Oceanic island biogeography through the lens of the General Dynamic Model: assessment and prospect

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ABSTRACT

The general dynamic model of oceanic island biogeography (GDM) has added a new dimension to theoretical island biogeography in recognizing that geological processes are key drivers of the evolutionary processes of diversification and extinction within remote islands. It provides a dynamic and essentially non-equilibrium framework generating novel predictions

for emergent diversity properties of oceanic islands and archipelagos. Its publication in 2008 coincided with, and spurred on, renewed attention to the dynamics of remote islands. We review progress, both in testing the GDM's predictions and in developing and enhancing ecological–evolutionary understanding of oceanic island systems through the lens of the GDM. In particular, we focus on four main themes: (1) macroecological tests using a space-for-time rationale; (2) extensions of theory to islands following different patterns of ontogeny; (3) the implications of GDM dynamics for lineage diversification and trait evolution; and (4) the potential for downscaling GDM dynamics to local-scale ecological patterns and processes within islands. We also consider the implications of the GDM for understanding patterns of non-native species diversity. We demonstrate the vitality of the field of island biogeography by identifying a range of potentially productive lines for future research.

Key words: archipelago, diversity theory, General Dynamic Model, island biogeography, island evolution, trait evolution, volcanic islands.

CONTENTS

I. INTRODUCTION: THE GENERAL DYNAMIC MODEL

"I believe that a principal cause of the rarity or extinction of old species on oceanic islands is the subsidences they have all experienced. This sinking of the island operates in various ways. 1. It reduces the number of spots suitable to the habits of the plant. 2. It accelerates that struggle for existence which must terminate in the more hardy or more prolific displacing the less hardy or less prolific. 3. It reduces both the numbers and kinds of insects to whose activity the fertilising process in plants, and hence their

propagation, is so largely due..." — Joseph Dalton Hooker, lecture of 27th August 1866 (Hooker, 1867)

The general dynamic model of oceanic island biogeography (hereafter GDM) depicts the responses of the key processes of immigration, speciation and extinction to the ontogeny of volcanic islands formed over oceanic plates *via* magma plumes (Whittaker *et al.*, 2007; Whittaker, Triantis & Ladle, 2008, 2010; Borregaard, Matthews & Whittaker, 2015). The GDM is based on three key premises: (*i*) that the processes of immigration, speciation and extinction operate as functions of island isolation and area, as represented within MacArthur & Wilson's (1967) equilibrium theory of island biogeography (ETIB); (*ii*) that diversification is driven by unutilized ecological opportunity and within-island allopatry; and (*iii*) that species carrying capacity and within-island allopatry vary over time with the geological ontogeny of the island. It is primarily in the incorporation of premise *iii* that the GDM is distinct from the ETIB and generates a unique set of predictions (see Whittaker *et al.*, 2008, for details).

The ETIB proposes that species richness of near-source islands is a dynamic outcome of opposing rates of immigration and extinction, whereas on more remote islands the dynamic also involves speciation by diversification of successful immigrant lineages (MacArthur & Wilson, 1963). The ETIB thus predicts that species richness of even remote islands constitutes a dynamic equilibrium, with predictable rates of turnover. The lower extinction rates (and higher equilibrium species richness) predicted for larger islands permits the accumulation of endemics, with greater proportions of endemism found on the most isolated of islands (the 'radiation zone'; MacArthur & Wilson, 1963, 1967). Efforts to test these hypotheses have been thwarted by a combination of: (*i*) the long timescales of *in situ* diversification processes; (*ii*) the confounding effects of extensive anthropogenic and geological disturbance to systems; (*iii*) complications of interactions with other nearby

islands, which can affect immigration and extinction rates; (*iv*) the implicit assumption that

oceanic islands are static, with no consistent, predictable ontogeny; and (*v*) until recently, the

lack of explicit, complete and adequately calibrated phylogenies that allow documentation of

diversification processes that are crucial for the model (Whittaker & Fernández-Palacios,

2007).

