrasting directional movements of evolutionary lineages. (**A**) Wilson's (*62*) taxon cycle describes the direction movement of ponerine ants from mainland to the Pacific islands, where derived forms evolve (inset: *Diacamma* sp., Sabah, by Steve Shattuck, 2012, http://Antwiki.org, license: https://creativecommons.org/licenses/by-sa/3.0/). (**B**) Fjeldså's (*66*) interpretation of Oscine (songbird) evolution, as an insular radiation in the region of present day New Guinea (using a reconstructed base map for c. 34 Ma), subsequently spreading throughout the globe to provide around half of the world's birds (inset: *Atrapia mayeri*, New Guinea, by Eden Cottee-Jones).
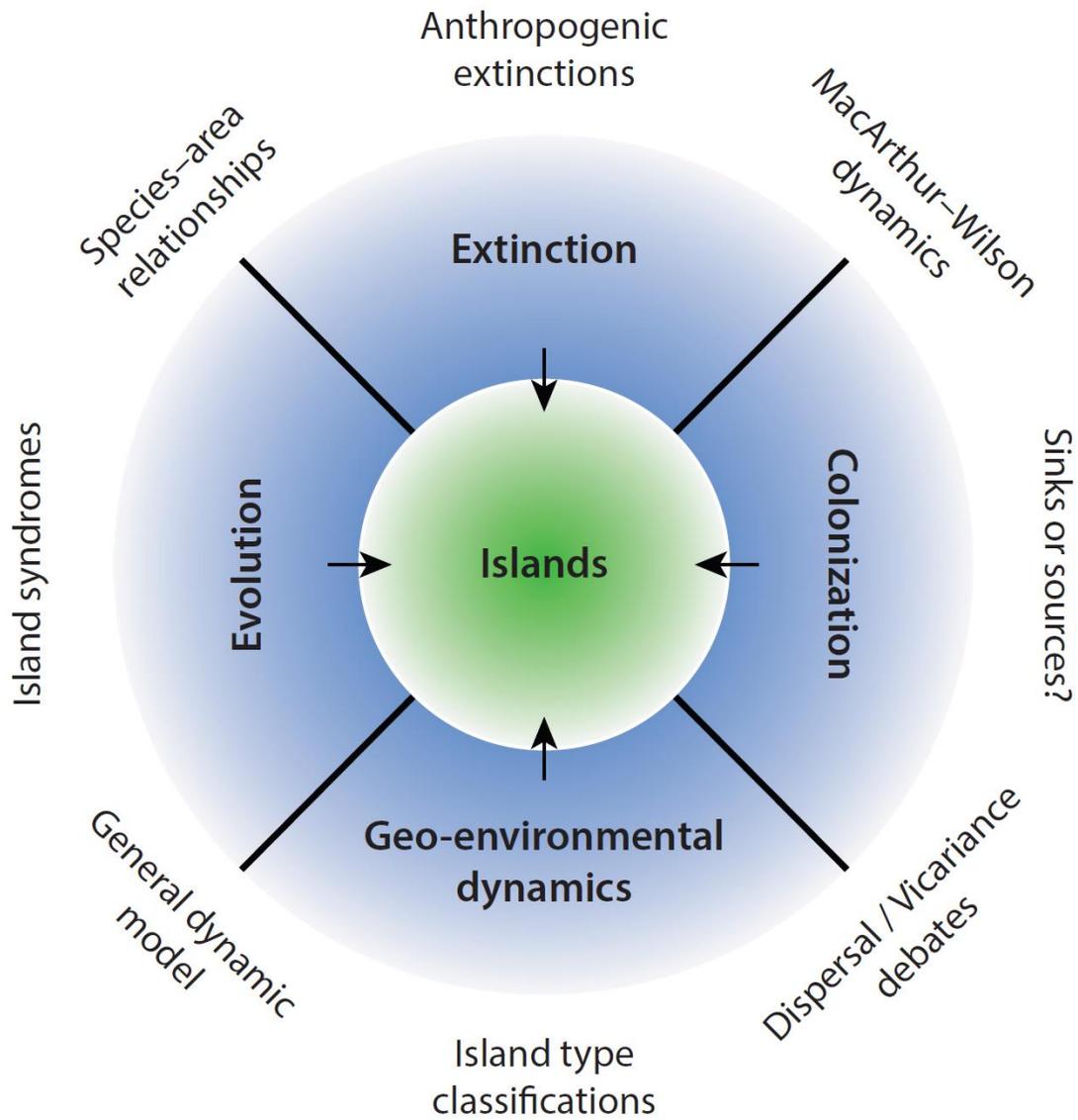
