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

Jairo Patiño[1,2,*], Robert J. Whittaker[3,4], Paulo A.V. Borges[2], José María Fernández-Palacios[5], Claudine Ah-Peng[6], Miguel Araújo[7,8], Sergio P. Ávila[9], Pedro Cardoso[2,10], Josselin Cornuault[11], Erik J. de Boer[12], Lea de Nascimento[5], Artur Gil[2], Aarón González-Castro[1], Daniel S. Gruner[13], Ruben Heleno[14], Joaquín Hortal[8,15], Juan Carlos Illera[16], Christopher Kaiser-Bunbury[17], Thomas J. Matthews[2,18], Anna Papadopoulou[19], Nathalie Pettorelli[20], Jonathan P. Price[21], Ana M. C. Santos[2,8,22], Manuel J. Steinbauer[23], Kostas A. Triantis[24], Luis Valente[25], Pablo Vargas[26], Patrick Weigelt[27] and Brent C. Emerson[1,28]

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

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

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

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ABSTRACT

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

Location Worldwide.

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

Results Questions were structured around four broad and partially overlapping island topics, including: (Macro)Ecology and Biogeography, (Macro)Evolution, Community Ecology, and Conservation and Management. These topics were then subdivided according to the following subject areas: global diversity patterns (5 questions in total); island ontogeny and past climate change (4); island rules and syndromes (3); island biogeography theory (4); immigration–speciation–extinction dynamics (5); speciation and diversification (4); dispersal and colonization (3); community assembly (6); biotic interactions (2); global change (5); conservation and management policies (5); and invasive alien species (4).

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

Keywords

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

INTRODUCTION

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

The seminal work of MacArthur and Wilson has subsequently stimulated a substantial research effort on island biogeography and biodiversity (Whittaker & Fernández-Palacios, 2007; Losos *et al.*, 2010), and promoted the exploration of islands as model systems for a more general understanding of biological communities (e.g. Warren *et al.*, 2015). The similarities between island archipelagos and fragmented continental landscapes have also triggered interest in applying MacArthur and Wilson's theory in conservation science; for instance, by deriving principles of protected area design and estimation of species extinctions in fragmented landscapes (e.g. Diamond, 1975). In addition to the colonization–extinction dynamics forming the core of MacArthur and Wilson's theory (MacArthur & Wilson, 1967), the authors included speciation as a term in the model within the 1963 description of equilibrium theory, and provided a 35-page chapter on '*evolutionary changes following colonization*' within their 1967 monograph. Evolutionary processes, however, were set aside from the early chapters of the monograph, excluded from statements of the *Core IBT* (Island Biogeography Theory) and the famous intersecting curves graphic, and were not explicitly integrated in the neutral mathematical formulation of the model (leading to the erroneous but oft repeated claim that they ignored speciation). The subsequent development of molecular genetic tools for evolutionary analysis have prompted renewed interest in the integration of speciation into the *Core IBT* (e.g. Emerson & Gillespie, 2008; Rosindell & Phillimore, 2011; Valente *et al.*, 2015), and improved estimation of historical immigration dynamics based on phylogenetic relationships among species (Ronquist & Sanmartín, 2011). The *Core IBT* is in essence a biologically neutral model – or close to it –, occupying the first 67 pages of the 1967 monograph, with much of the next 116 pages devoted to theory concerning population- and species-level traits of island biotas and their dynamics (MacArthur & Wilson, 1967). Progress on these latter themes has arguably been slower than on issues surrounding the *Core IBT*, but recent advances in genomic techniques, trait biology and analytical capacity should move forward this agenda (e.g. Gillespie *et al.*, 2012; Heleno & Vargas, 2015; Santos *et al.*, 2016a). Additionally, while the *Core IBT* referenced long-term biological dynamics, it did not take into account the dynamic nature of islands themselves, and here too, notable advances are being made (e.g. Whittaker *et al.*, 2008; Borregaard *et al.*, 2016; Fernández-Palacios *et al.*, 2016).

