

A reappraisal of the role of humans in the biotic disturbance of islands

THEMATIC SECTION
Humans and Island
Environments

JUAN D. DELGADO^{*1}, RODRIGO RIERA², RICARDO A. RODRÍGUEZ³, PABLO GONZÁLEZ-MORENO⁴ AND JOSÉ MARÍA FERNÁNDEZ-PALACIOS⁵

¹Department of Physical, Chemical and Natural Systems, Ecology Area, Universidad Pablo de Olavide, E-41013 Sevilla, Spain, ²Centro de Investigaciones Medioambientales del Atlántico (CIMA SL), 38107 Santa Cruz de Tenerife, Canary Islands, Spain, ³Department of Biology, Miami University, Oxford, OH 45056, USA, ⁴Centre for Agricultural Bioscience International, Egham, Wallingford, Oxfordshire, UK and ⁵Island Ecology and Biogeography Research Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUNETSPC), Universidad de La Laguna, Tenerife, Canary Islands, 38206 Spain

Date submitted: 4 August 2016; Date accepted: 22 March 2017; First published online 12 April 2017

SUMMARY

Traditionally, islands have been used as ecological and biogeographical models because of their assumed ecological simplicity, reduced ecosystem size and isolation. The vast number of Earth's oceanic islands play a key role in maintaining global biodiversity and serve as a rich source of evolutionary novelty. Research into the factors determining diversity patterns on islands must disentangle natural phenomena from anthropogenic causes of habitat transformation, interruption and enhancement of biological fluxes and species losses and gains in these geographically and ecologically limited environments. The anthropogenic ecological forcing of communication through global transport has profound implications regarding island–continent links. Anthropogenic disturbances along continental margins and insular coasts contribute to shaping island biotas in ecological time, but also have evolutionary consequences of global resonance. Patterns of human landscape and resource use (geographical space and ecological communities and species), as well as increasing ecological connectivity of oceanic islands and mainland, are chief driving forces in island biogeography that should be reappraised. Global indirect effects of human activities (i.e. climate change) may also affect islands and interact with these processes. We review the implications of direct and indirect anthropogenic disturbances on island biotic patterns, focusing on island size, isolation and introduced exotic species, as well as the unsettled issue of oceanic island ecological vulnerability.

Keywords: island disturbance, alien species, island area, isolation, vulnerability, island diversity patterns, global change, non-equilibrium, island landscape pattern

INTRODUCTION

Oceanic island ecosystems are well-defined biotic entities with different but usually high degrees of isolation, evolutionary novelty and biological irreplaceability, shaped by complex interactions between natural and anthropogenic disturbance regimes (Whittaker & Fernández-Palacios 2007; Kueffer & Fernández-Palacios 2010; Warren *et al.* 2015). Islands are not biologically isolated, but dynamically open ecological systems that receive and export living organisms, interacting with other islands and continents (Nunn 1994; Adersen 1995; Walter 2004). After major contributions such as the formulation of island biogeography theory (IBT; MacArthur & Wilson 1967), the natural history of islands (Carlquist 1974) or experimental zoogeography (Simberloff & Wilson 1969), there has been a continuous advancement in the modelling of islands from evolutionary, biogeographical and conservation angles (Diamond 1975b; Ricklefs & Bermingham 2002; Whittaker *et al.* 2008; Gillespie & Clague 2009; Warren *et al.* 2015).

An efficient biogeographical approach to conservation cannot undervalue the contribution of humans to loss of island biodiversity. Far from a mere confounding factor in biogeography, human influence is a driving force on island biotas in actual ecological time, with deep consequences in evolutionary time. Island–island and island–continent biotic communication can be complicated, accelerated or interrupted by the intervention of humans (Helmus *et al.* 2014).

Islands shelter a large proportion of Earth's biodiversity. Despite covering only *c.* 3% of the emerged lands, they sustain a disproportionately high biodiversity relative to their area, largely due to endemism (Lomolino & Heaney 2004). This is especially the case with volcanic islands (e.g. Hawaii) and microcontinents (e.g. Madagascar), rather than with land-bridge islands (Whittaker & Fernández-Palacios 2007). Oceanic islands show high rates of speciation, endemism and taxonomic exclusivity (Denslow 2003; Kier *et al.* 2009; Kueffer *et al.* 2009), and *c.* 180,000 islands harbour *c.* 20% of the world's plant and animal species (Kier *et al.* 2009).

Compared with continental biotas, oceanic islands have suffered an accelerated loss of species mainly during the

*Correspondence: Prof Juan D. Delgado e-mail: jddelgar@upo.es
Supplementary material can be found online at <https://doi.org/10.1017/S0376892917000236>

last two centuries, and most extinctions of endemic species have occurred on islands (Anderson 2002). At the same time, most cases of biological invasions by new and aggressive foreign species (including humans) are from oceanic islands (Anderson 1995; Gillespie 2001). As a consequence, many species disappear and others continue arriving at and colonizing islands, both naturally and as introductions.

Islands are not, as traditionally depicted, biodiversity sinks or the end of the colonization road (Preston 1968) for continental species (Patiño *et al.* 2015). Oceanic islands play a dynamic role in species evolution, biodiversity and extinction at the global scale, as sparse centres of evolutionary novelty for the continental taxocenosis, as well as for other islands (Losos & Ricklefs 2009). Besides, islands in the Anthropocene can be considered centres of particularly steep increases in species richness due to non-native taxa (Sax *et al.* 2002), which add novel ecological and evolutionary impacts in concurrence with secular landscape disturbance (Thomas 2013).

Interest in the weight of disturbances as shaping forces (either human or natural) of island biotic communities has been repeatedly expressed (Whittaker 1995; Anderson 2002; Garden 2005). A number of both natural and anthropogenic forces interact to trigger or accelerate biological impoverishment of island biotas (Whittaker 1995; Whittaker *et al.* 2008), and as a consequence, island species numbers tend to depart from biotic equilibrium (Walter 2004). Basic equilibrium models of island diversity are being developed in increasingly realistic geographical contexts with deviations towards non-equilibrium systems (Whittaker 1995; Whittaker *et al.* 2007, 2008). Walter (2004) raised concern about the limitations and limited generalization power of the equilibrium theory of island biogeography (ETIB) as based chiefly on rates of immigration and extinction. Particular island geographic attributes (place, or *eigenplace*; Walter 2004) should be considered to enhance modelling and to determine perspectives of conservation for focal island biodiversity. Both natural (Whittaker 1995) and anthropogenic (Ficetola & Padoa-Schioppa 2009; Helmus 2014) disturbances interact with background biotic fluxes to and from islands. The island life ontogenesis or geo-biotic life cycle from emergence to final submergence has been integrated with basic ETIB processes of immigration, extinction and speciation to better explain island biodiversity patterns (Whittaker *et al.* 2007, 2008), but to date, insufficient emphasis has been put on the determinant role of human perturbations of island ecosystems. Modern island biogeographical science contrives to analyse the role of humans as a species that is able to irreversibly transform island biotas and evolutionary pathways in a very short period of time (Richardson & Whittaker 2010). Hence, a thorough reappraisal of the human impact in configuring island ecological assemblages is urgently needed.