The GDM addresses point *iv* by extending the theory to incorporate a model of island

ontogeny, which is specific to volcanic oceanic islands and can be summarized in four phases

(Fig. 1A): in stage 1 (youth or building), the island builds up towards its maximum elevation

and area while possessing a relatively limited complexity of topography. During stage 2

(immaturity), island-building processes slow down and are overtaken by erosive processes,

generating a more complex topography. In stage 3 (maturity), the island gradually undergoes

cessation of constructive volcanism, followed by significant loss of elevation and area due to

erosion, dissection, and subsidence. Stage 4 (old age) completes the island's lifespan, as

island elevation, area and topographic variation are reduced and ultimately eliminated by

erosion and subsidence. Whereas the GDM as originally described by Whittaker *et al.* (2008)

focused on oceanic islands that have this particular ontogeny, best represented within hotspot

archipelagos (Whittaker & Fernández-Palacios, 2007), it has recently been extended also to

cover subduction-based arc islands and continental fragments (Borregaard *et al.*, 2015). In

articulating the model, Whittaker *et al.* (2008) set out a series of graphical models focused on

the temporal development of a single oceanic island and its biota (e.g. Fig. 1), but also

considered that, at any one time, a suite of islands exists in an archipelagic context, with

islands at different stages of the island life cycle.

The GDM differs from the ETIB, not only by including the geological dynamism of

(oceanic) islands, but also in the notion that species accumulation on islands is affected by

diversity-dependent dynamics. Taking from the ETIB the expectation of declining

immigration rate I following island formation, opposed by rising extinction rate E, the GDM further stipulates that there is an environmental carrying capacity (K species as opposed to K individuals), which limits the number of species of a given taxon that can be sustained on an island at any given time (Figs 1, 2). K is a function of the resource base provided by the island and is hypothesized to vary over time, in concert with changing island area and elevational range. K should be conceptualized as representing not so much a fixed ceiling, but rather an effect of diversity dependence on rates of immigration, speciation and extinction: and the realized species richness is not predicted to reach K, except perhaps at a very late stage of an island's life (Borregaard *et al.*, 2015, and see the discussion in Rabosky, 2013; Fig. 1B). In stages 1 and 2 of the island's ontogeny K exceeds the realized richness by a substantial margin, as immigrants are insufficiently numerous to fill the available resource space and there has been insufficient time for *in situ* speciation to close the gap. This gap represents unutilized ecological opportunity, which, according to the GDM logic, is predicted to stimulate adaptive radiation. Over time, as the island enters stage 3, the realized species richness approaches K and diversity-dependent effects drive speciation rates down and extinction rates up. In stage 4, K itself declines, and the species richness must in time track this decline until the point at which the island founders.

The generally low immigration rate of species to remote islands means that the realized richness at any point in time will likely remain below that of near-shore islands or equivalent mainland areas. Assuming that K is set purely by resource availability, realized richness will track but remain below K for most of the island's life cycle (Borregaard *et al.*, 2015), implying that over much of an island's lifespan, the system is arguably not in a dynamic equilibrium, contrary to the assumption within the ETIB. Alongside the hump-shaped trend in K, the higher topographic complexity in stages 2 and 3 in the life of hotspot

volcanic islands creates numerous possibilities for within-island allopatry, stimulating speciation by local adaptive or non-adaptive processes (Fig. 2).

The introduction of the GDM has reinvigorated research on the diversity dynamics of islands, leading to the hope that we may be on the way to a coherent and comprehensive theory of island diversity (Heaney, Balete & Rickart, 2013; Borregaard *et al.*, 2015; Fernández-Palacios, Kueffer & Drake, 2015*a*). By incorporating island geology and diversity-dependent dynamics it has led to some new insights and, perhaps more importantly, it has sharpened the focus on outstanding questions concerning our understanding of island biotas, such as the importance of the archipelagic context for the process of species assembly and evolution, and the links between the phylogenetic histories of individual clades and island-level diversity dynamics. In this review, we first view island biogeography through the lens of the GDM, and identify key recent advances and questions. Whittaker *et al.* (2008) identified a set of 10 predictions derivable from the GDM: several of which since have been the subjects of formal analysis, reviewed in Section II. We then show how the GDM framework can be extended by incorporating more geological and environmental complexity. We go on to review other recently published modelling and empirical analyses (Chen & He, 2009; Givnish *et al.*, 2009; Rosindell & Phillimore, 2011; Knope *et al.*, 2012; Rosindell & Harmon, 2013; Valente, Etienne & Phillimore, 2014; Triantis *et al.*, 2015) permitting the development of a broader framework of island evolutionary ecology. Throughout, we aim to identify promising avenues for further research.

