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New Directions in Island Biogeography

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Abstract

Aim: Much of our current understanding of ecological and evolutionary processes comes from island research. With increasing availability of data on distributions and phylogenetic relationships, and new analytical approaches to understanding the processes that shape species’ distributions and interactions, a prospective on this ever-interesting topic is timely.

Location: Islands globally.

Methods: We start by arguing that the reasons island research has achieved so much in the past also apply to the future. We then critically assess the current state of island biogeography, focusing on recent changes in emphasis, including research featured in this special issue of *Global Ecology and Biogeography*. Finally, we suggest promising themes for the future. We cover both ecological and evolutionary topics, although the greater emphasis on island ecology reflects our own backgrounds and interests.

Results: Much ecological theory has been directly or indirectly influenced by research on island biotas. Currently, island biogeography is reascent, with research focusing on, among other things, patterns and processes underlying species interaction networks, species coexistence and the assembly of island communities through ecological and evolutionary time. Continuing island research should provide additional insight into biological invasions and other impacts of human activities, functional diversity and ecosystem functioning, extinction and diversification, species pools and more. Deeper understanding of the similarities and differences between island and mainland systems will aid transferability of island theory to continental regions.

Main conclusions: As research in biogeography and related fields expands in new directions, islands continue to provide opportunities for developing insights, both as natural laboratories for ecology and evolution and because of the exceptions islands often present to the usual ‘rules’ of ecology. New data-collection initiatives are needed on islands worldwide and should be directed towards filling gaps in our knowledge of within-island distributions of species, as well as island species’ functional traits and phylogenetic relationships.
Introduction

“...we have the facts of distribution often presented to us in their simplest forms, along with others which become gradually more and more complex; and we are therefore able to proceed step by step in the solution of the problems they present.”

(Wallace, 1880, p. 234)

The nature of island biology research

Wallace (1880) argued that islands offer solutions to key ‘problems’ in biogeography, ecology, and evolutionary biology. But do biologists still believe this? Or has island biogeography become peripheral to the mainstream, pursued by a few enthusiasts mindful of early seminal contributions of island studies to these fields? Do islands continue to provide key insights and unique settings for research on important biogeographical, ecological, and evolutionary questions? We argue here that the answer to the last question is emphatically “yes”. While island-specific knowledge and understanding continue to grow, island biogeography is more integrated with mainstream research than ever before, and this integration will intensify over the coming decades.

Current themes in ecology, biogeography and evolutionary biology include the causes of variation in species richness, the assembly of ecological communities, mechanisms shaping the outcomes of evolutionary processes (including adaptive radiations), and the impact of global change on biodiversity (e.g. Sutherland et al., 2013). These issues are complex, involving scale-dependent processes, including species interactions, dispersal and colonization, gene flow and population dynamics, all played out in a heterogeneous world. Addressing such broad and complex issues will require the resolution of underlying mechanisms into straightforward hypotheses amenable to testing by experimental or comparative approaches. Islands can be powerful allies in such endeavours.

Island systems often present ecological, evolutionary and geological processes on timescales (usually so different among these processes) that are relatively similar, and often quite recent. On volcanic oceanic islands (Box 1), in particular, geological dynamics may be unusually fast and ecological dynamics relatively slow, aligning both quite closely with each other and with evolutionary dynamics (Rominger et al., this issue). Spatial scales tend to be compressed (e.g., by steep terrain) and spatial structure within archipelagos is discrete; local extinctions on oceanic islands are often global extinctions; and population differentiation between and within islands provides model systems for studying speciation. These features of islands provide a valuable testing ground for theory because they break typical scaling relationships that constrain the expression of many key biological processes within larger continental regions (Warren et al., 2015).

The importance of islands thus goes far beyond their shorelines and, ever since the seminal works of the great nineteenth century naturalists, much of the understanding gained from island-based studies has informed studies of mainland systems, as illustrated by many of the references highlighted in Tables 1 and S1. Indeed, during the 19th century, the work of Charles Darwin in the Galápagos Archipelago and of Alfred Russel Wallace in the Malay Archipelago, secured island biology in the foundation of contemporary research across most biological disciplines. Much of our current understanding of the ecological and evolutionary processes that shape diversity patterns comes from knowledge gained from islands. As Robert MacArthur and Edward O. Wilson (1967: 3) stated, “insularity is ... a universal feature of biogeography ... many of the principles graphically displayed in the Galápagos Islands ... apply in lesser or greater degree to all natural habitats.” Some discrete
habitats have been studied in the context of island theory, from mountaintops (or ‘sky islands’) to forest fragments and lakes (e.g. Brown, 1971, 1978; March & Bass, 1995), and island theory has provided the conceptual basis for much research on the ecological impacts of habitat fragmentation (Laurance, 2009). Island-like marine environments (e.g., marine lakes, i.e. pieces of seawater entirely surrounded by land; seamounts) also can be integrated within the general theories of island biogeography, according to Dawson (this issue). More generally, insularity within the contiguous landmasses of the continents remains under-appreciated (but see Steinbauer et al., in press b), and the same may apply to the oceans.

In their ‘equilibrium theory of island biogeography’ (ETIB; Box 1), MacArthur and Wilson (1963, 1967) applied insights from the population biology of the early-mid 20th century (birth and death processes) to island biogeography (colonization and extinction), and then to other disciplines (e.g., conservation biology). As well as leading to a paradigm shift within island research, this theory played a central role in the development of conservation theory (Pimm, 1991) and was a starting point for Hubbell’s (2001) development of the neutral theory of ecology.

Other theories and models that developed out of island research have become mainstays of ecology, conservation, and biogeography, sometimes with their island origins obscured (Tables 1, S1). The role of competition in patterns of species’ occurrences across archipelagos, the subject of sometimes acrimonious debate in the 1970s (e.g. Diamond, 1975; Connor & Simberloff, 1979), revitalized interest in studying mechanisms of community assembly (Simberloff & Collins, 2009). The ‘assembly rules’ (Box 1) debate also led to the current emphasis on formulating appropriate null models for community assembly (e.g. Weiher & Keddy, 1995), entailing the use of randomized null simulations for interpreting empirical results in biogeography (stemming from Connor & Simberloff, 1979; Gotelli & Graves, 1996). Further, the controversy raised by Jared Diamond’s (1975) analysis of the mechanisms of community assembly can be linked to Hubbell’s (2001) ‘unified neutral theory of biodiversity and biogeography’. Hubbell developed this theory “on the foundation of the ETIB” (Hubbell, 2001: 5), being partly based on the randomness of colonization and extinction of the ETIB, also by setting local communities in a geographical metacommunity, as islands are embedded in a colonization landscape. However, Hubbell defined neutrality at the individual level, with species being equivalent within a trophic guild and species’ abundance and diversity in a community being determined by random individual birth, death, and dispersal events. He also added a speciation term, using a model of random species formation. Hubbell’s theory can reproduce a wide range of community and biogeographic patterns, and it has initiated continuing debate on the nature of a world without ecological interactions (Ricklefs, 2006; Leigh, 2007; Rosindell et al., 2011).

