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REVIEW AND SYNTHESIS

Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson

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Abstract

The study of islands as model systems has played an important role in the development of evolutionary and ecological theory. The 50th anniversary of MacArthur and Wilson's (December 1963) article, 'An equilibrium theory of insular zoogeography', was a recent milestone for this theme. Since 1963, island systems have provided new insights into the formation of ecological communities. Here, building on such developments, we highlight prospects for research on islands to improve our understanding of the ecology and evolution of communities in general. Throughout, we emphasise how attributes of islands combine to provide unusual research opportunities, the implications of which stretch far beyond islands. Molecular tools and increasing data acquisition now permit reassessment of some fundamental issues that interested MacArthur and Wilson. These include the formation of ecological networks, species abundance distributions, and the contribution of evolution to community assembly. We also extend our prospects to other fields of ecology and evolution – understanding ecosystem functioning, speciation and diversification – frequently employing assets of oceanic islands in inferring the geographic area within which evolution has occurred, and potential barriers to gene flow. Although island-based theory is continually being enriched, incorporating non-equilibrium dynamics is identified as a major challenge for the future.

Keywords
Community assembly, diversification, ecosystem functioning, genomics, island biogeography, islands as model systems, speciation.

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INTRODUCTION

Fifty years ago, two young ecologists were disheartened by the descriptive and old-fashioned nature of their field, the importance of which was becoming overshadowed by revolutionary advances in molecular biology. In their 1963 paper, 'An equilibrium theory of insular zoogeography', R. H. MacArthur and E. O. Wilson took their first step in a landmark endeavour both to add statistical rigour to community ecology and to establish a conceptual foundation for further work. Inspired by previous advances in biology using insular systems, they recognised the utility of island

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Box 1 Island biogeography theory: a summary of MacArthur and Wilson's main hypothesis, and some definitions

IBT was inspired by two patterns of species richness that had been documented by the early 1960s – the species–area and species–distance relationships. The first of these describes the positive relationship between the area of habitat considered, and the number of species found within that area. This may be the oldest recognised ecological pattern, descriptions dating back to the mid-18th century (see Triantis *et al*. 2012). The second pattern describes the reduction in species richness of islands with distance from the source of colonisation. It had been expressed qualitatively by many authors prior to IBT, notably E. Mayr and P. J. Darlington (see MacArthur & Wilson 1963).

MacArthur & Wilson (1963) noted that the low species richness of remote islands had previously been attributed to the length of time available for species to colonise and their chances of reaching a remote island in that time. Inspired by density-dependent regulation of population sizes (Lack 1954), they proposed that island species diversity should rather be viewed as a diversity-dependent dynamic balance between immigration and extinction, and they made two assumptions concerning these processes. They assumed that the immigration rate for an island falls as the number of species on the island increases and that the rate of extinction of species increases as the number of species increases. Together, these two assumptions imply that diversity will tend towards equilibrium (Fig. 1).

At equilibrium, the number of species on the island stabilises, with the rate of immigration of new species balanced by the rate of extinction (Fig. 1). Based on this equilibrium, MacArthur & Wilson (1963) made two principal assumptions (Fig. 1) concerning the effects of island area and its distance from the source of colonisation, other things being equal. First, near islands will have higher immigration rates than far islands. Second, small islands will have higher extinction rates than large islands. Provided that the immigration and extinction curves are monotonic, and regardless of their precise shape, two main predictions can be drawn from these assumptions, other things being equal. First, near islands have more species than far islands. Second, large islands have more species than small islands.

Although MacArthur and Wilson were not the first to have such ideas (see Lomolino & Brown (2009) for Eugene G. Munroe's earlier and independent work), they were the first to develop and publicise them. We refer to this model as ***Core IBT***, to distinguish it clearly from other ideas that MacArthur and Wilson developed in both the 1963 paper, and final six chapters of their 1967 monograph (MacArthur & Wilson 1967). Exemplifying the importance of this distinction, although Core IBT does not incorporate speciation, MacArthur & Wilson (1963, 1967) nonetheless provided detailed insights as to the conditions under which speciation should occur on islands (Gillespie & Baldwin 2010). Likewise, although Core IBT does not consider species identity, this identity and the ecological differences between species are key to ideas expressed in chapters 5 and 7 of the 1967 monograph.

biotas as providing discrete, manageable and replicated microcosms of biological communities in general.

Two different conclusions can be drawn regarding the legacy of MacArthur & Wilson's (1963) theory (herein 'Island Biogeography Theory', IBT; Box 1; Fig. 1). On the one hand, viewed as a strict explanatory model for patterns of species diversity, appreciation of its utility has been mixed (e.g. Gilbert 1980; Williamson 1989; Schoener 2010). Despite being a good predictor of diversity patterns, the hypothesis of equilibrium, as originally defined, may be unfalsifiable (Simberloff 1976). On the other hand, MacArthur and Wilson's broader aim – using islands as model systems to develop a conceptual framework for their field – has been an unquestionable success. In the 50 years since IBT's conception, it has spawned or inspired many ecological and evolutionary models, not all of which concern islands. Likewise, the literature stemming from MacArthur & Wilson (1963, 1967) is colossal. It includes reviews of the validity of the core model (e.g. Simberloff 1976; Gilbert 1980; Schoener 2010), island biogeography (e.g. Whittaker and Fernández-Palacios 2007) and the wider legacy of their work to ecology and evolutionary biology (e.g. Losos & Ricklefs 2010) as well as related disciplines (see Appendix S1).

Compared to the broad literature reviewing IBT and its legacy, surprisingly little has been written about the wider contribution of island studies to our understanding of fundamental processes in ecology and evolution, the importance of which stretch far beyond islands (but see Grant 1998). Our aim in this review is to provide a forward-looking view of prospects

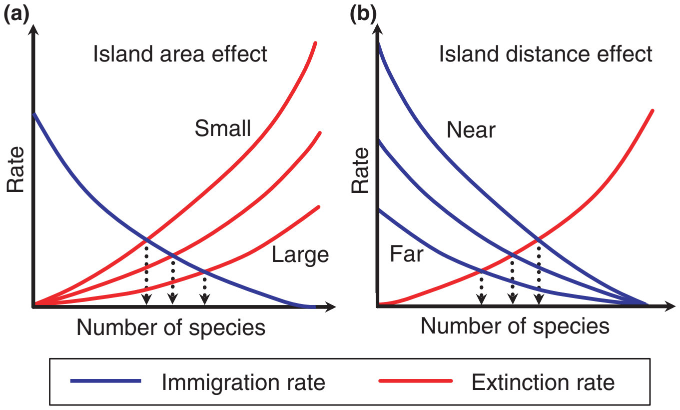

Figure 1 The Core IBT model (see Box 1 for definition), illustrating MacArthur & Wilson's (1963, 1967) assumptions regarding the following: (a) the effect of island area on extinction rate, and (b) the effect of distance from the mainland on immigration rate. Predicted species numbers appear on the *x*-axis, with dotted arrows marking equilibria between immigration and extinction rates.

Box 2 Glossary

Anagenetic species: a species confined to a region (e.g. island or archipelago) whose sister lineage occurs outside that region.
Cladogenetic species: a species confined to a region (e.g. island or archipelago) whose sister lineage is also confined to that region.
De novo community assembly: assembly of a community of species in an area where they were all previously absent.
De novo island: an island devoid of life upon formation, e.g. emerging as a result of volcanism or falling water level.
Ecological neutrality: the chances of an individual's reproduction and death are independent of its species identity.
Fragment island: an island formed by separation from another landmass or island, thereby bearing a biota upon formation, e.g. formed by plate tectonics or rising water level.
In situ: occurring within the geographical region of interest.

provided by islands for future advances in ecology and evolution.