II. FORMAL TESTS OF THE GDM

(1) Tests of the ATT² model: comparative analyses of island biotic diversity metrics

If the biotic diversity on islands is controlled by GDM dynamics, measures of diversity are predicted to show a hump-shaped trajectory as the island ages. However, even hotspot oceanic islands may persist for several million years, making empirical tests of this relationship between diversity and island age challenging. Most studies have used a chronofunction or space-for-time-substitution approach, whereby adjacent islands of different ages are used to represent different points in the life cycle of an island. As the maximum size attained by each island usually varies, the realized areas of different islands of the same age may vary widely, both within and especially between archipelagos. Area determines species richness, diversification and extinction rates, and thus varying area trajectories among islands may confound relationships between age and diversity metrics. To control for this problem analytically, Whittaker *et al.* (2008) tested the GDM using a regression model specifying a linear term for island area, alongside the hump-shaped relationship between time (island age) and diversity: i.e. diversity = [log]Area + Time – Time². This ATT² model permitted initial evaluation of the GDM by reference to data for native and single-island endemic (SIE) species from the Azores, Canaries, Galapagos, Marquesas and Hawaii, for various groups of invertebrates and for higher plants (14 data sets in all). The statistical tests were carried out using multiple linear regression and were found to offer broad support for the GDM (Whittaker *et al.*, 2008; for more sophisticated re-analyses see Bunnefeld & Phillimore, 2012; Steinbauer *et al.*, 2013).

Since publication of the original 2008 paper, the ATT² model has been evaluated using an array of different taxa, island systems and analytical implementations. These analyses mostly comprise data for plant and invertebrate taxa from sub-tropical to tropical archipelagos (e.g. Borges & Hortal, 2009; Cardoso *et al.*, 2010; Wagner, 2012; Cameron *et al.*, 2013;

Patiño *et al.*, 2013; Aranda *et al.*, 2014). The approach has been extended to near-shore

continental islands (e.g. Fattorini, 2009), submerged sea mounts (Hart & Pearson, 2011) and

mountain-top habitat islands (Barrantes, Yglesias & Fuchs, 2011). Analysis has involved

testing the ATT² model alongside alternative competitor models on a range of diversity

properties that the GDM predicts should have hump-shaped relationships to island age,

including species richness, the number and proportions of single island endemics (nSIE, pSIE,

respectively) and a set of simple diversification indices (e.g. the species:genus ratio). These

tests have provided much support for the model but fits are not universally significant or most

parsimonious in multi-model comparisons. Fits have generally been best for archipelagos that

include a full range of island ages and stages (e.g. the Canary Islands), whereas positive

relationships with island age (the rising limb of the postulated hump) are prominent for

younger archipelagos, e.g. Azores (e.g. Borges & Hortal, 2009; Bunnefeld & Phillimore,

2012).

The degree to which different taxa adhere to the predictions of the GDM may be

ecologically instructive. Whereas the ATT² model provides generally good fits for snails

(Cameron *et al.*, 2013), spiders (Cardoso *et al.*, 2010) and flowering plants (Whittaker *et

al.*, 2008; Steinbauer *et al.*, 2013) in a range of archipelagos, including the Canary Islands

and Hawaii, a hump-shaped time function is insignificant for bryophytes (Patiño *et al.*,

2013). Bryophytes disperse by air-borne spores and have high dispersal ability, and

consequently have island distributions characterized by little differentiation and low levels

of cladogenetic and anagenetic endemism (Patiño *et al.*, 2013). Hence, while most remote

islands are Darwinian (dominated by evolutionary processes) for other taxa, the diversity

pattern for bryophytes reflects ecological rather than evolutionary dynamics. By contrast,

the dynamics of cave-dwelling arthropods appear to proceed through an accelerated GDM

process, with the early loss of cave habitats during the island ageing process matched by an early peak in diversity of cave species (Borges & Hortal, 2009).

