



New Directions in Island Biogeography

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5 3 **New Directions in Island Biogeography**

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21 19
22 20 **Keywords:** community assembly, climatic niche, Equilibrium Theory of Island Biogeography,
23 21 evolutionary processes, general dynamic model, invasive species, marine environments,
24 22 natural laboratories, species–area relationship, species interactions.

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3 41 **Abstract**
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5 43 **Aim:** Much of our current understanding of ecological and evolutionary processes comes
6 44 from island research. With increasing availability of data on distributions and phylogenetic
7 45 relationships, and new analytical approaches to understanding the processes that shape
8 46 species' distributions and interactions, a prospective on this ever-interesting topic is timely.
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10 48 **Location:** Islands globally.
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12 50 **Methods:** We start by arguing that the reasons island research has achieved so much in the
13 51 past also apply to the future. We then critically assess the current state of island
14 52 biogeography, focusing on recent changes in emphasis, including research featured in this
15 53 special issue of *Global Ecology and Biogeography*. Finally, we suggest promising themes for
16 54 the future. We cover both ecological and evolutionary topics, although the greater emphasis
17 55 on island ecology reflects our own backgrounds and interests.
18 56

19 57 **Results:** Much ecological theory has been directly or indirectly influenced by research on
20 58 island biotas. Currently, island biogeography is renascent, with research focusing on, among
21 59 other things, patterns and processes underlying species interaction networks, species
22 60 coexistence and the assembly of island communities through ecological and evolutionary
23 61 time. Continuing island research should provide additional insight into biological invasions
24 62 and other impacts of human activities, functional diversity and ecosystem functioning,
25 63 extinction and diversification, species pools and more. Deeper understanding of the
26 64 similarities and differences between island and mainland systems will aid transferability of
27 65 island theory to continental regions.
28 66

29 67 **Main conclusions:** As research in biogeography and related fields expands in new directions,
30 68 islands continue to provide opportunities for developing insights, both as natural
31 69 laboratories for ecology and evolution and because of the exceptions islands often present
32 70 to the usual 'rules' of ecology. New data-collection initiatives are needed on islands
33 71 worldwide and should be directed towards filling gaps in our knowledge of within-island
34 72 distributions of species, as well as island species' functional traits and phylogenetic
35 73 relationships.
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Introduction

“In islands 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

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3 124 habitats have been studied in the context of island theory, from mountaintops (or 'sky
4 125 islands') to forest fragments and lakes (e.g. Brown, 1971, 1978; March & Bass, 1995), and
5 126 island theory has provided the conceptual basis for much research on the ecological impacts
6 127 of habitat fragmentation (Laurance, 2009). Island-like marine environments (e.g., marine
7 128 lakes, i.e. pieces of seawater entirely surrounded by land; seamounts) also can be integrated
8 129 within the general theories of island biogeography, according to Dawson (this issue). More
9 130 generally, insularity within the contiguous landmasses of the continents remains under-
10 131 appreciated (but see Steinbauer *et al.*, in press b), and the same may apply to the oceans.

11 132 In their 'equilibrium theory of island biogeography' (ETIB; Box 1), MacArthur and
12 133 Wilson (1963, 1967) applied insights from the population biology of the early-mid 20th
13 134 century (birth and death processes) to island biogeography (colonization and extinction),
14 135 and then to other disciplines (e.g., conservation biology). As well as leading to a paradigm
15 136 shift within island research, this theory played a central role in the development of
16 137 conservation theory (Pimm, 1991) and was a starting point for Hubbell's (2001) development
17 138 of the neutral theory of ecology.

18 139 Other theories and models that developed out of island research have become
19 140 mainstays of ecology, conservation, and biogeography, sometimes with their island origins
20 141 obscured (Tables 1, S1). The role of competition in patterns of species' occurrences across
21 142 archipelagos, the subject of sometimes acrimonious debate in the 1970s (e.g. Diamond,
22 143 1975; Connor & Simberloff, 1979), revitalized interest in studying mechanisms of community
23 144 assembly (Simberloff & Collins, 2009). The 'assembly rules' (Box 1) debate also led to the
24 145 current emphasis on formulating appropriate null models for community assembly (e.g.
25 146 Weiher & Keddy, 1995), entailing the use of randomized null simulations for interpreting
26 147 empirical results in biogeography (stemming from Connor & Simberloff, 1979; Gotelli &
27 148 Graves, 1996). Further, the controversy raised by Jared Diamond's (1975) analysis of the
28 149 mechanisms of community assembly can be linked to Hubbell's (2001) 'unified neutral
29 150 theory of biodiversity and biogeography'. Hubbell developed this theory "on the foundation
30 151 of the ETIB" (Hubbell, 2001: 5), being partly based on the randomness of colonization and
31 152 extinction of the ETIB, also by setting local communities in a geographical metacommunity,
32 153 as islands are embedded in a colonization landscape. However, Hubbell defined neutrality at
33 154 the individual level, with species being equivalent within a trophic guild and species'
34 155 abundance and diversity in a community being determined by random individual birth,
35 156 death, and dispersal events. He also added a speciation term, using a model of random
36 157 species formation. Hubbell's theory can reproduce a wide range of community and
37 158 biogeographic patterns, and it has initiated continuing debate on the nature of a world
38 159 without ecological interactions (Ricklefs, 2006; Leigh, 2007; Rosindell *et al.*, 2011).

39 160 We should also remember that Wright's (1983) species–energy theory, the impact of
40 161 which has mainly been in research on the causes of the latitudinal gradient in biodiversity,
41 162 stems from island research. Wright developed his theory as an extension of the ETIB,
42 163 particularly its species–area component, amalgamating it with Brown's (1981) focus on
43 164 energetics (see also Brown *et al.*, 2004). The simple replacement of 'area' by 'available
44 165 energy' in the ETIB, combined with Preston's (1962a, b) earlier model for the distribution of
45 166 species' abundances, focused attention on relationships between energy availability and
46 167 population sizes, extinction rates, and species richness. Similarly, Rosenzweig (1975)
47 168 reformulated ETIB for continental regions, replacing immigration with species formation.

48 169 Amid the excitement about the value of islands for understanding the world in
49 170 general, islands clearly are interesting in their own right. Islands are home to some of the
50 171 most bizarre and threatened species of the world, many of which are in the public

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3 172 consciousness: ‘Darwin’s finches’ of the Galápagos Islands; Komodo dragons of Indonesia;
4 173 the extinct Dodo of Réunion; moas of New Zealand; and elephant birds of Madagascar. Most
5 174 recorded extinctions are of island species (Diamond, 2005), and many leading global
6 175 conservation initiatives focus on islands as hotspots of biodiversity – e.g. six of the 25
7 176 hotspots defined by Myers *et al.* (2000) are archipelagos and four others are regions that
8 177 include many important islands. Islands are interesting; islands are attractive; islands are
9 178 valuable.

