

1 | **Strapline: SYNTHESIS Special Paper**

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

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

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65 **Word count:** 10496 [text] + 5431 [references] = 15927

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67

68 **ABSTRACT**

69

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

75

76 **Location** Worldwide.

77

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

85

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

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

95

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

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104 **Keywords**

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

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109 **INTRODUCTION**

110

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

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

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

155 themselves, and here too, notable advances are being made (e.g. Whittaker *et al.*, 2008;
156 Borregaard *et al.*, 2016; Fernández-Palacios *et al.*, 2016).
157 Fifty years on from its publication, MacArthur and Wilson's (1967) book remains
158 one of the most influential texts on ecology and evolution, with continued debate over its
159 strengths and limitations. It has been, and will continue to be, a springboard for research
160 on the origin and maintenance of biological communities, with particular reference to
161 marine island systems, but also extending to other island-like systems. Half a century
162 since this seminal contribution, it is time to review both the new and outstanding
163 challenges facing the broad discipline of island biology, as well as particularly promising
164 research avenues (see e.g. Warren *et al.*, 2015; Santos *et al.*, 2016b). The impact of their
165 monograph is discernibly very broad across island biology, not merely within the
166 biogeographical literature. In particular, this paper focuses on identifying the 50 most
167 fundamental questions for present and future island biology research. Inspired by
168 previous studies seeking to identify priority research questions within a scientific field
169 based on a cornucopia of proven methods (e.g. Pretty *et al.*, 2010; Sutherland *et al.*, 2011;
170 Sutherland *et al.*, 2013; Seddon *et al.*, 2014; Kennicutt *et al.*, 2015), we present the
171 outcome of a survey-based approach initiated at *Island Biology 2016: the 2nd*
172 *International Conference on Island Evolution, Ecology and Conservation*, which was
173 held at the University of Azores in Terceira Island, July 18–22, 2016.
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176 **MATERIALS AND METHODS**
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Comment [PL1]: This connection is not working. I think that the problem can be solved by leaving out the sentence "The impact..."

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

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

216 At the end of *Survey 1*, the original survey questions were ranked according to the
217 total number of questions scored as 'fundamental', and the top 80 questions selected (List
218 2). Then, the 44 new questions proposed by survey participants (List 3) were merged with
219 an equivalent number of questions from List 2, specifically the 44 lowest ranked key
220 questions, to create a second survey (*Survey 2*) with 88 questions (List 4). The questions
221 from List 4 were voted as 'fundamental' or 'not fundamental' by the 29 members of the
222 '50 fundamental questions in island biology' working group, and ranked. The top 44
223 questions of List 4 were then refined to eliminate redundant questions or ambiguities

Comment [PL2]: Odd sentence, should maybe be the number of respondents who scored these as fundamental

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

235

236 **Study shortcomings**

237 Across the different phases of this participative process, a determined effort was made to
238 select experts, questions and voters, representative of the full breadth of island biology
239 research. In addition, the inclusion of 48 questions suggested online by anonymous
240 attendees of the Island Biology 2016 conference further contributed to increase the
241 diversity of backgrounds and expertise reflected in the questions identified (see Fig. 1).
242 However, despite these efforts, it would be naive to regard our list as definitive and
243 unbiased, as it inevitably reflects the interests of the particular group of voters who were
244 contacted and participated in our survey (see e.g. Sutherland *et al.*, 2013; Seddon *et al.*,
245 2014). For instance, from the 27 initial questions on Palaeoecology &
246 Palaeobiogeography included in the online *Survey 1*, only one question [see Q28 in

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

255

256

257 **RESULTS**

258

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

267 In the final round of online voting (*Survey 3*), 303 people participated, with the 80
268 submitted questions receiving on average 286.6 (SD = 2.3) votes. A large proportion of
269 the 80 questions (77 out of the 80) were considered as 'fundamental' by the majority of

270 the voters, and the final ranking was thus based on the proportion of 'fundamental' votes
271 with respect to the total numbers of votes ('fundamental' + 'not fundamental') received
272 for each question. The percentage of fundamental votes varied between 79% (top) and
273 39% (the 80th question), while the last question making it into the top 50 attracted 62% of
274 positive votes.

