

A roadmap for island biology: 50 fundamental questions after 50 years of The Theory of Island Biogeography

Matthews, Thomas

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1 **Strapline: Special Paper**

2

3 **A roadmap for island biology: 50 fundamental questions after 50 years**

4 **of *The Theory of Island Biogeography***

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7

8 Jairo Patiño^{1,2,*}, Robert J. Whittaker^{3,4}, Paulo A.V. Borges², José María Fernández-
9 Palacios⁵, Claudine Ah-Peng⁶, Miguel Araújo^{7,8}, Sergio P. Ávila⁹, Pedro Cardoso^{2,10},
10 Josselin Cornuault¹¹, Erik J. de Boer¹², Lea de Nascimento⁵, Artur Gil², Aarón González-
11 Castro¹, Daniel S. Gruner¹³, Ruben Heleno¹⁴, Joaquín Hortal^{8,15}, Juan Carlos Illera¹⁶,
12 Christopher Kaiser-Bunbury¹⁷, Thomas J. Matthews^{2,18}, Anna Papadopoulou¹⁹, Nathalie
13 Pettorelli²⁰, Jonathan P. Price²¹, Ana M. C. Santos^{2,8,22}, Manuel J. Steinbauer²³, Kostas A.
14 Triantis²⁴, Luis Valente²⁵, Pablo Vargas²⁶, Patrick Weigelt²⁷ and Brent C. Emerson^{1,28}

15

16 ¹*Island Ecology and Evolution Research Group, Instituto de Productos Naturales y*
17 *Agrobiología, (IPNA-CSIC), La Laguna, Tenerife, Canary Islands, Spain, ²Centre for*
18 *Ecology, Evolution and Environmental Changes (cE3c)/Azorean Biodiversity Group &*
19 *University of the Azores, Angra do Heroísmo and Ponta Delgada, Azores, Portugal,*
20 ³*School of Geography and the Environment, University of Oxford, South Parks Road,*
21 *Oxford, UK, ⁴Center for Macroecology, Evolution and Climate, University of*
22 *Copenhagen, Copenhagen, Denmark, ⁵Island Ecology and Biogeography Research*
23 *Group. Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias*
24 *(IUETSPC) Universidad de La Laguna, Tenerife, Canary Islands, Spain, ⁶UMR PVBMT,*
25 *University of La Réunion, Pôle de Protection des Plantes, Saint-Pierre, La Réunion,*
26 *France, ⁷CIBIO/InBio-UE: Centro de Investigação em Biodiversidade e Recursos*
27 *Genéticos, Universidade de Évora, Évora, Portugal, ⁸Department of Biogeography and*
28 *Global Change, Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid, Spain,*
29 ⁹*CIBIO-Açores/INBIO: Centro de Investigação em Biodiversidade e Recursos Genéticos*
30 *and Departamento de Biologia, Faculdade de Ciências e Tecnologia, Universidade dos*
31 *Açores, Ponta Delgada, Açores, Portugal, ¹⁰Finnish Museum of Natural History,*
32 *University of Helsinki, Helsinki, Finland, ¹¹Groningen Institute for Evolutionary Life*
33 *Sciences, University of Groningen, Groningen, The Netherlands, ¹²Institute for*
34 *Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The*
35 *Netherlands, ¹³Department of Entomology, University of Maryland, College Park, MD,*
36 *USA, ¹⁴Centre for Functional Ecology, Department of Life Sciences, University of*
37 *Coimbra, 3000 Coimbra, Portugal, ¹⁵Departamento de Ecologia, Instituto de Ciências*

38 *Biologicas, Universidade Federal de Goiás, Goiânia, GO, Brazil,* ¹⁶*Research Unit of*
39 *Biodiversity (UO-CSIC-PA), Oviedo University, Campus of Mieres, Research Building,*
40 *Asturias, Spain,* ¹⁷*Ecological Networks, Department of Biology, TU Darmstadt,*
41 *Darmstadt, Germany,* ¹⁸*GEES (School of Geography, Earth and Environmental*
42 *Sciences), The University of Birmingham, Birmingham, UK,* ¹⁹*Department of*
43 *Integrative Ecology, Estación Biológica de Doñana (CSIC), Seville, Spain,* ²⁰*Institute of*
44 *Zoology, Zoological Society of London, London, UK,* ²¹*University of Hawai'i at Hilo,*
45 *Hilo, HI, United States,* ²²*Departamento de Ciencias de la Vida, Universidad de Alcalá.*
46 *Alcalá de Henares, Madrid, Spain,* ²³*Section Ecoinformatics and Biodiversity,*
47 *Department of Bioscience, Aarhus University, 8000 Aarhus C, Denmark,* ²⁴*Department*
48 *of Ecology and Taxonomy, Faculty of Biology, National and Kapodistrian University of*
49 *Athens, Athens, Greece,* ²⁵*Museum für Naturkunde, Leibniz-Institut für Evolutions- und*
50 *Biodiversitätsforschung, Berlin, Germany,* ²⁶*Royal Botanical garden of Madrid (CSIC-*
51 *RJB), Madrid, Spain,* ²⁷*Biodiversity, Macroecology and Biogeography, Georg-August-*
52 *University Göttingen, Göttingen, Germany,* ²⁸*School of Biological Sciences, University*
53 *of East Anglia, Norwich Research Park, Norwich, UK*

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56 **Running head:** 50 key research questions in island biology

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59 **Correspondence:** Jairo Patiño, Island Ecology and Evolution Research Group, Instituto
60 de Productos Naturales y Agrobiología (IPNA-CSIC), c/ Astrofísico Francisco Sánchez
61 3, La Laguna, Tenerife, Canary Islands, 38206, Spain
62 Emails: jpatino.llorente@gmail.com; jpatino@ipna.csic.es

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67 **ABSTRACT**

68

69 **Aims** The 50th anniversary of the publication of the seminal book, *The Theory of Island*
70 *Biogeography*, by Robert H. MacArthur and Edward O. Wilson is a timely moment to
71 review and identify key research foci that could advance island biology. Here we take a
72 collaborative horizon-scanning approach to identify 50 fundamental questions for the
73 continued development of the field.

74

75 **Location** Worldwide.

76

77 **Methods** We adapted a well-established methodology of horizon scanning to identify
78 priority research questions in island biology, and initiated it during the Island Biology
79 2016 conference held in the Azores. A multidisciplinary working group prepared an
80 initial pool of 187 questions. A series of online surveys was then used to refine a list of
81 the 50 top priority questions. The final shortlist was restricted to questions with a broad
82 conceptual scope, and which should be answerable through achievable research
83 approaches.

84

85 **Results** Questions were structured around four broad and partially overlapping island
86 topics, including: (Macro)Ecology and Biogeography, (Macro)Evolution, Community
87 Ecology, and Conservation and Management. These topics were then subdivided
88 according to the following subject areas: global diversity patterns (5 questions in total);
89 island ontogeny and past climate change (4); island rules and syndromes (3); island

90 biogeography theory (4); immigration–speciation–extinction dynamics (5); speciation
91 and diversification (4); dispersal and colonization (3); community assembly (6); biotic
92 interactions (2); global change (5); conservation and management policies (5); and
93 invasive alien species (4).

94

95 **Main conclusions** Collectively, this cross-disciplinary set of topics covering the 50
96 fundamental questions has the potential to stimulate and guide future research in island
97 biology. By covering fields ranging from biogeography, community ecology, and
98 evolution to global change, this horizon scan has the potential to foster the formation of
99 interdisciplinary research networks, enhancing joint efforts to better understand past,
100 present and future of island biotas.

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102

103 **Keywords**

104 Biodiversity conservation, community ecology, extinction, global change, island biology,
105 island biogeography theory, island evolution, island macroecology, research priorities

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107

108 **INTRODUCTION**

109

110 In 1967 Robert H. MacArthur and Edward O. Wilson published *The Theory of Island*
111 *Biogeography* (MacArthur & Wilson, 1967), where they expanded upon an earlier paper
112 in which they first described their equilibrium theory (MacArthur & Wilson, 1963). In
113 these works they developed a general mathematical theory to explain the regulation of
114 species richness on islands. Their theory was based on the argument that island biotas
115 eventually reach a dynamic equilibrium between processes that add species, particularly
116 by immigration (plus, for more remote islands, speciation; see MacArthur & Wilson,
117 1963), counterbalanced by processes that cause local extinction of species. Specifically,
118 the model at the core of their theory predicts that the rates of these two key processes are
119 determined by geographical context, represented in the first instance by island area and
120 isolation. Whereas their general theory was motivated by a desire to formulate ecological
121 and evolutionary theories based upon population level processes and to introduce a new
122 rigour into the discipline of island biogeography, their theorizing was inspired by
123 documented patterns of species abundance, species richness and turnover within and
124 across islands (Lomolino & Brown, 2009; Wilson, 2010).