Our aim in this paper is to review, exemplify and discuss local and global consequences of human perturbation of oceanic island biotic patterns. We focus on anthropogenic impacts, which are largely underrated or avoided by the ETIB corpus, as critical global factors in island biotic assembly. Our

specific objectives were: (a) to revise the role of isolation in a globally interconnected island scenario; (b) in attending to the relevance of islands for global biodiversity conservation, we revisit issues in some scarcely evaluated aspects of the effects of focal island landscape configuration, island–continent mutual relationships, size (area) and conservation status of ecosystems, with special interest in smaller islands; and (c) to address causes and explanations for the conventionally accepted inherent vulnerability of island biotas to invasions and other disturbances. Finally, we discuss alternative explanations for determinism, stochasticity and separation of island biotas from equilibrium, as results of anthropogenic interference, driving biodiversity patterns in oceanic islands.

NO TRUE ISLAND ISOLATION IN THE ‘PLANETARY VILLAGE’

In the Anthropocene (Gibbard & Walker 2014; Lewis & Maslin 2015), islands cannot be considered as sea-isolated entities (Helmus *et al.* 2014). Distance to the nearest land (isolation) is still an influential variable in natural island colonization patterns for many species (background island colonization and rescue effect); however, distance (isolation) per se seems not to be critical for the array of other human-linked taxa, such as commensal, pathogen or exploitable taxa.

Human population size and range, movement abilities by land, sea and especially by air and the telecommunication and geolocation skills of the satellital era have experienced several-fold increases. Humans have been reaching and thus significantly transforming islands at different technological levels and transport means for the last 5000 years at least (Smith & Davies 2012).

Particularly for remote islands, this involves geomorphological, ecological and evolutionary consequences. For instance, accelerated climate change threatens the integrity of low islands due to sea-level rise, survival of mangrove and coral reef ecosystems and the dynamics of barrier islands and continental margins (Wetzel *et al.* 2012). Many formerly remote archipelagos have been connected in order to satisfy global trade, settlement and leisure demands. Propagule traffic has reached a planetary scale in terms of biomass, individuals, populations, species and genes moved in ecological time (*c.* 3000 species of animals and plants travel daily by this means; GESAMP 1998).

Islands forming archipelagos are more connected than ever, favouring contact amongst individual island biotas. This increases risks of introductions of invasive species from companion islands in a pool and contributes to homogenization of island clusters from formerly distinct assemblages. There is limited published evidence of within-archipelago human-mediated transference of endemic species. Incidental human transport, however, as a factor of increasing colonization probabilities for insular endemics, has been reported for endemic reptiles to continental grounds (Fattorini 2010).

Some authors argue that, paradoxically, the human capacity to carry species to remote points, human-induced changes in

climate and the creation of hybrid landscapes contribute to increase overall biodiversity in the Anthropocene, even when many species are being lost at the same time, with replacement of native island landscapes by alien species in many islands (Chown *et al.* 2008; Thomas 2013).

LINKS AMONG ISLAND PHYSICAL TRAITS AND HUMAN OCCUPATION PATTERNS

Basic factors affecting island species diversification that are used as predictors of species richness include island age, altitude, area, topographical complexity and distance to mainland or isolation from any source, including other islands (Williamson 1988; Whittaker & Fernández-Palacios 2007). As these factors influence resource and space availability and habitability for humans, they are likely to determine patterns of occupation of island ecosystems, which will be affected accordingly.

Scarce information exists on how coastal occupation by exotic species and urban areas could prevent settlement of naturally dispersing propagules on islands, thus interfering or mixing with ongoing colonization processes. The ecological and genetic effects of such transport of alien taxa are foreseeable at the receptor islands. Sampling effects and the aspect of the island to prevailing winds respectively determine species and probable main routes for propagule dispersal from mainland. In the Canary Islands, capital cities are set favourable locations that are relatively protected from prevailing trade winds, and most operating harbours are on leeward coasts. These slopes are the most anthropogenically altered, and those facing the African coast, the nearest mainland source at *c.* 96 km from the archipelago, would be the first recipients of spontaneous propagules. Lower probabilities of propagule establishment, however, are expected for these island slopes, at least for vagrant birds, reptiles and even mammals such as bats, as well as some plants. The structure of the island biota is thus influenced by topographical aspects (windward versus leeward), prevailing winds and oceanic currents helping to channel the dispersal of propagules. However, potential propagule receptor areas, such as coastlines facing North Africa, are already occupied by intensive urbanization (Otto *et al.* 2007) and may become inadequate terrain for effective colonization. These urban areas also act as human-modified sources of alien taxa (Otto *et al.* 2014).

Low- to mid-level elevations can shelter the largest proportion of an island's endemism (Otto *et al.* 2007, 2012), and hence are susceptible to heavier biodiversity losses from human settlement. Steinbauer *et al.* (2012) found that the percentage of single island endemics was higher in the mid-elevation thermophilous scrub, the most negatively affected vegetation belt in the Canary Islands (Otto *et al.* 2012). However, the Canarian lowlands, especially on leeward slopes, are even more profoundly affected by urbanization and infrastructure. Leeward areas of Tenerife have gentler slopes and a mild climate, attracting tourism and commercial activity. A great proportion of plant and animal endemics are sheltered

in this semiarid, *Euphorbia*-dominated ecosystem ring situated from the littoral zone to *c.* 300 m altitude. The Canarian net of protected natural spaces covers *c.* 40% of the territory, but for most of the remaining 60% of legally unprotected land, dispersed, poorly planned development has been consuming natural areas at a dramatic pace.

The frequency and intensity of disturbance often drop with increasing land area, while species diversity increases (McGuinness 1984). Vulnerability to anthropogenic disturbances can indeed be higher in smaller islands, which are the most abundant at a global scale, and remote, smaller and lower islands are especially prone to species extinctions driven by abiotic and anthropogenic disturbance (e.g. Schoener *et al.* 2001 for Bahamian reptiles; Ficetola & Padoa-Schioppa 2009 for resident reptile species in 212 Mediterranean and Atlantic islands).