We should also remember that Wright’s (1983) species–energy theory, the impact of which has mainly been in research on the causes of the latitudinal gradient in biodiversity, stems from island research. Wright developed his theory as an extension of the ETIB, particularly its species–area component, amalgamating it with Brown’s (1981) focus on energetics (see also Brown et al., 2004). The simple replacement of ‘area’ by ‘available energy’ in the ETIB, combined with Preston’s (1962a, b) earlier model for the distribution of species’ abundances, focused attention on relationships between energy availability and population sizes, extinction rates, and species richness. Similarly, Rosenzweig (1975) reformulated ETIB for continental regions, replacing immigration with species formation.

Amid the excitement about the value of islands for understanding the world in general, islands clearly are interesting in their own right. Islands are home to some of the most bizarre and threatened species of the world, many of which are in the public...
consciousness: ‘Darwin’s finches’ of the Galápagos Islands; Komodo dragons of Indonesia; the extinct Dodo of Réunion; moas of New Zealand; and elephant birds of Madagascar. Most recorded extinctions are of island species (Diamond, 2005), and many leading global conservation initiatives focus on islands as hotspots of biodiversity – e.g. six of the 25 hotspots defined by Myers et al. (2000) are archipelagos and four others are regions that include many important islands. Islands are interesting; islands are attractive; islands are valuable.

A fresh impetus

As research priorities change, researchers are again looking to island systems to gain fundamental insights – about how species arise, how they interact, and how they are threatened by a changing world (Tables 1, S1). In 2007, the 40th anniversary of MacArthur and Wilson’s (1967) Princeton Monograph provided the occasion for a gathering of prominent biologists to assess the continuing impact of ETIB, and to examine how it has been extended and modified. That workshop, and the ensuing edited volume (Losos & Ricklefs, 2009), effectively brought to a close some older debates in island biogeography, including the ‘single large or several small’ (SLOSS) debate concerning the design of nature reserves (Laurance, 2009), and turned towards new horizons. Further momentum comes from new taxonomic, ecological, and molecular data (coupled with recent advances in analysing such data), and from new analytical approaches that allow stronger inference from island data (e.g. Bunnefeld & Phillimore, 2012). New syntheses in island biogeography are developing under a standard of multidisciplinarity and increasingly recognize the changing nature of the ‘stage’ on which life is played out (e.g. Whittaker et al., 2008; Gravel et al., 2011; Rosindell & Harmon, 2013; Fernández-Palacios et al., this issue). A range of current developments in ecology and evolutionary biology can also be integrated into island-based research, making this an opportune moment to help frame the future of island biogeography.

This special issue of Global Ecology and Biogeography originated in a symposium at the British Ecological Society–INTECOL 2013 meeting in London in August, 2013, which marked the centenary of the death of the great island biogeographer, Alfred Russel Wallace, and the 50th anniversary of the initial appearance of the equilibrium theory of island biogeography in the journal Evolution (MacArthur & Wilson, 1963). The purpose of this special issue is not to look back at the influence of the ETIB, but instead to build on the current excitement in the literature (e.g. Fernández-Palacios et al., 2015) and in recent conferences and highlight research directions being pioneered by a new generation of island biogeographers.

Although island research has recently contributed strongly to our understanding of species and lineage diversification (including ecological speciation and adaptive radiation; Box 1; e.g. Givnish, 1997; Schluter, 2000; Warren et al., 2015), this special issue has more of an ecological flavour, though by no means exclusively so. It highlights new insights into island biogeography theory, particularly in terms of the geological “life-cycles” of islands (also termed ontogeny; Box 1) – that were partially acknowledge by Darwin (1842) and Wilson (1963), changes in archipelago geography caused by sea-level fluctuations, species addition (both colonization and in situ speciation), species’ interactions, extinction, and area effects. The papers in this special issue focus strongly on processes not typically associated with the classical ETIB, particularly the roles of species’ interactions, community assembly, environmental change, and evolution, in shaping island and island-like communities (though most of these were discussed to some extent by MacArthur and Wilson, 1967). These
processes include seed-dispersal and pollination networks at large spatial scales, as well as
the influence of predation, mutualism and competition in structuring island communities.
You will also find new perspectives on marine environments and on community assembly
over ecological and evolutionary time. These topics inform our understanding of how global
change will affect ecological communities, providing guidance for conservation and
management. Finally, this issue covers niche (Box 1) evolution in relation to ecological
opportunity and its influence on geographic distribution, and how the dynamics of island
formation and demise, combined with changing sea levels and climates, influence the
composition of island biotas. In the remainder of this opening contribution to the special
issue, we highlight key areas of current research in island biogeography, locating the other
papers within this wider context, and look ahead to further developments in the coming
decade.

Advances and insights from island biogeography

Recent research on island systems has shifted towards broader themes in ecology and
evolution that are considered global priorities for future work (Sutherland et al., 2013).
Among these themes is community assembly, for which islands can provide community-level
entities with clear boundaries. The underlying processes are both local (e.g. physical
conditions, resource limitation, competition) and regional (e.g. colonization, evolutionary
diversification). The many islands of the world provide discrete ‘natural experiments’
replicated with respect to varying age, area, altitude, latitude, remoteness and local
ecological conditions. The low number of species relative to mainland systems provides a
level of simplicity that helps in understanding how species’ interactions shape communities.
Moreover, the ‘disharmony’ of many island biotas (i.e., the absence of entire groups of
species that would be found in continental settings; Whittaker & Fernández-Palacios, 2007;
Box 1) can be likened to manipulative experiments at a scale beyond the reach of
researchers.

Species’ interactions

Islands have figured prominently in research on how species interact. Early studies
emphasized competition, as exemplified by the work of Diamond (1975) and others on
‘assembly rules’ governing how species’ interactions influence community organization;
more recent research has considered the roles of predators, pathogens and mutualists,
including pollinators (e.g. Terborgh, 2001, Ricklefs & Bermingham, 2007). Network analysis,
developed over the last two decades, is helping ecologists to understand species’
interactions, particularly with respect to the organization of mutualistic networks involving
pollinators and seed-dispersers (Bascompte & Jordano, 2007). Island pollination and seed-
dispersal networks differ from those on the mainland (Traveset et al., this issue) because of
dispersal-driven biases in the types of species that can colonize islands (disharmony). Island
networks are often simpler than mainland ones in having fewer species (e.g. González-Castro
et al., 2012; Traveset et al., this issue), but they can be more complex owing to domination
by generalist species (e.g. Olesen et al., 2002; but see Olesen & Jordano, 2002).

Current research on interaction networks is taking a more macroecological/spatial
perspective, including recent advances in evaluating large-scale geographical patterns of
network properties (e.g. González-Castro et al., 2012; Trøjelsgaard & Olesen, 2013). Traveset
et al. (this issue) provide one of the first global comparisons of island and mainland
pollination networks. They found that oceanic island (Box 1) networks present higher niche
overlap among fewer species and links than mainland areas, and that, contrary to their expectations, pollinator/plant ratios, connectance, nestedness and modularity were similar in ecological communities on oceanic islands and mainlands (Box 1). In contrast, Nogales et al. (this issue) evaluated the modularity and nestedness patterns between two distant archipelagos (Canaries and Galápagos), finding very different patterns: the Canaries support highly nested networks and the Galápagos, modular ones.