125 The seminal work of MacArthur and Wilson has subsequently stimulated a
126 substantial research effort on island biogeography and biodiversity (Whittaker &
127 Fernández-Palacios, 2007; Losos *et al.*, 2010), and promoted the exploration of islands as
128 model systems for a more general understanding of biological communities (e.g. Warren
129 *et al.*, 2015). The similarities between island archipelagos and fragmented continental
130 landscapes have also triggered interest in applying MacArthur and Wilson's theory in

131 conservation science; for instance, by deriving principles of protected area design and
132 estimation of species extinctions in fragmented landscapes (e.g. Diamond, 1975). In
133 addition to the colonization–extinction dynamics forming the core of MacArthur and
134 Wilson's theory (MacArthur & Wilson, 1967), the authors included speciation as a term
135 in the model within the 1963 description of equilibrium theory, and provided a 35-page
136 chapter on ‘*evolutionary changes following colonization*’ within their 1967 monograph.
137 Evolutionary processes, however, were set aside from the early chapters of the
138 monograph, excluded from statements of the *Core IBT* (Island Biogeography Theory) and
139 the famous intersecting curves graphic, and were not explicitly integrated in the neutral
140 mathematical formulation of the model (leading to the erroneous but oft repeated claim
141 that they ignored speciation). The subsequent development of molecular genetic tools for
142 evolutionary analysis have prompted renewed interest in the integration of speciation into
143 the *Core IBT* (e.g. Emerson & Gillespie, 2008; Rosindell & Phillimore, 2011; Valente *et*
144 *al.*, 2015), and improved estimation of historical immigration dynamics based on
145 phylogenetic relationships among species (Ronquist & Sanmartín, 2011). The *Core IBT*
146 is in essence a biologically neutral model – or close to it –, occupying the first 67 pages
147 of the 1967 monograph, with much of the next 116 pages devoted to theory concerning
148 population- and species-level traits of island biotas and their dynamics (MacArthur &
149 Wilson, 1967). Progress on these latter themes has arguably been slower than on issues
150 surrounding the *Core IBT*, but recent advances in genomic techniques, trait biology and
151 analytical capacity should move forward this agenda (e.g. Gillespie *et al.*, 2012; Heleno
152 & Vargas, 2015; Santos *et al.*, 2016a). Additionally, while the *Core IBT* referenced long-
153 term biological dynamics, it did not take into account the dynamic nature of islands

154 themselves, and here too, notable advances are being made (e.g. Whittaker *et al.*, 2008;
155 Borregaard *et al.*, 2016; Fernández-Palacios *et al.*, 2016).

156 Fifty years on from its publication, MacArthur and Wilson's (1967) book remains
157 one of the most influential texts on ecology and evolution, with continued debate over its
158 strengths and limitations. It has been, and will continue to be, a springboard for research
159 on the origin and maintenance of biological communities, with particular reference to
160 marine island systems, but also extending to other island-like systems. Half a century
161 since this seminal contribution, it is time to review both the new and outstanding
162 challenges facing the broad discipline of island biology, as well as particularly promising
163 research avenues (see e.g. Warren *et al.*, 2015; Santos *et al.*, 2016b). In particular, this
164 paper focuses on identifying the 50 most fundamental questions for present and future
165 island biology research. Inspired by previous studies seeking to identify priority research
166 questions within a scientific field based on a cornucopia of proven methods (e.g. Pretty *et*
167 *al.*, 2010; Sutherland *et al.*, 2011; Sutherland *et al.*, 2013; Seddon *et al.*, 2014; Kennicutt
168 *et al.*, 2015), we present the outcome of a survey-based approach initiated at *Island*
169 *Biology 2016: the 2nd International Conference on Island Evolution, Ecology and*
170 *Conservation*, which was held at the University of Azores in Terceira Island, July 18–22,
171 2016.

172

173

174 **MATERIALS AND METHODS**

175

176 Prior to the Island Biology 2016 conference, a total of 21 conference attendees (see
177 author list) were identified by the five survey coordinators (JP, RJW, PAVB, JMFP and
178 BCE), to constitute the ‘50 fundamental questions in island biology’ working group in
179 which each member encompasses expertise in at least one of the following subject areas:
180 (i) (Macro-)Ecology and Biogeography, (ii) Speciation and Extinction, (iii) Community
181 Ecology, (iv) Biotic Interactions, (v) Conservation Biology and Global Change, (vi)
182 Dispersal and Colonization, and (vii) Palaeobiogeography and Palaeoecology. Two or
183 three members of the working group were assigned to each subject area, and they had the
184 possibility to recruit one or two more members to their panel. An eighth panel (viii) was
185 also formed to identify any key questions that fell outside the scope of the seven original
186 subject areas. Research interests within the ‘50 fundamental questions in Island Biology’
187 working group represent a broad array of geographic areas, model organisms, and
188 networks of international collaborators. The members of each subject group were asked
189 to identify at least 15 questions that they viewed as of fundamental interest within their
190 subject panel. Members were encouraged to consult broadly with colleagues, with the
191 mentioned option to invite non-conference attendees to join their panels, to provide
192 additional expertise. A total of 197 questions were compiled in this process, which were
193 screened for duplication or ambiguity by the five survey coordinators, resulting in a
194 curated list of 187 questions (hereafter termed List 1; Fig. 1). To facilitate the practical
195 implementation of the first voting, questions from List 1 were redistributed into four main
196 island biology topics (e.g. see Carlquist, 1974; Whittaker & Fernández-Palacios, 2007;
197 and Losos *et al.*, 2010): (i) Island (Macro)Ecology and Biogeography (52 questions)
198 included questions from the subject areas of (Macro-)Ecology and Biogeography, and

199 Palaeobiogeography and Palaeoecology; (ii) Island (Macro)Evolution (63 questions) was
200 used to group questions on Speciation and Extinction, and Dispersal and Colonization;
201 (iii) Island Community Ecology (27 questions) comprised questions from Community
202 Ecology, and Biotic Interactions; and (iv) Island Conservation and Management (45
203 questions) included questions from Conservation Biology and Global Change. The 407
204 conference attendees of the Island Biology 2016 conference (see
205 <http://www.islandbiology2016.uac.pt>) were invited to participate in four online surveys
206 (*Survey 1*), one for each of the four amended groups of topics above. Across the four
207 surveys, the conference attendees could score each question as ‘fundamental’, ‘not
208 fundamental’, or leave the answer blank. The order of the questions was randomized for
209 each new login, so that a specific order of presentation of questions could not bias the
210 outcome of the surveys; this strategy was retained for the two following online surveys
211 (see below). For each of the four topics, survey participants were also given the
212 opportunity to submit one additional question, if they felt such a question was missing
213 from List 1.

214 At the end of *Survey 1*, the original survey questions were ranked according to the
215 total number of participants who scored a given question as ‘fundamental’, and the top 80
216 questions selected (List 2). Then, the 44 new questions proposed by survey participants
217 (List 3) were merged with an equivalent number of questions from List 2, specifically the
218 44 lowest ranked key questions, to create a second survey (*Survey 2*) with 88 questions
219 (List 4). The questions from List 4 were voted as ‘fundamental’ or ‘not fundamental’ by
220 the 29 members of the ‘50 fundamental questions in island biology’ working group, and
221 ranked. The top 44 questions of List 4 were then refined to eliminate redundant questions

222 or ambiguities through discussions among the coordinators of the survey, and then
223 merged with the top 36 questions kept from List 2. The list of 80 questions (List 5) was
224 then subject to a third online survey (*Survey 3*) involving a broader participation by
225 extending the invitation to participate to approximately 400 attendees of the Island
226 Biology 2014 conference held in Honolulu, Hawaii, some of whom did not attend the
227 Island Biology 2016 conference, and also to the members of the following island biology
228 related interest groups: American Society of Naturalists; British Ecological Society;
229 Conservation Specialist Interest Group; Société Française d'Ecologie; Ecological Society
230 of America; Hellenic Ecological Society; International Biogeography Society; New
231 Zealand Ecological Society; the Spanish and the Portuguese Ecological Societies, and
232 other specific working groups and e-mailing lists related to island biology that the authors
233 could identify.

234

235 **Study shortcomings**

236 Across the different phases of this participative process, a determined effort was made to
237 select experts, questions and voters, representative of the full breadth of island biology
238 research. In addition, the inclusion of 48 questions suggested online by anonymous
239 attendees of the Island Biology 2016 conference further contributed to increase the
240 diversity of backgrounds and expertise reflected in the questions identified (see Fig. 1).
241 However, despite these efforts, it would be naive to regard our list as definitive and
242 unbiased, as it inevitably reflects the interests of the particular group of voters who were
243 contacted and participated in our survey (see e.g. Sutherland *et al.*, 2013; Seddon *et al.*,
244 2014). For instance, from the 27 initial questions on Palaeoecology &

245 Palaeobiogeography included in the online *Survey 1*, only one question [see Q28 in
246 Results section] remained in the final list of 50 questions. This may reflect the fact that
247 only about 10% of the final survey voters identified Palaeoecology &
248 Palaeobiogeography as one of their fields of expertise (see Results). Such biases in the
249 composition of the biologists sampled have undoubtedly influenced the balance of the
250 questions presented here. Despite such shortcomings, by performing several voting and
251 discussion rounds with a large group of experts from a wide range of organizations, fields
252 and geographical regions (see Results, below), we hope to have minimized the
253 consequences of individual preferences and other subjective choices.