Island size and environmental fragility have an inverse relationship: the smaller the island, the greater the impacts of human activities and synergies among them and natural phenomena such as sea-level change, extreme weather events (droughts), earthquakes and hurricanes (Maul 2005; Bunce *et al.* 2009). In addition to intrinsic population fluctuations, such events can accelerate extinction rates of island species, as for El Niño–Southern Oscillation events and the giant Galápagos tortoise (Loire *et al.* 2013). Generally lacking other resources or the possibility to exploit them, humans on small islands have tended to rely more on tourism. These habitats have then experienced heavy impacts derived from population pressures (Maul 2005). The effects of natural catastrophic events added to those of local human populations are the main threats to inhabited smaller island ecosystems (Baine *et al.* 2007).

Island ecological fragility may depend on the intensity of particular activities. The main human disturbances to biotas of small, remote and scarcely populated islands come from exploitation interests of powerful economies combined with a shift in the type of relationships between native populations and land uses (Pretto *et al.* 2010). Geopolitical issues have contributed to setting the ecological fate of many oceanic island communities through politically driven reclamation, building of artificial islands, oil prospecting, nuclear waste storage and militarization (e.g. air bases, harbours and weapon tests), as ongoing international conflicts within the Asia–Pacific region demonstrate (Valero 1994).

Nevertheless, the effects of the human presence on archipelagos could still be positive for smaller islands with more effective protection from further human impacts. They can sustain smaller human populations and have fewer resources, harsher environments and limited opportunities for human habitation (e.g. space, water and food), transportation structure or exploitation (Enoch & Warren 2008). Smaller islands can also shelter rare ecosystems or endemic species of global concern, and/or are assumed to be more ecologically fragile, attracting international protective and research efforts (Fernandes & Pinho 2017). These peculiarities of small islands would have the opposite effect to that expected by the disturbance hypothesis in the long term.

La Palma, El Hierro and other smaller islands in the Canaries are good examples. As western islands, El Hierro and La Palma are less affected by the major erosive processes that cause soil loss than larger and more eastern islands: El Hierro and La Palma have 6% and 8% of their island areas affected by this impact, respectively, compared with *c.* 40–60% eroded land of Fuerteventura, Gran Canaria and Tenerife (Rodríguez 2001). La Gomera is exceptional: although similar in size to La Palma and El Hierro, and with a large amount of forested area, it is older and has had no volcanic construction activity for the last million years, and its erosion rate is nearly 50% of the affected area (Rodríguez 2001).

El Hierro is geologically young (1.1 million years old; 14,000–13,000 years after being partially dismantled by massive landslides); its area, habitat availability and complexity, mature forest cover and hence terrestrial biodiversity are lower than for the other western islands including Tenerife, La Gomera and La Palma. Its human population density is accordingly low and, to a certain extent, constant, whereas the other larger islands of the archipelago tend to have growing populations. Unlike in most of the other islands, the El Hierro human population is distributed along or near the coast, but is also sparsely distributed at mid-range elevations. Furthermore, El Hierro is legally protected in various ways (*c.* 58.1% of the island area) and is considered to be a Biosphere Reserve (Fig. 1). Although there is a strong positive association between area and amount of protected space per island ($R^2 = 0.9425$; Fig. 1(a)), the proportion that is protected is greater for smaller islands and islets ($R^2 = 0.7489$; Fig. 1(b)).

The disturbance hypothesis (Gotelli 2004) supposes that small islands tend to suffer greater disturbance than large islands. If legal protection of islands is taken as a proxy for actual island ecosystem conservation (although this is untrue for Canarian coastal habitats), then some of the smaller islands do not necessarily have to suffer greater disturbances than larger islands, at least from direct human activities. If extinction is an inverse function of area, then extinction rates should be generally higher on small islands than on large islands or continents. However, this tendency may vary among archipelagos. Lord Howe Island has almost the same number of alien plants (230 species) as native plants (241 species), and 9 out of 15 native bird species have been directly or indirectly driven extinct by humans (Hickman & Hickman 2009). Lord Howe Island is not a drastic paradigm of human transformation compared to other Pacific islands, but provides another example of extinction in historical times in a location of high endemic diversity and recent control of human activities having positive conservation outcomes.

Also in Macaronesia, the Azores are a more extreme case of habitat loss than that of the Canaries. The Azores have lost 97% of their native habitats since European colonization 600 years ago (Terzopoulou *et al.* 2015). Single island endemic beetles were more prone to extinction than those that were endemic to several islands, and species of narrow geographic range and greater body size experienced greater risk of extinction (Terzopoulou *et al.* 2015). However, it

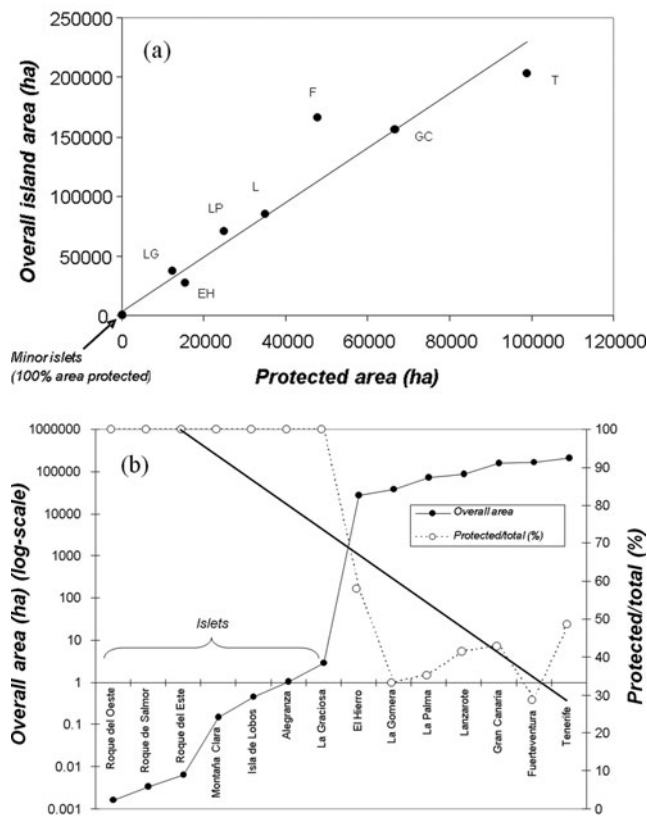


Figure 1 Relationship between island area and proportion of area protected for the Canary Islands. (a) Relationship between island area and protected area.