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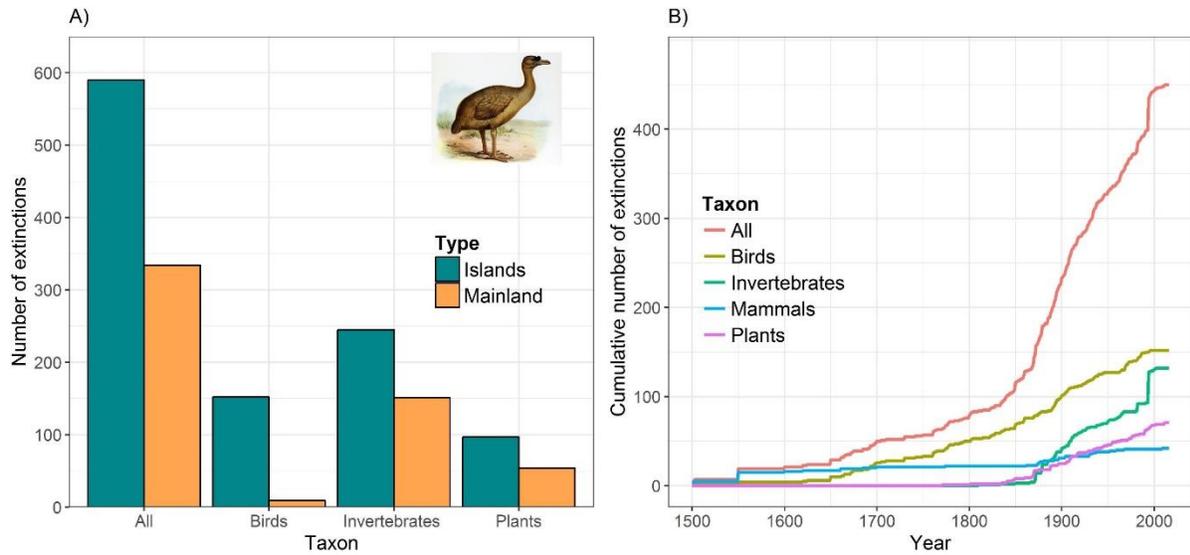
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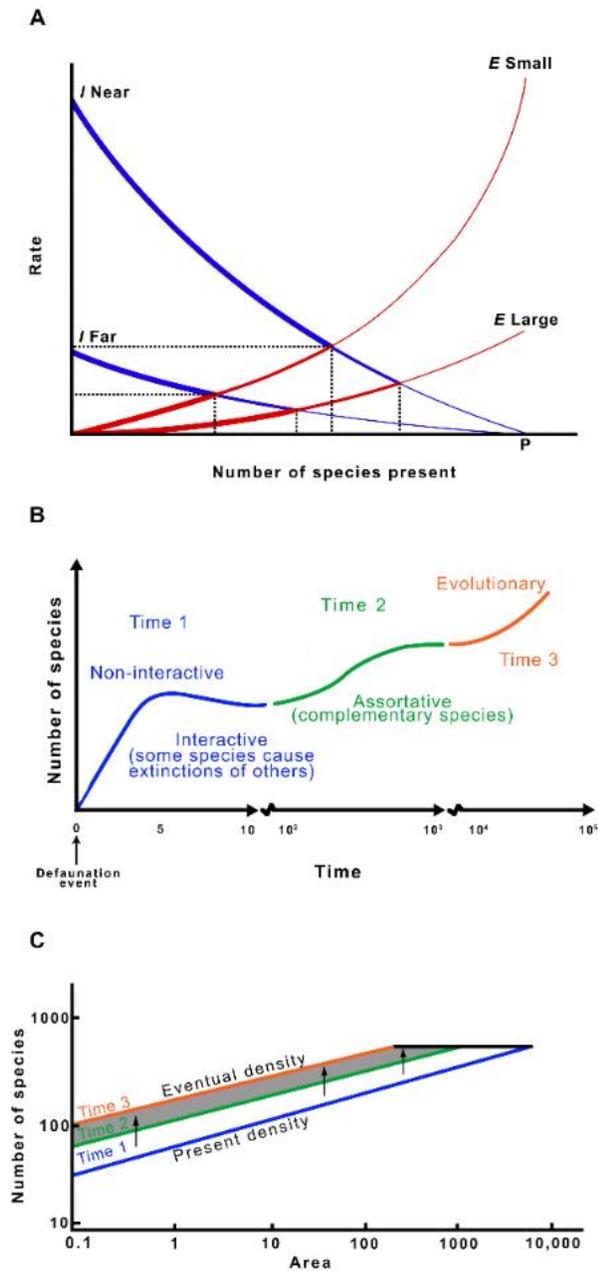
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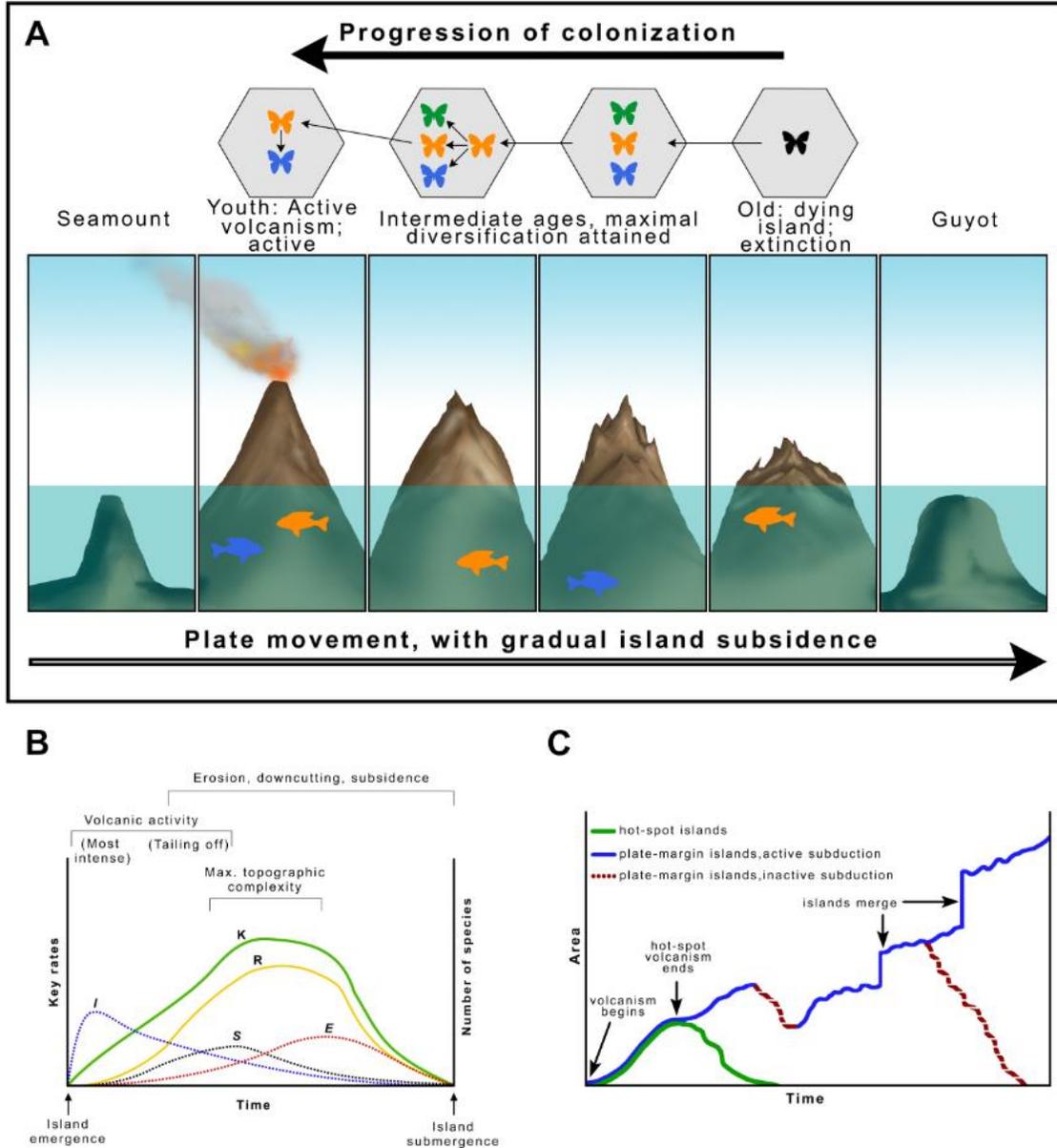correspondence between time points in B and C is our addition. (A,C modified from *8*, B modified from *82*).