254

255

256 **RESULTS**

257

258 The number of participants voting in the three rounds of online voting varied. In the first
259 online survey (*Survey 1*), the number of participants was distributed into the four topics
260 as follows: Island (Macro)Ecology and Biogeography (104 participants); Island
261 (Macro)Evolution (84); Island Community Ecology (82); Island Conservation and
262 Management (91). This round of voting was completely blind and no information about
263 the scientific profile of the participants was requested. In the second online survey
264 (*Survey 2*), only the 29 authors of this study voted, with each person voting on all the
265 questions irrespective of topic area.

266 In the final round of online voting (*Survey 3*), 303 people participated, with the 80
267 submitted questions receiving on average 286.6 (SD \pm 2.3) votes. A large proportion of

268 the 80 questions (77 out of the 80) were considered as ‘fundamental’ by the majority of
269 the voters, and the final ranking was thus based on the proportion of ‘fundamental’ votes
270 with respect to the total numbers of votes (‘fundamental’ + ‘not fundamental’) received
271 for each question. The percentage of fundamental votes varied between 79% (top) and
272 39% (the 80th question), while the last question making it into the top 50 attracted 62% of
273 positive votes.

274 The scientific profile of the third survey participants was highly diverse, being
275 distributed across thematic areas in island biology as identified by the participants
276 themselves as follows: Conservation, Management & Global Change (290 participants);
277 Community Ecology (141); Biogeography (137); Biotic Interactions (99); (Macro-
278)Ecology (76); Dispersal (69); (Macro-)Evolution (58); Island Theory (45);
279 Palaeoecology & Palaeobiogeography (30); and Plant or/& Animal Physiology (28). An
280 additional 45 participants identified with 11 less common disciplines. In total, 68.7%
281 (207) participants work on islands and/or island-habitat types, while 17.8% (54) voters
282 focus their research on other ecological systems. Only 10.2% (31) participants work both
283 on island and non-island systems. From the voters that provided information regarding
284 the geographic circumscription of their study areas, the following insular systems were
285 well represented: Oceania, including Australia, Melanesia, Micronesia, New Zealand,
286 Polynesia, Galápagos and Juan Fernández (57 participants); North Atlantic including
287 Macaronesia (39); Mediterranean (19); Caribbean (13); Indian Ocean, including the
288 Mascarenes, Socotra and Madagascar (13); and Indonesia (6).

289 Below we present the top 50 priority questions in island biology identified in the
290 present study. For convenience in presenting the results, questions were compiled into the

291 four main island topics used earlier (see List 1 above): (i) Island (Macro)Ecology and
292 Biogeography (including 16 questions); (ii) Island (Macro)Evolution (11); (iii) Island
293 Community Ecology (8); and (iv) Island Conservation and Management (15).
294 Information about each question's final rank (#) and percentage of votes received (%) is
295 also provided.

296

297 **Island (Macro)Ecology and Biogeography**

298 *Global diversity patterns*

299 Q1. What are the relative roles of spatial, historical and ecological processes in driving
300 taxonomic, phylogenetic and functional diversity patterns of insular systems? [# 7; %
301 = 75.2]

302 Q2. How do fundamental biogeographic processes interact through time and space to
303 establish the island species–area relationship? [# 22; % = 70.5]

304 Q3. How do taxonomic, phylogenetic and functional diversity compare between
305 islands and ecologically similar continental areas? [# 27; % = 68.7]

306 Q4. How important are islands as refuges for now extinct mainland lineages and/or
307 ecosystems? [# 45; % = 64.5]

308 Q5. How important are oceanic islands as generators of biodiversity and for the
309 assembly of continental biota through reverse-colonization and/or colonization *de*
310 *novo*? [# 49; % = 62.2]

311

312 The questions in this section share an emphasis on fundamental large-scale topics. The
313 first question [Q1], in particular, invokes a research agenda covering all types of island

314 systems and multiple facets of biodiversity. This question is a worthy reminder of the
315 importance of integrating the dynamics of historical/geographical, long-term
316 environmental, and contemporary ecological time-scales in analyses of insular biota.
317 Island biologists need to be aware of and integrate knowledge from other natural
318 sciences, in particular from earth systems science, in understanding long-term dynamics
319 of island platforms as theatres for the evolutionary play (e.g. Price & Clague, 2002;
320 Fernández-Palacios *et al.*, 2011; Ali & Aitchison, 2014; Skipwith *et al.*, 2016). How key
321 biogeographical processes of dispersal/migration, speciation and extinction interact to
322 shape the form of the island species–area relationship [Q2] remains an important topic
323 and particular how these processes and patterns vary among different island contexts,
324 including oceanic, continental-shelf, continental fragment, and habitat islands (e.g.
325 Triantis *et al.*, 2012; Patiño *et al.*, 2014b; Matthews *et al.*, 2016). Comparisons between
326 taxonomic (typically the species as unit of analysis), phylogenetic and functional
327 diversity responses across islands [see also Q29] and between islands and continents [Q3]
328 represent a very recent development, on which little research has so far been conducted
329 (but see e.g. Whittaker *et al.*, 2014 and; Weigelt *et al.*, 2015, for examples of intra and
330 inter-archipelago analyses respectively). Our perception of the roles of islands [Qs 4, 5]
331 as macroevolutionary sinks (*sensu* Goldberg *et al.*, 2005), rather than as sources, has been
332 challenged in recent years, and possibly needs to be reassessed (Bellemain & Ricklefs,
333 2008). It was long understood that, in general, whereas islands received colonist species
334 from continents, the reverse process rarely, if ever, happened (e.g. Carlquist, 1974). This
335 unidirectional view of island colonization was consistent with the notion that islands, as
336 species poor and disharmonic systems (i.e. lacking the full array of forms found on the

337 mainland) were typified by species that had become poor competitors (in the broad
338 sense). Moreover, islands were viewed as refugial holdouts of persistence for a number of
339 ancient forms (e.g. Yoder & Nowak, 2006; Vargas, 2007; Wood *et al.*, 2015; Shaw &
340 Gillespie, 2016), swept away by more recently evolved competitors from former
341 mainland bastions. More recently, it has become apparent that so-called back-
342 colonizations (or boomerangs sensu Caujapé-Castells, 2011) from islands to mainlands,
343 or movements across ocean basins via islands and colonization *de novo* of continents,
344 have occurred and include some colonist lineages that have had great importance in
345 shaping current biodiversity patterns. Examples include lineages of birds (e.g. Filardi &
346 Moyle, 2005; Jønsson *et al.*, 2011; Jønsson & Holt, 2015), insects (Grady & DeSalle,
347 2008) and plants (Carine *et al.*, 2004; Patiño *et al.*, 2015; Condamine *et al.*, 2016). For
348 the very reason that addressing these questions requires an integrative approach with the
349 intersection of disparate fields and methodological approaches, these broad questions [Qs
350 1–5] remain of central importance within island biology, with evident potential to
351 continue to generate significant changes in our understanding of this field.

352

353 *Island ontogeny and past climate change*

354 Q6. How do rates of colonization, speciation and extinction change during island
355 ontogeny? [# 9; % = 73.4]

356 Q7. How do diversification rates of island lineages change with island age? [# 38; %
357 = 66]

358 Q8. How important were past geological events and climate change in promoting
359 island colonization and altering dispersal pathways? [# 20; % = 70.5]

360 Q9. How has climate change influenced speciation and extinction within islands? [#
361 12; % = 72.7]

362 Questions 6–9 embrace specific challenges to our understanding of the long-term
363 dynamics of insular systems. Notwithstanding the diverse geological origins and
364 developmental histories of islands, a substantial number of them are remote, volcanic in
365 origin, and follow a broadly similar ontogeny. Typically, these islands begin with a
366 building phase, followed by a gradual shift into erosion and subsidence, eventually
367 leading to them becoming merely sub-ocean surface features. This developmental
368 pathway, or certain variants of it, and their biological consequences are integrated within
369 the general dynamic model of oceanic island biogeography (Whittaker *et al.*, 2008;
370 Borregaard *et al.*, 2016), which offers predictions concerning rates of colonization,
371 speciation, diversification and extinction and how they vary over the developmental
372 history of islands. Testing such predictions for speciation and extinction is challenging
373 (see [Qs 17–20]), and further complicated when island age is also integrated [Qs 6, 7]. It
374 requires a focus on comparing island-specific rates among islands of different maturity
375 across archipelagos, as opposed to within-lineage rates without implicit reference to
376 island specific rates (*sensu* Bennett & O'Grady, 2013), suggesting a need for innovative
377 approaches involving the comparative analysis of large numbers of time-calibrated
378 phylogenies.