The biodiversity of nearby source areas, combined with abiotic and biotic filters, can influence the diversity and character of island biotas (see Santos et al., this issue). Extensive analyses of Anolis lizards in the Caribbean (Losos, 2011) and Darwin’s finches (Aves: Geospizini) of the Galápagos Archipelago (Grant & Grant, 2008) have shown how communities can be shaped by competition and predation (e.g. Schoener, 1975; Spiller & Schoener, 1988). These studies provide clear examples of how the behaviour, habitat distribution, and phenotypes of populations can change in response to species’ interactions (Grant & Grant, 2006; 2010) – in some cases causing evolutionary change observable over decades (e.g. Losos et al., 2004; Grant & Grant, 2014). More recently, new models have arisen that describe the effects of trophic interactions in insular dynamics (e.g. Holt, 2009; Gravel et al., 2011). Following these recent models, Cirtwill & Stouffer (this issue) evaluated effects of trophic relationships on immigration and extinction probabilities, finding that the inclusion of bottom-up effects (e.g. resource availability) improves ETIB predictions. Santos et al. (this issue) made a first attempt to understand global patterns of functional diversity and assembly of island faunas in their analysis of parasitoid faunas (Box 1). They concluded that the main determinant of parasitoid community assembly may be the structure of host communities. However, lack of information on host species distributions and host–parasitoid relationships prevents testing this hypothesis and emphasizes how much information we are still missing.

Species’ interactions are often considered to drive Wilson’s (1959, 1961) ‘taxon cycle’ (Box 1), in which competitively superior new colonists progressively exclude older colonists. Patterns consistent with taxon cycles have been described through phylogeographic analyses in several systems (e.g. Ricklefs & Bermingham, 2002; Economo & Sarnat, 2012; Jønsson et al., 2014), but the underlying processes are poorly understood, particularly concerning the initiation of new expansion phases. Coevolutionary shifts in the balance between predators and their prey, or between pathogens and their hosts, might be involved (Ricklefs & Bermingham, 2002; Ricklefs, 2011). Regardless of the cause, species in expansion phases appear to colonize islands with little hindrance, suggesting that niche space on these islands is not filled. Many invasive species behave similarly (e.g. Sax et al., 2002). Moreover, although taxon cycles have been documented primarily in island systems, they undoubtedly occur within continental areas (Glazier, 1980; Erwin, 1985) and apply at all geographic scales (Ricklefs, 2011). Indeed, the coevolutionary dynamics postulated to drive taxon cycles might produce intrinsic dynamics in ecological systems generally, which could influence patterns of distribution, abundance and even species production (Ricklefs, 2015). Finally, the ability of “expanding” species to invade new ecosystems, including “reverse” colonization from fairly small oceanic and continental islands to continents (Bellemain & Ricklefs, 2008; Patiño et al., 2015), challenges the idea that continental communities are filled with species (but see Ricklefs, 2012; Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015).

**Area**

Understanding the relationship between area and biological diversity has long been a major research focus in biogeography and ecology (e.g. MacArthur & Wilson, 1967; Rosenzweig,
1995) and was recently the focus of a ‘virtual issue’ of the Journal of Biogeography (see Whittaker & Triantis, 2012). In examining species–area relationships, Triantis et al. (2012; also see Gray et al., 2004) drew attention to the fundamental distinction between species accumulation curves (‘SACs’ – the increase in species richness as a sampling property of progressively larger areas within regions) and island species–area relationships (‘ISARs’ – counts of species on different isolated islands). Their comprehensive meta-analysis of over 600 ISARs on true islands has now been added to by Matthews et al. (this issue), who used over 800 datasets from both habitat islands and true islands (Box 1) to evaluate how the slope (z) and intercept (c) of ISARs vary between island types. The slopes of the ISARs tended to be steeper on true islands, and oceanic islands had smaller intercepts than habitat islands within continental regions.

The dependence of extinction rate on island area (e.g. Ricklefs & Bermingham, 2007), in conjunction with the ‘target effect’ of larger islands being more likely to be colonised (Box 1; MacArthur, 1972), produces the familiar ISAR, reflecting the influence of island area on the dynamics of species gain and loss. Larger areas typically include more habitat types and support larger populations, promoting in situ speciation as well as reducing extinction rates. Losos and Schluter (2000) showed that the ISAR slope for Caribbean Anolis lizards increases above a critical island size that is apparently required for allopatric speciation within islands (Box 1). Building on that result, Algar and Mahler (this issue) found that the rate of climatic niche evolution in Anolis increases with island area, because of response to climatic opportunity, potentially contributing to adaptive diversification on larger islands. Consistent with a driving force on islands of response to opportunity, Steinbauer et al. (this issue) found high levels of climatic niche lability, rather than climatic niche conservatism or competitive displacement, within radiating plant clades in the Canary Islands.

Given those recent advances, it is not surprising that area affects not only species numbers, but also ecological interactions between island species (e.g. Holt, 2009; Gravel et al., 2011; Roslin et al., 2014). For islands in the Bahamas, Schoener et al. (this issue) found that competition and predation exhibited their largest effect sizes on intermediate-sized islands. They suggest that the harsher abiotic conditions, larger marine subsidies, lower spatial heterogeneity and greater stochastic effects typical of smaller islands shifted communities towards having fewer top predators compared to larger islands. In contrast, ant–plant mutualism decreased with increasing island area, while plant–pollinator mutualism showed the opposite trend.

The shifting stage

The recent history of island biogeographic investigation can be characterized as moving from a concept of islands as neutral, static and interchangeable landing pads for species (e.g. MacArthur & Wilson, 1963, 1967) to one in which their physical characteristics are critically important (e.g. Kalmar & Currie, 2006), and finally to a view of islands changing through time (e.g. Whittaker et al., 2008; Rijsdijk et al., 2014; Weigelt et al., 2016, Fernández-Palacios et al., this issue). These considerations are in accordance with the general paradigm that Earth is a dynamic planet, where changes can even occur in short time spans. The ‘General Dynamic Model’ of oceanic island biogeography (GDM; Box 1; Whittaker et al., 2008; see review by Borregaard et al., in press a) emphasizes the importance of island ontogeny and geological dynamics for biological processes on islands, including colonization, speciation and extinction. The GDM has been evaluated empirically, receiving considerable support (e.g. Whittaker et al., 2008; Borges & Hortal, 2009; Bunnefeld & Phillimore, 2012; Steinbauer et al., 2013; Valente et al., 2014). This model provides a good example of how island theory...
is linked to other research areas. It implies that, early in island ontogeny, the main process
acting is immigration, coupled with within-island and within-archipelago metapopulation
and metacommunity dynamics. At a later stage (called the immaturity stage), the dynamic
nature of island landscapes fosters the ascendance of evolutionary processes, at least on
larger islands. Finally, as the island reaches its maturity and starts to submerge (due to
erosion, downcutting, and subsidence), extinction increases and becomes the main driver of
species richness and island community dynamics.

The GDM, as originally formulated (Whittaker et al., 2008), was primarily applied to
oceanic hotspot islands (Box 1). It has now been extended to include subduction-based arc
islands and continental fragment islands (Box 1; Borregaard et al., this issue; see also Heaney
et al., 2013). Borregaard et al. (this issue) also formalized the logic of the GDM, expressing
the causal relationships as a directed graph model, which they used to evaluate the
generalized diagram of ‘key rates and properties’ of Whittaker et al. (2008). This latest
version of the GDM modifies the colonization and extinction curves and exposes a larger gap
between potential species richness (‘carrying capacity’) and actual species richness
throughout an island’s life cycle.