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

MATERIALS AND METHODS

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

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

At the end of *Survey* 1, the original survey questions were ranked according to the total number of participants who scored a given question as 'fundamental', and the top 80 questions selected (List 2). Then, the 44 new questions proposed by survey participants (List 3) were merged with an equivalent number of questions from List 2, specifically the 44 lowest ranked key questions, to create a second survey (*Survey* 2) with 88 questions (List 4). The questions from List 4 were voted as 'fundamental' or 'not fundamental' by the 29 members of the '50 fundamental questions in island biology' working group, and ranked. The top 44 questions of List 4 were then refined to eliminate redundant questions or ambiguities through discussions among the coordinators of the survey, and then merged with the top 36 questions kept from List 2. The list of 80 questions (List 5) was then subject to a third online survey (*Survey* 3) involving a broader participation by extending the invitation to participate to approximately 400 attendees of the Island Biology 2014 conference held in Honolulu, Hawaii, some of whom did not attend the Island Biology 2016 conference, and also to the members of the following island biology related interest groups: American Society of Naturalists; British Ecological Society; Conservation Specialist Interest Group; Société Française d'Ecologie; Ecological Society of America; Hellenic Ecological Society; International Biogeography Society; New Zealand Ecological Society; the Spanish and the Portuguese Ecological Societies, and other specific working groups and e-mailing lists related to island biology that the authors could identify.

Study shortcomings

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

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

RESULTS

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

In the final round of online voting (*Survey* 3), 303 people participated, with the 80 submitted questions receiving on average 286.6 (SD ± 2.3) votes. A large proportion of the 80 questions (77 out of the 80) were considered as ‘fundamental’ by the majority of the voters, and the final ranking was thus based on the proportion of ‘fundamental’ votes with respect to the total numbers of votes (‘fundamental’ + ‘not fundamental’) received for each question. The percentage of fundamental votes varied between 79% (top) and 39% (the 80th question), while the last question making it into the top 50 attracted 62% of positive votes.

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

Below we present the top 50 priority questions in island biology identified in the present study. For convenience in presenting the results, questions were compiled into the four main island topics used earlier (see List 1 above): (i) Island (Macro)Ecology and Biogeography (including 16 questions); (ii) Island (Macro)Evolution (11); (iii) Island Community Ecology (8); and (iv) Island Conservation and Management (15). Information about each question's final rank (#) and percentage of votes received (*%*) is also provided.

Island (Macro)Ecology and Biogeography

Global diversity patterns

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

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

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

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

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

The questions in this section share an emphasis on fundamental large-scale topics. The first question [Q1], in particular, invokes a research agenda covering all types of island systems and multiple facets of biodiversity. This question is a worthy reminder of the importance of integrating the dynamics of historical/geographical, long-term environmental, and contemporary ecological time-scales in analyses of insular biota. Island biologists need to be aware of and integrate knowledge from other natural sciences, in particular from earth systems science, in understanding long-term dynamics of island platforms as theatres for the evolutionary play (e.g. Price & Clague, 2002; Fernández-Palacios *et al.*, 2011; Ali & Aitchison, 2014; Skipwith *et al.*, 2016). How key biogeographical processes of dispersal/migration, speciation and extinction interact to shape the form of the island species–area relationship [Q2] remains an important topic and particular how these processes and patterns vary among different island contexts, including oceanic, continental-shelf, continental fragment, and habitat islands (e.g. Triantis *et al.*, 2012; Patiño *et al.*, 2014b; Matthews *et al.*, 2016). Comparisons between taxonomic (typically the species as unit of analysis), phylogenetic and functional diversity responses across islands [see also Q29] and between islands and continents [Q3] represent a very recent development, on which little research has so far been conducted (but see e.g. Whittaker *et al.*, 2014 and; Weigelt *et al.*, 2015, for examples of intra and inter-archipelago analyses respectively). Our perception of the roles of islands [Qs 4, 5] as macroevolutionary sinks (sensu Goldberg *et al.*, 2005), rather than as sources, has been challenged in recent years, and possibly needs to be reassessed (Bellemain & Ricklefs, 2008). It was long understood that, in general, whereas islands received colonist species from continents, the reverse process rarely, if ever, happened (e.g. Carlquist, 1974). This unidirectional view of island colonization was consistent with the notion that islands, as species poor and disharmonic systems (i.e. lacking the full array of forms found on the mainland) were typified by species that had become poor competitors (in the broad sense). Moreover, islands were viewed as refugial holdouts of persistence for a number of ancient forms (e.g. Yoder & Nowak, 2006; Vargas, 2007; Wood *et al.*, 2015; Shaw & Gillespie, 2016), swept away by more recently evolved competitors from former mainland bastions. More recently, it has become apparent that so-called back-colonizations (or boomerangs sensu Caujapé-Castells, 2011) from islands to mainlands, or movements across ocean basins via islands and colonization *de novo* of continents, have occurred and include some colonist lineages that have had great importance in shaping current biodiversity patterns. Examples include lineages of birds (e.g. Filardi & Moyle, 2005; Jønsson *et al.*, 2011; Jønsson & Holt, 2015), insects (Grady & DeSalle, 2008) and plants (Carine *et al.*, 2004; Patiño *et al.*, 2015; Condamine *et al.*, 2016). For the very reason that addressing these questions requires an integrative approach with the intersection of disparate fields and methodological approaches, these broad questions [Qs 1–5] remain of central importance within island biology, with evident potential to continue to generate significant changes in our understanding of this field.