Islands as model systems

Islands have played a key role in evolutionary theory from its inception; while the particular insights of Darwin regarding the fauna of the Galápagos Islands continue to receive much attention, the broader use of islands as tools by both Darwin and Wallace to establish the theory that was so controversial in their time is less often noted. Prior to their work, the prevailing view was that species were immutable and created independently. Differences in species assemblages across the planet were largely explained by historical patterns of species spread from a special point (or points) of creation and abiotic controls on distribution (Lomolino *et al.* 2010). A repeated theme in several chapters of *The Origin of Species* is Darwin's (1859) use of a variety of islands around the world to illustrate how presences, absences, affinities and patterns of species richness are at odds with these views and particularly with the notion that species are immutable. Islands provided Darwin the insights for his theory of descent from common ancestry, and from distinct geographical source areas. Studies of island biotas led Wallace (1855) to draw the same conclusions independently of Darwin, and later to defend evolutionary theory (Wallace 1880).

> If we look to the islands off the American shore, however much they may differ in geological structure, the inhabitants, though they may be all peculiar species, are essentially American. We may look back to past ages

Box 3 Connections between different insular systems

This article focuses on terrestrial islands surrounded by water that have arisen devoid of life (*de novo*; Box 2). However, many other insular systems are also relevant to some of the points raised and may provide substantial opportunities for research. From a biological perspective, a key characteristic that varies between insular systems is whether 'islands' (surrounded by water or otherwise) have arisen *de novo*, or as a result of the fragmentation of an existing landmass or habitat (Box 2; Gillespie & Roderick 2002). In *de novo* systems, species number rises following formation, as a result of the rate of colonisation exceeding that of extinction (Box 1). By contrast, on fragment 'islands', species number is expected to fall following formation (Box 1), because the rate of extinction should exceed that of colonisation (relaxation; Whittaker and Fernández-Palacios 2007). Origins aside, fragment islands surrounded by water can share many key attributes with the focal islands of this review (Table 1, column II).

Some lakes (especially those lacking connections to other lakes, e.g. by way of rivers) provide almost perfect analogues to islands surrounded by water. However, apparent '*de novo* origins' do not always carry the same implications, since even in the absence of connecting rivers, many lakes are filled by watercourses. Such lakes are therefore not devoid of life upon formation, even if species numbers increase following formation through colonisation exceeding extinction. Also, lake volume may be as relevant as area in assessing 'niche space'.

For terrestrial organisms on islands, even if they show varying abilities to cross the surrounding water and colonise other landmasses, water itself cannot be colonised (i.e. land is needed to reproduce). The same is often not true for the myriad of other insular systems (such as montane sky islands, caves, and fragmented landscapes or aquatic environments), since the intervening matrix consists of habitat from which some species may be able to colonise an 'island'. Furthermore, there may be transitory possibilities for organisms to inhabit the matrix (e.g. because some species, normally restricted to forest fragments, can inhabit the surrounding grassland in years of exceptional rainfall). A consequence of both of these tendencies is that isolation (and corresponding *in situ* evolutionary change and endemism) tends to be less pronounced per unit distance of surrounding matrix in many insular systems than it is for islands surrounded by water (e.g. Gillespie & Clague 2009).

Box 4 Examples of classic insights from islands into the ecology and evolution of communities

Communities are often but not always formed from the closest source pools

MacArthur & Wilson (1963, 1967) formalised expectations about distance to source pools in biota assembly; a corollary of Core IBT is that the largest proportion of island immigrants will come from the nearest mainland source. They also discussed numerous factors that may cause the geographical affinities of communities to differ from this prediction. These include long-distance dispersal events and a series of factors that can permute the effects of distance on dispersal such as the sizes of source and recipient areas, and the existence of stepping-stone islands. Other factors include wind and ocean currents, modes of dispersal, the elevation and topographic complexity of the landmasses concerned, and temporal dynamics of these variables (Whittaker and Fernández-Palacios 2007; Lomolino *et al.* 2010).

The simplicity of island systems in delimiting geographic areas has been exploited in numerous phylogenetic methods of historical biogeography to infer the effects of distance and direction of source pools in biota assembly (Ronquist & Sanmartín 2011). They have thus made it possible to identify situations that both support and contradict predictions regarding elementary models of dispersal and factors that permute the effect of distance. Examples conforming to predictions come from the Hawaiian Islands. Consistent with the direction of extreme storms, taxa with high aerial dispersal abilities have predominantly colonised the archipelago from the east. By contrast, insects capable of rafting have predominantly colonised from the southwest, consistent with the location of stepping-stone islands (Gillespie *et al.* 2012).

Cases that contradict predictions have frequently revealed unappreciated dispersal, and the conditions under which propagules are able to establish new populations. For example, in the presence of stepping-stone islands between remote islands and mainland source pools, some highly dispersive taxa (spiders and birds) appear to have colonised remote islands directly and independently from mainland sources (Gillespie *et al.* 2008). Such patterns lend support to the hypothesis that for these taxa single extreme long-distance dispersal events are more probable than the combined probability of consecutive shorter dispersal events (Nathan 2006).

Evolution can play a key role in community assembly

The spatial and temporal scales over which trait evolution occurs are recurrently controversial. For example, in response to the dramatic and frequent climatic shifts of the Quaternary, paleoecological data have long supported major continental-scale range shifts. Although such studies imply repeated community assembly and disassembly at timescales of 10 000–100 000 years, phenotypic change in response to such events is notably scarce (Bennett 1997). As a result of their isolated and replicated nature, islands have long been used to illustrate the existence of *in situ* evolutionary change in biota assembly. Evolutionary change following colonisation was originally inferred from the wealth of endemic species in island settings (Darwin 1859), and a mass of molecular data has since substantiated such inferences from morphology (Gillespie & Clague 2009). Further, numerous insular evolutionary patterns indicative of changes in selective pressures following arrival on islands are documented (Grant 1998; Losos & Ricklefs 2009), and are variably attributed to changes in population size, the abiotic environment, and the newfound presence or absence of particular other species (character displacement and character release, respectively).

***In situ* speciation is an important source of diversity**

On continents, in the absence of a fossil record, the facility with which species distributions can change over time may easily confound attempts to identify the precise geographical setting in which speciation has occurred. In combination with molecular phylogenetic data, the isolation, discrete nature, and high levels of endemism on islands have been key in demonstrating that *in situ* speciation can contribute significantly to biota assembly. Strong evidence for speciation having occurred within an island or archipelago is provided by the monophyly of species endemic to that region. Accordingly, for example, it appears that 150 species of diving beetle are the product of a single colonisation event followed by speciation within the island of New Guinea (Balke *et al.* 2007), and 1000 species of picture-winged *Drosophila* are the product of speciation within the Hawaiian archipelago (O'Grady *et al.* 2011). Islands have illustrated that the factors that interact to provide conditions necessary for *in situ* speciation include isolation (Manceau *et al.* 2010), age (Gillespie & Baldwin 2010) and area (Losos & Schluter 2000; Kisel & Barraclough 2010) of the region concerned, and variables often associated with area, such as topographic complexity and elevation (Whittaker *et al.* 2008).

> [...] and we find American types then prevalent on the American continent and in the American seas. We see in these facts some deep organic bond, prevailing throughout space and time, over the same areas of land and water, and independent of their physical conditions. The naturalist must feel little curiosity, who is not led to

Table 1 Under-explored or in need of revisiting: prospects for using islands to advance understanding in ecology and evolution in general. This is not intended as a comprehensive list, but rather reflects the interests and priorities of a working group on islands (the authors). Each row summarises a section in this article, with detail of promising approaches in the last column.