(b) Relationship between overall area (black line) and the ratio of protected/total island area. The fitted regression function (black line) in (b) is for values of the ratio of protected/total island area. Note: only one of the islets – La Graciosa – is inhabited. LG = La Gomera; EH = El Hierro; LP = La Palma; L = Lanzarote; F = Fuerteventura; GC = Gran Canaria; T = Tenerife.

has been found that increases in alien richness did not promote the homogenization in assemblages of Azorean epigeous arthropods (Florencio *et al.* 2013). Some aliens were revealed as habitat specialists forming new and heterogeneous communities in anthropogenically altered sites (Florencio *et al.* 2015). Current epigeic communities are complex products of the interaction between the historical extinction of native species and the emergence of invader alien specialists who have become integrated within the island biotas (Rigal *et al.* 2013; Florencio *et al.* 2015).

EXPLANATIONS FOR ISLAND VULNERABILITY

The greater fragility of insular biotas compared with continents is often assumed. However, the theoretical framework of ecology does not provide concrete arguments for greater susceptibility of islands compared with that of continents (Simberloff 1995; Sol 2000). The biotic rarity and vulnerability of smaller islands are linked most commonly

to limited geographical extents, elevation–area ratios and remoteness (Whittaker & Fernández-Palacios 2007). Small size, isolation and rarity combined with human fondness for islands and global transport capacity (Helmus *et al.* 2014) are favourable conditions for a greater disturbance pressure. The fact that exotic species can invade and displace native species that are well adapted to local environments is an intriguing paradox (Sax & Brown 2000) that has yet to be resolved. In proportion to their area, islands probably lose more native and endemic taxa to human-induced extinction than continents, due to spatial confinement, resource limitation, species rarity, small population size or behavioural vulnerability to invading competitors, predators and pathogens and new ecological pressures (i.e. land use changes) (Simberloff & Levin 1985; Richardson & Whittaker 2010).

Higher proneness to invasion by exotics may be explained by disproportionate ecological pressure (in terms of limited area occupied) and intrinsic patchy character compared to continental zones of comparable extent. Spatial constriction puts an inherently higher human population density (such as on many small- to medium-sized islands) in close vicinity with vulnerable biota. Islands shelter 20% of all plant, reptile and bird species on only 3% of the Earth's surface (da Fonseca *et al.* 2006), and in 2006, the world's islands sheltered *c.* 10% of the human population (550–650 million people) and held 13.1% of the UNESCO's World Heritage sites (Baldacchino 2006). Moreover, the human population in biodiversity hotspots is growing at a faster rate than the planet's average (Cincotta *et al.* 2000).

Human capabilities to reach remote islands are affected by island geographical configuration, distance to human source populations and geometric properties (Keegan & Diamond 1987). Island ecosystems are more physically restricted and functionally constrained than those of continents in terms of biomass production and population-level movements. Spatial limitations on islands imply that many of the smaller islands are not much larger than the ecosystems they contain; there are more rigid and sharply limited ecological niches on islands than on continents, because ecological interactions are geographically restricted (Walter 2004), in addition to intrinsic functional restrictions (i.e. movement and dispersal needs and trophic needs). Using the eigenplace concept of Walter (2004), taxa of smaller islands are differentially more prone to extinction because they are inherently limited in geographical range, so pressures towards further contraction (and also expansion) may be adverse. Under accelerated human encroachment of island ecosystems, many island species with restricted ranges can be readily displaced or extirpated.

For remote islands, lack of communication with continents or other islands is another factor affecting niche definition. Such communities are not well prepared for the pace and type of landscape change that are forced by human occupation, and these communities exhibit small tolerance to exotic competitors. Island assemblages have a very restricted geographic space for drifting or readapting when forced to compete with alien species. The ecological space available

in order to successfully undergo character displacement and to avoid high levels of competition with foreign invasive species is more limited in small, insular areas than in those of large islands or continents (Brown & Wilson 1956; Grant 1994; Losos 2000; Walter 2004; Muchhala & Potts 2007; Smith & Rausher 2008). This coincides with the fact that territory overlap is more common in insular than in mainland populations (Blondel & Aronson 1999).

More important than the absolute size of islands is the coherence between island size and the spatial manifestation of the amplitudes of ecological oscillation of which the arriving species are capable. The amplitude of ecological oscillation of species from continental taxocenosis may be many times greater than that of island endemics, which evolved within constrained ecosystems. This is in agreement with the evidence of natural selection that Darwin found in the Galápagos Islands. For example, a span of 22 years of coexistence between *Geospiza fortis* and *Geospiza magnirostris* (two species of Darwin's finches) was enough to produce significant interspecific differentiations in beak size and diet that are unobservable under allopatric conditions (Grant & Grant 2006). However, reinforced oscillatory behaviour due to insularity also implies large fluctuations of abundance, which are typical of insular populations that are strongly influenced by island size. If the arrival of an invasive species coincides with a situation in which there is a noteworthy local minimum of abundance of autochthonous species due to their intrinsic behavioural plasticity, the advantage will most probably be for the alien species. The accelerated rate of evolutionary change in island biotas has a cost regarding their differential susceptibility to invasions, a collateral risk of the reinforcement of the limited niche plasticity within any small set of isolated ecosystems.

DETERMINISM AND STOCHASTICITY IN AN ISLAND ASSEMBLY UNDER HUMAN INFLUENCE

Pivoting paradigms such as adaptive radiation, taxon cycle, assembly rules and equilibrium and meta-population models apply differently to the specific configuration of archipelagos (Whittaker & Fernández-Palacios 2007). Some limitations to generalizations from the ETIB have been identified (Shugart 2004; Walter 2004): (1) considering individual species as interchangeable units ignores unique aspects of particular species, which may in turn influence the fate of remaining and potentially interacting species; (2) species turnover on islands is difficult to determine empirically – long-term lists of changes in island biotas are often lacking and problematic to create, and there is incomplete (although improving) fossil evidence of recent human-caused extinctions and monitoring data for detecting newly acquired exotics; and (3) it is unclear whether islands continue to gain and lose species and, if so, how, once a certain diversity of species is attained.

These limitations are perhaps mostly intrinsic, but in part they could be caused, in the present context of biotic

homogenization, by the impact of human intervention on all components of island life. Both isolation and area alone can indeed explain island species diversity and how islands gain and lose species in some instances (e.g. Borges & Hortal 2009). The passive sampling hypothesis implies that area (through target effect) and isolation (through rescue effect) respectively increase and decrease diversity (Burns *et al.* 2010).