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11 180 **A fresh impetus**

12 181 As research priorities change, researchers are again looking to island systems to gain
13 182 fundamental insights – about how species arise, how they interact, and how they are
14 183 threatened by a changing world (Tables 1, S1). In 2007, the 40th anniversary of MacArthur
15 184 and Wilson’s (1967) Princeton Monograph provided the occasion for a gathering of
16 185 prominent biologists to assess the continuing impact of ETIB, and to examine how it has
17 186 been extended and modified. That workshop, and the ensuing edited volume (Losos &
18 187 Ricklefs, 2009), effectively brought to a close some older debates in island biogeography,
19 188 including the ‘single large or several small’ (SLOSS) debate concerning the design of nature
20 189 reserves (Laurance, 2009), and turned towards new horizons. Further momentum comes
21 190 from new taxonomic, ecological, and molecular data (coupled with recent advances in
22 191 analysing such data), and from new analytical approaches that allow stronger inference from
23 192 island data (e.g. Bunnefeld & Phillimore, 2012). New syntheses in island biogeography are
24 193 developing under a standard of multidisciplinary and increasingly recognize the changing
25 194 nature of the ‘stage’ on which life is played out (e.g. Whittaker *et al.*, 2008; Gravel *et al.*,
26 195 2011; Rosindell & Harmon, 2013; Fernández-Palacios *et al.*, this issue). A range of current
27 196 developments in ecology and evolutionary biology can also be integrated into island-based
28 197 research, making this an opportune moment to help frame the future of island
29 198 biogeography.

30 199 This special issue of *Global Ecology and Biogeography* originated in a symposium at
31 200 the British Ecological Society–INTECOL 2013 meeting in London in August, 2013, which
32 201 marked the centenary of the death of the great island biogeographer, Alfred Russel Wallace,
33 202 and the 50th anniversary of the initial appearance of the equilibrium theory of island
34 203 biogeography in the journal *Evolution* (MacArthur & Wilson, 1963). The purpose of this
35 204 special issue is not to look back at the influence of the ETIB, but instead to build on the
36 205 current excitement in the literature (e.g. Fernández-Palacios *et al.*, 2015) and in recent
37 206 conferences and highlight research directions being pioneered by a new generation of island
38 207 biogeographers.

39 208 Although island research has recently contributed strongly to our understanding of
40 209 species and lineage diversification (including ecological speciation and adaptive radiation;
41 210 Box 1; e.g. Givnish, 1997; Schluter, 2000; Warren *et al.*, 2015), this special issue has more of
42 211 an ecological flavour, though by no means exclusively so. It highlights new insights into
43 212 island biogeography theory, particularly in terms of the geological “life-cycles” of islands
44 213 (also termed ontogeny; Box 1) – that were partially acknowledge by Darwin (1842) and
45 214 Wilson (1963), changes in archipelago geography caused by sea-level fluctuations, species
46 215 addition (both colonization and *in situ* speciation), species’ interactions, extinction, and area
47 216 effects. The papers in this special issue focus strongly on processes not typically associated
48 217 with the classical ETIB, particularly the roles of species’ interactions, community assembly,
49 218 environmental change, and evolution, in shaping island and island-like communities (though
50 219 most of these were discussed to some extent by MacArthur and Wilson, 1967). These

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3 220 processes include seed-dispersal and pollination networks at large spatial scales, as well as
4 221 the influence of predation, mutualism and competition in structuring island communities.
5 222 You will also find new perspectives on marine environments and on community assembly
6 223 over ecological and evolutionary time. These topics inform our understanding of how global
7 224 change will affect ecological communities, providing guidance for conservation and
8 225 management. Finally, this issue covers niche (Box 1) evolution in relation to ecological
9 226 opportunity and its influence on geographic distribution, and how the dynamics of island
10 227 formation and demise, combined with changing sea levels and climates, influence the
11 228 composition of island biotas. In the remainder of this opening contribution to the special
12 229 issue, we highlight key areas of current research in island biogeography, locating the other
13 230 papers within this wider context, and look ahead to further developments in the coming
14 231 decade.
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20 234 **Advances and insights from island biogeography**

21 235 Recent research on island systems has shifted towards broader themes in ecology and
22 236 evolution that are considered global priorities for future work (Sutherland *et al.*, 2013).
23 237 Among these themes is community assembly, for which islands can provide community-level
24 238 entities with clear boundaries. The underlying processes are both local (e.g. physical
25 239 conditions, resource limitation, competition) and regional (e.g. colonization, evolutionary
26 240 diversification). The many islands of the world provide discrete 'natural experiments'
27 241 replicated with respect to varying age, area, altitude, latitude, remoteness and local
28 242 ecological conditions. The low number of species relative to mainland systems provides a
29 243 level of simplicity that helps in understanding how species' interactions shape communities.
30 244 Moreover, the 'disharmony' of many island biotas (i.e., the absence of entire groups of
31 245 species that would be found in continental settings; Whittaker & Fernández-Palacios, 2007;
32 246 Box 1) can be likened to manipulative experiments at a scale beyond the reach of
33 247 researchers.
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37 249 **Species' interactions**

38 250 Islands have figured prominently in research on how species interact. Early studies
39 251 emphasized competition, as exemplified by the work of Diamond (1975) and others on
40 252 'assembly rules' governing how species' interactions influence community organization;
41 253 more recent research has considered the roles of predators, pathogens and mutualists,
42 254 including pollinators (e.g. Terborgh, 2001, Ricklefs & Bermingham, 2007). Network analysis,
43 255 developed over the last two decades, is helping ecologists to understand species'
44 256 interactions, particularly with respect to the organization of mutualistic networks involving
45 257 pollinators and seed-dispersers (Bascompte & Jordano, 2007). Island pollination and seed-
46 258 dispersal networks differ from those on the mainland (Traveset *et al.*, this issue) because of
47 259 dispersal-driven biases in the types of species that can colonize islands (disharmony). Island
48 260 networks are often simpler than mainland ones in having fewer species (e.g. González-Castro
49 261 *et al.*, 2012; Traveset *et al.*, this issue), but they can be more complex owing to domination
50 262 by generalist species (e.g. Olesen *et al.*, 2002; but see Olesen & Jordano, 2002).

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54 263 Current research on interaction networks is taking a more macroecological/spatial
55 264 perspective, including recent advances in evaluating large-scale geographical patterns of
56 265 network properties (e.g. González-Castro *et al.*, 2012; Trøjelsgaard & Olesen, 2013). Traveset
57 266 *et al.* (this issue) provide one of the first global comparisons of island and mainland
58 267 pollination networks. They found that oceanic island (Box1) networks present higher niche
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3 268 overlap among fewer species and links than mainland areas, and that, contrary to their
4 269 expectations, pollinator/plant ratios, connectance, nestedness and modularity were similar
5 270 in ecological communities on oceanic islands and mainlands (Box 1). In contrast, Nogales *et*
6 271 *al.* (this issue) evaluated the modularity and nestedness patterns between two distant
7 272 archipelagos (Canaries and Galápagos), finding very different patterns: the Canaries support
8 273 highly nested networks and the Galápagos, modular ones.