	Why islands?									
	(II) Key attributes used									
(I) Research Questions	Hard boundaries	Isolation	Replicated nature	High endemism	*De novo* origin	Small size	Climatic stability	Known age	(III) Employment of key attributes	(IV) Promising approaches and study systems
Community assembly										
How important is arrival history in the sequence and outcome of community assembly?	•	•	•		•				(1) "Clean slates" for studying community assembly. (2) Facility of quantifying isolation.	*Approach*: *De novo* or sterilisable islands varying in their distance from the source, especially those that form matrices, with multiple islands at any one level of isolation. *Study systems*: *De novo* examples: those emerging by falling reservoir or lake levels. Sterilisable examples: any small islands that can be stripped of fauna and/or flora either artificially without causing ecological concern, or through extreme weather and other natural events.
How and why do species abundances change during the course of community assembly?	•	•	•	•	•				Barring unknown extinction and back-colonisation, the facility of inferring the timescale in which a lineage has occupied a community using phylogenetic branch lengths.	*Study systems*: Communities from oceanic archipelagos with high molecular phylogenetic coverage (including mainland relatives): e.g. birds and plants from Lesser Antilles, Hawaii, Canaries, Mascarenes.
Can we predict the contribution of anagenesis and cladogenesis to the assembly of a community, based on its size and isolation?	•	•	•						Facility of quantifying multiple cases of varying area and isolation	*Approach*: Comparison of model predictions for occurrence of anagenesis and cladogenesis with area and isolation of islands (e.g. Rosindell & Phillimore 2011) with empirical data sets incorporating a wider range of dispersal abilities, and speciation modes (from highly ecological to highly geographical).
Ecosystem functioning										
Does *in situ* evolution contribute to ecosystem functioning? If so, how, and to what degree?	•	•	•	•	•	•			Facility of identifying the geographic area within which evolution has occurred across a community or biota.	*Approach*: Archipelagos with small islands, some of which are highly preserved and with high endemism (therefore thousands to millions of years of *in situ* evolution), others highly transformed with introduced species (no endemism, *in situ* evolution is limited to the time period since human introduction). *Study systems*: e.g. Aldabra Group.
Speciation and diversification										
What is the genomic signature of speciation with and without gene flow?	•	•	•						Extreme differences in geographic isolation implicit in between-island vs. within-island comparisons: facility of	*Approach*: Radiations containing both inter- and intra-island comparisons. The latter ideally involving sympatry or low geographic isolation of diverging lineages. *Study systems*: e.g. Hawaiian *Tetragnatha*

(continued)

Table 1. (continued)

	Why islands?									
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(I) Research Questions	Hard boundaries	Isolation	Replicated nature	High endemism	*De novo* origin	Small size	Climatic stability	Known age	(III) Employment of key attributes	(IV) Promising approaches and study systems
									inferring low vs. high potential for gene flow independent of genetic data.	spiders & *Drosophila* fruiflies, Canarian *Tarphius* beetles.
Can gene flow promote speciation? If so, how?	•	•	•						As above.	*Approach*: As above. A role in speciation for phenomena associated with gene flow (e.g. increased genetic and phenotypic variance, reinforcement, coupling or immediate reproductive isolation) should meet two criteria: (1) occur in recently diverged species pairs, not just in more deeply diverged (post-speciation) pairs; (2) be absent from inter-island species pairs, or at least significantly less prevalent than for intra-island pairs. *Study systems*: As above.
Patterns of species richness										
Why are some lineages more diverse than others?	•			•			•	•	(1) High incidence of endemic lineages with identical distributions, (2) High incidence of intraspecific divergence occurring in the same context (geographic, ecological) as interspecific diversification occurred.	*Approach*: For species-rich vs. species-poor clades in a common island or archipelago setting, coupling of: (1) macroevolutionary phylogenetic studies to disentangle factors such as time and net rate of diversification in explaining differences in species richness, (2) population genomic studies of co-distributed species from within different clades, in which intraspecific divergence is occurring in the same context (geographic or ecological) as interspecific diversification has occurred. Widespread (multiple-island) members of insular clades otherwise composed of many single-island endemic species may be particularly good candidates. Comparisons can be made between different lineages along estimated time series following arrival. Coupling of (1) and (2) provides potential to examine the role of factors such as selection and gene flow in underlying differences in diversification rate.
What are the relative contributions of different modes of speciation (e.g.	•	•	•					•	(1) Facility of inferring barriers to gene flow, and temporal dynamics of these barriers. (2)	*Approach*: Extension of existing models (e.g. McPeek 2008; Pigot et al. 2010; Aguilee et al. 2013) to predict how variation in mode of speciation affects components relating to

(continued)

Table 1. (continued)

	Why islands?									
	(II) Key attributes used									
(I) Research Questions	Hard boundaries	Isolation	Replicated nature	High endemism	*De novo* origin	Small size	Climatic stability	Known age	(III) Employment of key attributes	(IV) Promising approaches and study systems
geographical, ecological) in driving patterns of species-richness?									Replicates of different temporal dynamic histories of barriers to gene flow.	species-richness patterns (e.g. shape of phylogenies, ecological trait distributions). *Study systems*: Archipelagos suitable for testing predictions should have a variable (and reconstructed) history of barriers to gene flow, and in-depth data relating to species-richness (phylogeny, and ecological traits) across multiple island clades to compare with the models (e.g. the Macaronesian archipelago).
What are the roles of equilibrium vs. non-equilibrium dynamics in governing observed patterns of species richness?	•		•	•	•				(1) Facility of inferring immigration, extinction (both local and total), and that speciation has occurred *in situ*. (2) "Clean slates" for studying community assembly.	*Approaches*: (1) Using 'geographic' lineage-based models to compare scenarios of unbounded (constant diversification rates) and bounded (declining diversification rates) diversity to a wider range of taxonomic and island systems (Rabosky & Glor 2010). (2) Extending current 'global scale' lineage-based models that were explicitly designed to test for equilibrium dynamics (Morlon et al. 2010) to give them a spatial structure and apply them to island systems. (3) Studying spatially-explicit individual-based models in their transient dynamics (including responses to perturbation, e.g. mass extinction) and developing phylogenetic inference tools that can be used to fit these models to phylogenetic data on islands. (4) Analysing the distinct signature that transient vs. equilibrium dynamics arising from individual-based models may leave on ecological (immigration – local extinction dynamics, species abundance distributions, species area relationships, distance-decay relationships) and macroevolutionary (phylogenies) island patterns. (5) Fitting stochastic models incorporating immigration, speciation and extinction (Valente et al. 2014) to phylogenetic data from communities on islands to test whether the whole community or specific clades are governed by equilibrium dynamics or are fundamentally non-equilibrial.

> inquire what this bond is. This bond, on my theory, is simply inheritance.. (Darwin 1859, p. 349–350).

The decades that followed saw the gradual acceptance of Darwin and Wallace's theory. However, contrary to other fields of biology in the early twentieth century, although ecology was quantitative at the population level, at other levels it remained highly descriptive, as did biogeography. IBT came from MacArthur and Wilson's desire to provide a mathematical foundation for community ecology. MacArthur & Wilson (1967) noted the difficulty of the task ahead of them, recognising that the fundamental processes underlying the ecology and evolution of communities ('dispersal, invasion, competition, adaptation and extinction') are 'among the most difficult in biology to study and understand'. They acknowledged that such a simplified theory would therefore have significant limitations, but felt that it would nonetheless provide a useful stimulus for future research.

> We do not seriously believe that the particular formulations advanced in the chapters to follow will fit for very long the exacting results of future empirical investigation. We hope instead that they will contribute to the stimulations of new forms of theoretical and empirical studies, which will lead in turn to a stronger general theory.. (MacArthur & Wilson 1967, p. 6).

The assets of islands as model systems for Darwin, Wallace, MacArthur and Wilson, are easily recognisable. On continents, species' ranges are often large. Further, it is easy to envisage dramatic range shifts as a result of changing climate, geology and subtle shifts in environmental tolerance. In contrast, islands provide comparatively small areas of land that are geographically discrete and isolated from other areas. Depending on the spatial scale and isolation considered, the boundaries of an island frequently present a long-standing limit to the distribution of either a species or population. As a consequence, identifying the present and historical ranges of species and populations, both in area and relative proximity, is often straightforward. Additionally, multiple islands may exist at a scale equivalent to (or smaller than) a single continent, providing natural ecological and evolutionary replicates. In the case of *de novo* islands (Box 2) of variable known age, such replicates can also serve as ecological and evolutionary time series.