For an archipelago of 34 islands in British Columbia, both deterministic (assembly rules) and stochastic (passive sampling) processes played non-exclusive roles in determining conifer community structure (Burns *et al.* 2010). However, assembly rules explain the abundance of individuals of a species on an island as a function of the number of other similar species (competing or facilitating) already present. Following Diamond's (1975a) assembly rules, particularly the rule of forbidden species combinations (Whittaker & Fernandez-Palacios 2007), the number of species should be a function of the degree of niche overlap or other measure of competence among the existing taxa pool. It can be gathered from Darwin's naturalization hypothesis that naturalization of introduced alien species on islands can be significantly inhibited by overlap between the ecological niches of related natives and aliens (Richardson & Whittaker 2010).

Non-equilibrium biotas are assumedly unsaturated with species (Whittaker 1995). On remote islands, cladogenesis and hence diversification is provided by open niches being filled by speciation from basal native taxa (Warren *et al.* 2015). Exotic species increase effective island species richness (Sax *et al.* 2002), but many of these imported taxa do not occupy empty (or artificially emptied) niches, instead occupying new niches created by human activities. Formerly empty niches in remote islands can thus be suddenly filled with relocated exotics. Such occupation could hamper or reduce cladogenesis and hence *in situ* speciation, but also could act as a selective pressure in evolution.

The evolution of island area, elevation, shape and relief, from island emergence through to the acquisition and building of its biota to its submergence, can be drastically changed by land use and extractive industries. Patterns of conifer diversity in islands of the Barkley Sound (British Columbia) were not consistent with ETIB predictions (Burns *et al.* 2010); instead, passive sampling (an aleatory process) and assembly rules (a deterministic process) might have operated as synergistic rather than mutually exclusive forces to shape island tree assemblages. Species–area curves deviated from a perfect rank–correlation for New Zealand and Aegean island bird faunas (Simberloff & Levin 1985); some species did not conform to species-specific minimum area requirements in their patterns of island occupation. Habitat differences between islands and anthropogenic extinctions emerged as the most probable causes, instead of equilibrium turnover. Logged native forest in the Solomon Islands showed incomplete recovery due to the persistence of pioneer tree species at least 50 years after disturbance (Katovai *et al.* 2016). The availability of potentially apt refuges for species may now depend directly on patterns of space use and intensity of

exploitation, which vary within and among islands and depend heavily on assemblage resilience (Katovai *et al.* 2016).

EQUILIBRIA VERSUS DISEQUILIBRIA IN HUMAN DISTURBANCE

Rather idiosyncratic and contingent patterns occur and should be studied island by island, due to the nature of technological pervasiveness and augmented biological communication through human transport. A human presence may alter the sequence of events of the island cycle from emergence to submergence. The destruction of habitats of previously extant species takes place at the same time that newly created habitats generate the conditions for the naturalization of introduced species. Before an island reaches the final stage of its evolution (terminal disappearance), human activities interact with (or take over) the inherent processes of geological dismantling. The concepts of vacant niche space and carrying capacity (K) would be better defined in the context of the amount of island niche space and the resource pool actually available for species to colonize after ecosystem deletions being triggered by humans.

Human impacts might perpetuate non-equilibrium states in disturbed island communities; they might extend the pre- or post-equilibrium phase of an island life cycle, depending on island age (Whittaker 1995; Shugart 2004; Whittaker *et al.* 2007). Some human activities have a great capacity to reset and simplify island species diversity, perpetuating non-equilibrium conditions (Whittaker *et al.* 2008). Although, in reality, island ontogeny does not have to change appreciably, the final stages of island evolution – those involving irreversible decreases in K due to the transformation of island ecosystems – would become more unpredictable than anticipated (Whittaker *et al.* 2007). On the other hand, with changes in K , realized species richness, and possibly speciation rate, would potentially decrease. The natural, background rates of immigration and extinction are also disturbed under this human domain. Immigration may be modified if impacts in coastal source areas (both mainland and source islands), which are heavily transformed by development (especially coastal), alter the spontaneous rate of dispersal of propagules to recipient island ecosystems (disturbance of background passive sampling).

Exotic species presence on islands will be increasingly determined by forced connectivity amongst islands and continents by means of human transportation (Helmus *et al.* 2014). However, the variance due to noise from alien species contributions and from other direct impacts is expected to be large and can *a priori* be explained by geographic factors such as island area, isolation (greatly overcome by global transport), topography and disturbance (Ficetola & Padoa-Schioppa 2009; Helmus *et al.* 2014). Thus, using actual species richness could add bias because a greater richness can be attained simply by adding aliens to the overall figure of natives and endemics.

On the other hand, it is often assumed that declines in native island plant species could be partly affected by introduced aliens. However, there is still little consensus on the causality of native plant extinctions by aliens. Many cases of positive correlations between alien and native plant diversity have been reported, whereas neat negative effects have barely been acknowledged (Caujapé-Castells *et al.* 2010). Negative impacts may often depend on the facilitation effect of the disturbed island landscape for alien taxa.

Introduction is not necessarily equivalent to invasion or biotic homogenization in the case of exotic plants in oceanic islands (Kueffer *et al.* 2010). Species introduced by humans on islands can remain locally confined without necessarily becoming invasive or incorporated into the local flora. However, post-introduction processes and particular disturbance profiles in the recipient territory can determine invasion success and therefore the composition of exotic flora and the effects on native species and communities (Pretto *et al.* 2010).

Moreover, some insularity parameters traditionally put forward in the IBT become diluted in this multivariate anthropogenic context. For example, Kueffer *et al.* (2010) could not explain alien species richness per group of islands (for a total of 30 groups) in terms of island area, latitude or distance to the continent (nor previous presence of other aliens or richness of native flora). Instead, their models were best supported by indicators of human development and diversity of habitats, island age or the oceanic region. In addition, these parameters could be dependent, to some extent, on the degree of landscape transformation of oceanic islands by humans, and perhaps also an unexplored inherent susceptibility to invasion (i.e. island age-related resistance, or even type of island origin – volcanic or continental fragments).

CONCLUSIONS

Further steps in generalizing the IBT would refine projections of how island biodiversity and species composition will behave after including human disturbance parameters in the models. The mechanisms underlying anthropogenic effects (such as those which induces alien invasion success) as factors shaping island communities remain poorly understood. Integrating natural and anthropogenic disturbances has a clear need for further research. Island biogeography might have experienced a sharp shift (Helmus *et al.* 2014); after millions of years of being mostly shaped by area, isolation and natural disturbances (see Whittaker 1995), island biogeography is now and will be increasingly governed by pervasive global connectedness, forced by ubiquitous humans. However, disturbance regimes and geographical conditions vary greatly from island to island. This opens new research scenarios for IBT and raises new and complex conservation issues. Hence, following Walter's (2004) eigenplace notion, human determinants of species richness should be approached on a more realistic, geographically explicit, per-island basis. Island biogeography could gain in functionality from a conservation perspective if multifactorial anthropogenic

change is dynamically integrated with basic parsimonious island biogeography.