379 Improved geodynamic data concerning past climate change, wind connectivity,
380 ocean currents, and sea-level oscillations over the Pleistocene permit the development of
381 more sophisticated models for inferring shifts in the configuration of islands and their
382 environment (area, isolation and climate) through time, and their availability has

383 generated increasing interest in the implications of these long-term changes for island
384 biodiversity patterns and processes (e.g. Carine, 2005; Dalsgaard *et al.*, 2013; Ali &
385 Aitchison, 2014; Rijdsdijk *et al.* 2014; Ávila *et al.*, 2016; Borregaard *et al.*, 2016;
386 Fernández-Palacios, 2016; Fernández-Palacios *et al.*, 2016; Steinbauer *et al.*, 2016a,b;
387 Weigelt *et al.*, 2016). Integrating colonization dynamics into these models [Q8] may
388 benefit from recent comparative phylogenetic approaches (Ronquist & Sanmartín, 2011),
389 while understanding how climate change has influenced rates and patterns of speciation
390 and extinction on islands [Q9] appears to be a particularly challenging area of study.

391

392 *Island rules and syndromes*

393 Q10. Is trait evolution fundamentally different on islands than on continents? [# 42;

394 % = 64.9]

395 Q11. How robust are the various island rules and syndromes relating to body size,

396 loss of dispersal, coloration, breeding system, woodiness, and clutch size, among

397 others? [# 47; % = 63.3]

398 Q12. To what extent are island populations genetically impoverished, compared to

399 comparable mainland populations? [# 50; % = 62]

400

401 Since the earliest days of scientific study of island biology, it has been understood that

402 islands possess peculiar forms and otherwise atypical subsets of ecological and

403 taxonomic groups (an aspect of island disharmony). Some part of this arises from a

404 colonization filter through dispersal limitation. Following successful colonization and

405 establishment on an island, recently arrived colonists are potentially exposed to a range of

406 novel biotic and abiotic conditions that have, in many instances, triggered notable
407 morphological, behavioural and ecological shifts (e.g. Kavanagh & Burns, 2014; Traveset
408 *et al.*, 2015). Indeed, many of these features were remarked upon and formalized into
409 syndromes or rules in classic works, particularly in *Island Life* by Alfred Russel Wallace
410 (1880) and *Island Biology* by Sherwin Carlquist (Carlquist, 1974). Not surprisingly,
411 chapter seven of MacArthur & Wilson's book (1967), entitled '*Evolutionary Changes*
412 *Following Colonization*', dealt with some of the most intriguing island syndromes, such
413 as the loss of dispersal capacity. Specifically, questions 10 and 11 reflect the long-lasting
414 interest in phenomena such as flightlessness, gigantism, super-generalism, or secondary
415 woodiness (reviewed in e.g. Jost, 2007; Whittaker & Fernández-Palacios, 2007; Losos &
416 Parent, 2010; Lens *et al.*, 2013), where empirical evidence has often provided conflicting
417 signals (e.g. for the loss of dispersability, see Cody & Overton, 1996; Patiño *et al.*, 2013;
418 Kavanagh & Burns, 2014; Vargas *et al.*, 2014).

419 A few decades ago, a number of seminal studies (e.g. Frankham, 1997) introduced
420 the idea that island populations are typically characterized by low levels of genetic
421 diversity [Q12]. Recent analyses of spatial distribution of genetic variation across island
422 and continental regions have, however, provided evidence that the expectation of low
423 genetic diversity cannot always be generalized to island assemblages (e.g. Fernández-
424 Mazuecos & Vargas, 2011; Hutsemékers *et al.*, 2011; García-Verdugo *et al.*, 2015; but
425 see Illera *et al.*, 2016). It seems likely that future research on island syndromes will need
426 to continue to pay critical attention to: (i) the statistical robustness of the patterns
427 concerned (e.g. Meiri *et al.*, 2008); (ii) causal explanations for the patterns, including the
428 extent to which they reflect *in situ* evolutionary change *versus* non-random

429 colonization/persistence (e.g. Valido *et al.*, 2004; Lomolino *et al.*, 2013); and (iii) the
430 mechanistic explanations for such distinctive evolutionary pathways (e.g. Burns *et al.*,
431 2012; Novosolov *et al.*, 2013; Itescu *et al.*, 2014). As these island-specific syndromes
432 develop from the same eco-evolutionary processes that operate on mainlands, research on
433 islands and continental counterparts (e.g. closely related taxa) [Q12] will be key to
434 enhancing our fundamental understanding of the underlying mechanisms.

435

436 *Island biogeography theory*

437 Q13. How do the dynamics of island communities scale up to generate the
438 biogeographical patterns predicted by island biogeographical theories? [# 37; % =
439 66.3]

440 Q14. How can we reconcile island biogeography theories with other ecological and
441 evolutionary theories to contribute to a general biodiversity theory? [# 15; % = 72.1]

442 Q15. How applicable are island biogeographical theories derived from real islands to
443 other forms of insular system, such as sky islands and seamounts? [# 48; % = 62.7]

444 Q16. How can we best incorporate population genetic and/or phylogenetic data to
445 advance models of island biogeography? [# 28; % = 68.3]

446

447 Island biogeography has always been a driver for the development of general theories in
448 ecology and evolution. Hubbell's (2001) '*neutral theory of biodiversity and*
449 *biogeography*' is one prominent example of how reflection on island theory (specifically
450 MacArthur and Wilson's theory) in a broader context, has continued to generate novel
451 research directions (e.g. Warren *et al.*, 2015; Santos *et al.*, 2016b). Neutral theory

452 provides one approach to scaling up from local scale species abundance distribution
453 patterns and dynamics to emergent biogeographical patterns [Q13], as exemplified by
454 recent work by Rosindell and colleagues (e.g. Rosindell & Phillimore, 2011; Rosindell &
455 Harmon, 2013). Although questions specifically on species abundance distributions failed
456 to make the final cut in the present survey, the significance of improving understanding
457 of species abundances in insular settings, and how they link to other macroecological
458 patterns (such as species–area relationships) is implicit in questions 13, 14, and 33 (see
459 e.g. Fattorini *et al.*, 2016).

460 Another facet of island theory that can be traced back directly to MacArthur &
461 Wilson (1967) is the application of theory developed with marine islands (i.e. ‘real
462 islands’) in mind to other insular contexts [Q15], be they mountain tops (sky islands, e.g.
463 Sklenář *et al.*, 2014; Steinbauer *et al.*, 2016b), or other **habitat islands** isolated by a
464 contrasting non-water matrix type (e.g. Kisel *et al.*, 2011; Matthews *et al.*, 2016).
465 **MacArthur & Wilson** themselves highlighted the application of their equilibrium theory
466 to habitat islands in the context of the fragmentation of formerly extensive, contiguous
467 ecosystems by anthropogenic land use change, and this remains an area of interest and
468 contention, with the quantitative implications of such processes for biodiversity
469 conservation remaining uncertain (Triantis *et al.*, 2010; Axelsen *et al.*, 2013; He &
470 Hubbell, 2013; Matthews *et al.*, 2016).

471 Island biogeographic theory invokes historical biological processes (colonization,
472 speciation, extinction) to explain contemporary species distribution patterns, which has
473 yielded a large body of phylogenetic and population genetic island-focussed research.
474 Such studies help advance models of island biogeography [Q16], link short term, within-

475 island ecological processes to patterns emerging on large spatial or evolutionary scales,
476 and thus help to unify theories of ecology and biogeography (e.g. Johnson *et al.*, 2000;
477 Steinbauer, 2017; see also Qs 17–20). Future statistical advances toward this goal may
478 include comparing the fit of data among the predictions of competing phylogenetic and
479 population genetic simulation models (e.g. Chan *et al.*, 2014; Patiño *et al.*, 2015), or
480 combining phylogenetic and population genetic perspectives into unified statistical
481 frameworks (e.g. Rannala & Yang, 2003). Combining a phylogenetic perspective with
482 population genetic approaches may also help to establish links between
483 macroevolutionary patterns and underlying microevolutionary mechanisms (e.g. Ricklefs
484 & Bermingham, 2001; Jordal & Hewitt, 2004; Roderick *et al.*, 2012; Paun *et al.*, 2016),
485 thus advancing our understanding of island biogeographic history.