Here our focus is on islands surrounded by water, although we acknowledge that other insular systems (e.g. montane sky islands and lakes; Box 3) frequently provide equivalent insights and opportunities for research. Likewise, our emphasis is on terrestrial islands that have arisen *de novo* from the perspective of biological colonisation (e.g. volcanic islands, and those that have previously been totally submerged due to changes in water level). Islands formed by the fragmentation of existing landmasses can present similar opportunities, but also exhibit fundamental differences in the way their biotas were formed (Box 3; Gillespie & Roderick 2002). Although we are concerned primarily with the native biota of islands, we acknowledge that humans have also had a major impact on many island systems by decimating populations of native species and introducing alien species, some of which have become invasive. Although most such introductions have been ecologically undesirable, they may at times provide useful points of comparison for understanding native biotas (see, for example, our section on Ecosystem Functioning). In many groups, native and introduced species can be readily distinguished, but this is not always the case. Further, human impacts on native island biotas are better known for some archipelagos than others (especially human-induced extinctions; Steadman 2006; Whittaker and Fernández-Palacios 2007). Therefore, caution is often needed in making inferences about natural processes from contemporary communities.

In the last 50 years, consistent with MacArthur and Wilson's study theme, but independent of Core IBT (Box 1), islands have provided a number of important insights into community (and biota) assembly. In Box 4 we provide some classic examples, largely made possible by genetic tools unavailable to MacArthur and Wilson. Following this theme, we detail prospects for future advances in ecology and evolution using islands as model systems (summarised in Table 1). We suggest that, in addition to theoretical advances, continued development and availability of genetic tools will be key, as they have been over the last 50 years. Coming years should see not only wider coverage across taxa and individuals, but also greater genomic depth, even for non-model organisms.

In contrast to 1963, when advances in molecular biology simply appeared to overshadow ecology and evolution, today genetic tools present an important means with which to reinforce these fields. Accordingly, rather than match future prospects with MacArthur and Wilson's emphases of a half century ago, we consider a range of situations (Table 1, column I) in which we believe that the assets of islands as model systems (Table 1, columns II and III) combined with recent advances in theory, molecular genetics, and data acquisition, provide potential to better understand processes underlying ecological communities and biota. For much of the twentieth century, these processes were addressed within relatively distinct disciplines of ecology and evolutionary biology. We argue that the aforementioned assets of islands to ecologists and evolutionists alike make them attractive study systems in the integration of these disciplines (Schoener 2011).

LOOKING FORWARD: PROSPECTS OF ISLANDS AS MODEL SYSTEMS FOR ECOLOGY AND EVOLUTION

Community assembly

Understanding how biological communities form and why they differ are key objectives in ecology. The subject is challenging in that community assembly involves interactions at different scales of organisation, space and time. It can be expected therefore, that uncovering a mechanism at one scale may provide little insight into mechanisms operating at other scales. MacArthur & Wilson (1967) recognised that, as a result of their discrete and replicated nature, islands are key systems in understanding the component parts of any community assembly process, at a scale that includes immigration, establishment, anagenetic evolutionary change, speciation, and local extinction. Moreover, although Core IBT (Box 1) considers all species as ecologically indistinguishable, in chapter 5 of the 1967 monograph MacArthur and Wilson expanded their scope to consider the identity and ecology of species capable of forming a community. Diamond (1975) also had this perspective in elaborating a set of assembly rules governing island species composition. Though much controversy has ensued (see Whittaker and Fernández-Palacios 2007; Simberloff & Collins 2010), the important message is that, as result of their discrete and replicated nature, islands provide excellent settings in which to make predictions about community assembly, in particular how different lineages respond and interact during the process. Here we look at prospects of island-based approaches to refine predictions about how communities form.

The role of arrival history in the assembly of ecological networks

Since Core IBT (Box 1) does not consider species identity, the sequence of immigration is effectively random. The problem is that the process of building up a network of ecological interactions is poorly known; both this process and resulting species compositions may be greatly influenced by the order and timing of arrivals, and by the ecological characteristics of both newly arriving and established taxa (e.g. Fukami *et al.* 2010). Arrival history is particularly relevant when feedback loops reinforce ecological interactions. Important insights regarding the role of interaction networks in community assembly have come from two island systems; Krakatau and mangrove islands in the Florida Keys. Repopulation of the Krakatau islands following the violent eruption in 1883 showed that the final outcome in terms of species composition could not be entirely predicted, reflecting in part historical contingency and stochastic components of colonisation sequence and associated cross-trophic level linkages (reviewed by Whittaker and Fernández-Palacios 2007). The repopulation of Simberloff & Wilson's (1971) artificially defaunated mangrove islands in the Florida Keys demonstrated shifts in trophic structure over time, and that the proportion of specialist species increased during food-web assembly relative to generalist species (Piechnik *et al.* 2008).

The availability of such empirical data from islands has recently made it possible to test an extension to Core IBT. While retaining the simplicity of Core IBT in modelling complex phenomena with few parameters, Gravel *et al.* (2011) have shown how species interactions could easily be incorporated with important consequences for the shape of the species-area relationship and even for the number of trophic levels expected in fragmented systems. Realistic network structures and assembly sequences are predicted simply by assuming a sequential and conditional assembly process (e.g. a predator/pollinator requiring at least one prey/plant to establish and persist). Thus, accounting for species identity in IBT provides a powerful framework to investigate the reciprocal feedbacks between assembly dynamics and community structure (Gravel *et al.* 2011, and references therein).

Notwithstanding this advance, there is still much to learn about how arrival history influences the build-up of ecological interactions and resulting species compositions. Small *de novo* or sterilised islands that differ in their isolation from the mainland (see Table 1 for examples) provide important opportunities to vary arrival history in a predictable and replicated manner. Such 'experiments' have more confounding factors than microcosm experiments in which important variables such as the traits of organisms are easily controlled, but have the advantage of being natural, and including higher organisms. First, little is known about how arrival interval influences ecological networks and the outcome of community assembly; in a microcosm experiment, the spacing of arrivals had a strong influence, as a result of competition and indirect facilitation (Fukami *et al.* 2007). These intervals are easily manipulated in island settings, arrivals being more closely spaced on near islands than far ones. Second, an untested hypothesis is that stochastic variability in arrival sequence increases with distance from the source (Thornton 1996). Replicates of *de novo* or sterilised islands both near and far from a mainland source (Table 1) would provide the opportunity to test this hypothesis, and evaluate the consequences of arrival history on ecological networks and the outcome of community assembly. Species compositions should be more variable among islands in which stochastic variability of arrival is high, than among those in which its effect is lower. However, the precise relationship between variability of arrival and species composition may be complex; strong ecological interactions and feedbacks could amplify stochastic variability, while facultative changes in a species' ecological position (e.g. diet, see Terborgh 2010) could have dampening effects. Such empirical studies, that effectively manipulate arrival history within natural systems, have great potential to refine our understanding of the roles of arrival history vs. ecological networks in driving deterministic sequences and outcomes of community assembly.

How and why species abundances change during community assembly

Ecological communities can be characterised not only by the number of species they support, but also by the relative abundances of those species. Although continual changes in species abundance are implicit both in *de novo* community assembly (Box 2) and dynamic equilibrium, few theories address these dynamics. Given that Core IBT (Box 1) does not consider species identities or population sizes, a logical extension of that theory is to consider how abundance distributions across species, and the abundance of individual species, change following colonisation of an island by founding individuals. An appropriate null hypothesis for population change is the assumption of ecological neutrality (Hubbell 2001). Such an approach has been taken by extending individual-based ecological neutral theory (Hubbell 2001) to predict species abundance distributions on islands over timescales that cover immigration, extinction, and *in situ* evolution (Rosindell & Phillimore 2011), and with reference to the approach to and attainment of dynamic equilibrium (Rosindell & Harmon 2013). Clearly, however, factors such as ecological release, unequal competitive abilities, predation, parasitism, and changes in environmental conditions, are expected to influence abundance dynamics in very non-neutral ways. For example, the taxon cycle describes a pattern in which lineages go through sequential phases of expansion and contraction during the assembly of an insular community (MacArthur &

Wilson 1967; Ricklefs & Bermingham 2002, and references therein). It has been suggested that expansion is driven by ecological release from predation or disease in a new environment, and that subsequent decline is the result of 'counteradaptation' of insular enemy species (Ricklefs & Bermingham 2002, and references therein). Carlquist (1966) also highlighted a loss of competitive ability in island lineages, as one of his 24 principles of dispersal and evolution. He posited loss of genetic variability or evolutionary specialisation as potential causes, although he lacked a comprehensive explanation for the latter. Specialisation to local environments might increase fitness on the generational timescale upon which selection acts, but reduce tolerance to changes arising over longer timescales, such as new arrivals and major environmental change, as well as reducing evolutionary lability in response to such events.