The main theoretical consequences for IBT of human disruption of the equilibria and biotic structuring of islands we have discussed in this work are thus:

- (1) Human activities on islands introduce new and underrated stochasticity that could either enhance or hamper ongoing biogeographical processes. The sign of the effect would be dependent on the taxa and environmental conditions affecting their dispersal, establishment and reproductive outputs. Frequent ecological reset of natural disturbances to oceanic islands cannot be equated to the chronic alteration of landscape by humans. The former involves recurrence in island biotic assembly, whereas the latter implies permanent (often irreversible) seclusion or erasing of assemblages. The time or stability to attain equilibria for vulnerable, long-lived larger island taxa are insufficient under chronic human disturbance. A growing number of biogeographers even doubt whether there is true species turnover in human-impacted islands.
- (2) Speciation rates in human-occupied habitats on small islands are as difficult to measure as naturally occurring speciation; human pressure is itself a selective force with evolutionary consequences for island biotas.
- (3) Propagule source areas are altered irreversibly and passive sampling processes suffer disruption. Human-forced landscape changes at continental margins affect islands and vice versa. The synergistic effects of coastal development and degradation alter natural patterns of propagule dispersal between source and receptor areas at both global and local island scales.
- (4) Vulnerability is due to the interacting intrinsic physical and ecological attributes of islands and their species, and to contingent landscape use patterns by humans. Despite being mostly contingent, island geographical location, aspect to prevailing abiotic drivers (e.g. wind and current) and shape factors should help to predict which basal island landscapes will receive maximum impacts and experience higher biodiversity loss.
- (5) The most vulnerable island ecosystems are being biotically homogenized. This is a sort of continentalization process (i.e. a dilution of the rarity and diversity of the island biota, which tends to resemble that of the continent). Homogenization amongst islands may also occur. Colonization rates are being artificially increased for a limited set of introduced exotic generalists, which are succeeding regardless of natural isolation. Homogenization also occurs due to effective areal encroachment of native taxa by human development and exotic competitors, precluding further speciation. The area threshold for *in situ* speciation is artificially lowered by human impacts. Such new ecological pressures also enhance extinction rates of native taxa.
- (6) Smaller islands can receive more protective efforts than large ones. Larger islands have greater unprotected areas

compared to the smaller islands, and it is in these unprotected natural spaces where biodiversity losses are significantly larger.

All of these synergistic processes are contributing to the homogenization and masking of both species–area and species–isolation relationships at a global scale (Helmus *et al.* 2014), as synergies between the human disturbance of island territories and exotic taxa introductions speed up. Isolation is becoming a rare exception in biogeography: it is a function of the socioeconomic isolation of islands, and there is need to define and contextualize isolation in biogeography. In general, species richness of small and remote islands located in areas of economic interest may be increasing after all, against ETIB basal predictions, at unprecedented rates. Nevertheless, small and remote islands in the intertropical region harbour the bulk of island endemism and biodiversity, compared to the vast number of islands occurring along the continental margins at higher latitudes. This implies a gain in richness at the individual island scale, at the cost of losing native and endemic biodiversity globally.

ACKNOWLEDGEMENTS

We would like to thank the editors and one anonymous reviewer for improving this work. We also thank Professor Paulo A.V. Borges (Azorean Biodiversity Group) for his suggestions and valuable references contributing to the manuscript.

Supplementary material

To view supplementary material for this article, please visit <https://doi.org/10.1017/S0376892917000236>

References

- Adersen, H. (1995) Research on islands: classic, recent, and prospective approaches. In: *Islands. Biological Diversity and Ecosystem Function*, eds. P.M. Vitousek, L. Loope & H. Adersen, pp. 7–21. Heidelberg, Germany: Springer-Verlag.
- Anderson, A.J. (1995) Prehistoric Polynesian impact on the New Zealand environment: Te Whenua Hou. In: *Historical Ecology in the Pacific Islands*, eds. P.V. Kirch & T.L. Hunt, pp. 271–283. New Haven, CT: Yale University Press.
- Anderson, A.J. (2002) Faunal collapse, landscape change and settlement history in remote Oceania. *World Archaeology* 33: 375–390.
- Baine, M., Howard, M., Kerr, S., Edgar, G. & Toral, V. (2007) Coastal and marine resource management in the Galapagos Islands and the Archipelago of San Andres: issues, problems and opportunities. *Ocean and Coastal Management* 50: 148–173.
- Baldacchino, G. (2006) Islands, island studies. *Island Studies Journal* 1: 3–18.
- Blondel, J. & Aronson, J. (1999) *Biology and Wildlife of the Mediterranean Region*. Oxford, UK/New York, NY: Oxford University Press.
- Borges, P.A.V. & Hortal, J. (2009) Time, area and isolation: factors driving the diversification of Azorean arthropods. *Journal of Biogeography* 36: 178–191.
- Brown, W.L. & Wilson, E.O. (1956) Character displacement. *Systematic Zoology* 5: 49–64.
- Bunce, M., Mee, M., Rodwell, L.D. & Gibb, R. (2009) Collapse and recovery in a remote small island – a tale of adaptive cycles or downward spirals? *Global Environmental Change* 19: 213–226.
- Burns, K.C., Berg, J., Bialynicka-Birula, A., Kratchmer, S. & Shortt, K. (2010) Tree diversity on islands: assembly rules, passive sampling and the theory of island biogeography. *Journal of Biogeography* 37: 1876–1883.
- Carlquist, S. (1974) *Island Biology*. New York, NY/London, UK: Columbia University Press.
- Caujapé-Castells, J., Tye, A., Crawford, D.J., Santos-Guerra, A., Sakai, A., Beaver, K., Lobin, W., Vincent-Florens, F.B., Moura, M., Jardim, R., Gomes, I. & Kueffer, C. (2010) Conservation of oceanic island floras: present and future global challenges. *Perspectives in Plant Ecology, Evolution and Systematics* 12: 107–129.
- Chown, S.L., Sinclair, B.J. & van Vuuren, D.J. (2008) DNA barcoding and the documentation of alien species establishment on sub-Antarctic Marion Island. *Polar Biology* 31: 651–655.
- Cincotta, R.P., Wisniewski, J. & Engelman, R. (2000) Human population in the biodiversity hotspots. *Nature* 404: 990–992.
- da Fonseca, G.A.B., Mittermeier, R.A. & Mittermeier, C.G. (2006) *Conservation of Island Biodiversity: Importance, Challenges and Opportunities*. Washington, DC: Centre for Applied Biodiversity Science.
- Denslow, J.S. (2003) Weeds in paradise: thoughts on the invasibility of tropical islands. *Annals of the Missouri Botanical Garden* 90: 119–127.
- Diamond, J. (1975a) Assembly of species communities. In: *Ecology and Evolution of Communities*, eds. M.L. Cody & J. Diamond, pp. 342–444. Cambridge, MA: Belknap.
- Diamond, J.M. (1975b) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* 7: 129–146.
- Enoch, M.P. & Warren, J.P. (2008). Automobile use within selected island states. *Transportation Research Part A: Policy and Practice* 42: 1208–1219.
- Fattorini, S. (2010) Influence of recent geography and paleogeography on the structure of reptile communities in a land-bridge archipelago. *Journal of Herpetology* 44: 242–252.
- Fernandes, R. & Pinho, P. (2017) The distinctive nature of spatial development on small islands. *Progress in Planning* 112: 1–18.
- Ficetola, G.F. & Padoa-Schioppa, E. (2009) Human activities alter biogeographical patterns of reptiles on Mediterranean islands. *Global Ecology and Biogeography* 18: 214–222.
- Florencio, M., Cardoso, P., Lobo, J.M., Azevedo, E.B. & Borges, P.A.V. (2013) Arthropod assemblage homogenization in oceanic islands: the role of exotic and indigenous species under landscape disturbance. *Diversity and Distributions* 19: 1450–1460.
- Florencio, M., Lobo, J.M., Cardoso, P., Almeida-Neto, M. & Borges, P.A.V. (2015) The colonisation of exotic species does not have to trigger faunal homogenisation: lessons from the assembly patterns of arthropods on oceanic islands. *PLoS ONE* 10(5): e0128276.
- Garden, D. (2005) *Australia, New Zealand and the Pacific: An Environmental History*. Santa Barbara, CA: ABC-CLIO.