9 274 The biodiversity of nearby source areas, combined with abiotic and biotic filters, can
10 275 influence the diversity and character of island biotas (see Santos *et al.*, this issue). Extensive
11 276 analyses of *Anolis* lizards in the Caribbean (Losos, 2011) and Darwin's finches (Aves:
12 277 Geospizini) of the Galápagos Archipelago (Grant & Grant, 2008) have shown how
13 278 communities can be shaped by competition and predation (e.g. Schoener, 1975; Spiller &
14 279 Schoener, 1988). These studies provide clear examples of how the behaviour, habitat
15 280 distribution, and phenotypes of populations can change in response to species' interactions
16 281 (Grant & Grant, 2006; 2010) – in some cases causing evolutionary change observable over
17 282 decades (e.g. Losos *et al.*, 2004; Grant & Grant, 2014). More recently, new models have
18 283 arisen that describe the effects of trophic interactions in insular dynamics (e.g. Holt, 2009;
19 284 Gravel *et al.*, 2011). Following these recent models, Cirtwill & Stouffer (this issue) evaluated
20 285 effects of trophic relationships on immigration and extinction probabilities, finding that the
21 286 inclusion of bottom-up effects (e.g. resource availability) improves ETIB predictions. Santos
22 287 *et al.* (this issue) made a first attempt to understand global patterns of functional diversity
23 288 and assembly of island faunas in their analysis of parasitoid faunas (Box 1). They concluded
24 289 that the main determinant of parasitoid community assembly may be the structure of host
25 290 communities. However, lack of information on host species distributions and host–parasitoid
26 291 relationships prevents testing this hypothesis and emphasizes how much information we are
27 292 still missing.

28 293 Species' interactions are often considered to drive Wilson's (1959, 1961) 'taxon cycle'
29 294 (Box 1), in which competitively superior new colonists progressively exclude older colonists.
30 295 Patterns consistent with taxon cycles have been described through phylogeographic
31 296 analyses in several systems (e.g. Ricklefs & Bermingham, 2002; Economo & Sarnat, 2012;
32 297 Jønsson *et al.*, 2014), but the underlying processes are poorly understood, particularly
33 298 concerning the initiation of new expansion phases. Coevolutionary shifts in the balance
34 299 between predators and their prey, or between pathogens and their hosts, might be involved
35 300 (Ricklefs & Bermingham, 2002; Ricklefs, 2011). Regardless of the cause, species in expansion
36 301 phases appear to colonize islands with little hindrance, suggesting that niche space on these
37 302 islands is not filled. Many invasive species behave similarly (e.g. Sax *et al.*, 2002). Moreover,
38 303 although taxon cycles have been documented primarily in island systems, they undoubtedly
39 304 occur within continental areas (Glazier, 1980; Erwin, 1985) and apply at all geographic scales
40 305 (Ricklefs, 2011). Indeed, the coevolutionary dynamics postulated to drive taxon cycles might
41 306 produce intrinsic dynamics in ecological systems generally, which could influence patterns of
42 307 distribution, abundance and even species production (Ricklefs, 2015). Finally, the ability of
43 308 "expanding" species to invade new ecosystems, including "reverse" colonization from fairly
44 309 small oceanic and continental islands to continents (Bellemain & Ricklefs, 2008; Patiño *et al.*,
45 310 2015), challenges the idea that continental communities are filled with species (but see
46 311 Ricklefs, 2012; Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015).

312 313 **Area**

314 Understanding the relationship between area and biological diversity has long been a major
315 research focus in biogeography and ecology (e.g. MacArthur & Wilson, 1967; Rosenzweig,

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3 316 1995) and was recently the focus of a ‘virtual issue’ of the *Journal of Biogeography* (see
4 317 Whittaker & Triantis, 2012). In examining species–area relationships, Triantis *et al.* (2012;
5 318 also see Gray *et al.*, 2004) drew attention to the fundamental distinction between species
6 319 accumulation curves (‘SACs’ – the increase in species richness as a sampling property of
7 320 progressively larger areas within regions) and island species–area relationships (‘ISARs’ –
8 321 counts of species on different isolated islands). Their comprehensive meta-analysis of over
9 322 600 ISARs on true islands has now been added to by Matthews *et al.* (this issue), who used
10 323 over 800 datasets from both habitat islands and true islands (Box 1) to evaluate how the
11 324 slope (z) and intercept (c) of ISARs vary between island types. The slopes of the ISARs tended
12 325 to be steeper on true islands, and oceanic islands had smaller intercepts than habitat islands
13 326 within continental regions.

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16 327 The dependence of extinction rate on island area (e.g. Ricklefs & Bermingham, 2007),
17 328 in conjunction with the ‘target effect’ of larger islands being more likely to be colonised (Box
18 329 1; MacArthur, 1972), produces the familiar ISAR, reflecting the influence of island area on
19 330 the dynamics of species gain and loss. Larger areas typically include more habitat types and
20 331 support larger populations, promoting *in situ* speciation as well as reducing extinction rates.
21 332 Losos and Schluter (2000) showed that the ISAR slope for Caribbean *Anolis* lizards increases
22 333 above a critical island size that is apparently required for allopatric speciation within islands
23 334 (Box 1). Building on that result, Algar and Mahler (this issue) found that the rate of climatic
24 335 niche evolution in *Anolis* increases with island area, because of response to climatic
25 336 opportunity, potentially contributing to adaptive diversification on larger islands. Consistent
26 337 with a driving force on islands of response to opportunity, Steinbauer *et al.* (this issue) found
27 338 high levels of climatic niche lability, rather than climatic niche conservatism or competitive
28 339 displacement, within radiating plant clades in the Canary Islands.

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30 340 Given those recent advances, it is not surprising that area affects not only species
31 341 numbers, but also ecological interactions between island species (e.g. Holt, 2009; Gravel *et al.*
32 342 *et al.*, 2011; Roslin *et al.*, 2014). For islands in the Bahamas, Schoener *et al.* (this issue) found
33 343 that competition and predation exhibited their largest effect sizes on intermediate-sized
34 344 islands. They suggest that the harsher abiotic conditions, larger marine subsidies, lower
35 345 spatial heterogeneity and greater stochastic effects typical of smaller islands shifted
36 346 communities towards having fewer top predators compared to larger islands. In contrast,
37 347 ant–plant mutualism decreased with increasing island area, while plant–pollinator
38 348 mutualism showed the opposite trend.