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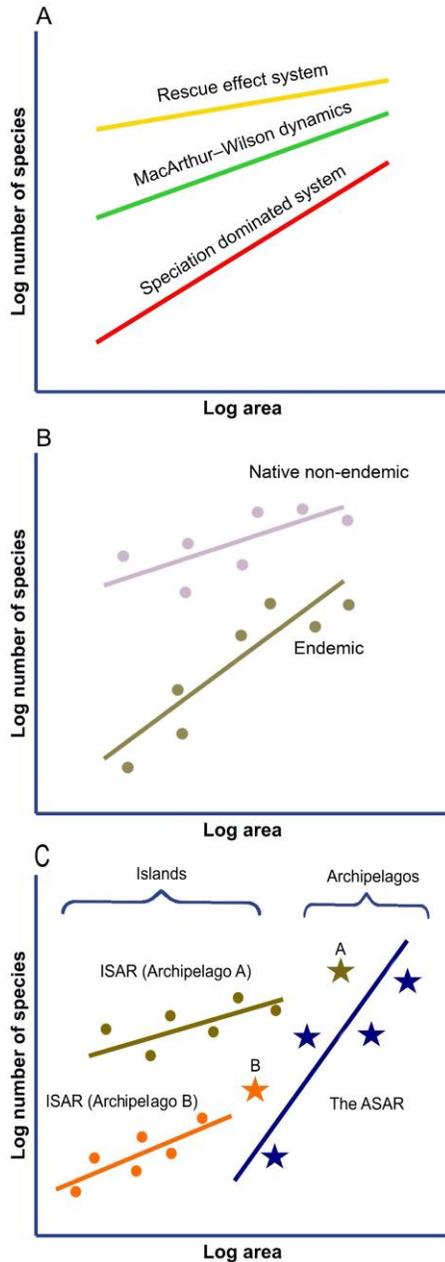
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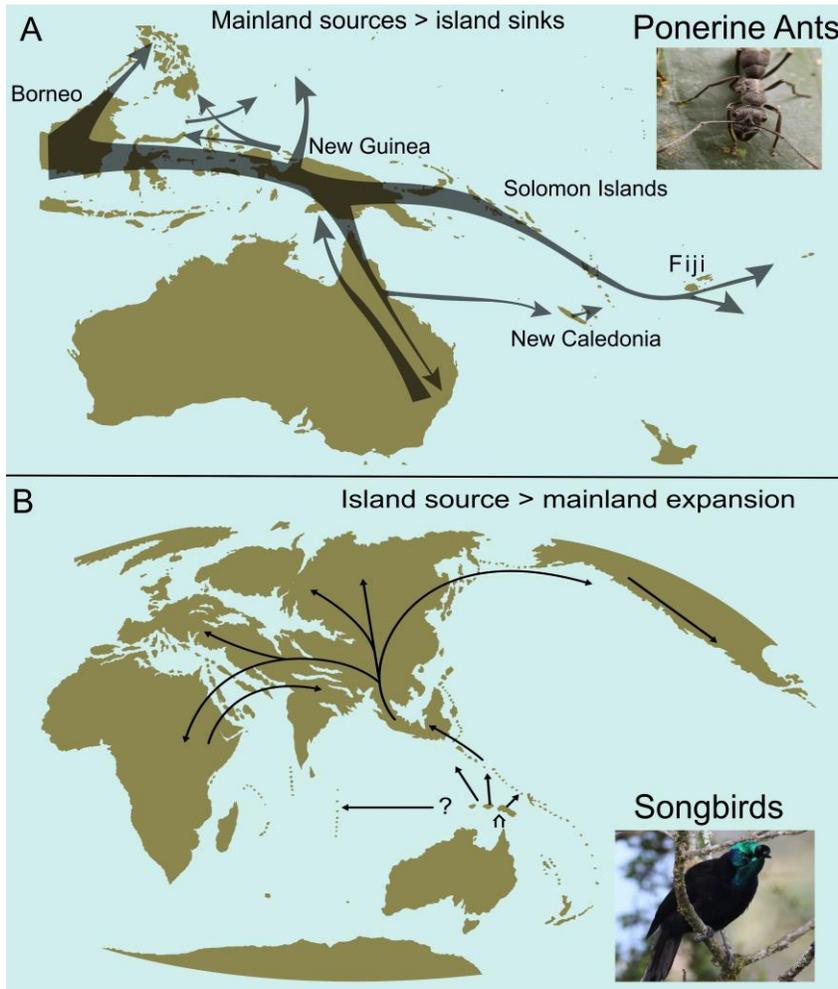
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