A practical limitation of these macroecological tests is that the ATT² model involves three parameters and most oceanic archipelagos suitable for testing GDM predictions have too few islands (<10) for confident model fitting. To counter this, rather than fitting models separately for each archipelago, Bunnefeld & Phillimore (2012) proposed the use of mixed-effects models that can incorporate data from multiple islands, archipelagos and taxa into a single analysis. Although this approach entails the inclusion of different climates, biogeographical regions and island geological dynamics, the approach has recovered significant ATT^2 fits and yielded additional novel insights (e.g. Steinbauer *et al.*, 2013; Cameron *et al.*, 2013; Patiño *et al.*, 2013). For instance, the hump-shaped relationship for Hawaiian land snails is largely driven by two families that appear relatively dispersal-limited, and which have radiated extensively within Hawaii: the Achatinellidae, a group of tree snails confined to the Pacific Basin, and the strictly Hawaiian snail family Amastridae (Cameron *et al.*, 2013).

While these efforts to evaluate the ATT² model have been productive, it is important to caution that a number of important assumptions have to be made. Tests of the GDM depend on the quality of the inventory data (Gray & Cavers, 2014), the quality and precision of calibrated phylogenies, and the dating of island surfaces, which typically over-simplify complicated and idiosyncratic island-developmental dynamics (e.g. Carracedo *et al.*, 2002; Fernández-Palacios, 2011).

(2) Next steps in the use of macroecological metrics

The comparative analyses reviewed above have followed Whittaker *et al.* (2008) in focusing on the species richness of endemic or native non-endemic species. However, the GDM also

predicts that a number of other macroecological properties of island assemblages should change over the life cycle of islands, which may allow a more robust evaluation of the model and open novel opportunities for combining ecological and evolutionary research on island biota. Relevant properties might include within-island species–area relationships, species abundance distributions (SADs), species' range–size distributions, interspecific abundance–occupancy relationships, and functional trait space occupancy and packing. Several of these macroecological themes, largely unexplored in the context of the GDM (but see Rigal *et al.*, 2013), are discussed further below (Section IV).

III. INCORPORATING GEOLOGICAL AND ENVIRONMENTAL COMPLEXITY INTO ISLAND BIOGEOGRAPHY

The central tenet of the GDM framework is that processes of ecology and evolution are shaped by the intrinsic environmental dynamics of oceanic islands. This framework allows a broader theory of island biogeography, which integrates the complexity of temporal dynamics of island formation and the spatial configuration of archipelagos. Even so, the model articulated by Whittaker *et al.* (2008) assumed a highly simplified island ontogeny. In this section, we extend their framework to introduce greater realism and flexibility.

(1) The varied ontogenies of oceanic islands and archipelagos

(a) (*a*) *Island environmental dynamics related to the ageing process*

The GDM represented island geological dynamics as a scenario of build-up and erosion, best matched by classic hotspot archipelagos (Courtillot *et al.*, 2003), although highly simplified even for these systems. Volcanic hotspot islands are formed in relatively discrete time frames, by plate movements over active magma plumes in the Earth's mantle, yet also experience

episodes of building and erosion iteratively during the active phase. The result is that each volcanic island has a partly idiosyncratic ontogeny. Durations of active volcanism, the maximum size and elevation attained, the speed and extent of island subsidence and the longevity of islands can each vary substantially, and especially so between islands of different archipelagos (Figs 3 and 4; and see: Carracedo *et al.*, 2002; Price & Elliott-Fisk, 2004; Fernández-Palacios *et al.*, 2011).