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43 350 **The shifting stage**

44 351 The recent history of island biogeographic investigation can be characterized as moving from
45 352 a concept of islands as neutral, static and interchangeable landing pads for species (e.g.
46 353 MacArthur & Wilson, 1963, 1967) to one in which their physical characteristics are critically
47 354 important (e.g. Kalmar & Currie, 2006), and finally to a view of islands changing through time
48 355 (e.g. Whittaker *et al.*, 2008; Rijdsdijk *et al.*, 2014; Weigelt *et al.*, 2016, Fernández-Palacios *et al.*
49 356 *et al.*, this issue). These considerations are in accordance with the general paradigm that Earth
50 357 is a dynamic planet, where changes can even occur in short time spans. The ‘General
51 358 Dynamic Model’ of oceanic island biogeography (GDM; Box 1; Whittaker *et al.*, 2008; see
52 359 review by Borregaard *et al.*, in press a) emphasizes the importance of island ontogeny and
53 360 geological dynamics for biological processes on islands, including colonization, speciation
54 361 and extinction. The GDM has been evaluated empirically, receiving considerable support
55 362 (e.g. Whittaker *et al.*, 2008; Borges & Hortal, 2009; Bunnefeld & Phillimore, 2012; Steinbauer
56 363 *et al.*, 2013; Valente *et al.*, 2014). This model provides a good example of how island theory

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3 364 is linked to other research areas. It implies that, early in island ontogeny, the main process
4 365 acting is immigration, coupled with within-island and within-archipelago metapopulation
5 366 and metacommunity dynamics. At a later stage (called the immaturity stage), the dynamic
6 367 nature of island landscapes fosters the ascendance of evolutionary processes, at least on
7 368 larger islands. Finally, as the island reaches its maturity and starts to submerge (due to
8 369 erosion, downcutting, and subsidence), extinction increases and becomes the main driver of
9 370 species richness and island community dynamics.

10 371 The GDM, as originally formulated (Whittaker *et al.*, 2008), was primarily applied to
11 372 oceanic hotspot islands (Box 1). It has now been extended to include subduction-based arc
12 373 islands and continental fragment islands (Box 1; Borregaard *et al.*, this issue; see also Heaney
13 374 *et al.*, 2013). Borregaard *et al.* (this issue) also formalized the logic of the GDM, expressing
14 375 the causal relationships as a directed graph model, which they used to evaluate the
15 376 generalized diagram of 'key rates and properties' of Whittaker *et al.* (2008). This latest
16 377 version of the GDM modifies the colonization and extinction curves and exposes a larger gap
17 378 between potential species richness ('carrying capacity') and actual species richness
18 379 throughout an island's life cycle.

19 380 The GDM does not include recent dramatic variations in climate and sea-level
20 381 changes associated with Pleistocene glacial cycles (Ali & Aitchison, 2014; Rijdsdijk *et al.*, 2014).
21 382 To address these factors, Fernández-Palacios *et al.* (this issue) have produced a model of
22 383 archipelagic island biogeography that combines the interconnected effects of sea-level
23 384 changes, island area and isolation on immigration and extinction rates and, consequently, on
24 385 species richness (see also Weigelt *et al.*, 2016). Furthermore, based on their model they
25 386 enunciated testable predictions, regarding, for instance, species' genetic structure and
26 387 extinction likelihood, which should enhance in the near future the study of the impact of sea
27 388 level changes on the contemporary biotas of oceanic islands. Rominger *et al.* (this issue)
28 389 have also incorporated archipelagic dynamics in their study of community assembly on the
29 390 Hawaiian Islands. Hotspot archipelagos such as the Hawaiian Islands provide a time series
30 391 over which one can investigate the evolutionary development of island biotas. Using
31 392 extensive genetic and molecular phylogenetic information, Rominger *et al.* examined the
32 393 development of ecological communities over the time series of the archipelago, where the
33 394 major subaerial islands range from <0.5 Ma (Hawaii) to more than 5 Ma (Kauai), and new
34 395 soils continue to form from recent lava flows on the youngest island, Hawaii. They found
35 396 that ecological communities are initially driven by immigration, but that this shifts to *in situ*
36 397 diversification after about 1 million years, resulting in changes in interaction network
37 398 structure and ecological specialization (increase in modularity and decrease in nestedness)
38 399 with increasing dominance of evolutionary change over time.

40 401 **Human influences and biological invasions**

41 402 Patterns of diversity and community organization on islands have, in many instances, been
42 403 affected by human activities. The impacts of humans, and their commensals, on island biotas
43 404 started in pre-historic times, as reflected by numerous extinctions apparent in the fossil
44 405 record (Olson, 1990; Whittaker & Fernández-Palacios, 2007; Duncan *et al.*, 2013). Habitat
45 406 conversion is one of the main threats to island species (e.g. Caujapé-Castells *et al.*, 2010;
46 407 Triantis *et al.*, 2010), together with alien (Box 1) competitors, herbivores, predators and
47 408 pathogens (e.g. Sax *et al.*, 2002; Reaser *et al.*, 2007; Caujapé-Castells *et al.*, 2010).
48 409 Extinctions also affect functional diversity (Boyer *et al.*, 2014), which can influence
49 410 ecosystem functioning. In some cases, introduced predators and herbivores have
50 411 dramatically impacted local populations, sometimes shifting the entire ecological character

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3 412 of an island – e.g. goats (Coblentz, 1978) and brown tree snakes (Savidge, 1987). In some
4 413 archipelagos (e.g. Galápagos and Hawaii), the number of alien plant species surpasses that of
5 414 natives, although it remains unclear how disruptive alien species are for interaction
6 415 networks (e.g. Olesen *et al.*, 2002; Padrón *et al.*, 2009; Heleno *et al.*, 2013; Nogales *et al.*,
7 416 this issue; but see Traveset & Richardson, 2006; Traveset *et al.*, 2013).

8 417 The native biotas of oceanic islands have developed through historic colonizations.
9 418 What have changed with human transport and deliberate introductions are the rate of
10 419 accumulation of new species and the appearance of species with limited dispersal ability
11 420 that would not reach many islands without human assistance. Introduced species (and also
12 421 historic extinctions) provide opportunities to observe how new species fit into established
13 422 communities (Sax *et al.*, 2002; Nogales *et al.*, this issue), and how their introduction alters
14 423 community relationships. Blackburn *et al.* (this issue) used structural equation modelling to
15 424 explore these questions, and found that both native and alien plants and birds have
16 425 strikingly similar (positive) ISARs. They found that alien species richness was strongly
17 426 positively related to both native species richness and human population size, interpreting
18 427 human population size as a measure of propagule pressure, and native species richness as a
19 428 proxy for the island environment. These results suggest that native and alien species
20 429 richness respond similarly to the same factors on islands, while biotic resistance (*sensu*
21 430 Elton, 1958) is not a major influence.
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24 433 **The future of island biogeography**

25 434 Island biogeography is currently enjoying a renaissance (Fernández-Palacios *et al.*, 2015).
26 435 Much of the knowledge gathered through the last decades from different research areas is
27 436 being synthesized in new theories and models – two of them being included in this special
28 437 issue (Borregaard *et al.*, in press b; Fernández-Palacios *et al.*, in press; Table 1), while existing
29 438 ones are being tested and updated with new and more powerful analytical tools and new
30 439 molecular, ecological and distributional data. Because islands' circumscribed geography and
31 440 discrete nature allow the study of the geography of processes that are, in fact, occurring
32 441 everywhere – including within large continental regions and ocean basins (examples in Table
33 442 1) – we believe this integration of knowledge arising from island studies will surely have an
34 443 impact in terms of understanding other systems.