Knowing how species abundances change over timescales encompassing both evolutionary change and *in situ* speciation would aid our understanding of community assembly, but such information is difficult to obtain. Nonetheless, barring extinction and back-colonisation (see Appendix S2), the ages of endemic populations on *de novo* islands can be inferred from genetic distances to their source populations on the mainland or other islands. Testing predictions for the relationship between species abundance and age using a neutral model (Rosindell & Phillimore 2011), including predictions concerning the approach to dynamic equilibrium as well as population behaviour at equilibrium, would be informative about the processes underlying species abundance distributions. Failure to reject such a model would imply a key role for dispersal and available space on an island in explaining abundance dynamics, while deviation from its predictions would implicate other ecological processes. For example, under ecologically neutral models, high abundance is achieved via the slow process of drift and therefore the highest abundance class would be predominantly occupied by old species, while under ecological release abundant species should be predominantly recent arrivals. If competition or predation were involved in the decline of an island population from the highest abundance class, the mean time to extinction would be shorter than under the ecologically neutral model (Ricklefs 2006). Studies of the species age-abundance relationship on islands testing predictions of alternative models should provide insight into the role of ecological differences between species in moulding species abundance distributions.

How evolution may influence community assembly: predicting the effects of geographic area and isolation

While evolution and speciation were absent from Core IBT (Box 1), MacArthur & Wilson (1963) included a term for speciation by *in situ* cladogenesis in the first mathematical statement of the equilibrium model. They left out speciation by anagenetic change as their focus at this point was on the establishment of equilibrium species numbers, which is unchanged by anagenesis. They also explicitly recognised the important role of speciation in contributing to species richness within sufficiently isolated archipelagos, in what they termed the 'radiation zone'. They thus recognised within their theory that the contribution of speciation to species richness would increase with island isolation. Integrating ecological neutral theory into island biogeography, Rosindell & Phillimore (2011) recently made more precise predictions regarding the location of zones of anagenesis and cladogenesis at equilibrium, with respect to island isolation and area. Cladogenetic species (Box 2) are predicted to occur above thresholds in both island area and isolation, and in greater numbers on the largest and most distant islands. Anagenetic species richness (Box 2) is also predicted to increase with island area, but to peak on islands of intermediate isolation.

This humped distribution of anagenetic species with distance results from a trade-off: immigration must be small enough to escape the homogenising effects of gene flow with the mainland population that prevent divergence (Johnson *et al.* 2000), but also frequent enough to initiate anagenesis repeatedly and keep temporal turnover high enough to prevent anagenetic species from persisting for long enough to radiate and become cladogenetic. Consistent with these predictions, support has been obtained for a model in which highest species richness occurs among lineages of intermediate dispersal ability, such that dispersal is sufficiently frequent to allow repeated colonisation across geographic barriers, but sufficiently limited to restrict gene flow across these barriers (Claramunt *et al.* 2012; Agnarsson *et al.* 2014). However, this model assumes that a lineage's dispersal ability remains constant through time. In reality, many cases of reduced dispersal ability following island colonisation are known, both in animals and plants, and are principally attributed to changes in selective regimes following island colonisation (Carlquist 1966; Grant 1998). Such insular changes are known to influence the spatial scale at which population differentiation occurs (Blondel *et al.* 1999). Thus, any generalisation on how dispersal ability influences island species richness remains provisional, and future studies might compare focal lineages of high dispersal ability that readily lose this ability (e.g. birds) with those that do so rarely (e.g. mosses and ferns).

An additional explanation for isolation promoting anagenesis is that under a low rate of colonisation populations are exposed to less competition, which gives them more time to differentiate anagenetically before they are displaced (Price 2008; Rosindell & Phillimore 2011). However, these factors work in the opposite direction to the 'rescue effect', in which at low isolation the more frequent arrival of propagules protects island populations from extinction through the demographic and genetic contributions of later immigrants (Brown & Kodric-Brown 1977).

A low rate of colonisation of remote islands also tends to promote cladogenesis by leaving niches 'open' for long periods, allowing them to be filled as readily by *in situ* speciation as by dispersal (Gillespie & Baldwin 2010). Intuitively, island area may also affect the potential for species diversification both by increasing opportunities for intra-island allopatry and by adaptation to more diverse habitats that can be accommodated on larger islands (Losos & Schluter 2000). Furthermore, larger areas imply larger population sizes, likely increasing both the number of advantageous mutations and the efficiency with which selection acts upon them (Gavrilets & Losos 2009). Several island-based studies have confirmed the importance of area in cladogenesis (Losos & Schluter 2000; Kisel &

Barraclough 2010; Rabosky & Glor 2010). However, beyond Rosindell & Phillimore's (2011) test of their own predictions with island bird data, how the interplay between isolation and area influences the relative importance of anagenesis and cladogenesis largely remains to be evaluated (but see Johnson *et al.* 2000; Valente *et al.* 2014). Islands provide key settings for such future empirical and theoretical study of biota assembly.

Ecosystem functioning

With the prospect of human activities leading to a global ecological crisis, Loreau (2010) has called for the unification of population, community, ecosystem and evolutionary ecology into a single discipline of evolutionary ecosystem ecology. One of the greatest challenges in this integration was identified as the gap between evolutionary biology, which seeks principles at the levels of genes, individuals and populations, and ecosystem ecology, which seeks principles at the higher organisational level of the ecosystem (Loreau 2010). We believe that islands provide excellent systems to explore whether coupling evolutionary and ecosystem dynamics can lead towards a better understanding of the processes shaping ecosystems. First, the small size and isolation of islands has long made them systems of choice for illuminating the role of species interactions on ecosystem functioning (for a recent example, see Fukami *et al.* 2006). Second, the very high proportion of endemic lineages (subspecies, species, and higher orders) on islands makes for communities in which the contribution of *in situ* evolution to community assembly is both large and relatively easily identified (e.g. Gillespie 2004; Clegg 2010).

Determining the relative roles of in situ *evolution and ecological fitting in ecosystem functioning*

Despite the high incidence of readily detectable *in situ* adaptive evolutionary change in the assembly of insular biotas, its importance at a small (community) scale within continents has been questioned. Janzen (1985) proposed that a Costa Rican forest community is principally assembled in the absence of *in situ* evolutionary change, by a process that he termed 'ecological fitting': a combination of immigration, environmental filtering and species interactions. His hypothesis stemmed from observation that the majority of species represented have vast distributions across the Americas, and little phenotypic variability between sites.

Beyond an understanding of the importance of different processes in community assembly, a useful future direction is to understand how assembly processes influence ecosystem functioning (Venail *et al.* 2008; Fukami *et al.* 2010). *In situ* evolution might influence ecosystem functioning as a result of both adaptation of individual species to the local environment and coevolution of two or more component species (Schoener 2011). Does *in situ* evolution therefore contribute to ecosystem productivity, efficiency or other properties, and to what degree? This question has strong implications for society in predicting and mitigating the impacts of human-induced global change. While some landmark studies have recently approached the problem using microbial systems (see e.g. Venail *et al.* 2008), islands, as a result of their isolation and replicated nature, may be excellent model systems with which to investigate such issues with higher organisms. Archipelagos containing many small (ca. 1–100 km^2) islands can provide replicates of two different situations, in which the physical environment (climate, geology and topography) is similar both within and among islands, or nearly so: (1) islands supporting native habitat in which human influence is minimal, and many taxa are endemic and (2) islands in which human influence has been dramatic, and much of the biota is introduced, with little native habitat and fewer endemic taxa remaining. The presence of single-island endemic species or subspecies would suggest a substantial role for *in situ* evolution in the assembly of the former community, while it would be negligible or absent from the latter. An example of an archipelago that could meet these conditions is the Aldabra Group (Box 5 case study).