The GDM does not include recent dramatic variations in climate and sea-level
changes associated with Pleistocene glacial cycles (Ali & Aitchison, 2014; Rijsdijk et al., 2014).
To address these factors, Fernández-Palacios et al. (this issue) have produced a model of
archipelagic island biogeography that combines the interconnected effects of sea-level
changes, island area and isolation on immigration and extinction rates and, consequently, on
species richness (see also Weigelt et al., 2016). Furthermore, based on their model they
enunciated testable predictions, regarding, for instance, species’ genetic structure and
extinction likelihood, which should enhance in the near future the study of the impact of sea
level changes on the contemporary biotas of oceanic islands. Rominger et al. (this issue)
have also incorporated archipelagic dynamics in their study of community assembly on the
Hawaiian Islands. Hotspot archipelagos such as the Hawaiian Islands provide a time series
over which one can investigate the evolutionary development of island biotas. Using
extensive genetic and molecular phylogenetic information, Rominger et al. examined the
development of ecological communities over the time series of the archipelago, where the
major subaerial islands range from <0.5 Ma (Hawaii) to more than 5 Ma (Kauai), and new
soils continue to form from recent lava flows on the youngest island, Hawaii. They found
that ecological communities are initially driven by immigration, but that this shifts to in situ
diversification after about 1 million years, resulting in changes in interaction network
structure and ecological specialization (increase in modularity and decrease in nestedness)
with increasing dominance of evolutionary change over time.

Human influences and biological invasions
Patterns of diversity and community organization on islands have, in many instances, been
affected by human activities. The impacts of humans, and their commensals, on island biotas
started in pre-historic times, as reflected by numerous extinctions apparent in the fossil
record (Olson, 1990; Whittaker & Fernández-Palacios, 2007; Duncan et al., 2013). Habitat
conversion is one of the main threats to island species (e.g. Caujapé-Castells et al., 2010;
Triantis et al., 2010), together with alien (Box 1) competitors, herbivores, predators and
pathogens (e.g. Sax et al., 2002; Reaser et al., 2007; Caujapé-Castells et al., 2010).
Extinctions also affect functional diversity (Boyer et al., 2014), which can influence
ecosystem functioning. In some cases, introduced predators and herbivores have
dramatically impacted local populations, sometimes shifting the entire ecological character
of an island – e.g. goats (Coblentz, 1978) and brown tree snakes (Savidge, 1987). In some archipelagos (e.g. Galápagos and Hawaii), the number of alien plant species surpasses that of natives, although it remains unclear how disruptive alien species are for interaction networks (e.g. Olesen et al., 2002; Padrón et al., 2009; Heleno et al., 2013; Nogales et al., this issue; but see Traveset & Richardson, 2006; Traveset et al., 2013).

The native biotas of oceanic islands have developed through historic colonizations. What have changed with human transport and deliberate introductions are the rate of accumulation of new species and the appearance of species with limited dispersal ability that would not reach many islands without human assistance. Introduced species (and also historic extinctions) provide opportunities to observe how new species fit into established communities (Sax et al., 2002; Nogales et al., this issue), and how their introduction alters community relationships. Blackburn et al. (this issue) used structural equation modelling to explore these questions, and found that both native and alien plants and birds have strikingly similar (positive) ISARs. They found that alien species richness was strongly positively related to both native species richness and human population size, interpreting human population size as a measure of propagule pressure, and native species richness as a proxy for the island environment. These results suggest that native and alien species richness respond similarly to the same factors on islands, while biotic resistance (sensu Elton, 1958) is not a major influence.

The future of island biogeography

Island biogeography is currently enjoying a renaissance (Fernández-Palacios et al., 2015). Much of the knowledge gathered through the last decades from different research areas is being synthesized in new theories and models – two of them being included in this special issue (Borregaard et al., in press b; Fernández-Palacios et al., in press; Table 1), while existing ones are being tested and updated with new and more powerful analytical tools and new molecular, ecological and distributional data. Because islands’ circumscribed geography and discrete nature allow the study of the geography of processes that are, in fact, occurring everywhere – including within large continental regions and ocean basins (examples in Table 1) – we believe this integration of knowledge arising from island studies will surely have an impact in terms of understanding other systems.

Despite this surge of research activity, some avenues for future research remain relatively unexplored. Heaney et al. (2013) and Warren et al. (2015) proposed a number of research questions that involve islands as key elements for understanding the ecological and evolutionary processes shaping communities in general. More particularly, they refer to questions related to (i) community assembly – the importance of arrival history (or priority effects; Box 1) for community assembly, changes in species’ abundance that might occur after colonization, the influence of existing species on the establishment of newly arrived species, and influence of island area and isolation on community assembly, equilibrium, and evolution; (ii) ecosystem functioning – particularly the contribution of in situ evolution to changes in rates of energy flux and nutrient cycling; and (iii) speciation and diversification – the role of gene flow in speciation, and the more rapid diversification of some lineages in comparison with others. These priorities reinforce the need to incorporate non-equilibrium dynamics and different modes of speciation in future island models. Here we complement these prospects and propose some questions that we feel should be pursued. We first discuss broad research directions that are not island-specific, but to which islands might
contribute important insights. We then briefly cover additional questions that may not be so directly transferable to continental areas.

Islands, particularly oceanic islands that have long been isolated from the mainland, have their own peculiarities (e.g. species with unusual adaptations as in the cases of woodpecker finches and blood-sucking finches on the Galápagos Islands, dragon’s blood trees on Socotra and Macaronesia, pollinating reptiles on many islands). To transfer knowledge appropriately from islands to broader contexts requires understanding both the similarities that promote transferability and the differences that limit it. For example, adaptive radiation, a process widely studied on islands (e.g. Givnish et al., 2009; Losos, 2011; Steinbauer et al., this issue), occurs differently on islands and continental areas. In island systems, speciation tends to occur in isolation within lineages (e.g. Pinto et al., 2008), while on continents it is common for radiations to involve evolution in many lineages, interacting through antagonistic or mutualistic relationships. Island–mainland (or species pool) comparisons seem to be a logical way to proceed, but few studies have taken this approach (but see Santos et al., 2011a, 2011b; Patiño et al., 2015; Traveset et al., this issue). Some that have done so have questioned old assumptions about islands – for example: island communities do not always have lower diversity than mainland communities (e.g. Algar & Losos, 2011; Patiño et al., 2015); the island rule does not hold true for many taxa (Box 1; e.g. Meiri et al., 2008; Itescu et al., 2014); island systems are not necessarily dominated by species with high dispersal capacities (e.g. Vargas et al., 2012; Heleno & Vargas, 2015). With more data and analytical approaches available than ever before, more effort should be directed towards understanding the generality of patterns and processes that have been widely acknowledged as being predominant on islands, and that have long been used to separate island from mainland systems.