Island ontogeny and past climate change

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

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

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

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

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

Improved geodynamic data concerning past climate change, wind connectivity, ocean currents, and sea-level oscillations over the Pleistocene permit the development of more sophisticated models for inferring shifts in the configuration of islands and their environment (area, isolation and climate) through time, and their availability has generated increasing interest in the implications of these long-term changes for island biodiversity patterns and processes (e.g. Carine, 2005; Dalsgaard *et al.*, 2013; Ali & Aitchison, 2014; Rijsdijk *et al*. 2014; Ávila *et al.*, 2016; Borregaard *et al.*, 2016; Fernández-Palacios, 2016; Fernández-Palacios *et al.*, 2016; Steinbauer *et al.*, 2016a,b; Weigelt *et al.*, 2016). Integrating colonization dynamics into these models [Q8] may benefit from recent comparative phylogenetic approaches (Ronquist & Sanmartín, 2011), while understanding how climate change has influenced rates and patterns of speciation and extinction on islands [Q9] appears to be a particularly challenging area of study.

Island rules and syndromes

Q10. Is trait evolution fundamentally different on islands than on continents? [# *42*; *% = 64.9*]

Q11. How robust are the various island rules and syndromes relating to body size, loss of dispersal, coloration, breeding system, woodiness, and clutch size, among others? [# *47*; *% = 63.3*]

Q12. To what extent are island populations genetically impoverished, compared to comparable mainland populations? [# *50*; *% = 62*]

Since the earliest days of scientific study of island biology, it has been understood that islands possess peculiar forms and otherwise atypical subsets of ecological and taxonomic groups (an aspect of island disharmony). Some part of this arises from a colonization filter through dispersal limitation. Following successful colonization and establishment on an island, recently arrived colonists are potentially exposed to a range of novel biotic and abiotic conditions that have, in many instances, triggered notable morphological, behavioural and ecological shifts (e.g. Kavanagh & Burns, 2014; Traveset *et al.*, 2015). Indeed, many of these features were remarked upon and formalized into syndromes or rules in classic works, particularly in *Island Life* by Alfred Russel Wallace (1880) and *Island Biology* by Sherwin Carlquist (Carlquist, 1974). Not surprisingly, chapter seven of MacArthur & Wilson's book (1967), entitled '*Evolutionary Changes Following Colonization*', dealt with some of the most intriguing island syndromes, such as the loss of dispersal capacity. Specifically, questions 10 and 11 reflect the long-lasting interest in phenomena such as flightlessness, gigantism, super-generalism, or secondary woodiness (reviewed in e.g. Jost, 2007; Whittaker & Fernández-Palacios, 2007; Losos & Parent, 2010; Lens *et al.*, 2013), where empirical evidence has often provided conflicting signals (e.g. for the loss of dispersability, see Cody & Overton, 1996; Patiño *et al.*, 2013; Kavanagh & Burns, 2014; Vargas *et al.*, 2014).