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

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

293 four main island topics used earlier (see List 1 above): (i) Island (Macro)Ecology and
294 Biogeography (including 16 questions); (ii) Island (Macro)Evolution (11); (iii) Island
295 Community Ecology (8); and (iv) Island Conservation and Management (15).

296 Information about each question's final rank (#) and percentage of votes received (%) is
297 also provided.

298

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

300 *Global diversity patterns*

301 Q1. What are the relative roles of spatial, historical and ecological processes in driving
302 taxonomic, phylogenetic and functional diversity patterns of insular systems? [# 7; %
303 = 75.2]

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

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

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

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

313

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

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

339 mainland) were typified by species that had become poor competitors (in the broad
340 sense). Moreover, islands were viewed as refugial holdouts of persistence for a number of
341 ancient forms (e.g. Yoder & Nowak, 2006; Vargas, 2007; Wood *et al.*, 2015; Shaw &
342 Gillespie, 2016), swept away by more recently evolved competitors from former
343 mainland bastions. More recently, it has become apparent that so-called back-
344 colonizations (or boomerangs sensu Caujapé-Castells, 2011) from islands to mainlands,
345 or movements across ocean basins via islands and colonization *de novo* of continents,
346 have occurred and include some colonist lineages that have had great importance in
347 shaping current biodiversity patterns. Examples include lineages of birds (e.g. Filardi &
348 Moyle, 2005; Jönsson *et al.*, 2011; Jönsson & Holt, 2015), insects (Grady & DeSalle,
349 2008) and plants (Carine *et al.*, 2004; Patiño *et al.*, 2015; Condamine *et al.*, 2016). For
350 the very reason that addressing these questions requires an integrative approach with the
351 intersection of disparate fields and methodological approaches, these broad questions [Qs
352 1–5] remain of central importance within island biology, with evident potential to
353 continue to generate significant changes in our understanding of this field.

354

355 *Island ontogeny and past climate change*

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

358 Q7. How do diversification rates of island lineages change with island age? [# 38; %
359 = 66]

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

362 Q9. How has climate change influenced speciation and extinction within islands? [#

363 12; % = 72.7]

364 Following on from the above themes, questions 6–9 embrace specific challenges to our
365 understanding of the long-term dynamics of insular systems. Notwithstanding the diverse
366 geological origins and developmental histories of islands, a substantial number of them
367 are remote, volcanic in origin, and follow a broadly similar ontogeny. Typically, these
368 islands begin with a building phase, followed by a gradual shift into erosion and
369 subsidence, eventually leading to them becoming merely sub-ocean surface features. This
370 developmental pathway, or certain variants of it, and their biological consequences are

371 integrated within the general dynamic model of oceanic island biogeography (Whittaker
372 *et al.*, 2008; Borregaard *et al.*, 2016), which offers predictions concerning rates of
373 colonization, speciation, diversification and extinction and how they vary over the
374 developmental history of islands. Testing such predictions for speciation and extinction is
375 challenging (see [Qs 17–20]), and further complicated when island age is also integrated
376 [Qs 6, 7]. It requires a focus on comparing island-specific rates among islands of different
377 maturity across archipelagos, as opposed to within-lineage rates without implicit
378 reference to island specific rates (*sensu* Bennett & O’Grady, 2013), suggesting a need for
379 innovative approaches involving the comparative analysis of large numbers of time-
380 calibrated phylogenies.

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

Comment [PL3]: Which themes? The first set of questions? Either make more explicit, or leave out. It does not seem to play a role.

Comment [PL4]: Is this what you mean?