Community assembly on oceanic islands involves (i) the dispersal of species from an external species pool, following which the species are then (ii) subjected to abiotic and biotic filters that determine the island or within-island assemblage. These two steps also occur on continental islands, although they are less important as newly formed continental islands already possess a diverse biota. The species pool can be defined as the group of species that can potentially colonize a local site (Cornell & Harrison, 2014); the species pool is generally thought of as a static and independent (i.e. extrinsic) unit (Mittelbach & Schemske, 2015). The species pool concept has been widely used as a null model for identifying processes (e.g. environmental filtering, limiting similarity) that shape the taxonomic, phylogenetic or trait structure of communities (e.g. Carstensen et al., 2013; Weigelt et al., 2015; Santos et al., this issue). Although this top-down framework has been widely applied (e.g. MacArthur & Wilson, 1963; Hubbell, 2001), it fails to incorporate the dynamic nature of the species pool, and the importance of dispersal, speciation and extinction for the maintenance of the species pool over time and space. Archipelagos can help us understand how local species assemblages and regional species pools are linked within continents, as each archipelago can be viewed as a regional pool that feeds, and is fed by, the dynamics occurring within and between its constituent islands (local assemblages; Grant & Grant, 2008). Species arising in allopatry might colonize other islands, achieving secondary sympatry and becoming part of the archipelagic species pool (islands feed the pool), eventually colonizing other islands within the archipelago (the pool feeds the islands).

The Earth is currently going through dramatic environmental changes (e.g. pollution, climate changes, land use change, biodiversity loss) that are affecting many of the planet’s ecosystem support systems, and that can ultimately lead to species’ extinctions and further deterioration of human societies. Islands are also subject to these impacts (e.g. Savidge,
1987; Sax et al., 2002; Duncan et al., 2013; Boyer & Jetz, 2014; Bellard et al., 2014) and can be useful tools for understanding the consequences of environmental change. First, as islands (or archipelagos) are discrete and geographically isolated, most of their populations cannot easily escape these impacts. Second, as many islands are among the last territories to be colonized by humans, the impact of human activity has been occurring for a shorter period of time, which provides the opportunity to disentangle the effects of climate change on the extinction of local communities.

Biological invasions can fundamentally change the local biotic environment (e.g. van der Wal et al., 2008). Islands have been particularly affected by invasions (Sax et al., 2002), with many island faunas and floras now being dominated by introduced species (e.g. Azores, Hawaii). Islands offer great opportunities for research into biological invasions because of their well delimited boundaries and, in many cases, relatively brief periods of human occupation (Sax et al., 2002) and knowledge of approximate human arrival dates. Further, as many islands are within archipelagos, they have been subject to similar evolutionary histories and ecological forces, providing replicated units with varying degrees of species’ introductions. Sax and Gaines (2008) described four principal knowledge gaps in invasion research: (i) the need to further understand the role of propagule pressure, (ii) the dynamics of time-lags to extinction, (iii) the effects of alien species on native species’ abundance, and (iv) the impact of land-use changes on native species diversity. To these, we add the important question of how invasive species affect ecosystem functioning: do they replace native species’ functions, add functions not previously performed, or become redundant in terms of the ecosystem functions they provide?

Some questions that apply specifically to island systems also address research priorities for ecology more generally. Trait diversity and phylogenetic diversity have been widely used over the past decade as tools to ascertain the processes that shape community assembly, particularly in continental areas. Typically, ecologists assume that communities are shaped either by limiting similarity (resulting in coexistence of species that are overdispersed in ecological and trait space) or environmental filtering (causing clustered patterns), with contradictions when traits are not phylogenetically conserved (Pausas & Verdú, 2010). So far, few studies on island systems have analysed community organization from this perspective (but see Cardillo & Meijaard, 2010; Santos et al., this issue). Island systems, with their relative simplicity, could be used to combine such research with investigation of other processes potentially involved in community assembly, but which are more difficult to address in continental contexts (e.g. convergent evolution, adaptive radiation). Our knowledge of the biogeography of trait and phylogenetic diversity is still limited. For example, what is the relationship between trait and/or phylogenetic diversity and species richness on islands? Does this relationship differ from that found in mainland systems? How are trait and/or phylogenetic diversity related to island area and age?

One of ETIB’s main predictions is that species on islands are continually being turned over through extinction and colonization, with species richness becoming stable through time (MacArthur & Wilson, 1967). Yet, few studies have addressed the dynamics of these processes (but see Valente et al., 2015). One prediction that should be evaluated is that islands have a mix of young and old species, which can now be assessed through phylogenetic reconstructions (Ricklefs & Bermingham, 2001, 2008; Cadena et al., 2005; Valente et al., 2014). However, this pattern could also arise in a non-saturated island, where no extinctions have occurred. Quantifying extinctions, particularly the timing of extinctions, is difficult in most island settings. One approach that could be more fully explored is fitting
species’ age distributions to models that incorporate extinction, assuming time-
555 homogeneous processes (Ricklefs, 2009).
556
Where species diversification occurs within islands, we would also like to understand
557 how this process varies over the geological ontogeny of individual islands. According to the
558 General Dynamic Model (Whittaker et al., 2008; Borregaard et al., this issue), speciation rate
559 should be higher in relatively young islands, which provide opportunities for diversification
due to empty ecological niche space, and when extinction rates may be relatively low.
560 Although a few studies have looked into this question using modelling approaches (e.g.
561 Rabosky & Glor, 2010; Valente et al., 2014), empirical evaluation is largely lacking (see,
however, Fritz et al., 2012).

Concluding remarks
From the observations and patterns described by naturalists during the first European
expeditions around the globe, to the studies by Darwin and Wallace, and to the
development of the Equilibrium Theory of Island Biogeography (Box 1), islands have long
influenced our understanding of ecological and evolutionary patterns and processes (Table
1, S1). This interest continues to the present, reinvigorated by new perspectives and
analytical approaches to community ecology, evolutionary diversification and biogeographic
distributions of species. This special issue of Global Ecology and Biogeography is a reflection
of the continued relevance of island systems for understanding ecology and evolution more
generally. We hope you agree that the papers in this special issue set a good collective
example for continuing research on island systems.

Existing datasets from island systems are globally valuable and have provided
important insights for ecology and evolution, largely because of the relative simplicity and
possibility for independent replication offered by islands and archipelagos. However,
although databases for island characteristics, and for species distributions and ecological
requirements, traits, and phylogenetic relationships continue to grow (e.g. Cardillo &
Meijaard, 2010; Weigelt et al., 2013, 2015; Whittaker et al., 2014; Santos et al., this issue),
many gaps need filling to realize the full potential of future research. Inventories of island
floras and faunas, particularly of non-vertebrate groups, are far from complete (e.g. Hortal et
al., 2007; Schipper et al., 2008; Santos et al., 2010), with many species still waiting to be
described. Detailed information on the distribution of species within islands, which could be
used for investigation of community assembly and, in some systems, adaptive radiation, is
still limited in many cases. More information on functional traits and phylogenetic
relationships may help us to interpret community assembly and structure in terms of
ecological and evolutionary processes, including adaptive radiation. We advocate a
continuing effort to build comprehensive island data for multiple taxa, to serve the wider
scientific community in the coming decades.