A few decades ago, a number of seminal studies (e.g. Frankham, 1997) introduced the idea that island populations are typically characterized by low levels of genetic diversity [Q12]. Recent analyses of spatial distribution of genetic variation across island and continental regions have, however, provided evidence that the expectation of low genetic diversity cannot always be generalized to island assemblages (e.g. Fernández-Mazuecos & Vargas, 2011; Hutsemékers *et al.*, 2011; García-Verdugo *et al.*, 2015; but see Illera et al., 2016). It seems likely that future research on island syndromes will need to continue to pay critical attention to: (i) the statistical robustness of the patterns concerned (e.g. Meiri *et al.*, 2008); (ii) causal explanations for the patterns, including the extent to which they reflect *in situ* evolutionary change *versus* non-random colonization/persistence (e.g. Valido *et al.*, 2004; Lomolino *et al.*, 2013); and (iii) the mechanistic explanations for such distinctive evolutionary pathways (e.g. Burns *et al.*, 2012; Novosolov *et al.*, 2013; Itescu *et al.*, 2014). As these island-specific syndromes develop from the same eco-evolutionary processes that operate on mainlands, research on islands and continental counterparts (e.g. closely related taxa) [Q12] will be key to enhancing our fundamental understanding of the underlying mechanisms.

Island biogeography theory

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

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

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

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

Island biogeography has always been a driver for the development of general theories in ecology and evolution. Hubbell's (2001) '*neutral theory of biodiversity and biogeography*' is one prominent example of how reflection on island theory (specifically MacArthur and Wilson's theory) in a broader context, has continued to generate novel research directions (e.g. Warren *et al.*, 2015; Santos *et al.*, 2016b). Neutral theory provides one approach to scaling up from local scale species abundance distribution patterns and dynamics to emergent biogeographical patterns [Q13], as exemplified by recent work by Rosindell and colleagues (e.g. Rosindell & Phillimore, 2011; Rosindell & Harmon, 2013). Although questions specifically on species abundance distributions failed to make the final cut in the present survey, the significance of improving understanding of species abundances in insular settings, and how they link to other macroecological patterns (such as species–area relationships) is implicit in questions 13, 14, and 33 (see e.g. Fattorini *et al.*, 2016).

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

Island biogeographic theory invokes historical biological processes (colonization, speciation, extinction) to explain contemporary species distribution patterns, which has yielded a large body of phylogenetic and population genetic island-focussed research. Such studies help advance models of island biogeography [Q16], link short term, within-island ecological processes to patterns emerging on large spatial or evolutionary scales, and thus help to unify theories of ecology and biogeography (e.g. Johnson *et al.*, 2000; Steinbauer, 2017; see also Qs 17–20). Future statistical advances toward this goal may include comparing the fit of data among the predictions of competing phylogenetic and population genetic simulation models (e.g. Chan *et al.*, 2014; Patiño *et al.*, 2015), or combining phylogenetic and population genetic perspectives into unified statistical frameworks (e.g. Rannala & Yang, 2003). Combining a phylogenetic perspective with population genetic approaches may also help to establish links between macroevolutionary patterns and underlying microevolutionary mechanisms (e.g. Ricklefs & Bermingham, 2001; Jordal & Hewitt, 2004; Roderick *et al.*, 2012; Paun *et al.*, 2016), thus advancing our understanding of island biogeographic history.