486

487

488 **Island (Macro)Evolution**

489 *Immigration–speciation–extinction dynamics*

490 Q17. How does the spatial configuration of an archipelago (e.g. intra-archipelagic
491 connectivity) influence colonization, speciation and extinction over time? [# 23; % =
492 70.1]

493 Q18. What is the nature of the relationship between rates of extinction and island
494 isolation, if any? [# 46; % = 64.1]

495 Q19. How do the extinction probabilities of island endemic species compare to those
496 of non-endemic species? [# 33; % = 67.2]

497 Q20. How important are diversity-dependent processes for island colonization,
498 speciation and extinction? [# 11; % = 73]

499 Q21. How do anthropogenic extinctions affect estimates of speciation and natural
500 extinction on island systems? [# 43; % = 64.8]

501

502 Island biodiversity emerges from the accumulation of species through time by
503 colonization and establishment from outside areas, anagenetic change, and extensive
504 diversification, all being counterbalanced by the depletive effects of extinction. The
505 relative roles of these macroevolutionary processes are predicted to be functionally
506 interrelated (e.g. MacArthur & Wilson, 1963, 1967; Emerson & Kolm, 2005; Emerson &
507 Gillespie, 2008; Whittaker *et al.*, 2008; Rominger *et al.*, 2016), but understanding their
508 dynamics over time remains a central challenge in island biology. Geographical context
509 plays an important role in determining how colonization, extinction and speciation [Qs
510 17, 18] dynamically vary and interact over time (see Cabral *et al.*, 2014; Papadopoulou &
511 Knowles, 2015b). While the effect of geography on macroevolution is well understood
512 for some processes (e.g. cladogenesis generally increases with island area; see Kisel &
513 Barraclough, 2010), for others, this relationship remains largely unknown (e.g. extinction
514 *versus* isolation in Q18). Time-calibrated phylogenies have been of particular interest in
515 investigating the processes of speciation and colonization, but they provide no direct
516 evidence for extinction. Thus, while rates of diversification can be derived directly from
517 dated phylogenies, estimating the underlying rates of colonization, speciation and
518 extinction is more challenging. However, it is now possible to apply a model-based
519 approach to estimate how these processes vary through time (Valente *et al.*, 2014, 2015),

520 suggesting that there is further potential for phylogenetics to inform island biogeography.
521 It is important that we note here that Q18 does not, in fact, specify a context involving
522 extinction of endemic species, and the question of how extinction rate varies with
523 isolation can be posed for a wide range of island systems and degrees of isolation,
524 including for instance among non-endemic species on habitat islands (as e.g. Brown &
525 Kodric-Brown, 1977).

526 Endemic species distributions have been used together with comparative
527 phylogenetic analysis to infer colonization, speciation and extinction dynamics with
528 island ontogeny (Emerson & Oromí, 2005; Givnish *et al.*, 2009; Rosindell & Phillimore,
529 2011; Shaw & Gillespie, 2016), and may provide a further means to address the influence
530 of geographical context. Gains may also be made if it were possible to infer per species
531 contemporary extinction risk due to anthropogenic change processes (a theme covered at
532 least partially by Q19), which may also aid conservation strategies (e.g. Qs 42–45).
533 Several models of island biogeography have either implicitly (the taxon cycle, see
534 Ricklefs & Bermingham, 2002) or explicitly (the general dynamic model, Whittaker *et*
535 *al.*, 2008) related the single island endemic status of species to increased extinction
536 probability relative to other species on the same island. Thus, question 19 can be
537 addressed not only in a contemporary conservation context but also in relation to longer-
538 term natural turnover. Although extinction is a difficult parameter to quantify, simply
539 understanding whether there is a fundamental difference in extinction risk between
540 endemic and non-endemic species [Q19] would be a significant step forward.

541 MacArthur and Wilson (1967) expressed their intuition of a negative feedback of
542 diversity on the accumulation of species on an island [Q20], either through an increased

543 extinction rate or through a decreased colonization rate by means of niche saturation by
544 early colonists. Their argument illustrates the early foundation of a still debated question:
545 is there a limit to the number of species a given area can sustain? This question has been
546 the subject of recent discussions (Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015)
547 and its longevity pertains in part to the difficulty of measuring turnover rates let alone
548 negative diversity feedbacks on evolutionary processes such as speciation. However, a
549 number of recent methodological developments (Rabosky, 2006; Etienne *et al.*, 2012;
550 Valente *et al.*, 2015) promise improved analytical power and have already revealed that
551 diversity-dependence in both colonization and speciation can potentially be inferred from
552 empirical data based on island phylogenies (Valente *et al.*, 2015). The issue of diversity-
553 dependence [Q20] is central to understanding island biodiversity dynamics, equilibrium
554 and biotic interactions on evolutionary time-scales [Q6] and promises to remain a key
555 topic over at least the next few years.

556 There is no a single path to extinction, and the role of humans as drivers of
557 distribution range shifts and extinctions in both recent historical and prehistorical time
558 has increasingly gained relevance on islands. This significance can be mirrored in the
559 species listed by the IUCN as extinct, of which 61% were confined to islands (Tershy *et*
560 *al.*, 2015), and among the 20 world territories with the highest percentages of extinct and
561 threatened species in both bird and mammal group lists, 19 and 17 are insular,
562 respectively (Vié *et al.*, 2009); remarkable statistics given that the 19 bird and 17
563 mammal territories themselves represent a mere 0.6% and 1.9% of the Earth's subaerial
564 landmass, respectively (Vié *et al.*, 2009). Compounding these issues is the unknown
565 degree to which island taxa have been eliminated as a consequence of human

566 colonization of islands and before their scientific documentation [Q21]. For birds in the
567 Pacific, to take the most infamous example, extrapolations from the relatively small
568 number of islands studied in detail, suggest that hundreds of undocumented species
569 extinctions may have taken place following Polynesian colonization (Steadman, 2006),
570 undermining efforts to estimate natural rates of speciation and extinction from these
571 insular systems [Q21].

572

573 *Speciation and diversification*

574 Q22. What functional traits (e.g. relating to dispersal capacity, reproduction, trophic
575 ecology) are associated with high diversification rates within and across island
576 systems? [# 2; % = 77.9]

577 Q23. What traits best predict which groups will undergo adaptive radiation on
578 islands? [# 17; % = 71.1]

579 Q24. What is the relative importance of ecological *versus* geographical speciation on
580 islands? [# 31; % = 67.8]

581 Q25. What is the influence of gene flow among islands and/or between islands and
582 mainland areas on speciation rates? [# 19; % = 70.8]

583

584 Spectacular species radiations are perhaps the best known feature of oceanic islands
585 (Losos & Ricklefs, 2009). However, the majority of lineages either do not diversify at all,
586 or only to a very limited extent, with high diversification rates typically restricted to a
587 limited number of lineages within an island or archipelago (for animals see e.g. Ricklefs
588 & Bermingham, 2007; and Illera *et al.*, 2012; and for plants see e.g. Patiño *et al.*, 2014a).

589 Answering the question of why only some lineages diversify is central to a deeper
590 understanding of island community assembly, the origin of biological diversity in general
591 [Q22], and adaptive radiations in particular [Q23]. Diversified lineages are often
592 associated with ecological divergence and adaptive radiation, but non-ecological
593 mechanisms are also expected in insular settings where the interaction of geology,
594 topography and climate promote speciation by local geographic isolation [Q24].

595 As the number of independent phylogenetic and population genetic studies
596 increases, comparative analyses can shed light on the functional traits associated with
597 accelerated diversification rates [Q22]. This approach has recently demonstrated that a
598 herbaceous dry-fruited ancestral syndrome is frequently associated with diversified plant
599 lineages across different archipelagos (García-Verdugo *et al.*, 2014). A more complete
600 understanding of the contribution and functional relevance of speciation to island
601 community assembly will require not only identifying the traits associated with
602 diversification, but also the drivers underlying their change, and thus those traits that
603 underscore adaptive radiation [Q23]. Distinguishing among the drivers of natural
604 selection, sexual selection and non-selective processes for speciation is not a trivial task,
605 as multiple drivers may underlie trait divergence. This interconnectedness among the
606 different drivers of speciation and diversification [Qs 22–24] is exemplified by delphacid
607 planthoppers of the genus *Nesosydne* in the Hawaiian islands. The species of *Nesosydne*
608 are recognised as an adaptive radiation linked to host plant use, however, sexual selection
609 and non-selective processes also contribute to reproductive isolation via divergence of
610 sexual signals (Goodman *et al.*, 2015). Another interesting aspect of trait evolution will

611 be to determine whether similar traits promote high diversification rates in both islands
612 and mainland areas [see Q10].

613 Molecular data can provide insight into the importance of geography and gene
614 flow in the speciation process, both within islands and among islands and mainland areas
615 [Qs 24, 25]. Intuitively, small amounts of gene flow would seem likely to retard
616 speciation, but it is increasingly recognised that, at least under some circumstances,
617 introgression may promote speciation, and that this might be particularly relevant within
618 insular settings (see Warren *et al.*, 2015; Faria *et al.*, 2016). To understand the influence
619 of gene flow among islands and mainland areas on speciation rates [Q25], robust
620 estimates of historical gene flow are required. The advent of high-throughput cost-
621 effective genomic sequencing approaches for non-model organisms will fuel further
622 advances in our understanding of the interplay between isolation, gene flow and
623 speciation (e.g. Papadopoulou & Knowles, 2015a).