35 444 Despite this surge of research activity, some avenues for future research remain
36 445 relatively unexplored. Heaney *et al.* (2013) and Warren *et al.* (2015) proposed a number of
37 446 research questions that involve islands as key elements for understanding the ecological and
38 447 evolutionary processes shaping communities in general. More particularly, they refer to
39 448 questions related to (i) community assembly – the importance of arrival history (or priority
40 449 effects; Box 1) for community assembly, changes in species' abundance that might occur
41 450 after colonization, the influence of existing species on the establishment of newly arrived
42 451 species, and influence of island area and isolation on community assembly, equilibrium, and
43 452 evolution; (ii) ecosystem functioning – particularly the contribution of *in situ* evolution to
44 453 changes in rates of energy flux and nutrient cycling; and (iii) speciation and diversification –
45 454 the role of gene flow in speciation, and the more rapid diversification of some lineages in
46 455 comparison with others. These priorities reinforce the need to incorporate non-equilibrium
47 456 dynamics and different modes of speciation in future island models. Here we complement
48 457 these prospects and propose some questions that we feel should be pursued. We first
49 458 discuss broad research directions that are not island-specific, but to which islands might
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3 459 contribute important insights. We then briefly cover additional questions that may not be so
4 460 directly transferable to continental areas.

5 461 Islands, particularly oceanic islands that have long been isolated from the mainland,
6 462 have their own peculiarities (e.g. species with unusual adaptations as in the cases of
7 463 woodpecker finches and blood-sucking finches on the Galápagos Islands, dragon's blood
8 464 trees on Socotra and Macaronesia, pollinating reptiles on many islands). To transfer
9 465 knowledge appropriately from islands to broader contexts requires understanding both the
10 466 similarities that promote transferability and the differences that limit it. For example,
11 467 adaptive radiation, a process widely studied on islands (e.g. Givnish *et al.*, 2009; Losos, 2011;
12 468 Steinbauer *et al.*, this issue), occurs differently on islands and continental areas. In island
13 469 systems, speciation tends to occur in isolation within lineages (e.g. Pinto *et al.*, 2008), while
14 470 on continents it is common for radiations to involve evolution in many lineages, interacting
15 471 through antagonistic or mutualistic relationships. Island–mainland (or species pool)
16 472 comparisons seem to be a logical way to proceed, but few studies have taken this approach
17 473 (but see Santos *et al.*, 2011a, 2011b; Patiño *et al.*, 2015; Traveset *et al.*, this issue). Some
18 474 that have done so have questioned old assumptions about islands – for example: island
19 475 communities do not always have lower diversity than mainland communities (e.g. Algar &
20 476 Losos, 2011; Patiño *et al.*, 2015); the island rule does not hold true for many taxa (Box 1; e.g.
21 477 Meiri *et al.*, 2008; Itescu *et al.*, 2014); island systems are not necessarily dominated by
22 478 species with high dispersal capacities (e.g. Vargas *et al.*, 2012; Heleno & Vargas, 2015). With
23 479 more data and analytical approaches available than ever before, more effort should be
24 480 directed towards understanding the generality of patterns and processes that have been
25 481 widely acknowledged as being predominant on islands, and that have long been used to
26 482 separate island from mainland systems.

27 483 Community assembly on oceanic islands involves (i) the dispersal of species from an
28 484 external species pool, following which the species are then (ii) subjected to abiotic and biotic
29 485 filters that determine the island or within-island assemblage. These two steps also occur on
30 486 continental islands, although they are less important as newly formed continental islands
31 487 already possess a diverse biota. The species pool can be defined as the group of species that
32 488 can potentially colonize a local site (Cornell & Harrison, 2014); the species pool is generally
33 489 thought of as a static and independent (i.e. extrinsic) unit (Mittelbach & Schemske, 2015).
34 490 The species pool concept has been widely used as a null model for identifying processes (e.g.
35 491 environmental filtering, limiting similarity) that shape the taxonomic, phylogenetic or trait
36 492 structure of communities (e.g. Carstensen *et al.*, 2013; Weigelt *et al.*, 2015; Santos *et al.*, this
37 493 issue). Although this top-down framework has been widely applied (e.g. MacArthur &
38 494 Wilson, 1963; Hubbell, 2001), it fails to incorporate the dynamic nature of the species pool,
39 495 and the importance of dispersal, speciation and extinction for the maintenance of the
40 496 species pool over time and space. Archipelagos can help us understand how local species
41 497 assemblages and regional species pools are linked within continents, as each archipelago can
42 498 be viewed as a regional pool that feeds, and is fed by, the dynamics occurring within and
43 499 between its constituent islands (local assemblages; Grant & Grant, 2008). Species arising in
44 500 allopatry might colonize other islands, achieving secondary sympatry and becoming part of
45 501 the archipelagic species pool (islands feed the pool), eventually colonizing other islands
46 502 within the archipelago (the pool feeds the islands).

47 503 The Earth is currently going through dramatic environmental changes (e.g. pollution,
48 504 climate changes, land use change, biodiversity loss) that are affecting many of the planet's
49 505 ecosystem support systems, and that can ultimately lead to species' extinctions and further
50 506 deterioration of human societies. Islands are also subject to these impacts (e.g. Savidge,

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3 507 1987; Sax *et al.*, 2002; Duncan *et al.*, 2013; Boyer & Jetz, 2014; Bellard *et al.*, 2014) and can
4 508 be useful tools for understanding the consequences of environmental change. First, as
5 509 islands (or archipelagos) are discrete and geographically isolated, most of their populations
6 510 cannot easily escape these impacts. Second, as many islands are among the last territories to
7 511 be colonized by humans, the impact of human activity has been occurring for a shorter
8 512 period of time, which provides the opportunity to disentangle the effects of climate change
9 513 on the extinction of local communities.

11 514 Biological invasions can fundamentally change the local biotic environment (e.g. van
12 515 der Wal *et al.*, 2008). Islands have been particularly affected by invasions (Sax *et al.*, 2002),
13 516 with many island faunas and floras now being dominated by introduced species (e.g. Azores,
14 517 Hawaii). Islands offer great opportunities for research into biological invasions because of
15 518 their well delimited boundaries and, in many cases, relatively brief periods of human
16 519 occupation (Sax *et al.*, 2002) and knowledge of approximate human arrival dates. Further, as
17 520 many islands are within archipelagos, they have been subject to similar evolutionary
18 521 histories and ecological forces, providing replicated units with varying degrees of species'
19 522 introductions. Sax and Gaines (2008) described four principal knowledge gaps in invasion
20 523 research: (i) the need to further understand the role of propagule pressure, (ii) the dynamics
21 524 of time-lags to extinction, (iii) the effects of alien species on native species' abundance, and
22 525 (iv) the impact of land-use changes on native species diversity. To these, we add the
23 526 important question of how invasive species affect ecosystem functioning: do they replace
24 527 native species' functions, add functions not previously performed, or become redundant in
25 528 terms of the ecosystem functions they provide?