Island (Macro)Evolution

Immigration–speciation–extinction dynamics

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

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

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

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

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

Island biodiversity emerges from the accumulation of species through time by colonization and establishment from outside areas, anagenetic change, and extensive diversification, all being counterbalanced by the depletive effects of extinction. The relative roles of these macroevolutionary processes are predicted to be functionally interrelated (e.g. MacArthur & Wilson, 1963, 1967; Emerson & Kolm, 2005; Emerson & Gillespie, 2008; Whittaker *et al.*, 2008; Rominger *et al.*, 2016), but understanding their dynamics over time remains a central challenge in island biology. Geographical context plays an important role in determining how colonization, extinction and speciation [Qs 17, 18] dynamically vary and interact over time (see Cabral *et al.*, 2014; Papadopoulou & Knowles, 2015b). While the effect of geography on macroevolution is well understood for some processes (e.g. cladogenesis generally increases with island area; see Kisel & Barraclough, 2010), for others, this relationship remains largely unknown (e.g. extinction *versus* isolation in Q18). Time-calibrated phylogenies have been of particular interest in investigating the processes of speciation and colonization, but they provide no direct evidence for extinction. Thus, while rates of diversification can be derived directly from dated phylogenies, estimating the underlying rates of colonization, speciation and extinction is more challenging. However, it is now possible to apply a model-based approach to estimate how these processes vary through time (Valente *et al.*, 2014, 2015), suggesting that there is further potential for phylogenetics to inform island biogeography. It is important that we note here that Q18 does not, in fact, specify a context involving extinction of endemic species, and the question of how extinction rate varies with isolation can be posed for a wide range of island systems and degrees of isolation, including for instance among non-endemic species on habitat islands (as e.g. Brown & Kodric-Brown, 1977).

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

MacArthur and Wilson (1967) expressed their intuition of a negative feedback of diversity on the accumulation of species on an island [Q20], either through an increased extinction rate or through a decreased colonization rate by means of niche saturation by early colonists. Their argument illustrates the early foundation of a still debated question: is there a limit to the number of species a given area can sustain? This question has been the subject of recent discussions (Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015) and its longevity pertains in part to the difficulty of measuring turnover rates let alone negative diversity feedbacks on evolutionary processes such as speciation. However, a number of recent methodological developments (Rabosky, 2006; Etienne *et al.*, 2012; Valente *et al.*, 2015) promise improved analytical power and have already revealed that diversity-dependence in both colonization and speciation can potentially be inferred from empirical data based on island phylogenies (Valente *et al.*, 2015). The issue of diversity-dependence [Q20] is central to understanding island biodiversity dynamics, equilibrium and biotic interactions on evolutionary time-scales [Q6] and promises to remain a key topic over at least the next few years.

There is no a single path to extinction, and the role of humans as drivers of distribution range shifts and extinctions in both recent historical and prehistorical time has increasingly gained relevance on islands. This significance can be mirrored in the species listed by the IUCN as extinct, of which 61% were confined to islands (Tershy *et al.*, 2015), and among the 20 world territories with the highest percentages of extinct and threatened species in both bird and mammal group lists, 19 and 17 are insular, respectively (Vié *et al.*, 2009); remarkable statistics given that the 19 bird and 17 mammal territories themselves represent a mere 0.6% and 1.9% of the Earth's subaerial landmass, respectively (Vié *et al.*, 2009). Compounding these issues is the unknown degree to which island taxa have been eliminated as a consequence of human colonization of islands and before their scientific documentation [Q21]. For birds in the Pacific, to take the most infamous example, extrapolations from the relatively small number of islands studied in detail, suggest that hundreds of undocumented species extinctions may have taken place following Polynesian colonization (Steadman, 2006), undermining efforts to estimate natural rates of speciation and extinction from these insular systems [Q21].

Speciation and diversification

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

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

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

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

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

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

As the number of independent phylogenetic and population genetic studies increases, comparative analyses can shed light on the functional traits associated with accelerated diversification rates [Q22]. This approach has recently demonstrated that a herbaceous dry-fruited ancestral syndrome is frequently associated with diversified plant lineages across different archipelagos (García-Verdugo *et al.*, 2014). A more complete understanding of the contribution and functional relevance of speciation to island community assembly will require not only identifying the traits associated with diversification, but also the drivers underlying their change, and thus those traits that underscore adaptive radiation [Q23]. Distinguishing among the drivers of natural selection, sexual selection and non-selective processes for speciation is not a trivial task, as multiple drivers may underlie trait divergence. This interconnectedness among the different drivers of speciation and diversification [Qs 22–24] is exemplified by delphacid planthoppers of the genus *Nesosydne* in the Hawaiian islands. The species of *Nesosydne* are recognised as an adaptive radiation linked to host plant use, however, sexual selection and non-selective processes also contribute to reproductive isolation via divergence of sexual signals (Goodman *et al.*, 2015). Another interesting aspect of trait evolution will be to determine whether similar traits promote high diversification rates in both islands and mainland areas [see Q10].