The current excitement around islands reflects island biogeography’s being a vibrant,
active field of research. We hope this enthusiasm will continue and that the knowledge and
theories developed from island systems will continue to produce insight into the natural
world more generally.
Acknowledgments

The symposium that led to this special issue of Global Ecology and Biogeography was supported by the Biogeography Research Group of the Royal Geographical Society (with the IBG – Institute of British Geographers). We gratefully acknowledge this support. AMCS was supported by a Marie Curie Intra-European Fellowship (IEF 331623 ‘COMMSTRUCT’). We thank David Currie for accepting our proposal for the special issue, and also the editor (Michael Borregaard), José María Fernández-Palacios and one anonymous referee for constructive comments on the manuscript.

Biosketch

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Richard Field is mainly interested in biogeography, macroecology and plant ecology, with particular focus on biodiversity and the drivers structuring ecological communities, particularly on islands.

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Author contributions: A.M.C.S., R.F. and R.E.R. conceived and designed the review, and A.M.C.S. led the writing of the paper with significant contributions from R.F. and R.E.R.
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**Box 1. Glossary**

This glossary gives definitions of terms as we use them in the paper. Some of them (e.g. oceanic islands) have a range of definitions in the literature.

*Adaptive radiation*: the evolutionary process by which a single ancestral species diverges into an array of species that exhibit a wide range of ecological, phenotypic and behavioural diversity.

*Alien species*: a species that has been introduced in a new region outside its natural geographic range due to human actions (also known as exotic, exogenous, non-indigenous or non-native, among other terms).

*Allopatric speciation*: speciation that occurs when two populations are geographically isolated from each other, and originate distinct species.

*Archipelago*: a group of islands located reasonably close to each other, and that usually share a common geological origin.

*Assembly rules*: rules that describe the composition of biotas based on competition processes. These have been controversial.

*Character displacement*: the process by which traits of similar species diverge when such species co-occur geographically, as a consequence of competition scaling directly with similarity.

*Checkerboard distributions*: patterns presented by two or more ecologically similar species, where they have mutually exclusive and non-overlapping distributions.

*Connectance*: the proportion of all possible links that occur in a network.

*Continental Island sensu lato*: islands that have originated from the fragmentation (either recent – continental *sensu stricto*. or landbridge islands, or ancient – continental fragments) of the continental shelf and therefore have been connected to the continent in some point during its history. The fragmentation may result from sea-level rise or tectonic processes.

*Density compensation*: process leading to abnormally high abundance of species inhabiting islands with species-poor biotas.

*Disharmony*: the absence from an island of entire groups of species that would occur in continental settings.

*Ecological release*: expansion of the range, habitat and/or resource usage that occurs after a colonizing species enters an environment where natural enemies (competitors, parasites, predators) are missing.

*Equilibrium Theory of Island Biogeography*: a theoretical model by MacArthur and Wilson (1967) that postulates that the number of species present on an island will be determined by the dynamic relationship between immigration and extinction rates. In turn, immigration
rates depend greatly on the island isolation, while extinction rates are mainly associated with island area.

**General Dynamic Model of oceanic island biogeography**: a conceptual model by Whittaker et al. (2008) describing changes in diversity and ecological and evolutionary processes that are associated with the changes in the physiographic characteristics of volcanic oceanic islands (e.g. area, altitude) that occur throughout its ontogeny.

**Habitat island**: a discrete patch of habitat that is surrounded by a matrix of contrasting (usually unsuitable) habitat(s).

**Hotspot archipelago**: an archipelago of volcanic origin where islands are formed over near-stationary thermal plumes located in the Earth’s upper mantel. Tectonic plate movements cause the islands to drift from that point, originating a series of islands of different ages.

**Incidence functions**: functions that describe how the probability of occurrence of a species varies with certain island characteristics (e.g. area, isolation, species richness).

**Island ontogeny**: the development of an island, from its formation through its development and subsequent degradation and disappearance.

**Island rule**: the tendency of small animals to evolve to larger sizes and large animals to evolve to smaller sizes on islands.

**Mangrove islands**: islands where the land area is mostly or totally below tidal water (at high tide), being overwash banks covered mainly by mangrove plants. They are usually located rather close to the mainland, and might, or might not, have been connected to the mainland coastal habitats.

**Metacommunity**: a group of communities that are linked through dispersal.

**Metapopulation**: a group of spatially separated populations that are connected by gene flow, extinction and recolonization.

**Modularity**: the occurrence of semi-independent groups (also called modules) of interacting species.

**Nestedness (in respect to network analysis)**: a metric of the generalist–specialist balance in ecological communities. A network is nested when specialists interact with a subset of the group of species with which generalists interact.

**Niche**: the requirements (resources or physical conditions) of a population or species that allow it to survive in the focal certain area.

**Oceanic Island**: island formed due to volcanic activity, that has never been connected to another landmass. Upon their formation, oceanic islands are devoid of life, and so their biotas are assembled from colonization and/or speciation.
Parasitoid: an organism (usually an insect) that develops through adulthood by feeding on or in the body of a host (usually an arthropod), eventually killing it.

Priority effects: the effects that the first species that colonize an area cause on the subsequent colonizers, as a result of colonizing first.

Sympatric speciation: speciation that occurs when populations are not geographically isolated from each other.

Target effect: the increased probability that a larger island has of being colonized than a smaller one, resulting from random dispersal.

Taxon cycle: sequential phases of expansion and contraction of species’ ranges, which are usually associated with shifts in the species’ ecological niches.

True island: a piece of land that is surrounded by water.
Table 1. A non-exhaustive summary of theories, processes and patterns that a) have originated in island studies, or b) have not originated from island studies, but have received an important theoretical and/or analytical input from island studies. Examples (citations) of each theory, process or pattern are given for different types of island (see Box 1), and also for mainland systems. Many of these examples (indicated by #) are not exclusive to one particular theory, process or pattern, and could indeed also be included in one or more different sections. * indicates the studies that are part of this special issue. See Appendix 1 (Data Sources) for references not in the main reference list. The expanded online version of this table (Table S1) additionally categorizes the examples by taxon.

**Appendix 1 – Data sources**
List of references for the examples cited in Table 1 and Table S1 that are not in the main reference list.

**Supplementary Material (online only)**
Table S1.
Expanded version of Table 1. A non-exhaustive summary of theories, processes and patterns that a) have originated in island studies, or b) have not originated from island studies, but have received an important theoretical and/or analytical input from island studies. Examples (citations) of each theory, process or pattern are given for different types of island (see Box 1, main paper), and also for mainland systems. Many of these examples (indicated by #) are not exclusive to one particular theory, process or pattern, and could indeed also be included in one or more different sections. The main taxa used in each example are displayed in the columns. Symbols are as follows: f(x) - Theoretical study (no use, or very limited use, of empirical data); Arthropods; Other terrestrial invertebrates; Mammals; Reptiles; Amphibians; Birds; Fish; Marine invertebrates; Plants; Microorganisms. * indicates the studies that are part of this special issue. See main paper for references: main reference list and Appendix 1 (Data Sources).
### Theories/Patterns that have originated mainly from island studies

#### Adaptive radiation

* **Oceanic Islands**: Algar *et al*., this issue; Blonder *et al*., 2016; Gillespie *et al*., 2004; Givnish *et al*., 2009; Grant & Grant, 2008; Losos, 2011; Pinto *et al*., 2008