29 529 Some questions that apply specifically to island systems also address research
30 530 priorities for ecology more generally. Trait diversity and phylogenetic diversity have been
31 531 widely used over the past decade as tools to ascertain the processes that shape community
32 532 assembly, particularly in continental areas. Typically, ecologists assume that communities
33 533 are shaped either by limiting similarity (resulting in coexistence of species that are
34 534 overdispersed in ecological and trait space) or environmental filtering (causing clustered
35 535 patterns), with contradictions when traits are not phylogenetically conserved (Pausas &
36 536 Verdú, 2010). So far, few studies on island systems have analysed community organization
37 537 from this perspective (but see Cardillo & Meijaard, 2010; Santos *et al.*, this issue). Island
38 538 systems, with their relative simplicity, could be used to combine such research with
39 539 investigation of other processes potentially involved in community assembly, but which are
40 540 more difficult to address in continental contexts (e.g. convergent evolution, adaptive
41 541 radiation). Our knowledge of the biogeography of trait and phylogenetic diversity is still
42 542 limited. For example, what is the relationship between trait and/or phylogenetic diversity
43 543 and species richness on islands? Does this relationship differ from that found in mainland
44 544 systems? How are trait and/or phylogenetic diversity related to island area and age?

48 545 One of ETIB's main predictions is that species on islands are continually being turned
49 546 over through extinction and colonization, with species richness becoming stable through
50 547 time (MacArthur & Wilson, 1967). Yet, few studies have addressed the dynamics of these
51 548 processes (but see Valente *et al.*, 2015). One prediction that should be evaluated is that
52 549 islands have a mix of young and old species, which can now be assessed through
53 550 phylogenetic reconstructions (Ricklefs & Bermingham, 2001, 2008; Cadena *et al.*, 2005;
54 551 Valente *et al.*, 2014). However, this pattern could also arise in a non-saturated island, where
55 552 no extinctions have occurred. Quantifying extinctions, particularly the timing of extinctions,
56 553 is difficult in most island settings. One approach that could be more fully explored is fitting

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3 554 species' age distributions to models that incorporate extinction, assuming time-
4 555 homogeneous processes (Ricklefs, 2009).

5 556 Where species diversification occurs within islands, we would also like to understand
6 557 how this process varies over the geological ontogeny of individual islands. According to the
7 558 General Dynamic Model (Whittaker *et al.*, 2008; Borregaard *et al.*, this issue), speciation rate
8 559 should be higher in relatively young islands, which provide opportunities for diversification
9 560 due to empty ecological niche space, and when extinction rates may be relatively low.
10 561 Although a few studies have looked into this question using modelling approaches (e.g.
11 562 Rabosky & Glor, 2010; Valente *et al.*, 2014), empirical evaluation is largely lacking (see,
12 563 however, Fritz *et al.*, 2012).
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17 566 **Concluding remarks**

18 567 From the observations and patterns described by naturalists during the first European
19 568 expeditions around the globe, to the studies by Darwin and Wallace, and to the
20 569 development of the Equilibrium Theory of Island Biogeography (Box 1), islands have long
21 570 influenced our understanding of ecological and evolutionary patterns and processes (Table
22 571 1, S1). This interest continues to the present, reinvigorated by new perspectives and
23 572 analytical approaches to community ecology, evolutionary diversification and biogeographic
24 573 distributions of species. This special issue of *Global Ecology and Biogeography* is a reflection
25 574 of the continued relevance of island systems for understanding ecology and evolution more
26 575 generally. We hope you agree that the papers in this special issue set a good collective
27 576 example for continuing research on island systems.

28 577 Existing datasets from island systems are globally valuable and have provided
29 578 important insights for ecology and evolution, largely because of the relative simplicity and
30 579 possibility for independent replication offered by islands and archipelagos. However,
31 580 although databases for island characteristics, and for species distributions and ecological
32 581 requirements, traits, and phylogenetic relationships continue to grow (e.g. Cardillo &
33 582 Meijaard, 2010; Weigelt *et al.*, 2013, 2015; Whittaker *et al.*, 2014; Santos *et al.*, this issue),
34 583 many gaps need filling to realize the full potential of future research. Inventories of island
35 584 floras and faunas, particularly of non-vertebrate groups, are far from complete (e.g. Hortal *et al.*,
36 585 2007; Schipper *et al.*, 2008; Santos *et al.*, 2010), with many species still waiting to be
37 586 described. Detailed information on the distribution of species within islands, which could be
38 587 used for investigation of community assembly and, in some systems, adaptive radiation, is
39 588 still limited in many cases. More information on functional traits and phylogenetic
40 589 relationships may help us to interpret community assembly and structure in terms of
41 590 ecological and evolutionary processes, including adaptive radiation. We advocate a
42 591 continuing effort to build comprehensive island data for multiple taxa, to serve the wider
43 592 scientific community in the coming decades.

44 593 The current excitement around islands reflects island biogeography's being a vibrant,
45 594 active field of research. We hope this enthusiasm will continue and that the knowledge and
46 595 theories developed from island systems will continue to produce insight into the natural
47 596 world more generally.
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3 601 **Acknowledgments**
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11 609 constructive comments on the manuscript.
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16 613 **Biosketch**
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18 615 Ana M. C. Santos is currently a post-doctoral researcher at the Museo Nacional de Ciencias
19 616 Naturales (CSIC; Madrid, Spain). Her research interests include community ecology, island
20 617 biogeography and entomology. Her current work focuses on cross-scale variations of
21 618 community assembly and structure.
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24 620 Richard Field is mainly interested in biogeography, macroecology and plant ecology, with
25 621 particular focus on biodiversity and the drivers structuring ecological communities,
26 622 particularly on islands.
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29 624 Robert E. Ricklefs has a long standing interest in the distribution of birds on islands,
30 625 particularly in the West Indies. He is currently working on the host and geographic
31 626 distributions of malarial parasites of island birds.
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34 628 Author contributions: A.M.C.S., R.F. and R.E.R. conceived and designed the review, and
35 629 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

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3 1063 rates depend greatly on the island isolation, while extinction rates are mainly associated
4 1064 with island area.
5 1065
6 1066 *General Dynamic Model of oceanic island biogeography*: a conceptual model by Whittaker *et*
7 1067 *al.* (2008) describing changes in diversity and ecological and evolutionary processes that are
8 1068 associated with the changes in the physiographic characteristics of volcanic oceanic islands
9 1069 (e.g. area, altitude) that occur throughout its ontogeny.
10 1070
11 1071 *Habitat island*: a discrete patch of habitat that is surrounded by a matrix of contrasting
12 1072 (usually unsuitable) habitat(s).
13 1073
14 1074 *Hotspot archipelago*: an archipelago of volcanic origin where islands are formed over near-
15 1075 stationary thermal plumes located in the Earth's upper mantle. Tectonic plate movements
16 1076 cause the islands to drift from that point, originating a series of islands of different ages.
17 1077
18 1078 *Incidence functions*: functions that describe how the probability of occurrence of a species
19 1079 varies with certain island characteristics (e.g. area, isolation, species richness).
20 1080
21 1081 *Island ontogeny*: the development of an island, from its formation through its development
22 1082 and subsequent degradation and disappearance.
23 1083
24 1084 *Island rule*: the tendency of small animals to evolve to larger sizes and large animals to
25 1085 evolve to smaller sizes on islands.
26 1086
27 1087 *Mangrove islands*: islands where the land area is mostly or totally below tidal water (at high
28 1088 tide), being overwash banks covered mainly by mangrove plants. They are usually located
29 1089 rather close to the mainland, and might, or might not, have been connected to the mainland
30 1090 coastal habitats.
31 1091
32 1092 *Metacommunity*: a group of communities that are linked through dispersal.
33 1093
34 1094 *Metapopulation*: a group of spatially separated populations that are connected by gene flow,
35 1095 extinction and recolonization.
36 1096
37 1097 *Modularity*: the occurrence of semi-independent groups (also called modules) of interacting
38 1098 species.
39 1099
40 1100 *Nestedness (in respect to network analysis)*: a metric of the generalist–specialist balance in
41 1101 ecological communities. A network is nested when specialists interact with a subset of the
42 1102 group of species with which generalists interact.
43 1103
44 1104 *Niche*: the requirements (resources or physical conditions) of a population or species that
45 1105 allow it to survive in the focal certain area.
46 1106
47 1107 *Oceanic Island*: island formed due to volcanic activity, that has never been connected to
48 1108 another landmass. Upon their formation, oceanic islands are devoid of life, and so their
49 1109 biotas are assembled from colonization and/or speciation.
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1111 *Parasitoid*: an organism (usually an insect) that develops through adulthood by feeding on or
1112 in the body of a host (usually an arthropod), eventually killing it.