Within Hawaii, which is the classic hotspot archipelago, the first *c.* 1 million years of island building are characterized by consistent volcanic activity, at the same time that a large part of the biota is assembled (Wagner & Funk, 1995). Substantial areas of such islands, especially in proximity to active vents, may be repeatedly covered by new flows, creating patches of substrate of varying properties and many different stages of ecosystem development. As substrates become recolonized, they undergo weathering and release nutrients to plants, so that the island surface becomes characterized by a patchwork of landscape units of different ages, soil qualities and nutrient levels. Patches spared by flows of lava can provide isolated refuges (in Hawaiian 'kipukas'), contributing to population subdivision, bottleneck effects, and micro-allopatry, potentially fuelling speciation (Carson, Lockwood & Craddock, 1990; Carson, 1992).

The resulting heterogeneity of habitats is further enhanced by the action of local meteorological processes that come into play as islands gain elevation and start interacting with airflow and circulation patterns. In archipelagos such as Hawaii and the Canary islands, the largest and highest islands (Fig. 3) eventually reach an inversion layer that prevents rain clouds from passing over the summit of the mountain, directing winds around and between the higher peaks. Together, these processes may lead to very strong mesoclimatic differences and thus high diversity of major ecosystem types over remarkably small areas (Whittaker & Fernández-Palacios, 2007; Fernández-Palacios *et al.*, 2014), resulting in a potentially

important role for habitat diversity in contributing to island diversity (e.g. Triantis *et al.*, 2003; Cardoso *et al.*, 2010).

The high heterogeneity of soil types, climate and habitats produced on young/intermediate-stage islands results in a network of patches that should facilitate intra-island allopatry among populations and stimulate local adaptation and drift (Fig. 2 and see, for example: Carson *et al.*, 1990; Carson, 1992; Macías-Hernández *et al.*, 2013). These characteristics and dynamics are predicted to result in elevated speciation rates in the early life stages of the island (Fig. 1; Whittaker *et al.*, 2008). The extension of some islands into higher elevations with distinct climate space and biomes also open them up to colonization from a wider array of source pools, with subsequent opportunities for colonizing lineages to undergo niche expansion into relatively unsaturated, geographically adjacent ecosystems and providing further impetus for *in situ* diversification processes.

It has been suggested that high-elevation habitats may on the whole be expected to experience lower immigration rates (and thus higher *in situ* speciation and endemism) than lowland habitats, because they are typically further away from potential source areas with similar habitats (e.g. all nearby islands have lowland areas, not all have highlands). This argument is supported by analyses of plant data for the Canary Islands (Steinbauer *et al.*, 2012). However, evidence from Hawaii suggests that numerous temperate lineages have colonized (Baldwin & Wagner, 2010) and radiated adaptively, with some species becoming specialized to low-elevation and tropical niches; e.g. Madiinae (Baldwin & Robichaux, 1995), the Hawaiian endemic mints (Lindqvist *et al.*, 2003), and *Schiedea* (Soltis *et al.*, 1996). These observations suggest interesting further lines of future research focusing on whether colonizing lineages from different source pools and habitat affinities exhibit differential rates of island evolution.

As islands age, volcanic activity diminishes, and surfaces and soils age (lowering nutrient availability; Hedin, Vitousek & Matson, 2003). Islands lose elevation by both erosion and subsidence (Fig. 3; Price & Clague, 2002), leading directly to the local extinction of species adapted to high-elevation habitats. This loss of ecosystem types at higher elevations (Fernández-Palacios *et al.*, 2014) is enhanced by climatic changes after glacial episodes, where inter-glacial warming and sea-level rise combine to reduce high-elevation area. The main effect of such changes in regional climate regime is to accelerate extinction rates, although the impact on the composition and species carrying capacity of particular islands will depend on their position within the global circulation pattern (Nogué *et al.*, 2013).