624

625 *Dispersal and colonization*

626 Q26. What is the importance of founder effects for the evolution of island lineages?
627 [# 8 % = 74.4]

628 Q27. How frequent is inter-island dispersal and is it enough to form an archipelago-
629 wide metacommunity, or are islands better understood as functionally independent
630 communities? [# 26 % = 69.1]

631 Q28. How can palaeoecology contribute to the understanding of species arrival,
632 establishment and spread on islands? [# 35 % = 66.8]

633

634 High dispersal rates among islands will push populations toward genetic homogeneity,
635 whereas low dispersal rates will facilitate divergence among populations on different
636 islands and high rates of inter-island cladogenetic speciation (Emerson & Faria, 2014).
637 Despite colonization, establishment and divergence rates being crucial within island
638 biogeographic theory, both the frequency of dispersal events between islands [Qs 26, 27]
639 and actual dispersal mechanism responsible for inter-island colonization are unknown for
640 most species (for plants see Heleno & Vargas, 2015). The arrival of colonizing
641 propagules to remote islands is intrinsically a rare event and even when they make this
642 journey, successful colonization is contingent on their reproduction and the establishment
643 of a viable population, which can be equally challenging. In the extreme, the founder may
644 be a single gravid female, a female with stored sperm, or a parthenogenetic individual, or
645 at most, a small group of individuals. Thus, the limited genetic diversity transported by
646 these individuals may be decisive for the outcome. Theory suggests that such founder
647 effects may be a driver of insular evolution, speciation and further diversification (e.g.
648 Mayr, 1954; Carson, 1968; Templeton, 1980), but they may equally select for
649 evolutionary lineages that are less negatively affected by low genetic variation and
650 inbreeding. Importantly, and while the relevance of these founder effects can be
651 particularly clear for the evolution of island lineages [Q26], they can also be highly
652 relevant for evolution within habitat islands such as caves, lakes or mountain tops (e.g.
653 Wessel *et al.*, 2013). This may be particularly relevant if reduced dispersal ability is a
654 characteristic of island lineages in general and highly diversified lineages in particular
655 [see Qs 11 and 22].

656 One of the key attributes that make islands ideal models for ecology and evolution
657 is their well-defined borders (Whittaker & Fernández-Palacios, 2007). However, most
658 islands are embedded in regional groups of islands so that the nearest coast is not of a
659 continent but of another island. In addition, islands of high elevation are environmentally
660 diverse (at least in climatic regimes) and source regions for potential colonisers can then
661 differ between habitats (Steinbauer, 2017). Therefore, archipelago configurations and
662 environmental gradients can blur the lines of what seems the most relevant unit to study
663 for particular topics within island biology: the archipelago, the island, or ecozones within
664 the island. Intuitively, the relevance of archipelago-level process will largely depend on
665 the frequency of inter-island dispersal, so that when dispersal is low, island-level
666 processes dominate, and when dispersal is high, archipelago-level processes become
667 increasingly relevant. Ultimately, inter-island dispersal can be so important that single-
668 island populations are better understood in their broader context, as part of an
669 archipelagic metapopulation (Hanski, 1998). As the empirical observation of inter-island
670 movements is logistically challenging, population genetic data are particularly valuable
671 for estimating the frequency of inter-island dispersal and thus for exploring question 27.
672 Recent studies are providing novel insights in this direction (e.g. García-Verdugo *et al.*,
673 2014; Garrick *et al.*, 2014; Spurgin *et al.*, 2014; Hendrickx *et al.*, 2015; Vargas *et al.*,
674 2015; Faria *et al.*, 2016), but more research is needed to generate fine-grained spatial
675 genetic data within focal archipelagos and to provide general answers.

676 Palaeoecology is a field of emerging importance in island biology. Palaeoecology
677 has been used to understand the consequences of human colonization, frequently
678 characterised by concomitant waves of extinction (Sadler, 1999; van der Geer *et al.*,

679 2016). In addition, climate data have been integrated in attempts to distinguish plant
680 community compositional changes in response to shifts in climate from those in response
681 to human activity (e.g. Nogué *et al.*, 2013). Extending the application of palaeoecology to
682 investigate species arrival, establishment, and spread on islands [Q28] may be more
683 feasible for species of recent origin, such as those that were introduced by early human
684 colonizers. However, there is also potential for the analysis of much older native species,
685 where temporal patterns of trait change can also be integrated [see Q23] to understand
686 radiations (e.g. DeMiguel, 2016). Finally, alongside palaeoecological techniques, the
687 emerging field of palaeogenomics, based on the analysis of ancient DNA, can become
688 increasingly relevant for conservation by informing management and restoration
689 decisions [see Qs 42–46, below] of island ecosystems under past and present
690 anthropogenic pressure (e.g. Wilmshurst *et al.*, 2014).

691

692 **Island Community Ecology**

693 *Community assembly*

694 Q29. How do taxonomic, phylogenetic and functional diversities of island
695 communities change during assembly and disassembly of island systems? [# 39; % =
696 65.7]

697 Q30. How do island area, elevation and isolation influence the community
698 composition and dynamics of island systems? [# 1; % = 78.9]

699 Q31. What are the relative roles of island age, phylogenetic group and functional
700 ecology in determining natural (background) extinction rates among oceanic island
701 taxa? [# 21; % = 70.5]

702 Q32. How does the order of colonization influence emergent outcomes in the
703 assembly of island biotas? [# 13; % = 72.1]

704 Q33. How important are rare species for the functioning of island communities? [#
705 30; % = 67.8]

706 Q34. How does *in situ* evolution drive the functioning of island ecosystems? [# 14; %
707 = 72]

708

709 Comparisons of species richness among islands are evolving with the incorporation of
710 more informative estimators of diversity using taxonomic, phylogenetic and functional
711 trait data. How these measures of diversity respond to island ontogenetic change at the
712 community level, and how they are influenced by other abiotic parameters [Qs 29–31]
713 remains largely unexplored (but see Santos *et al.*, 2011, 2016a; Whittaker *et al.*, 2014;
714 Cardoso *et al.*, 2015). The unpredictability that accompanies island assembly by
715 colonization raises the question of how important colonization order (i.e. priority effects)
716 may be in explaining assembly patterns on both ecological and evolutionary timescales
717 [Q32]. For example, for evolutionary patterns of assembly it has been suggested that a
718 ‘founder takes all’ density-dependence principle may account for tendencies towards
719 monophyly in diverse genera of flowering plants that have diversified *in situ* on certain
720 oceanic archipelagos (Silvertown, 2004; Silvertown *et al.*, 2005). In addition,
721 phylogenetic evidence supports the proposition that a ‘progression-rule’ pattern of
722 younger species being derived from older species found on successively older islands is
723 commonplace among oceanic archipelagos (Carstensen *et al.*, 2013; Shaw & Gillespie,
724 2016). Waters *et al.* (2013) suggest that it is likely that dispersal of related lineages is

725 ongoing, but that establishment of the first founding lineages effectively reduces the
726 probability of establishment by subsequent migrants (see also Schaefer *et al.*, 2011).
727 Extending this logic, one can propose that abundance or range size differences between
728 functionally similar species may be a consequence of colonization order, although over
729 longer time scales, taxon cycle dynamics may develop a sequential pattern of
730 colonization, followed by population expansion and subsequent contraction of range of
731 earlier colonists (e.g. Wilson, 1961; Ricklefs & Bermingham, 2002; Carstensen *et al.*,
732 2013; Economo *et al.*, 2015). Given the historical dimension to this topic, comparative
733 phylogenetic analyses for the estimation of relative colonization times should continue to
734 be a profitable approach.

735 The majority of the species on Earth present restricted distributions and/or small
736 abundances, with comparatively few being cosmopolitan in distribution. Remote islands
737 possess high numbers of endemic species, which are, by nature of the limited size of
738 islands, rare in the sense that they have small global ranges. What is less clear is whether,
739 in the absence of human interference, island endemic species are also rare in terms of
740 population sizes and local density, which constitutes distinct forms of rarity. The
741 implications of the potential loss of rare species for other species with which they
742 interact, and for overall patterns of ecosystem form and function, remain under-
743 researched [Q33], with most illustrations of ecological cascades focussed on a limited
744 range of vertebrate taxa (e.g. giant tortoise, bird communities), which may well have
745 originally been rare only in the sense of having restricted ranges. To address this issue
746 will require better data on species distribution and abundance as well as systematic and

747 comprehensive community-level assessments of ecosystem form and function (e.g.
748 Traveset *et al.*, 2013; Trøjelsgaard *et al.*, 2013).