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

Dispersal and colonization

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

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

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

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

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

Palaeoecology is a field of emerging importance in island biology. Palaeoecology has been used to understand the consequences of human colonization, frequently characterised by concomitant waves of extinction (Sadler, 1999; van der Geer *et al.*, 2016). In addition, climate data have been integrated in attempts to distinguish plant community compositional changes in response to shifts in climate from those in response to human activity (e.g. Nogué *et al.*, 2013). Extending the application of palaeoecology to investigate species arrival, establishment, and spread on islands [Q28] may be more feasible for species of recent origin, such as those that were introduced by early human colonizers. However, there is also potential for the analysis of much older native species, where temporal patterns of trait change can also be integrated [see Q23] to understand radiations (e.g. DeMiguel, 2016). Finally, alongside palaeoecological techniques, the emerging field of palaeogenomics, based on the analysis of ancient DNA, can become increasingly relevant for conservation by informing management and restoration decisions [see Qs 42–46, below] of island ecosystems under past and present anthropogenic pressure (e.g. Wilmshurst *et al.*, 2014).

Island Community Ecology

Community assembly

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

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

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

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

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

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

Comparisons of species richness among islands are evolving with the incorporation of more informative estimators of diversity using taxonomic, phylogenetic and functional trait data. How these measures of diversity respond to island ontogenetic change at the community level, and how they are influenced by other abiotic parameters [Qs 29–31] remains largely unexplored (but see Santos *et al.*, 2011, 2016a; Whittaker *et al.*, 2014; Cardoso *et al.*, 2015). The unpredictability that accompanies island assembly by colonization raises the question of how important colonization order (i.e. priority effects) may be in explaining assembly patterns on both ecological and evolutionary timescales [Q32]. For example, for evolutionary patterns of assembly it has been suggested that a 'founder takes all' density-dependence principle may account for tendencies towards monophyly in diverse genera of flowering plants that have diversified *in situ* on certain oceanic archipelagos (Silvertown, 2004; Silvertown *et al.*, 2005). In addition, phylogenetic evidence supports the proposition that a 'progression-rule' pattern of younger species being derived from older species found on successively older islands is commonplace among oceanic archipelagos (Carstensen *et al.*, 2013; Shaw & Gillespie, 2016). Waters *et al.* (2013) suggest that it is likely that dispersal of related lineages is ongoing, but that establishment of the first founding lineages effectively reduces the probability of establishment by subsequent migrants (see also Schaefer *et al.*, 2011). Extending this logic, one can propose that abundance or range size differences between functionally similar species may be a consequence of colonization order, although over longer time scales, taxon cycle dynamics may develop a sequential pattern of colonization, followed by population expansion and subsequent contraction of range of earlier colonists (e.g. Wilson, 1961; Ricklefs & Bermingham, 2002; Carstensen *et al.*, 2013; Economo *et al.*, 2015). Given the historical dimension to this topic, comparative phylogenetic analyses for the estimation of relative colonization times should continue to be a profitable approach.

The majority of the species on Earth present restricted distributions and/or small abundances, with comparatively few being cosmopolitan in distribution. Remote islands possess high numbers of endemic species, which are, by nature of the limited size of islands, rare in the sense that they have small global ranges. What is less clear is whether, in the absence of human interference, island endemic species are also rare in terms of population sizes and local density, which constitutes distinct forms of rarity. The implications of the potential loss of rare species for other species with which they interact, and for overall patterns of ecosystem form and function, remain under-researched [Q33], with most illustrations of ecological cascades focussed on a limited range of vertebrate taxa (e.g. giant tortoise, bird communities), which may well have originally been rare only in the sense of having restricted ranges. To address this issue will require better data on species distribution and abundance as well as systematic and comprehensive community-level assessments of ecosystem form and function (e.g. Traveset *et al.*, 2013; Trøjelsgaard *et al.*, 2013).