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1114 *Priority effects*: the effects that the first species that colonize an area cause on the
1115 subsequent colonizers, as a result of colonizing first.

1116

1117 *Sympatric speciation*: speciation that occurs when populations are not geographically
1118 isolated from each other.

1119

1120 *Target effect*: the increased probability that a larger island has of being colonized than a
1121 smaller one, resulting from random dispersal.

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1123 *Taxon cycle*: sequential phases of expansion and contraction of species' ranges, which are
1124 usually associated with shifts in the species' ecological niches.

1125

1126 *True island*: a piece of land that is surrounded by water.

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3 1128 Table 1. A non-exhaustive summary of theories, processes and patterns that a) have
4 1129 originated in island studies, or b) have not originated from island studies, but have received
5 1130 an important theoretical and/or analytical input from island studies. Examples (citations) of
6 1131 each theory, process or pattern are given for different types of island (see Box 1), and also
7 1132 for mainland systems. Many of these examples (indicated by #) are not exclusive to one
8 1133 particular theory, process or pattern, and could indeed also be included in one or more
9 1134 different sections. * indicates the studies that are part of this special issue. See Appendix 1
10 1135 (Data Sources) for references not in the main reference list. The expanded online version of
11 1136 this table (Table S1) additionally categorizes the examples by taxon.
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17 **Appendix 1 – Data sources**

18 1141 List of references for the examples cited in Table 1 and Table S1 that are not in the main
19 1142 reference list.
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24 **Supplementary Material (online only)**

25 1147
26 1148 Table S1.

27 1149 Expanded version of Table 1. A non-exhaustive summary of theories, processes and patterns
28 1150 that a) have originated in island studies, or b) have not originated from island studies, but
29 1151 have received an important theoretical and/or analytical input from island studies. Examples
30 1152 (citations) of each theory, process or pattern are given for different types of island (see Box
31 1153 1, main paper), and also for mainland systems. Many of these examples (indicated by #) are
32 1154 not exclusive to one particular theory, process or pattern, and could indeed also be included
33 1155 in one or more different sections. The main taxa used in each example are displayed in the
34 1156 columns. Symbols are as follows: $f(x)$ - Theoretical study (no use, or very limited use, of
35 1157 empirical data);  - Arthropods;  - Other terrestrial invertebrates;  - Mammals;
36 1158  - Reptiles;  - Amphibians;  - Birds;  - Fish;  - Marine invertebrates;  -
37 1159 Plants;  - Microorganisms. * indicates the studies that are part of this special issue. See
38 1160 main paper for references: main reference list and Appendix 1 (Data Sources).
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8 **Theories/Patterns that have originated mainly from island studies**
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10 **Adaptive radiation**

11 * *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[#]

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

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

14 *Non-Island Systems*: Hughes *et al.*, 2006; Pincheira-Donoso *et al.*, 2015
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18 **Ecological release and Density compensation**

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

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

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

22 *Non-Island Systems*: Adams & Rohlf, 2000; Davies *et al.*, 2007; Schmitt & Holbrook, 1990
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26 **Body size evolution and the "island rule"**

27 *Oceanic Islands*: Clegg & Owens, 2002; Lomolino, 2005[#]

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

29 *Habitat Islands*: Schmidt & Jensen, 2003

30 *Non-Island Systems*: McClain *et al.*, 2006
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34 **Taxon cycle**

35 *Oceanic Islands*: Economo *et al.*, 2012; Jønsson *et al.*, 2014[#]; Ricklefs & Bermingham, 2002; Ricklefs & Cox, 1972; Wilson, 1961

36 *Non-Island Systems*: Economo *et al.*, 2015; Erwin, 1985; Glazier, 1980; Hoagstrom *et al.*, 2014
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39 **Equilibrium Theory of Island Biogeography**
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5 * *Oceanic Islands*: * Fernández-Palacios *et al.*, this issue; Heaney, 2000 #; MacArthur & Wilson, 1963, 1968; Rosindell & Harmon, 2013 #

6 *Continental Islands*: Cody, 2006; Foufopoulos & Mayer, 2007; Jones & Diamond, 1976

7 *Mangrove Islands*: Simberloff & Wilson, 1969, 1970

8 * *Habitat Islands*: Bossard, 2014; Brown, 1971, 1978; * Dawson, this issue; Hart & Pearson, 2011; March & Bass, 1995; Schoener, 1974; Smith, 1979

9 *Non-Island Systems*: Rosenzweig, 1975 #

10 11 12 **General Dynamic Model of Island Biogeography**

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

15 16 17 **Assembly rules, Checkerboard distributions and Null models in ecology**

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

20 *Continental Islands*: Cody, 2006

21 *Habitat Islands*: Englund *et al.*, 2009

22 *Non-Island Systems*: Gotelli & Ellison, 2002; Gotelli & Graves, 1996; Gotelli *et al.*, 1997; Rautenbach *et al.*, 2014; Sanders *et al.*, 2007

23 24 25 26 27 **Unified Neutral Theory of Biodiversity and Biogeography**

28 *Oceanic Islands*: Rosindell & Phillimore, 2011 #

29 *Continental Islands*: Hubbell, 2001, 2009

30 *Habitat Islands*: Dornelas *et al.*, 2006; Gilbert *et al.*, 2006

31 *Non-Island Systems*: Ricklefs, 2006; Rosindell *et al.*, 2015

32 33 34 35 36 **Theories/patterns not originated on island systems, but that have benefited from them**

37 38 **Natural Selection and Speciation**

39 *Oceanic Islands*: Calsbeek & Cox, 2010; Darwin, 1859; Grant & Grant, 2008, 2016; Roderick & Gillespie, 1998; Rowe *et al.*, 2016 #; Savolainen *et al.*, 2006;

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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

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; Inchausti & Weimerskirch, 2002[#]

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Continental Islands: Hanski, 2009[#]; Nieminen, 1996; Nieminen & Hanski, 1998; Zalewski, 2004

Habitat Islands: Bay *et al.*, 2008; Hanski & Ovaskainen, 2000

Non-Island Systems: Levins, 1969, 1970

Ecological Succession

Oceanic Islands: Edwards & Thorton, 2001; Magnússon *et al.*, 2014; Mueller-Dombois & Bohemer, 2013; Thornton *et al.*, 1993; Whitaker *et al.*, 1989

Continental Islands: Lavoie & Fillion, 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[#]; Tscharrntke & 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[#]; Coblenz, 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

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For Peer Review

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.