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

393

394 *Island rules and syndromes*

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

396 % = 64.9]

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

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

399 others? [# 47; % = 63.3]

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

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

402

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

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

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

406 colonization filter through dispersal limitation. Following successful colonization and

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

408 novel biotic and abiotic conditions that have, in many instances, triggered notable
409 morphological, behavioural and ecological shifts (e.g. Kavanagh & Burns, 2014; Traveset
410 *et al.*, 2015). Indeed, many of these features were remarked upon and formalized into
411 syndromes or rules in classic works, particularly in *Island Life* by Alfred Russel Wallace
412 (1880) and *Island Biology* by Sherwin Carlquist (Carlquist, 1974). Not surprisingly,
413 chapter seven of MacArthur & Wilson's book (1967), entitled '*Evolutionary Changes*
414 *Following Colonization*', dealt with some of the most intriguing island syndromes, such
415 as the loss of dispersal capacity. Specifically, questions 10 and 11 reflect the long-lasting
416 interest in phenomena such as flightlessness, gigantism, super-generalism, or secondary
417 woodiness (reviewed in e.g. Jost, 2007; Whittaker & Fernández-Palacios, 2007; Losos &
418 Parent, 2010; Lens *et al.*, 2013), where empirical evidence has often provided conflicting
419 signals (e.g. for the loss of dispersability, see Cody & Overton, 1996; Patiño *et al.*, 2013;
420 Kavanagh & Burns, 2014; Vargas *et al.*, 2014). A few decades ago, a number of seminal
421 studies (e.g. Frankham, 1997) introduced the idea that island populations are typically
422 characterized by low levels of genetic diversity [Q12]. Recent analyses of spatial
423 distribution of genetic variation across island and continental regions have, however,
424 provided evidence that the expectation of low genetic diversity cannot always be
425 generalized to island assemblages (e.g. Fernández-Mazuecos & Vargas, 2011;
426 Hutsemékers *et al.*, 2011; García-Verdugo *et al.*, 2015; but see Illera *et al.*, 2016). It
427 seems likely that future research on island syndromes will need to continue to pay critical
428 attention to: (i) the statistical robustness of the patterns concerned (e.g. Meiri *et al.*,
429 2008); (ii) causal explanations for the patterns, including the extent to which they reflect
430 *in situ* evolutionary change versus non-random colonization/persistence (e.g. Valido *et*

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

437

438 *Island biogeography theory*

439 Q13. How do the dynamics of island communities scale up to generate the
440 biogeographical patterns predicted by island biogeographical theories? [# 37; % =
441 66.3]

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

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

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

448

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

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

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

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

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

488
489

490 **Island (Macro)Evolution**

491 *Immigration–speciation–extinction dynamics*

492 Q17. How does the spatial configuration of an archipelago (e.g. intra-archipelagic
493 connectivity) influence colonization, speciation and extinction over time? [# 23; % =
494 70.1]

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

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

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

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

503

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

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

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

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

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

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

Comment [PL5]: Or just humans?

Comment [PL6]: Subaerial?

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

574

575 *Speciation and diversification*

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

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

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

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

585

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

591 Answering the question of why only some lineages diversify is central to a deeper
592 understanding of island community assembly, the origin of biological diversity in general
593 [Q22], and adaptive radiations in particular [Q23]. Diversified lineages are often
594 associated with ecological divergence and adaptive radiation, but non-ecological
595 mechanisms are also expected in insular settings where the interaction of geology,
596 topography and climate promote speciation by local geographic isolation [Q24].
597 As the number of independent phylogenetic and population genetic studies
598 increases, comparative analyses can shed light on the functional traits associated with
599 accelerated diversification rates [Q22]. This approach has recently demonstrated that a
600 herbaceous dry-fruited ancestral syndrome is frequently associated with diversified plant
601 lineages across different archipelagos (Garcia-Verdugo *et al.*, 2014). A more complete
602 understanding of the contribution and functional relevance of speciation to island
603 community assembly will require not only identifying the traits associated with
604 diversification, but also the drivers underlying their change, and thus those traits that
605 underscore adaptive radiation [Q23]. Distinguishing among the drivers of natural
606 selection, sexual selection and non-selective processes for speciation is not a trivial task,
607 as multiple drivers may underlie trait divergence. This interconnectedness among the
608 different drivers of speciation and diversification [Qs 22–24] is exemplified by delphacid
609 planthoppers of the genus *Nesosydne* in the Hawaiian islands. *Nesosydne* are recognised
610 as an adaptive radiation linked to host plant use, however, sexual selection and non-
611 selective processes also contribute to reproductive isolation via divergence of sexual
612 signals (Goodman *et al.*, 2015). Another interesting aspect of trait evolution will be to

Comment [PL7]: Genus is, so "Nesosydne is recognized", but "the species of Nesosydne are"

613 determine whether similar traits promote high diversification rates in both islands and
614 mainland areas [see Q10].