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

Biotic interactions

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

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

The Quaternary period (the last 2.588 Myr) has been a period of major climatic fluctuation between glacial and inter-glacial conditions, which have driven associated eustatic changes in sea-level, with an amplitude of the order of 120–130 m. Interglacial periods are times of high sea-level stands while the lowest sea-levels are typical of late glacial stages (e.g. the Last Glacial Maximum c. 21 ka). These changes result in altered island area, elevation, and effective degree of isolation, largely in synchrony with changing regional climate regimes. Indeed, many islands have emerged and submerged, or joined and been parted from larger land-masses, reiteratively, during this period.

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

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

Island Conservation and Management

Global change

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

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

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

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

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

The Earth's ecosystems and their biotas are increasingly transformed by direct and indirect human pressures (e.g. Barnosky *et al.*, 2012), a process particularly evident on many islands (Caujapé-Castells *et al.*, 2010; Kueffer & Kaiser-Bunbury, 2014; Tershy *et al.*, 2015). Thus, it remains crucial to better understand how island systems may respond to anthropogenic threats such as habitat loss, biological invasion and climate change. This urgency is clearly captured by our survey-based approach, with the two first questions of this subsection focusing on how island and continental biotas differ in their response to global-change processes in which humans are increasingly dominant [Qs 37, 38]. Island organisms are often characterized by globally small population sizes, limited geographical distribution ranges, and endemics of narrow distribution, driven by limited habitat availability and unique traits resulting from prolonged evolutionary isolation (e.g. Whittaker & Fernández-Palacios, 2007). It is generally thought that these features, in combination with multiple anthropogenic change agents on islands, combine to make island species more prone to human-induced extinction than their continental counterparts [Qs 37, 38]. Despite long-standing hypotheses (e.g. Elton, 1958), most studies have focussed either on island or continental systems, and more comparative studies are urgently needed, to provide better resolution on levels of island endangerment and the specific factors and combinations of them that drive extinction risk (but see e.g. Bowen & Vuren, 1997; Siliceo & Díaz, 2010; Traveset *et al.*, 2016).

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

Conservation and management policies

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

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

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

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

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

Whereas island biologists are well aware that solutions to island conservation problems require broad interdisciplinary approaches (Kingsford *et al.*, 2009), the questions in this and the next section [Qs 42–50] are deliberately oriented to scientific issues within island biology that may inform management strategies [Q42]. While the impacts of non-native species [Q43, see also Qs 47–50] are not unique to islands, remote islands provide some of the most familiar and dramatic cases (e.g. the impact of brown tree snake on Guam, and of rats, cats, rabbits, mongoose and goats on many islands), with much recent effort devoted to developing effective control and eradication methods that minimize non-target effects [Qs 42–46]. The scale of the problem is such that, despite notable successes (see e.g. Olivera *et al.*, 2010; Rivera-Parra *et al.*, 2012; Nogales *et al.*, 2013; Stokstad, 2013; Robinson & Copson, 2014), increased efforts are evidently needed. The integration of biodiversity conservation goals with those of other stakeholders [Qs 42, 46] is an area where much less published work exists and the potential for political conflict is rife (e.g. Fernández-Palacios & de Nascimento, 2011; Fernandes *et al.*, 2015), but in which the engagement of biologists with other specialists in the development of strategies and monitoring of impacts is surely crucial (e.g. Gil *et al.*, 2011; Bentz *et al.*, 2013).