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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); - 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).

	$f(x)$										
Theories/Patterns that have originated mainly from island studies											
Adaptive radiation											
<i>Oceanic Islands</i>											
* Algar <i>et al.</i> , this issue						X					
Blonder <i>et al.</i> , 2016											X
Gillespie <i>et al.</i> , 2004		X									
Givnish <i>et al.</i> , 2009											X
Grant & Grant, 2008							X				
Losos, 2011						X					
Pinto <i>et al.</i> , 2008 #						X					
<i>Continental Islands</i>											
Baldwin, 2007											X
van der Geer <i>et al.</i> , 2010				X							
<i>Habitat Islands</i>											
Dawson & Hammer, 2005									X		
Seehausen, 2006								X			

*Non-Island Systems*Hughes *et al.*, 2006

X

Pincheira-Donoso *et al.*, 2015

X

Ecological release and Density compensation*Oceanic Islands*

Grant & Grant, 2006

X

Lack, 1947

X

Novosolov *et al.*, 2016 #

X

Schluter, 1988

X

* Steinbauer *et al.*, this issue

X

Wright, 1980 #

X

*Continental Islands*Barun *et al.*, 2015

X

Case, 1975

X

Lomolino, 1984

X

MacArthur, 1972

X

Schluter & McPhail, 1992

X

Schoener & Spiller, 1987

X

X

*Habitat Islands*Hobbs *et al.*, 2012

X

Martin & Pfennig, 2011

X

McGrady-Steed & Morin, 2000

X

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Non-Island Systems

Adams & Rohlf, 2000						X				
Davies <i>et al.</i> , 2007			X							
Schmitt & Holbrook, 1990								X		

Body size evolution and the "island rule"

Oceanic Islands

Clegg & Owens, 2002								X		
Lomolino, 2005 #			X		X					

Continental Islands

Lawlor, 1982			X							
Meiri, 2007					X					
Montesinos <i>et al.</i> , 2012						X				

Habitat Islands

Schmidt & Jensen, 2003			X							
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Non-Island Systems

McClain <i>et al.</i> , 2006									X	
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Taxon cycle

Oceanic Islands

Economo <i>et al.</i> , 2012	X									
Jønsson <i>et al.</i> , 2014 #								X		
Ricklefs & Bermingham, 2002					X					
Ricklefs & Cox, 1972								X		
Wilson, 1961	X									

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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 #

Continental Islands

Hubbell, 2001, 2009

Habitat Islands

Dornelas *et al.*, 2006

Gilbert *et al.*, 2006

Non-Island Systems

Ricklefs, 2006











Rosindell *et al.*, 2015

	$f(x)$	Butterfly	Snail	Frog	Lizard	Iguana	Bird	Fish	Jellyfish	Leaf	Pond
Englund <i>et al.</i> , 2009											
Gotelli & Ellison, 2002						X					
Gotelli & Graves, 1996	X										
Gotelli <i>et al.</i> , 1997								X			
Rautenbach <i>et al.</i> , 2014					X						
Sanders <i>et al.</i> , 2007						X					
Unified Neutral Theory of Biodiversity and Biogeography											
<i>Oceanic Islands</i>											
Rosindell & Phillimore, 2011 #								X			
<i>Continental Islands</i>											
Hubbell, 2001, 2009											X
<i>Habitat Islands</i>											
Dornelas <i>et al.</i> , 2006									X		
Gilbert <i>et al.</i> , 2006											X
<i>Non-Island Systems</i>											
Ricklefs, 2006								X			
Rosindell <i>et al.</i> , 2015	X										

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	$f(x)$										
<i>Continental Islands</i>											
Ali & Huber, 2000				X							
Alsos <i>et al.</i> , 2015										X	
<i>Habitat Islands</i>											
Huth <i>et al.</i> , 2015	X										
<i>Non-Island Systems</i>											
Bellemain & Ricklefs, 2008 #		X		X	X	X	X			X	
Brochet <i>et al.</i> , 2009										X	
Dawson & Hammer, 2008 #											X
Nicholson <i>et al.</i> , 2005 #					X						
O'Grady & DeSalle, 2008 #		X									
Patiño <i>et al.</i> , 2015 #										X	
Species-area relationship											
<i>Oceanic Islands</i>											
Aranda <i>et al.</i> , 2013										X	
Kisel <i>et al.</i> , 2010 #		X	X	X	X		X			X	
Lomolino & Weiser, 2001 #		X	X	X	X	X	X			X	
Losos & Schluter, 2000					X						
Ricklefs & Lovette, 1999		X		X	X	X	X				
Santos <i>et al.</i> , 2010 #		X	X	X	X	X	X			X	
Scheiner, 2003 #	X										
Triantis <i>et al.</i> , 2012 #		X	X	X	X	X	X			X	
Wright, 1983 #							X			X	



Continental Islands

Azeria, 2004								X	
Conroy <i>et al.</i> , 1999			X						
Dennis <i>et al.</i> , 2012	X							X	
Murakami & Hirao, 2010	X								
Wang <i>et al.</i> , 2010			X		X			X	

Habitat Islands

Matthews <i>et al.</i> , 2015								X	
Patterson & Atmar, 1986 #			X						
Watling & Donnelly, 2006 #	X	X	X	X	X			X	

Non-Island Systems

Baselga, 2010	X								
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Metapopulation dynamics

Oceanic Islands

Farrington & Petren, 2011								X	
Garcia-Verdugo <i>et al.</i> , 2010									X
Inchausti & Weimerskirch, 2002 #								X	

Continental Islands

Hanski, 2009 #	X		X					X	
Nieminen, 1996	X								
Nieminen & Hanski, 1998	X								
Zalewski, 2004	X								

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Habitat Islands

Bay *et al.*, 2008

X

Hanski & Ovaskainen, 2000

X

Non-Island Systems

Levins, 1969, 1970

X

Ecological Succession

Oceanic Islands

Edwards & Thorton, 2001

X

Magnússon *et al.*, 2014

X

Mueller-Dombois & Bohemer, 2013

X

Thornton *et al.*, 1993

X

Whitaker *et al.*, 1989

X

Continental Islands

Lavoie & Fillion, 2001

X

Rydin & Borggård, 1988

X

Mangrove Islands

Piechnick *et al.*, 2008

X

Habitat Islands

McClanahan, 2014

X

Pinotti *et al.*, 2015

X

Non-Island Systems

Clements, 1916

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Dauber & Wolters, 2005

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Letcher, 2010

X

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