To examine the contribution of *in situ* evolution to ecosystem functioning, suitable measures for comparison between islands may include net primary production, various measures based on nutrient cycling, and measures based on plant–soil

Box 5 A case study archipelago for inferring the relative role of *in situ* evolution and ecological fitting in ecosystem functioning: the Aldabra Group of the western Indian Ocean

The Aldabra Group of the Seychelles in the western Indian Ocean may present a suitable example of an archipelago with the features needed to understand the relative contribution of ecological fitting (Box 6) and *in situ* evolution in ecosystem functioning. The approach compares (1) a community in which the majority of lineages have undergone *in situ* evolution following their arrival and (2) a community created by ecological fitting of species that have evolved elsewhere. Within the Aldabra Group, the former situation occurs on the islands of Aldabra Atoll (UNESCO World Heritage Site), which are among the least disturbed of all low latitude islands, with many endemic species (Stoddart & Wright 1967). By contrast, the neighbouring islands of Assumption, Cosmoledo and Astove frequently present the latter situation. Although once similar to the islands of Aldabra Atoll, they have been extensively transformed by human activity. In particular, the mixed scrub community of Assumption is composed of many introduced plant species, despite being similar in overall species richness to that of Aldabra Atoll (Stoddart *et al.* 1970). Such islands are also very similar to those of Aldabra Atoll in size, topography and climate, and therefore present informative points of comparison.

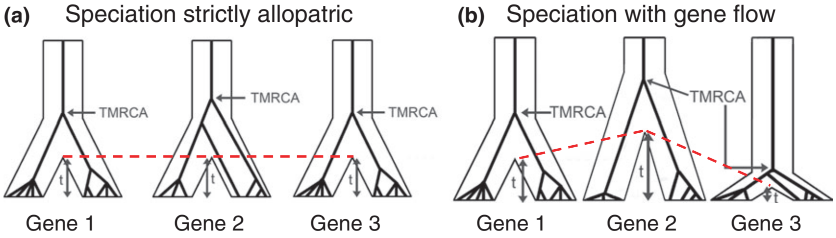

Figure 2 Predictions regarding genomic signatures of different speciation modes after Bachtrog *et al.* (2006). t, time since divergence; TMRCA, time since most recent common ancestor. (a) speciation strictly allopatric, no difference in t between loci; (b) speciation with gene flow, t differs.

feedbacks (Vitousek 2004; Bardgett & Wardle 2010). Within this framework, linking the diversity of decomposers and of decomposition rates appears to be a particularly promising avenue to investigate (see Ehrenfeld 2003). Clearly, ability to eliminate confounding variables is key to the strength of an island-based test. Notably, species richness may vary between islands and is known to influence ecosystem functioning (Hooper *et al.* 2005; Bardgett & Wardle 2010). Although differences in species number between islands resulting from *in situ* cladogenesis are a true reflection of *in situ* evolution, those resulting from immigration are not. As a starting point for approximation, the number of immigration events contributing to an island community can often be inferred from taxonomy, and comparisons are possible between islands in which they are constant, or nearly so. Going a step further, with increasing availability of molecular phylogenetic data and advances in analytical interpretation, it is becoming possible to quantify immigration with ever-increasing accuracy (e.g. Ronquist & Sanmartín 2011; Cornuault *et al.* 2013).

Geography, gene flow, and species diversification

Island systems have proven key in studying the process of population differentiation, as a result of being discrete, geographically isolated, replicated, and small in size relative to continents (e.g. Grant & Grant 2008). We illustrate how this situation provides underappreciated potential for investigating what are currently important topics in the biology of speciation, i.e. how divergence-with-gene flow may lead to speciation, and distinguishing the effects of geography and ecology on genomic divergence and speciation (Feder *et al.* 2013; Seehausen *et al.* 2014). With respect to intraspecific divergence, the substantial environmental heterogeneity of many islands provides suitable settings for examining how different lineages respond to common environmental and geographical variation. We illustrate how this feature can aid in understanding why some lineages are more diverse than others. Although these prospects are the furthest removed from Core IBT, we believe that by addressing problems in a rapidly moving field, they present the most immediate potential for advances using islands as model systems.

Determining the genomic signature of speciation with and without gene flow

In an insightful paper, Bachtrog *et al.* (2006) proposed that different levels of gene flow during speciation can be distinguished using genealogical analysis of multilocus datasets from closely related species. They argued that under strict allopatry (i.e., no gene flow), all regions of the genome will have a single divergence history, and vary only in their coalescence times (Fig. 2a). By contrast, in geographical contexts allowing gene flow (e.g. sympatry, parapatry, and when populations are separated but sufficiently close to allow regular dispersal between them), species may share regions that have not yet diverged functionally, or that function sufficiently well in the recipient species as to be maintained by selection. As a result, in the presence of gene flow, they predicted that the genome will be a mosaic of different regions with disparate divergence times (Fig. 2b). To the best of our knowledge, these predictions remain to be explicitly tested using independent (non-genetic) inferences regarding the geographic context of divergence.

Islands provide ideal systems to test these predictions because of the frequent replication of two geographic extremes within the same island radiation. First, such radiations frequently include sister-species pairs in which each member of the pair is endemic to a different island, and in which the two islands have never been connected. Such pairs provide cases for divergence in full allopatry, in which opportunities for gene flow are minimal when inter-island distance exceeds the organism's regular dispersal ability. Second, some such radiations also contain sympatric or closely occurring sister species endemic to the same island (e.g. Hawaiian *Tetragnatha* and *Drosophila:* Gillespie & Baldwin 2010; O'Grady *et al.* 2011). These have high potential to have diverged in the presence of intermittent or ongoing gene flow. Under these conditions, same-island vs. different-island species pairs offer a promising investigative framework. Coalescent analyses (Sousa & Hey 2013) of multiple species pairs from the same island radiation within such a framework would provide the data to test whether the alternatives proposed by Bachtrog *et al.* (2006) correctly depict genomic patterns of divergence in nature. If the alternatives are supported, such results may offer a baseline to infer levels of gene flow during speciation, in cases where past biogeography (geographic proximity of lineages) is highly uncertain. Such comparisons should also provide a test of the role of gene flow in shaping patterns of divergence across the genome (Feder *et al.* 2013).

Assessing the role of gene flow in speciation

Beyond characterisation of how gene flow shapes patterns of genomic divergence, its consequences in promoting or retarding speciation can be expected to vary greatly between taxa, stages of divergence, and spatial contexts (Abbott *et al.* 2013).

Three main mechanisms by which gene flow may promote speciation have been proposed. First, it can increase the genetic variance upon which selection can act (Smadja & Butlin 2011), potentially serving as a multilocus macromutation (Mallet 2007, and references therein), which may expand the range of phenotypic variance on which natural selection can act. Second, counterintuitively, it can promote reproductive isolation, by increasing the potential for reinforcement (Smadja & Butlin 2011; Abbott *et al.* 2013) or by coupling genetic incompatibilities with ecological loci under disruptive selection (Seehausen 2013). Third, it can create new species directly in the form of reproductively isolated hybrids (Abbott *et al.* 2013). Clearly, however, the efficacy of the first two mechanisms must also depend on conditions under which the homogenising effects of gene flow are overcome. Due to such difficulties, the predominant impact of hybridisation on speciation remains controversial (Barton 2013; Servedio *et al.* 2013).

Empirical data shedding light on the genome-wide build-up of barriers to gene flow are growing rapidly, via genome scans and association mapping using large sets of individuals from diverging lineages. This includes transects across hybrid zones, replicated combinations of lineages at different locations, and the comparison of closely related populations and species with different divergence times (Abbott *et al.* 2013). However, as emphasised by Butlin & Ritchie (2009), the new plethora of genomic data will not clarify the genetics of speciation unless it is possible to distinguish changes that have contributed to divergence and reproductive isolation from those that are carried along in its wake.