749 Similarly, the importance of local assembly and *in situ* evolution for ecosystem
750 functioning [Q34] remains underexplored (see Warren *et al.*, 2015). As one of the few
751 case studies in the literature, Rominger *et al.* (2016) compiled ecological, genetic and
752 phylogenetic data from a suite of Hawaiian endemic arthropods across a geological
753 chronosequence to investigate the relative roles of dispersal and *in situ* differentiation in
754 the assembly of plant–herbivore networks. Similar, comparative, plot-based and
755 experimental approaches to exploit the natural chronosequences provided by oceanic
756 islands hold promise for addressing questions [e.g. Qs 29, 32] posed in this section
757 seeking to integrate ecological and evolutionary theory (e.g. Heleno *et al.*, 2010;
758 Trøjelsgaard *et al.*, 2013).

759

760 *Biotic interactions*

761 Q35. How do climate and sea-level changes influence biotic interactions on islands?
762 [# 18; % = 71]

763 Q36. How do biotic interactions (within and between trophic levels) influence
764 immigration, extinction and speciation rates on islands? [# 3; % = 77.2]

765

766 The Quaternary period (the last 2.588 Myr) has been a period of major climatic
767 fluctuation between glacial and inter-glacial conditions, which have driven associated
768 eustatic changes in sea-level, with an amplitude of the order of 120–130 m. Interglacial
769 periods are times of high sea-level stands while the lowest sea-levels are typical of late

770 glacial stages (e.g. the Last Glacial Maximum c. 21 ka). These changes result in altered
771 island area, elevation, and effective degree of isolation, largely in synchrony with
772 changing regional climate regimes. Indeed, many islands have emerged and submerged,
773 or joined and been parted from larger land-masses, reiteratively, during this period.

774 On theoretical grounds, islands affected by such processes are expected to have
775 shown pulses of enhanced immigration and/or extinction, e.g. with sea-level rise after the
776 LGM driving pulses of extinction, especially from former land-bridge islands. In turn
777 these changes must be linked to altered patterns of biotic interaction via competition,
778 predation, predator-release, altered pollination or dispersal networks [Q35]. Recent
779 improvements in understanding of both regional climate and sea-level adjustments open
780 the possibility to search for such effects in the structure of contemporary island biotas.
781 Conversely, over time, ecological and evolutionary adjustments in biotic interactions can
782 be expected to alter rates of immigration, extinction and speciation and thus equilibrial
783 levels of species diversity (Wilson, 1969; Whittaker & Jones, 1994; Gravel *et al.*, 2011)
784 [Q36], although quantifying such effects remains challenging. Similarly, how those
785 interactions and dynamics have been and may be modified under future climate change
786 and, for instance associated sea-level change, is a topic of considerable uncertainty
787 (Tylianakis, 2009; Montoya & Raffaelli, 2010). In a recent review, Barraclough (2015)
788 summarises that, among other consequences, ecological interactions among species can
789 promote evolutionary changes through coevolution, and/or alter evolutionary outcomes
790 by influencing selection pressures relative to specific abiotic conditions. Such divergent
791 outcomes depend on species numbers and the distribution of interaction strengths across
792 the interaction network space.

793 One framework for analysing changes in interaction networks was provided by
794 Holt (1996, 2009) who put forward a model on the spatial limitations to food web size
795 and structure, based on *Core IBT*, called the trophic theory of island biogeography. In a
796 subsequent development, Gravel *et al.* (2011) developed a stochastic model of multi-
797 species occupancy dynamics, which showed that trophic interactions could have a
798 substantial impact on how immigration and extinction rates determine patterns of species
799 richness on islands. Their model focuses on herbivory or predation, but it does not
800 consider mutualistic interactions (like pollination or seed dispersal) or host–parasite
801 interactions, which are crucial for biodiversity maintenance and island colonization.
802 Nonetheless, Gravel *et al.* (2011) also found that immigration–extinction dynamics could
803 promote greater occupancy of generalist versus specialist taxa in small areas. Although
804 their approach is promising, it relies on mechanistic models for simplifying and linking
805 whole-community empirical evidence (Barraclough, 2015). Further improvements to
806 such models, for example, by incorporating mutualistic and/or host-parasite interactions,
807 will be of value for understanding the role of biotic interactions in island community
808 assembly.

809

810 **Island Conservation and Management**

811 *Global change*

812 Q37. How, if at all, do island biotas differ from continental biotas in their response to
813 global change? [# 32; % = 67.5]

814 Q38. Are island species more prone to extinction than their closest relatives on the
815 mainland, and if so, why? [# 4; % = 75.5]

816 Q39. How can we identify which island taxa are most at risk from global change and
817 what are their risk-associated traits? [# 5; % = 75.4]

818 Q40. What determines anthropogenic extinction rates among island taxa? [# 25; % =
819 69.7]

820 Q41. How do anthropogenic changes within islands impact on the capacity of island
821 species to respond successfully to climate change? [# 44; % = 65.3]

822

823 The Earth's ecosystems and their biotas are increasingly transformed by direct and
824 indirect human pressures (e.g. Barnosky *et al.*, 2012), a process particularly evident on
825 many islands (Caujapé-Castells *et al.*, 2010; Kueffer & Kaiser-Bunbury, 2014; Tershy *et*
826 *al.*, 2015). Thus, it remains crucial to better understand how island systems may respond
827 to anthropogenic threats such as habitat loss, biological invasion and climate change. This
828 urgency is clearly captured by our survey-based approach, with the two first questions of
829 this subsection focusing on how island and continental biotas differ in their response to
830 global-change processes in which humans are increasingly dominant [Qs 37, 38]. Island
831 organisms are often characterized by globally small population sizes, limited
832 geographical distribution ranges, and endemics of narrow distribution, driven by limited
833 habitat availability and unique traits resulting from prolonged evolutionary isolation (e.g.
834 Whittaker & Fernández-Palacios, 2007). It is generally thought that these features, in
835 combination with multiple anthropogenic change agents on islands, combine to make
836 island species more prone to human-induced extinction than their continental
837 counterparts [Qs 37, 38]. Despite long-standing hypotheses (e.g. Elton, 1958), most
838 studies have focussed either on island or continental systems, and more comparative

839 studies are urgently needed, to provide better resolution on levels of island endangerment
840 and the specific factors and combinations of them that drive extinction risk (but see e.g.
841 Bowen & Vuren, 1997; Siliceo & Díaz, 2010; Traveset *et al.*, 2016).

842 Despite the increasing interest in species responses to ongoing global change,
843 current predictions and conclusions greatly vary among regions and taxa (e.g. Urban,
844 2015). Rising rates of extinction create an urgent need to identify the traits and
845 mechanisms that render species vulnerable to extinction [Qs 39, 40], by answering
846 questions such as to what extent phylogenetic lineages are equally at risk from the same
847 anthropogenic threats (e.g. Ducatez & Shine, 2016). Although some traits (e.g. large-
848 bodied animals, flightlessness, strong ecological specialization) have been associated
849 with species rarity and their proneness to extinction (e.g. Boyer, 2008; Kirkpatrick &
850 Peischl, 2012; Illera *et al.*, 2016), case studies document that adaptive mechanisms can
851 counter the genetic disadvantages associated with small population sizes, rescuing
852 species from the negative consequences of anthropogenic environmental change (e.g.
853 Lavergne *et al.*, 2012). Therefore, studies that identify the level of risk that global change
854 poses to species and the specific traits that contribute to extinction risk on islands should
855 remain a priority [Qs 39, 40], with a particular focus on how climate change may interact
856 with other threat factors [Q41]. Gaining such information can help identify, forecast and
857 mitigate anthropogenic threats, ultimately leading to the development of more cost-
858 effective preventative and management strategies (Cardillo & Meijaard, 2012).

859

860 *Conservation and management policies*

861 Q42. How can we identify islands that are more susceptible to biodiversity loss in the
862 coming decade, and what are the most efficient and cost-effective methods (i.e.
863 policy; education; research; management) for safeguarding their biodiversity? [# 6; %
864 = 75.3]

865 Q43. What are the best strategies for *in situ* conservation of island species impacted
866 by non-native species? [# 16; % = 71.6]

867 Q44. What are the most effective methods for responding to the anthropogenic
868 extinction crisis on islands? [# 29; % = 68.3]

869 Q45. How can we best implement long-term monitoring schemes on islands to
870 provide quantitative evidence of changes within island ecological systems? [# 36; %
871 = 66.7]

872 Q46. How can conservation interests best be integrated with other island stakeholder
873 interests (particularly tourism) on populated islands? [# 41; % = 65.3]

874

875 Whereas island biologists are well aware that solutions to island conservation problems
876 require broad interdisciplinary approaches (Kingsford *et al.*, 2009), the questions in this
877 and the next section [Qs 42–50] are deliberately oriented to scientific issues within island
878 biology that may inform management strategies [Q42]. While the impacts of non-native
879 species [Q43, see also Qs 47–50] are not unique to islands, remote islands provide some
880 of the most familiar and dramatic cases (e.g. the impact of brown tree snake on Guam,
881 and of rats, cats, rabbits, mongoose and goats on many islands), with much recent effort
882 devoted to developing effective control and eradication methods that minimize non-target
883 effects [Qs 42–46]. The scale of the problem is such that, despite notable successes (see

884 e.g. Olivera *et al.*, 2010; Rivera-Parra *et al.*, 2012; Nogales *et al.*, 2013; Stokstad, 2013;
885 Robinson & Copson, 2014), increased efforts are evidently needed. The integration of
886 biodiversity conservation goals with those of other stakeholders [Qs 42, 46] is an area
887 where much less published work exists and the potential for political conflict is rife (e.g.
888 Fernández-Palacios & de Nascimento, 2011; Fernandes *et al.*, 2015), but in which the
889 engagement of biologists with other specialists in the development of strategies and
890 monitoring of impacts is surely crucial (e.g. Gil *et al.*, 2011; Bentz *et al.*, 2013).