Invasive alien species

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

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

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

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

Biotic invasions constitute one of the greatest threats to island native biodiversity (e.g. Caujapé-Castells *et al.*, 2010; Kueffer *et al.*, 2010; McCreless *et al.*, 2016). Given their geographic isolation, replicated numbers and discrete zonal ecosystems, islands are model systems for understanding how biological invasions affect community structure and ecosystem function, eventually leading to more efficient conservation and management strategies. A major challenge and a priority in island conservation is to better understand the responses of ecosystems (Kueffer *et al.*, 2010) and, particularly, biotic interactions networks (Sax & Gaines, 2008; Heleno *et al.*, 2013) to invasion [Q47]. It has been proposed that the underlying determinants and subsequent outcomes of invasions may vary depending on the invasion stage (i.e. the introduction–naturalization–invasion continuum; for a review see Richardson & Pyšek, 2012). Little is known (but see Traveset *et al.*, 2013) about how the different invasion stages negatively impact geographic distributions and biotic interactions of native insular biotas [Q48]. With a majority of the economic and practical efforts focused on the 'invasion' stage (Richardson & Pyšek, 2012), research that broadens and improves our understanding of the factors implicated in the establishment and naturalization of introduced organisms [Q48] will have important consequences for the management and control of biological invasions on islands.

Following the logic of MacArthur and Wilson (1967; see also the 'saturation point' proposed by Sax & Gaines, 2008), the natural and/or anthropogenic addition of new colonizers can potentially result in the local extinction of measurable numbers of native species, with knock-on consequences for ecosystem functions performed by lost species (e.g. McConkey & Drake, 2006). More information is needed on the functional roles played by alien species on islands and the extent to which some may become effective substitutes for extinct native species [Q49] (Traveset *et al.*, 2013). The existing literature shows a clear bias towards certain taxonomic groups (for birds, see e.g. Heleno *et al.*, 2013) and the limited evidence to date suggests that introductions rarely fully compensate the functional roles of lost native species (Sobral *et al.*, 2016; but see Olesen *et al.,* 2002). Studies in which the effects of new natural colonizers and those introduced by humans are compared [Q50] remain virtually absent, due at least in part to the difficulties in defining nativeness in organisms for which there is no historical (e.g. fossil, observation) and/or molecular evidence (e.g. Essl *et al.*, 2015; Patiño & Vanderpoorten, 2015).

DISCUSSION

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

It is clear that addressing many of the 50 questions will benefit from an interdisciplinary and integrative approach. To take one methodological area as illustrative, phylogenetics has been a core element within research across the first three subject areas of our study. It features explicitly within five questions [Qs 1, 3, 16, 29, 31], and is implicit within many others [e.g. Qs 7, 18, 20, 32]. As the number of published phylogenies increases, researchers will likely find new ways to exploit them, and novel approaches published in recent years (e.g. Ronquist & Sanmartín, 2011) provide a firm foundation for continued advances. We suggest that the field is likely to see increased efforts to integrate across large numbers of independent phylogenies to address macroecological and macroevolutionary questions in island biology.

Despite the long and critical influence of islands on ecological and evolutionary theories, the focus of efforts has typically remained limited to the scale of individual islands or single archipelagos. In the coming years, the analysis of biogeographical dynamics performed through the comparative study of multiple archipelagos may provide us with a better understanding of the regulation of biodiversity at higher levels of spatial organization (e.g. Price & Wagner, 2011; Cabral *et al.*, 2014; Triantis *et al.*, 2015). To achieve this will require suitable comparable data across islands and archipelagos, and it is here that we believe that much progress can be made over the next 50 years. Coarse-grained analyses of island-scale biota such as those of Price and Wagner (2011), Cabral *et al.* (2014), Patiño *et al.* (2014b) and Triantis *et al.* (2015) can reveal recurrent patterns that either invoke or suggest process-based explanations. We predict that analogous but spatially fine-grained comparative analyses across islands and archipelagos will prove equally enlightening. Recent plot- or site-based approaches among and within habitats within islands (e.g. Heleno *et al.*, 2010; Emerson *et al.*, 2017), among islands (e.g. Rominger *et al.*, 2016) and among archipelagos (Cicconardi *et al.*, 2017) offer useful and powerful frameworks. The key will be to coordinate across geographic regions to generate comparable data through replicated (or at least comparable) sampling. Such sampling can be directed towards questions from across the four subject areas within which the 50 questions have been grouped, with the importance for conservation and management having already been demonstrated (Heleno *et al.*, 2010). Such sampling calls for increased connectivity among research programs. This is in itself a logistical and financial challenge, but with the potential for high rewards.

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

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BIOSKETCH

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

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

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