Island radiations such as those proposed above, with both inter-island and intra-island sister-species pairs, would provide an ideal framework to address these issues. A further advantage would be afforded by the presence of both inter-island and intra-island pairs that differ significantly in their degree of divergence, ranging from incipient species to species that exhibit complete or nearly complete reproductive isolation. In such a comparative framework, a role in speciation for phenomena associated with gene flow (e.g. increased genetic and phenotypic variance, reinforcement, coupling, or immediate reproductive isolation) should meet two criteria. First, these phenomena should be observed in recently diverged species pairs, not just in older (post-speciation) pairs. Second, they should be absent from inter-island species pairs, or at least significantly less prevalent than for intra-island pairs.

Understanding why some lineages are more diverse than others

The proliferation of life on islands has progressed much farther within some lineages than others. For example, among the 88 native genera of weevils (Coleoptera, Curculionidae) occurring naturally within the Canary Islands, there is an average of only three species per genus (Whittaker and Fernández-Palacios 2007, and references therein). However, 128 species, more than one-third of all the native weevil species in the Canary Islands, belong to a single genus, *Laparocerus* (A. Machado, pers. comm.). Such island-based patterns raise an important and more general question – why have some lineages diversified so extensively, while others have not? A first step in responding to this question is to assume that diversity increases unbounded through time, and to distinguish between two alternative explanations for diversity variation among clades: differences in the time available for diversification, and differences in net diversification rate. Studies using dated phylogenies have variably supported both explanations (e.g. Rabosky *et al.* 2007; Cornuault *et al.* 2013). A second step involves considering alternative explanations for diversity dynamics such as diversity-dependence and bounded diversity, equilibrium dynamics and periods of diversity decline (Morlon 2014, and references therein). The co-distribution of both diversified and non-diversified lineages across the same island or archipelago offers researchers some degree of control over the time, geographical area and environmental heterogeneity available for diversification. It also offers some control over the environmental changes experienced by clades during their evolutionary history. Such settings seem ideal to identify fundamental differences in the way species from diversified lineages respond to heterogeneity and temporal variation in environment and geography, compared to species belonging to lineages that have not diversified.

Phylogenetic analyses chart the histories of species over deep timescales, revealing, for example, differences in diversification rates among lineages. The integration of population-level studies with such higher order phylogenetic studies may provide greater opportunity to connect phylogenetic pattern with evolutionary and ecological process. In a recent review, Losos & Ricklefs (2009) suggest that detailed population-level studies can chart the course of evolution over short time periods, directly measuring the extent to which natural selection changes in strength and direction over time. This approach can be broadened to incorporate intraspecific-level studies with geographically explicit sampling of individuals for the reconstruction of gene genealogies to reveal the extent to which natural selection, or alternative mechanisms (e.g. differences in neutral divergence resulting from differences in dispersal ability; Agnarsson *et al.* 2014), may explain evolutionary change. Island radiations are ideal systems for such an approach, because it is frequently apparent that the arena within which interspecific diversification has occurred is similar to the arena within which intraspecific diversification is occurring (e.g. Ricklefs & Bermingham 2002). This likely results from the hard boundaries, isolation and climatic stability of islands (Table 1), despite geological dynamics (Whittaker *et al.* 2008). Population genomic comparisons of lineages from species-rich and species-poor clades in the same island or archipelago setting provide real potential to determine the relative roles of factors such as the strength of selection and gene flow in rendering one lineage more species-rich than another.

HOPES FOR THE FUTURE OF ISLAND-BASED THEORY

For many, MacArthur & Wilson's (1963) model is the foremost example of using islands as model systems. It can be seen as the founding core of a theory that has been and continues to be greatly extended, providing a quantitative baseline against which deviation can be tested. As such it has not just improved our understanding of island communities, but also brought important insights in ecology, evolution, biogeography and community assembly in general (e.g. Hubbell

Box 6 Equilibrium vs. non-equilibrium, and the potential nature of equilibria

MacArthur and Wilson's IBT explains species richness on an island from a dynamic balance between colonisation and extinction events (Box 1). While the theory has been greatly expanded (e.g. Brown & Kodric-Brown 1977; Hubbell 2001; Hanski 2010; Gravel *et al.* 2011; Rosindell & Phillimore 2011), the hypothesis of equilibrium dynamics is rarely brought into question (but see Simberloff 1976, 1983; Gilbert 1980; Steadman 2006; Whittaker and Fernández-Palacios 2007).

Two separate explanations for a lack of equilibrium are frequently confused, both on ecological and evolutionary timescales. In one scenario, a biota is governed by processes that cause species richness to tend towards equilibrium, but this equilibrium has not been reached, and in some cases may never be reached. We refer to this situation as ***unattained equilibrium***. It may occur when: (1) there has been insufficient time for the equilibrium in question to be reached. Examples include islands that are young (be they *de novo* or fragment islands; Brown 1971), recently sterilised, large, or highly isolated; (2) there is a lag in the response time of extinction, allowing equilibrium to be temporarily exceeded (Gillespie 2004; Gavrilets & Losos 2009); (3) environmental fluctuations or disturbances outpace the time to equilibrium (McGuiness 1984; Whittaker 2000). In a second scenario, species richness is simply not governed by equilibrium dynamics. We refer to this as ***fundamental non-equilibrium***. For example, on evolutionary (and potentially ecological) timescales, diversity may accumulate without limit (Emerson & Kolm 2005; Morlon *et al.* 2010), there being no *a priori* reason to believe that extinction should balance species accumulation.

A largely overlooked addition to IBT is E. O. Wilson's (1969) hypothesis that equilibria can themselves shift during the course of what is described today as community assembly (Fig. 3). He envisaged a time-progressive sequence in the relative importance of the actions of species interactions (such as competitive exclusion), environmental filtering, adaptation, and co-evolution during community assembly, leading to changes in the position of the equilibrium between immigration and extinction. Four equilibria were recognised on a hypothetical relative timescale:

(1) Non-interactive: an equilibrium reached prior to the attainment of sufficiently high population densities to make species interference (including competitive exclusion) a major factor in extinction,
(2) Interactive: an equilibrium in which species interactions (including competitive exclusion) are a major factor in survivorship,
(3) Assortative: an equilibrium occurring in response to environmental filtering, that is, the peculiar physical conditions of the local environment and interactions with other species over the long term,
(4) Adaptive (to distinguish this from the equilibrium that follows, we avoid using Wilson's term 'evolutionary'): an equilibrium reached when populations have had time to undergo evolutionary adaptive change in response to both local environmental conditions and to other species. Such island populations may or may not be considered separate species from their continental relatives.

The first three of these equilibria are based on empirical data from the Florida mangrove experiments that E. O. Wilson conducted with D. Simberloff (Simberloff & Wilson 1971). In Fig. 3, we present a modified version of E. O. Wilson's (1969) schema, to which we have added a fifth equilibrium, more easily studied since the advent of molecular phylogenetics, in which the effect of speciation (as well as immigration), offsets extinction:

(5) Radiative: an equilibrium occurring when lineages resulting from the adaptive phase have had time to undergo speciation (cladogenesis) *within* the island or archipelago of interest.

E. O. Wilson (1969) considered his four equilibria as a time-progressive sequence, with evolutionary processes in the fourth being clearly distinguished from ecological processes in the previous three. Today, evolutionary responses are widely recognised to occur on timescales that are as short as ecological ones (Schoener 2011), and indeed natural selection will operate throughout the five phases of equilibria. We therefore see the schema as a continuum, rather than a discrete sequence, and acknowledge that at each phase, the processes leading to the previous equilibrium will still operate. Following Janzen (1985), we refer to the process of environmental filtering and species interactions leading to the accommodation of extra species in the assortative equilibrium as 'ecological fitting'. We refer to the process of *in situ* adaptation, both to the environment and to other species, allowing accommodation of extra species in the adaptive equilibrium as 'evolutionary packing'.