* **Continental Islands**: Baldwin, 2007; van der Geer *et al*., 2010

* **Habitat Islands**: Dawson & Hammer, 2005; Seehausen, 2006

* **Non-Island Systems**: Hughes *et al*., 2006; Pincheira-Donoso *et al*., 2015

#### Ecological release and Density compensation

* **Oceanic Islands**: Grant & Grant, 2006; Lack, 1947; Novosolov *et al*., 2016; Schluter, 1988; Steinbauer *et al*., this issue; Wright, 1980

* **Continental Islands**: Barun *et al*., 2015; Case, 1975; Lomolino, 1984; MacArthur, 1972; Schluter & McPhail, 1992; Schoener & Spiller, 1987

* **Habitat Islands**: Hobbs *et al*., 2012; Martin & Pfennig, 2011; McGrady-Steed & Morin, 2000

* **Non-Island Systems**: Adams & Rohlf, 2000; Davies *et al*., 2007; Schmitt & Holbrook, 1990

#### Body size evolution and the "island rule"

* **Oceanic Islands**: Clegg & Owens, 2002; Lomolino, 2005

* **Continental Islands**: Lawlor, 1982; Meiri, 2007; Montesinos *et al*., 2012

* **Habitat Islands**: Schmidt & Jensen, 2003

* **Non-Island Systems**: McClain *et al*., 2006

#### Taxon cycle

* **Oceanic Islands**: Economou *et al*., 2012; Jønsson *et al*., 2014; Ricklefs & Bermingham, 2002; Ricklefs & Cox, 1972; Wilson, 1961

* **Non-Island Systems**: Economou *et al*., 2015; Erwin, 1985; Glazier, 1980; Hoagstrom *et al*., 2014

#### Equilibrium Theory of Island Biogeography
For Peer Review

Oceanic Islands: * Fernández-Palacios et al., this issue; Heaney, 2000 *; MacArthur & Wilson, 1963, 1968; Rosindell & Harmon, 2013 *
Continental Islands: Cody, 2006; Foufopoulos & Mayer, 2007; Jones & Diamond, 1976
Mangrove Islands: Simberloff & Wilson, 1969, 1970
* Habitat Islands: Bossard, 2014; Brown, 1971, 1978; * Dawson, this issue; Hart & Pearson, 2011; March & Bass, 1995; Schoener, 1974; Smith, 1979
Non-Island Systems: Rosenzweig, 1975 *

General Dynamic Model of Island Biogeography

* Oceanic Islands: Borges & Hortal, 2009; * Borregaard et al., this issue; Bunnefeld & Phillimore, 2012; Cameron et al., 2013; Fattorini, 2009; Steinbauer et al., 2013; Valente et al., 2014; Whittaker et al., 2008

Assembly rules, Checkerboard distributions and Null models in ecology

* Oceanic Islands: Connor & Simberloff, 1979; Connor et al., 2013; Diamond, 1975a; Gotelli, 2000 *; Mayr & Diamond, 2001; * Santos et al., this issue *; Simberloff & Collins, 2009
Continental Islands: Cody, 2006
Habitat Islands: Englund et al., 2009
Non-Island Systems: Gotelli & Ellison, 2002; Gotelli & Graves, 1996; Gotelli et al., 1997; Rautenbach et al., 2014; Sanders et al., 2007

Unified Neutral Theory of Biodiversity and Biogeography

Oceanic Islands: Rosindell & Phillimore, 2011 *
Habitat Islands: Dornelas et al., 2006; Gilbert et al., 2006
Non-Island Systems: Ricklefs, 2006; Rosindell et al., 2015

Theories/patterns not originated on island systems, but that have benefited from them

Natural Selection and Speciation

Oceanic Islands: Calsbeek & Cox, 2010; Darwin, 1859; Grant & Grant, 2008, 2016; Roderick & Gillespie, 1998; Rowe et al., 2016 *; Savolainen et al., 2006;
Long distance dispersal and Colonization Routes

Oceanic Islands: Carlquist, 1966; Heleno & Vargas, 2015; Nathan, 2006; Vargas et al., 2012; Wada et al., 2012
Continental Islands: Ali & Huber, 2000; Alsos et al., 2015
Habitat Islands: Huth et al., 2015
Non-Island Systems: Bellemain & Ricklefs, 2008; Brochet et al., 2009; Dawson & Hammer, 2008; Nicholson et al., 2005; O’Grady & DeSalle, 2008; Patiño et al., 2015

Species-area relationship

Oceanic Islands: Aranda et al., 2013; Kisel et al., 2010; Lomolino & Weiser, 2001; Losos & Schluter, 2000; Ricklefs & Lovette, 1999; Santos et al., 2010; Scheiner, 2003; Triantis et al., 2012; Wright, 1983
Continental Islands: Holt et al., 1999; Kurt & Howe, 1979; Panitsa et al., 2006; Roslin et al., 2014; Schoener et al., this issue; Sfenthourakis, 1996
Habitat Islands: Brown & Dinsmore, 1988; Belmaker et al., 2007; Hanski et al., 2013; He & Hubbel, 2011; Krauss et al., 2003; Matthews et al., this issue; Newmark, 1986; Wagner et al., 2014
Non-Island Systems: Kisel et al., 2011; Qian et al., 2007; Storch et al., 2012

Nestedness patterns

Oceanic Islands: Cook & Quinn, 1995; Darlington, 1957; Florencio et al., 2015
Continental Islands: Azeria, 2004; Conroy et al., 1999; Dennis et al., 2012; Murakami & Hirao, 2010; Wang et al., 2010
Habitat Islands: Matthews et al., 2015; Patterson & Atmar, 1986; Watling & Donnelly, 2006
Non-Island Systems: Baselga, 2010

Metapopulation dynamics

Oceanic Islands: Farrington & Petren, 2011; Garcia-Verdugo et al., 2010; Inchaisti & Weimerskirch, 2002
Continental Islands: Hanski, 2009; Nieminen, 1996; Nieminen & Hanski, 1998; Zalewski, 2004
Habitat Islands: Bay et al., 2008; Hanski & Ovaskainen, 2000

Ecological Succession
Oceanic Islands: Edwards & Thornton, 2001; Magnusson et al., 2014; Mueller-Dombois & Bohemer, 2013; Thornton et al., 1993; Whitaker et al., 1989
Continental Islands: Lavoie & Filion, 2001; Rydin & Borgegård, 1988
Mangrove Islands: Piechnick et al., 2008
Habitat Islands: McClanahan, 2014; Pinotti et al., 2015
Non-Island Systems: Clements, 1916; Dauber & Wolters, 2005; Letcher, 2010

Trophic Theory and Interaction Networks
Oceanic Islands: González-Castro et al., 2012; Nogales et al., this issue; Olesen et al., 2002; Rominger et al., this issue; Traveset et al., this issue
Continental Islands: Strong & Leroux, 2014; Terborgh, 2009; Terborgh et al., 2001
Mangrove Islands: Cirtwill & Stouffer, this issue; Gravel et al., 2011
Habitat Islands: Harvey & MacDougall, 2014; Holt, 2009; Tscharntke & Brandl, 2004
Non-Island Systems: Amaresakare, 2008; Pimm, 1982

Conservation Theory - Invasive species, Extinction and Habitat fragmentation
Oceanic Islands: Bellard et al., 2014; Blackburn et al., this issue; Boyer et al., 2014; Coblentz, 1978; Duncan et al., 2013; Kueffer et al., 2010; Sax et al., 2002; Triantis et al., 2010; Walsh et al., 2013
Continental Islands: Gasc et al., 2010; Pattermore & Wilcove, 2012; Pretto et al., 2012; van de Crommenacker et al., 2015
Habitat Islands: Diamond, 1975b, 1981; Krauss et al., 2010; Larsen et al., 2005; Laurence, 2009; Lindenmayer, 2015; Simberlogg & Abele, 1976; Tjørve, 2010
Appendix 1 – Data sources
List of references for the examples cited in Table 1 and Table S1 that are not in the main reference list.