(b) (*b*) *Islands with complex geologies*

An important deviation from the simplistic GDM island ontogeny is the merging of multiple volcanoes into a single island, as is generally accepted to have happened in the formation of Tenerife from three proto-islands (Fernández-Palacios, 2011). The volcanoes may be either approximately coetaneous (erupting simultaneously, e.g. Isabela, Galápagos) or formed by successive eruption episodes (Maui and Big Island, Hawaii; Tenerife and La Palma, Canary islands; La Réunion, Mascarenes; or Tahiti, Society Islands). The island of La Réunion is a typical example of an island composed of two volcanoes at different ontogenetic stages: one summit [Piton des Neiges, 3070 m above sea level (a.s.l.)] is inactive and is losing elevation to erosion, while the other (Piton de la Fournaise, 2613 m a.s.l.) is active and growing (Lénat, Gibert-Malengreau & Galdéano, 2001). These kinds of dynamics indicate the need either for a more complex ontogenetic model, or for changing the scale of analysis to individual volcanic edifices within a particular island, and their interrelationships and connectivity over time. Examples of papers following the latter approach include Hochkirch & Görzig (2009) and

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Macías-Hernández *et al.* (2013), while a more macroecological approach to downscaling the GDM for within-island application is provided by Otto *et al.* (2016).

(2) Archipelagic dynamics

Hotspots usually form coherent archipelagos comprising several islands at different stages, but, as already highlighted, the environmental histories of individual islands/archipelagos may vary substantially. Within the Hawaiian archipelago, for example, O'ahu was in the past briefly conjoined to Moloka'i, which then became conjoined with Lana'i, Maui, and Kaho'olawe to form Maui Nui (Carson & Clague, 1995; Price & Elliott-Fisk, 2004), although they are currently separate islands. Within the extant Canary islands, Pleistocene sea-level changes saw Fuerteventura and Lanzarote joined together into a single island (Mahan) as recently as the end-Pleistocene sea-level minimum (Fernández-Palacios *et al.*, 2011). Similarly, the islands of Faial and Pico in the Azores may have been conjoined recently (Rijsdijk *et al.*, 2014).

Recent studies have highlighted the role of the archipelagic context in shaping the build-up of island biota. For example, in their analyses of vascular plant diversity of 23 archipelagos, Cabral *et al.* (2014) analysed the relative explanatory power of spatial and temporal connectivity between islands compared to classic biogeographical and climatic predictor variables. Whereas classic island biogeographical factors including area, age, elevation and isolation had high explanatory power for island species richness, intra-archipelagic spatial factors (number of islands, mean inter-island distance, area range, archipelago area and connectivity) had a strong effect on species turnover between islands. These findings support the notion that the spatial arrangement of islands within an archipelago and how this changes over time may have an important influence on gene flow

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and differentiation within archipelagos (Wagner & Funk, 1995; Amorim *et al.*, 2012; Ali & Aitchison, 2014; Carvalho *et al.*, 2015).

(a) (*a*) *Dynamics of island connectivity*

The gradual appearance and disappearance of islands creates spatial and temporal variation in the connectivity and isolation of islands, and affects rates of between-island immigration. On a shorter timescale, climatically driven sea-level changes also create marked archipelagic dynamics during glaciation cycles (Wallace, 1881; Miller *et al.*, 2005; Fernández-Palacios *et al.*, 2011). Whereas the biogeographical consequences of such sea-level changes are well appreciated in continental islands (e.g. Voris, 2000; Inger & Voris, 2001; Meijaard, 2003), the associated changes in area and connectivity have so far received comparatively less attention in the biogeography of oceanic islands (but see Ali & Aitchison, 2014; Rijsdijk *et al.*, 2014; Fernández-Palacios *et al.*, 2015*b*). At least three important consequences have been suggested: (*a*) changes in temperature and precipitation impact the elevational distribution of species and ecosystems, potentially leading to the emergence or disappearance of entire ecosystems, particularly those of the highest elevations (Fernández-Palacios *et al.*, 2014); (*b*) shifts in marine currents and wind regimes may greatly affect relationships to source areas, dispersal routes and dispersal rhythms of diaspores (Fernández-Palacios, Carine & Caujapé-Castells, 2013); and (*c*) sea-level changes may lead to island transgressions, and depending on the bathymetry of the zone may drastically alter the configuration of islands within an archipelago (Ali & Aitchison, 2014; Rijsdijk *et al.*, 2014)