- Gibbard, P.L. & Walker, M.J.C. (2014) The term 'Anthropocene' in the context of formal geological classification. *Geological Society of London Special Publications* **395**: 29–37.
- Gillespie, R.G. & Clague, D.A. (eds.). (2009) *Encyclopedia of Islands*. Berkeley, CA: University of California Press.
- Gillespie, R.G. (2001) Oceanic islands: models of diversity. In: *Encyclopedia of Biodiversity* (Second Edition), ed. S.A. Levin, pp. 590–599. Waltham, MA: Academic Press.
- Gotelli, N.J. (2004) Assembly rules. In: *Foundations of Biogeography: Classic Papers with Commentaries*, eds. M.V. Lomolino, D.F. Sax, & J.H. Brown, pp. 1027–1035. Chicago, IL: University of Chicago Press.
- Grant, P.R. & Grant, B.R. (2006) Evolution of character displacement in Darwin's finches. *Science* **313**: 224–226.
- Grant, P.R. (1994) Ecological character displacement. *Science* **266**: 746–747.
- Helmus, M.R., Mahler, D.L. & Losos, J.B. (2014) Island biogeography of the Anthropocene. *Nature* **513**: 543–546.
- Hickman, C.S. & Hickman, C.S. (2009). Lord Howe Island. In: *Encyclopedia of Islands*, eds. R.G. Gillespie & D.A. Clague. Berkeley, CA: University of California Press.
- GESAMP (IMO/FAO/UNESCO-IOC/WMO/WHO/IAEA/UN/UNEP Joint Group of Experts on the Scientific Aspects of Marine Pollution) (1998) *Opportunistic Settlers and the Problem of the Ctenophore Mnemiopsis leidyi Invasion in the Black Sea*. London, UK: International Maritime Organization.
- Katovai, E., Sirikolo, M., Srinivasan, U., Edwards, W. & Laurance, W.F. (2016) Factors influencing tree diversity and compositional change across logged forests in the Solomon Islands. *Forest Ecology and Management* **372**: 53–63.
- Keegan, W.F. & Diamond, J.M. (1987) Colonization of islands by humans: a biogeographical perspective. *Advances in Archaeological Method and Theory* **10**: 49–92.
- Kier, G., Kreft, H., Ming, T., Jetz, W., Ibsch, P.L., Nowicki, C., Mutke, J. & Barthlott, W. (2009) A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences of the United States of America* **23**: 9322–9327.
- Kueffer, C. & Fernández-Palacios, J.M. (2010) Comparative ecological research on oceanic islands. *Perspectives in Plant Ecology, Evolution and Systematics* **12**: 81–82.
- Kueffer, C., Daehler, C.C., Torres-Santana, C.W., Lavergne, C., Meyer, J.Y., Otto, R. & Silva, L. (2010) A global comparison of plant invasions on oceanic islands. *Perspectives in Plant Ecology, Evolution and Systematics* **12**: 145–161.
- Kueffer, C., Kronauer, L. & Edwards, P.J. (2009) Wider spectrum of fruit traits in invasive than native floras may increase the vulnerability of oceanic islands to plant invasions. *Oikos* **118**: 1327–1334.
- Lewis, S.L. & Maslin, M.A. (2015) Defining the Anthropocene. *Nature* **519**: 171–180.
- Loire, E., Chiari, Y., Bernard, A., Cahais, V., Romiguier, J., Nabholz, B., Lourenço, J.M. & Galtier, N. (2013) Population genomics of the endangered giant Galápagos tortoise. *Genome Biology* **14**: R136.
- Lomolino, M.V. & Heaney, L.R. (2004) *Frontiers of Biogeography: New Directions in the Geography of Nature*. Sunderland, MA: Sinauer Associates.
- Losos, J. (2000) Ecological character displacement and the study of adaptation. *Proceedings of the National Academy of Sciences of the United States of America* **97**: 5693–5695.
- Losos, J.B. & Ricklefs, R.E. (2009) Adaptation and diversification on islands. *Nature* **457**: 830–836.
- MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.
- Maul, G. (2005) Small Islands. In: *Encyclopedia of Coastal Science*, ed. M.L. Schwartz, pp. 883–887. The Netherlands: Springer.
- McGuinness, K.A. (1984) Equations and explanations in the study of species area curves. *Biological Review* **59**: 423–440.
- Muchhala, N. & Potts, M.D. (2007) Character displacement among bat-pollinated flowers of the genus *Burmeistera*: analysis of mechanism, process and pattern. *Proceedings of the Royal Society of London B* **274**: 2731–2737.
- Nunn, P.D. (1994) *Oceanic Islands*. Oxford, UK: Blackwell.
- Otto, R., Arteaga, M.A., Delgado, J.D., Arévalo, J.R., Blandino, C. & Fernández-Palacios, J.M. (2014) Road edge effect and elevation patterns of native and alien plants on an oceanic island (Tenerife, Canary Islands). *Folia Geobotanica* **49**: 65–82.
- Otto, R., Barone, R., Delgado, J.D., Arévalo, J.R., Garzón-Machado, V., Cabrera-Rodríguez, F. & Fernández-Palacios, J.M. (2012) Diversity and distribution of the last remnants of endemic juniper woodlands on Tenerife, Canary Islands. *Biodiversity and Conservation* **21**: 1811–1834.
- Otto, R., Krüsi, B.O. & Kienast, F. (2007) Degradation of an arid coastal landscape in relation to land use changes in Southern Tenerife (Canary Islands). *Journal of Arid Environments* **70**: 527–539.
- Patiño, J., Carine, M., Mardulyn, P., Devos, N., Mateo, R.G., González-Mancebo, J.M., Shaw, A.J. & Vanderpoorten, A. (2015) Approximate Bayesian computation reveals the crucial role of oceanic islands for the assembly of continental biodiversity. *Systematics Biology* **64**: 579–589.
- Preston, F.W. (1968) On modelling islands. *Ecology* **49**: 592–594.
- Preto, F., Celesti-Grapow, L., Carli, E. & Blasi, C. (2010) Influence of past land use and current human disturbance on non-native plant species on small Italian islands. *Plant Ecology* **210**: 225–239.
- Richardson, D.M. & Whittaker, R.J. (2010) Conservation biogeography – foundations, concepts and challenges. *Diversity and Distributions* **16**: 313–320.
- Ricklefs, R.E. & Bermingham, E. (2002) The concept of the taxon cycle in biogeography. *Global Ecology and Biogeography* **11**: 353–361.
- Rigal, F., Whittaker, R.J., Triantis, K.A. & Borges, P.A.V. (2013) Integration of non-indigenous species within the interspecific abundance–occupancy relationship. *Acta Oecologica – International Journal of Ecology* **48**: 69–75.
- Rodríguez, A. (2001) Erosión y desertificación. In: *Naturaleza de las Islas Canarias. Ecología y Conservación*, eds. J.M. Fernández-Palacios & J.L. Martín Esquivel, pp. 317–321. Santa Cruz de Tenerife, Spain: Turquesa.
- Sax, D.F., Gaines, S.D. & Brown, J.H. (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *The American Naturalist* **160**: 766–783.
- Sax, D.V. & Brown, J.H. (2000) The paradox of invasion. *Global Ecology & Biogeography* **9**: 363–371.
- Schoener, T.W., Spiller, D.A. & Losos, J.B. (2001) Predators increase the risk of catastrophic extinction of prey populations. *Nature* **412**: 183–186.
- Shugart, H.H. (2004) *How the Earthquake Bird Got Its Name and Other Tales of an Unbalanced Nature*. New Haven, CT/London, UK: Yale University Press.