Hanski, I. (2009) The theories of island biogeography and metapopulation dynamics - science marches forward but the legacy of good ideas lasts for a long time. *The


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Table S1. Expanded version of Table 1. A non-exhaustive summary of theories, processes and patterns that a) have originated in island studies, or b) have not originated from island studies, but have received an important theoretical and/or analytical input from island studies. Examples (citations) of each theory, process or pattern are given for different types of island (see Box 1, main paper), and also for mainland systems. Many of these examples (indicated by *) are not exclusive to one particular theory, process or pattern, and could indeed also be included in one or more different sections. The main taxa used in each example are displayed in the columns. Symbols are as follows: \( f(x) \) - Theoretical study (no use, or very limited use, of empirical data); \( \square \) - Arthropods; \( \triangle \) - Other terrestrial invertebrates; \( \triangleleft \) - Mammals; \( \blacktriangleleft \) - Reptiles; \( \blacktriangle \) - Amphibians; \( \lozenge \) - Birds; \( \blacklozenge \) - Fish; \( \blacklozenge \) - Marine invertebrates; \( \lozenge \) - Plants; \( \blacklozenge \) - Microorganisms. * indicates the studies that are part of this special issue. See main paper for references: main reference list and Appendix 1 (Data Sources).

### Theories/Pattems that have originated mainly from island studies

#### Adaptive radiation

**Oceanic Islands**
- * Algar *et al.*, this issue
- Blonder *et al.*, 2016
- Gillespie *et al.*, 2004
- Givnish *et al.*, 2009
- Grant & Grant, 2008
- Losos, 2011
- Pinto *et al.*, 2008 *

**Continental Islands**
- Baldwin, 2007
- van der Geer *et al.*, 2010

**Habitat Islands**
- Dawson & Hammer, 2005
- Seehausen, 2006
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<td>* Steinbauer et al., this issue</td>
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<td>Wright, 1980</td>
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<td><strong>Continental Islands</strong></td>
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<td>Martin &amp; Pfennig, 2011</td>
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<td>McGrady-Steed &amp; Morin, 2000</td>
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### Body size evolution and the "Island rule"

**Oceanic Islands**
- Clegg & Owens, 2002
- Lomolino, 2005
- Economo et al., 2012
- Jønsson et al., 2014
- Ricklefs & Bermingham, 2002
- Ricklefs & Cox, 1972
- Wilson, 1961

**Continental Islands**
- Lawlor, 1982
- Meiri, 2007
- Montesinos et al., 2012

**Habitat Islands**
- Schmidt & Jensen, 2003

**Non-Island Systems**
- Adams & Rohlf, 2000
- Davies et al., 2007
- Schmitt & Holbrook, 1990
- McClain et al., 2006

### Taxon cycle

**Oceanic Islands**
- Economo et al., 2012
- Jønsson et al., 2014
- Ricklefs & Bermingham, 2002
- Ricklefs & Cox, 1972
- Wilson, 1961
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<td>MacArthur &amp; Wilson, 1963, 1968</td>
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### Non-Island Systems
Rosenzweig, 1975 *

### General Dynamic Model of Island Biogeography

#### Oceanic Islands
- Borges & Hortal, 2009
- * Borregaard et al., this issue
- Bunnefeld & Phillimore, 2012
- Cameron et al., 2013
- Fattorini, 2009
- Steinbauer et al., 2013
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- Whittaker et al., 2008

### Assembly rules, Checkerboard distributions and Null models in ecology

#### Oceanic Islands
- Connor & Simberloff, 1979
- Connor et al., 2013
- Diamond, 1975a
- Gotelli, 2000 *
- Mayr & Diamond, 2001
- * Santos et al., this issue *
- Simberloff & Collins, 2009

#### Continental Islands
- Cody, 2006
For Peer Review

### Habitat Islands
- Englund et al., 2009

### Non-Island Systems
- Gotelli & Ellison, 2002
- Gotelli & Graves, 1996
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- Rautenbach et al., 2014
- Sanders et al., 2007

### Unified Neutral Theory of Biodiversity and Biogeography

#### Oceanic Islands
- Rosindell & Phillimore, 2011 *

#### Continental Islands
- Hubbell, 2001, 2009

#### Habitat Islands
- Dornelas et al., 2006
- Gilbert et al., 2006

#### Non-Island Systems
- Ricklefs, 2006
- Rosindell et al., 2015
Theories/patterns not originated on island systems, but that have benefited from them

**Natural Selection and Speciation**

*Oceanic Islands*
- Calsbeek & Cox, 2010
- Darwin, 1859
- Grant & Grant, 2008, 2016
- Roderick & Gillespie, 1998
- Rowe et al., 2016
- Savolainen et al., 2006
- Stuessy et al., 2006

*Continental Islands*
- Clegg et al., 2002
- Comes et al., 2008
- Lescak et al., 2015

*Habitat Islands*
- Barluenga et al., 2006
- Gao et al., 2015
- Juan et al., 2010

**Long distance dispersal and Colonization Routes**

*Oceanic Islands*
- Carlquist, 1966
- Heleno & Vargas, 2015
- Nathan, 2006
- Vargas et al., 2012
- Wada et al., 2012
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<td>Sfenthourakis, 1996</td>
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<td>Murakami &amp; Hirao, 2010</td>
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**Metapopulation dynamics**

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| <strong>Oceanic Islands</strong>      |                  |         |
| Farrington &amp; Petren, 2011|                  | X       |
| Garcia-Verdugo <em>et al.</em>, 2010|           |         |
| Inchaisti &amp; Weimerskirch, 2002 |              | X       |
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| <strong>Continental Islands</strong>  |                  |         |
| Hanski, 2009            |                  | X       |
| Nieminen, 1996          |                  | X       |
| Nieminen &amp; Hanski, 1998 |                  | X       |
| Zalewski, 2004          |                  | X       |</p>
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Ecological Succession

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<td>Amaresakare, 2008</td>
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<td>Pimm, 1982</td>
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Conservation Theory - Invasive species, Extinction and Habitat fragmentation

**Oceanic Islands**

- Bellard et al., 2014
- Blackburn et al., this issue
- Boyer et al., 2014
- Cob lentz, 1978
- Duncan et al., 2013
- Kueffer et al., 2010
- Sax et al., 2002
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- Gasc et al., 2010
- Pattermore & Wilcove, 2012
- Pretto et al., 2012
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**Habitat Islands**

- Diamond, 1975b, 1981
- Krauss et al., 2010
- Larsen et al., 2005
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- Simberloff & Abele, 1976
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