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

626

627 *Dispersal and colonization*

628 Q26. What is the importance of founder effects for the evolution of island lineages?

629 [# 8 % = 74.4]

630 Q27. How frequent is inter-island dispersal and is it enough to form an archipelago-

631 wide metacommunity, or are islands better understood as functionally independent

632 communities? [# 26 % = 69.1]

633 Q28. How can palaeoecology contribute to the understanding of species arrival,

634 establishment and spread on islands? [# 35 % = 66.8]

635

Comment [PL8]: Or hybridization? Wiki definition: "the movement of a [gene \(gene flow\)](#) from one species into the gene pool of another by the repeated [backcrossing](#) of an [interspecific hybrid](#) with one of its parent species." note that the hybrid crosses with a parent. Hybridization is the more general term

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

658 One of the key attributes that make islands ideal models for ecology and evolution
659 is their well-defined borders (Whittaker & Fernández-Palacios, 2007). However, most
660 islands are embedded in regional groups of islands so that the nearest coast is not of a
661 continent but of another island. In addition, islands of high elevation are environmentally
662 diverse (at least in climatic regimes) and source regions for potential colonisers can then
663 differ between habitats (Steinbauer, 2017). Therefore, archipelago configurations and
664 environmental gradients can blur the lines of what seems the most relevant unit to study
665 for particular topics within island biology: the archipelago, the island, or ecozones within
666 the island. Intuitively, the relevance of archipelago-level process will largely depend on
667 the frequency of inter-island dispersal, so that when dispersal is low, island-level
668 processes dominate, and when dispersal is high, archipelago-level processes become
669 increasingly relevant. Ultimately, inter-island dispersal can be so important that single-
670 island populations are better understood in their broader context, as part of an archipelago
671 meta-population (Hanski, 1998). As the empirical observation of inter-island movements
672 is logistically challenging, population genetic data are particularly valuable for estimating
673 the frequency of inter-island dispersal and thus for exploring question 27. Recent studies
674 are providing novel insights in this direction (e.g. García-Verdugo *et al.*, 2014; Garrick *et*
675 *al.*, 2014; Spurgin *et al.*, 2014; Hendrickx *et al.*, 2015; Vargas *et al.*, 2015; Faria *et al.*,
676 2016), but more research is needed to generate fine-grained spatial genetic data within
677 focal archipelagos and provide general answers.

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

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

693

694 **Island Community Ecology**

695 *Community assembly*

696 | Q29. How do taxonomic, phylogenetic and functional diversity of island
697 communities change during assembly and disassembly of island systems? [# 39; % =
698 65.7]

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

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

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

706 Q33. How important are rare species for the functioning of island communities? [#
707 30; % = 67.8]

708 Q34. How does *in situ* evolution drive the functioning of island ecosystems? [# 14; %
709 = 72]

710

711 Comparisons of species richness among islands are evolving with the incorporation of
712 more informative estimators of diversity using taxonomic, phylogenetic and functional
713 trait data. How these measures of diversity respond to island ontogenetic change at the
714 community level, and how they are influenced by other abiotic parameters [Qs 29–31]
715 remains largely unexplored (but see Santos *et al.*, 2011, 2016a; Whittaker *et al.*, 2014;
716 Cardoso *et al.*, 2015). The unpredictability that accompanies island assembly by
717 colonization raises the question of how important colonization order (i.e. priority effects)
718 may be in explaining assembly patterns on both ecological and evolutionary timescales
719 [Q32]. For example, for evolutionary patterns of assembly it has been suggested that a
720 ‘founder takes all’ density-dependence principle may account for tendencies towards
721 monophyly in diverse genera of flowering plants that have diversified *in situ* on certain
722 oceanic archipelagos (Silvertown, 2004; Silvertown *et al.*, 2005). In addition,
723 phylogenetic evidence supports the proposition that a ‘progression-rule’ pattern of
724 younger species being derived from older species found on successively older islands is
725 commonplace among oceanic archipelagos (Carstensen *et al.*, 2013; Shaw & Gillespie,
726 2016). Waters *et al.* (2013) suggest that it is likely that dispersal of related lineages is

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

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

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

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

761

762 *Biotic interactions*

763 Q35. How do climate and sea-level changes influence biotic interactions on islands?
764 [# 18; % = 71]

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

767

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

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

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

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

811

812 **Island Conservation and Management**

813 *Global change*

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

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

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

820 Q40. What determines anthropogenic extinction rates among island taxa? [# 25; % =
821 69.7]

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

824

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

Comment [PL9]: "and what are their risk-associated traits?"