- Simberloff, D. (1995) Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science* **49**: 87–97.
- Simberloff, D. & Levin, B. (1985) Predictable sequences of species loss with decreasing island area – land birds in two archipelagos. *New Zealand Journal of Ecology* **8**: 11–20.
- Simberloff, D.S. & Wilson, E.O. (1969) Experimental zoogeography of islands: the colonisation of empty islands. *Ecology* **50**: 278–296.
- Smith, C.M. & Davies, E.T. (2012) *Emigration beyond Earth: Human Adaptation and Space Colonization*. New York, NY: Springer Science + Business.
- Smith, R.A. & Rausher, M.D. (2008) Experimental evidence that selection favors character displacement in the ivyleaf morning glory. *The American Naturalist* **171**: 1–9.
- Sol, D. (2000) Are islands more susceptible to be invaded than continents? Birds say no. *Ecography* **23**: 687–692.
- Steinbauer, M. J, Otto, R., Naranjo-Cigala, A., Beierkuhnlein, C. & Fernández-Palacios, J.M. (2012) Increase of island endemism with altitude – speciation processes on oceanic islands. *Ecography* **35**: 23–32.
- Terzopoulou, S., Rigal, F., Whittaker, R.J., Borges, P.A.V. & Triantis, K.A. (2015) Drivers of extinction: the case of Azorean beetles. *Biology Letters* **11**: 1–4.
- Thomas, C.D. (2013) The Anthropocene could raise biological diversity. *Nature* **502**: 7.
- Valero, G.M.C. (1994) Spratly archipelago dispute: Is the question of sovereignty still relevant? *Marine Policy* **18**: 314–344.
- Walter, H.S. (2004) The mismeasure of islands: implications for biogeographic theory and the conservation of nature. *Journal of Biogeography* **31**: 177–197.
- Warren, B.H., Simberloff, D., Ricklefs, R.E., Aguilee, R., Condamine, F.L., Gravel, D., Morlon, H., Mouquet, N., Rosindell, J., Casquet, J., Conti, E., Cornuault, J., Fernández-Palacios, J.M., Hengl, T., Norder, S.J., Rijsdijk, K.F., Sanmartin, I., Strasberg, D., Triantis, K.A., Valente, L.M., Whittaker, R.J., Gillespie, R.G., Emerson, B.C. & Thebaud, C. (2015) Islands as model systems in ecology and evolution: prospects fifty years after MacArthur–Wilson. *Ecology Letters* **18**: 200–217.
- Wetzel, F.T., Kissling, W.D., Beissmann, H. & Penn, D.J. (2012) Future climate change driven sea-level rise: secondary consequences from human displacement for island biodiversity. *Global Change Biology* **18**: 2707–2719.
- Whittaker, R.J. & Fernandez-Palacios, J.M. (2007) *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford, UK: Oxford University Press.
- Whittaker, R.J. (1995) Disturbed island ecology. *Trends in Ecology and Evolution* **10**: 421–425.
- Whittaker, R.J., Ladle, R.J., Araújo, M.B., Fernandez-Palacios, J.M., Delgado, J.D. & Arévalo, J.R. (2007) The island immaturity – speciation pulse model of island evolution: an alternative to the ‘diversity begets diversity’ model. *Ecography* **30**: 321–327.
- Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* **35**: 977–994.
- Williamson, M. (1988) Relationship of species number to area, distance and other variables. In: *Analytical Biogeography*, eds. A.A. Myers & P.S. Giller, pp. 91–115. London, UK: Chapman & Hall.