2001; Hanski 2010; Losos & Ricklefs 2010). However, despite its success in predicting diversity patterns, over the 50 years since its publication, the ability of IBT to identify underlying processes has received a range of critiques (Gilbert 1980; Williamson 1989; Steadman 2006). In particular, the central premise of IBT – that of an equilibrium between immigration and local extinction – remains equivocal and difficult to test (Simberloff 1976, 1983; Gilbert 1980). Incorporating the possibility of non-equilibrium dynamics (both on ecological and evolutionary timescales) remains one of the greatest challenges for the future (Box 6). We therefore advocate a judicious use of island-based theory. This should include using the assets of islands in allowing theories to be simple, but also remaining critical and continuing to question the core hypotheses and assumptions involved. Here, we consider some hopes for the future of island-based theory with these views in mind.

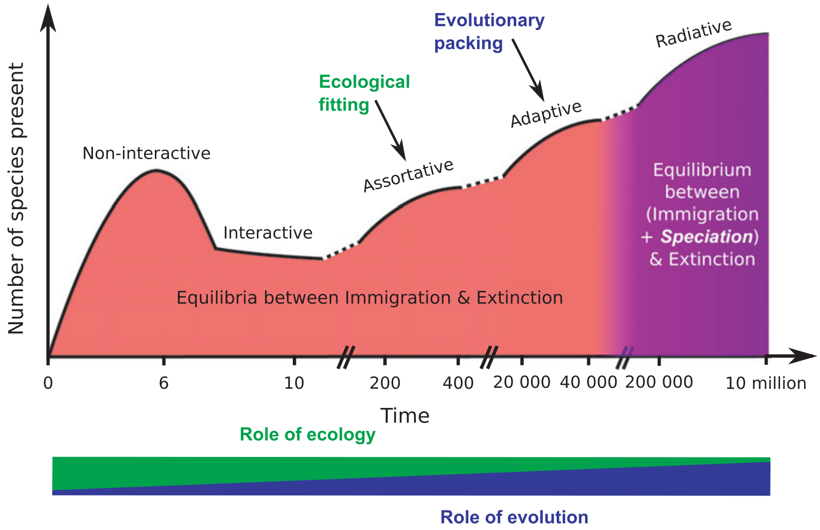

Figure 3 A schematic hypothesis for the time-progressive continuum of equilibria involved in community assembly (Box 6), modified from E. O. Wilson's (1969) Brookhaven paper. Following Wilson (1969), a hypothetical relative time scale is used. Equilibria between immigration and *local* extinction are shaded red, while the equilibrium among immigration, speciation and *local* extinction is shaded purple. Once populations have differentiated *in situ* to the species level, local extinction events will also be total extinction events.

Modes of speciation

In order to explain the spatial distribution of species diversity, *in situ* speciation needs to be taken into account. Accordingly, recent island-based models have incorporated speciation (e.g. Rosindell & Phillimore 2011). Ideally however, future island models should incorporate different modes of speciation, in particular geographical speciation (for which geographical isolation is the component initiating genetic divergence) and ecological speciation (i.e. as a result of ecologically-based divergent selection). Further, many permutations of these simplified scenarios are possible; different speciation events on any one island may follow different modes, and any single speciation event may result from a combination of different modes, especially when geographical settings change during speciation (Butlin *et al.* 2008). The latter may particularly apply when geological and environmental dynamics induce repetitive island connection and separation (Whittaker and Fernández-Palacios 2007). Geographical isolation may thus contribute only intermittently to speciation. Likewise, progressive phases of community assembly on islands (Box 6, Fig. 3) may alter the shape and strength of ecological selective pressures that contribute to speciation. Variation in island size (e.g. owing to sea level fluctuations) affects the overall probability of speciation (Losos & Schluter 2000; Kisel & Barraclough 2010) and may therefore also affect the contributing mode(s) of speciation (Whittaker *et al.* 2008; Losos & Ricklefs 2009). Aguilée *et al.* (2013) recently developed a model allowing for such variable history, in which ecological speciation includes temporary and repetitive geographical isolation. They show that temporal variation in geographic setting, inducing changes in the contribution of different speciation modes, is likely to facilitate speciation, possibly generating adaptive radiation. In this context, models predicting biodiversity patterns that can be compared to empirical data are, however, still lacking. Realistic phylogenies (including tree imbalance and deceleration in the rate of lineage accumulation) can be obtained purely from ecological speciation (McPeek 2008) as well as purely from geographical speciation (Pigot *et al.* 2010). We therefore need new models to make quantitative predictions to assess the contribution of different modes of speciation in community assembly (Moen & Morlon 2014). These might include not only phylogenies, but also ecological traits and species ranges. Such models provide the potential to more precisely predict the influence of area and temporal connectivity of available land on the spatial distribution of species diversity.

Understanding equilibrium vs. non-equilibrium dynamics

If species richness is to a large extent explained by non-equilibrium dynamics (Box 6), non-equilibrium models and a better theoretical understanding of dynamics outside of equilibrium are still required (Whittaker and Fernández-Palacios 2007). For example, fundamental non-equilibrium models (see Box 6 for definition) could be achieved by integrating classic MacArthur & Wilson immigration–extinction processes with time-variable macroevolutionary birth–death models of *in situ* diversification with no upper limits to diversity (Valente *et al.* 2014). This might be achieved with extinction rates that are constantly outstripped by the input of new species from immigration and speciation, and so diversity grows without bound. An alternative way to approach non-equilibrium theory is simply to study the transient behaviour of models that would in theory eventually equilibrate, but do not have the opportunity due to lack of time or continuous environmental change (i.e. unattained equilibrium, Box 6; Ricklefs & Bermingham 2001).

In the case of equilibrium models such as IBT, a better understanding of the time it takes to reach equilibrium would be useful. Perhaps the equilibrium towards which we are heading is a moving target (e.g. Box 6, Fig. 3)? If so, in some cases it may never be reached. To resolve these questions we must study and model predictions over the time scales in which equilibrium would be expected to be reached. This could include phylogenetic data, fossil data and ecological time series. In addition to studying the colonisation of newly formed or sterilised islands, changes in island characteristics (e.g. area, isolation, and topographic complexity) due to ontogeny (Whittaker *et al.* 2008) or sea level change (Rijsdijk *et al.* 2014) provide underexploited situations in which to test whether equilibrium dynamics apply.

CONCLUSIONS

Fifty years after MacArthur & Wilson's (1963) classic article, we are at an opportune moment for taking new approaches to our understanding of ecology and evolution using islands as model systems. Until recently there has been a predominant gap between ecological studies that are explicitly spatial and consider short timescales, and evolutionary studies considering longer timescales but in which the spatial scale of phenomena is unclear (Schoener 2011). The combination of assets offered by islands as model systems to both ecologists and evolutionists should continue to place them centre stage as tools with which to close this gap. Of primary importance in this endeavour is the acquisition of DNA sequence data at the genomic level at an ever-increasing rate, and for non-model organisms. This is providing ecologists and evolutionary biologists with unprecedented opportunities to uncover the history of lineages at the community level (Sousa & Hey 2013; Ellegren 2014). Many of the future prospects presented here will be feasible (or are becoming feasible) only as a result of this technological advance. Of equal importance, we are in a period in which islands as model systems are receiving considerable new theoretical input (e.g. Gravel *et al.* 2011; Rosindell & Phillimore 2011). Consistent with MacArthur & Wilson's (1963, 1967) intuition, the implications of these island-based prospects are not restricted to islands, rather they extend to our understanding of ecology and evolution in general.

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All authors are directly or indirectly members of a working group who conceived this review, contributed to the conceptual framework and drafted sections of text, many of which were incorporated to a greater or lesser degree. BHW wrote most of the manuscript, coordinated the ideas and input from all co-authors and benefited throughout from substantial technical and conceptual support and experience from all co-authors. CT, DSi, BCE, RER and RGG provided substantial senior guidance regarding contents and format. RA, FLC, BCE, DG, HM, NM, JR and DSi contributed large blocks of time in writing and/or figure preparation. All authors read and commented on drafts of the manuscript.

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