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

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

861

862 *Conservation and management policies*

863 Q42. How can we identify islands that are more susceptible to biodiversity loss in the
864 coming decade, and what are the most efficient and cost-effective methods (i.e.
865 policy, education, research, management) for safeguarding their biodiversity? [# 6; %
866 = 75.3]

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

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

871 Q45. How can we best implement long-term monitoring schemes on islands to
872 provide quantitative evidence of changes within island ecological systems? [# 36; %
873 = 66.7]

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

876

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

886 e.g. Olivera *et al.*, 2010; Rivera-Parra *et al.*, 2012; Nogales *et al.*, 2013; Stokstad, 2013;
887 Robinson & Copson, 2014), increased efforts are evidently needed. The integration of
888 biodiversity conservation goals with those of other stakeholders [Qs 42, 46] is an area
889 where much less published work exists and the potential for political conflict is rife (e.g.
890 Fernández-Palacios & de Nascimento, 2011; Fernandes *et al.*, 2015), but in which the
891 engagement of biologists with other specialists in the development of strategies and
892 monitoring of impacts is surely crucial (e.g. Gil *et al.*, 2011; Bentz *et al.*, 2013).
893
894 *Invasive alien species*
895 Q47. What are the impacts of novel biotic interactions between and among alien and
896 native species on island biodiversity and ecosystem functioning? [# 10; % = 73.3]
897 Q48. How does the invasion stage (i.e. colonization, establishment, and long-term
898 adaptation) of alien taxa affect distribution ranges and biotic interactions of native
899 insular biotas? [# 24; % = 69.8]
900 Q49. To what extent can alien species act as functional substitutes for extinct native
901 species on islands? [# 40; % = 65.5]
902 Q50. How do the ecological effects of introduced species differ from those of
903 naturally arriving colonist species on islands? [# 34; % = 66.9]
904
905 Biotic invasions constitute one of the greatest threats to island native biodiversity (e.g.
906 Caujapé-Castells *et al.*, 2010; Kueffer *et al.*, 2010; McCreless *et al.*, 2016). Given their
907 geographic isolation, replicated numbers and discrete zonal ecosystems, islands are
908 model systems for understanding how biological invasions affect community structure

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

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

932 compensate the functional roles of lost native species (Sobral *et al.*, 2016; but see Olesen
933 *et al.*, 2002). Studies in which the effects of new natural colonizers and those introduced
934 by humans are compared [Q50] remain virtually absent, due at least in part to the
935 difficulties in defining nativeness in organisms for which there is no historical (e.g. fossil,
936 observation) and/or molecular evidence (e.g. Essl *et al.*, 2015; Patiño & Vanderpoorten,
937 2015).

938
939

940 **DISCUSSION**

941

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

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

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

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

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

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

992

993

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1019

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Comment [PL10]: Single-page paper?

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1556 **BIOSKETCH**

1557 The ‘50 fundamental questions in island biology’ working group is composed of a set
1558 of island biologists, including biogeographers, ecologists, phylogeneticists,
1559 paleontologists, and conservation biologists, who share an interest in understanding how

1560 evolutionary mechanisms interact with ecological processes to shape patterns in
1561 biodiversity across spatial and temporal scales.

1562

1563 Author contributions: J.P. and B.C.E. conceived the original idea with the contribution of
1564 R.J.W., P.A.V.B., and J.M.F.P. All authors compiled the first list of questions (*List 1*).

1565 J.P., R.J.W. and B.C.E. analyzed the data and prepared a first draft of the paper, to which
1566 all authors contributed.

1567 **Figure 1** Conceptual scheme showing the procedure used to identify the 50 fundamental questions in island biology (50FQIB).