891

892 *Invasive alien species*

893 Q47. What are the impacts of novel biotic interactions between and among alien and
894 native species on island biodiversity and ecosystem functioning? [# 10; % = 73.3]

895 Q48. How does the invasion stage (i.e. colonization, establishment, and long-term
896 adaptation) of alien taxa affect distribution ranges and biotic interactions of native
897 insular biotas? [# 24; % = 69.8]

898 Q49. To what extent can alien species act as functional substitutes for extinct native
899 species on islands? [# 40; % = 65.5]

900 Q50. How do the ecological effects of introduced species differ from those of
901 naturally arriving colonist species on islands? [# 34; % = 66.9]

902

903 Biotic invasions constitute one of the greatest threats to island native biodiversity (e.g.
904 Caujapé-Castells *et al.*, 2010; Kueffer *et al.*, 2010; McCreless *et al.*, 2016). Given their
905 geographic isolation, replicated numbers and discrete zonal ecosystems, islands are
906 model systems for understanding how biological invasions affect community structure

907 and ecosystem function, eventually leading to more efficient conservation and
908 management strategies. A major challenge and a priority in island conservation is to
909 better understand the responses of ecosystems (Kueffer *et al.*, 2010) and, particularly,
910 biotic interactions networks (Sax & Gaines, 2008; Heleno *et al.*, 2013) to invasion [Q47].
911 It has been proposed that the underlying determinants and subsequent outcomes of
912 invasions may vary depending on the invasion stage (i.e. the introduction–naturalization–
913 invasion continuum; for a review see Richardson & Pyšek, 2012). Little is known (but
914 see Traveset *et al.*, 2013) about how the different invasion stages negatively impact
915 geographic distributions and biotic interactions of native insular biotas [Q48]. With a
916 majority of the economic and practical efforts focused on the ‘invasion’ stage
917 (Richardson & Pyšek, 2012), research that broadens and improves our understanding of
918 the factors implicated in the establishment and naturalization of introduced organisms
919 [Q48] will have important consequences for the management and control of biological
920 invasions on islands.

921 Following the logic of MacArthur and Wilson (1967; see also the ‘saturation
922 point’ proposed by Sax & Gaines, 2008), the natural and/or anthropogenic addition of
923 new colonizers can potentially result in the local extinction of measurable numbers of
924 native species, with knock-on consequences for ecosystem functions performed by lost
925 species (e.g. McConkey & Drake, 2006). More information is needed on the functional
926 roles played by alien species on islands and the extent to which some may become
927 effective substitutes for extinct native species [Q49] (Traveset *et al.*, 2013). The existing
928 literature shows a clear bias towards certain taxonomic groups (for birds, see e.g. Heleno
929 *et al.*, 2013) and the limited evidence to date suggests that introductions rarely fully

930 compensate the functional roles of lost native species (Sobral *et al.*, 2016; but see Olesen
931 *et al.*, 2002). Studies in which the effects of new natural colonizers and those introduced
932 by humans are compared [Q50] remain virtually absent, due at least in part to the
933 difficulties in defining nativeness in organisms for which there is no historical (e.g. fossil,
934 observation) and/or molecular evidence (e.g. Essl *et al.*, 2015; Patiño & Vanderpoorten,
935 2015).

936

937

938 **DISCUSSION**

939

940 We conducted this horizon-scanning exercise to help advance the field of island biology
941 through the identification of 50 key questions to coincide with the 50th anniversary of
942 MacArthur and Wilson's seminal monograph. The intention was to generate and select
943 questions of broad scope, answerable through realistic research approaches. Although
944 updates of the present list of questions will be necessary in the coming years, we hope
945 that this contribution will supplement recent efforts to pinpoint challenges and advances
946 in island biology research (e.g. Fernández-Palacios *et al.*, 2015; Warren *et al.*, 2015;
947 Borges *et al.*, 2016; Borregaard *et al.*, 2016; Santos *et al.*, 2016b), as it captures many of
948 the top issues and challenges identified as cross-cutting subject areas. Such a multilateral
949 approach may foster the formation of interdisciplinary networks formed by island
950 ecologists, evolutionary biologists, managers and policy makers.

951 It is clear that addressing many of the 50 questions will benefit from an
952 interdisciplinary and integrative approach. To take one methodological area as

953 illustrative, phylogenetics has been a core element within research across the first three
954 subject areas of our study. It features explicitly within five questions [Qs 1, 3, 16, 29, 31],
955 and is implicit within many others [e.g. Qs 7, 18, 20, 32]. As the number of published
956 phylogenies increases, researchers will likely find new ways to exploit them, and novel
957 approaches published in recent years (e.g. Ronquist & Sanmartín, 2011) provide a firm
958 foundation for continued advances. We suggest that the field is likely to see increased
959 efforts to integrate across large numbers of independent phylogenies to address
960 macroecological and macroevolutionary questions in island biology.

961 Despite the long and critical influence of islands on ecological and evolutionary
962 theories, the focus of efforts has typically remained limited to the scale of individual
963 islands or single archipelagos. In the coming years, the analysis of biogeographical
964 dynamics performed through the comparative study of multiple archipelagos may provide
965 us with a better understanding of the regulation of biodiversity at higher levels of spatial
966 organization (e.g. Price & Wagner, 2011; Cabral *et al.*, 2014; Triantis *et al.*, 2015). To
967 achieve this will require suitable comparable data across islands and archipelagos, and it
968 is here that we believe that much progress can be made over the next 50 years. Coarse-
969 grained analyses of island-scale biota such as those of Price and Wagner (2011), Cabral
970 *et al.* (2014), Patiño *et al.* (2014b) and Triantis *et al.* (2015) can reveal recurrent patterns
971 that either invoke or suggest process-based explanations. We predict that analogous but
972 spatially fine-grained comparative analyses across islands and archipelagos will prove
973 equally enlightening. Recent plot- or site-based approaches among and within habitats
974 within islands (e.g. Heleno *et al.*, 2010; Emerson *et al.*, 2017), among islands (e.g.
975 Rominger *et al.*, 2016) and among archipelagos (Cicconardi *et al.*, 2017) offer useful and

976 powerful frameworks. The key will be to coordinate across geographic regions to
977 generate comparable data through replicated (or at least comparable) sampling. Such
978 sampling can be directed towards questions from across the four subject areas within
979 which the 50 questions have been grouped, with the importance for conservation and
980 management having already been demonstrated (Heleno *et al.*, 2010). Such sampling
981 calls for increased connectivity among research programs. This is in itself a logistical and
982 financial challenge, but with the potential for high rewards.

983 The 50 fundamental questions identified in this paper emphasize the potential for
984 island biology to inspire and guide empirical, theoretical and applied research questions
985 related to ecological, evolutionary and conservation science. We hope that this first list of
986 questions compiled under the legacy of MacArthur and Wilson's *Theory of Island*
987 *Biogeography Theory* provides a source of inspiration for constructive discussions about
988 the future agenda of island research and a fruitful arena for the coming generations of
989 island biologists.

990

991

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1552

1553 **BIOSKETCH**

1554 The ‘**50 fundamental questions in island biology**’ working group is composed of a set
1555 of island biologists, including biogeographers, ecologists, phylogeneticists,
1556 palaeontologists, and conservation biologists, who share an interest in understanding how
1557 evolutionary mechanisms interact with ecological processes to shape patterns in
1558 biodiversity across spatial and temporal scales.

1559

1560 Author contributions: J.P. and B.C.E. conceived the original idea with the contribution of
1561 R.J.W., P.A.V.B., and J.M.F.P. All authors compiled the first list of questions (*List 1*).
1562 J.P., R.J.W. and B.C.E. analyzed the data and prepared a first draft of the paper, to which
1563 all authors contributed.

1564 **Figure 1** Conceptual scheme showing the procedure used to identify the 50 fundamental questions in island biology (50FQIB).