Sea-level fluctuations have direct effects on island land area and on the submergence or emergence of islands. For some—but by no means all—oceanic islands, the sea-level minimum of the last glacial maximum (*c*. 120 m below present sea level *c*. 18–13 ka) (Miller *et al.*, 2005) caused substantial changes to island size (Rijsdijk *et al.*, 2014; Fernández-

Palacios *et al.*, 2015*b*). However, perhaps the most important consequence of sea-level fluctuations is how they affect the spatial and temporal connectivity of islands (Ali & Aitchison, 2014; Rijsdijk *et al.*, 2014). Low-lying seamounts may have emerged as islands above sea level and acted as stepping-stones during extreme glacial sea-level minima, allowing species to disperse between islands, while other, now separate, islands were joined together into a larger island (examples above).

(b) (*b*) *The effect of archipelago characteristics on speciation and richness dynamics*

The effects of varying island connectivity on the evolutionary dynamics upon oceanic islands remain poorly understood (Gillespie & Roderick, 2014), although a number of patterns should be expected on theoretical grounds. High spatial connectivity should increase rates of immigration and cause homogenization of archipelago floras and faunas while reducing the number of single-island endemics. At the same time, connectivity serves to reduce extinction rates by facilitating metapopulation dynamics and rescue effects (*sensu* Brown & Kodric-Brown, 1977). Finally, the process of repeated merging and separation of populations on distinct islands may have been an important driver of speciation dynamics (Ali & Aitchison, 2014), and may increase the potential for adaptive evolution by increasing the genetic variation within species (Carson *et al.*, 1990).

A central, and yet unanswered, question in island biogeography is whether most diversification occurs between populations within islands (labelled 'cladogenesis' in the original paper by Whittaker *et al.*, 2008), or between populations on separate islands (which is anagenesis as seen from the perspective of a single island). In the most common usage of these terms, anagenesis is diversification from the mainland ancestor, and cladogenesis is diversification into two or more species within the focal area (Stuessy, Crawford & Marticorena, 1990; Stuessy *et al.*, 2006, 2013). Anagenetic island endemic species are

typically widely distributed and exhibit effective dispersal (i.e. gene flow) across several islands, thus inhibiting between-island diversification.

Given the dynamic nature of island connectivity, it is a challenge to assess the relative prevalence of archipelago-level anagenetic speciation, between-island cladogenesis and within-island cladogenesis. For example, three single island endemics might occur on three intermittently connected islands, such as the Maui Nui complex of Maui, Lanai and Kahoolawe, where species A occurs on island A and shares a common ancestor with species B and C; species B occurs on island B, and shares a common ancestor with species C on island C. As the islands on which B and C occur have been intermittently joined and separated due to fluctuating sea level, it may be impossible to determine whether their origins should be termed anagenesis or cladogenesis at the island level, and whether the speciation events involved were entirely allopatric or not. Similarly, inter-island dispersal and local extinction make it difficult to infer the relative rates of anagenesis and cladogenesis from contemporary distributions. One example of this is given below (*Amarantus brownei* on Nihoa), a second concerns the two endemic species of *Rubus* in Hawaii, which turned out to be derived from two separate colonization events (Howarth, Gardner & Morden, 1997).

Under the GDM, the relative ratio of anagenetically and cladogenetically derived species is predicted to vary across an island's lifetime. Specifically, it is predicted that (*a*) within-island cladogenesis should peak in the intermediate/mature stages of an island's ontogeny, while, with time (*b*) those lineages that have radiated to produce sister species within the island should eventually collapse, and (*c*) at the penultimate step of that process should produce a pattern of 'false anagenesis' (i.e. one endemic form remaining of a once larger clade). For example, the enigmatic *Amaranthus brownei* from the island of Nihoa (an old remnant in the Northwest Hawaiian Islands), is the sole native representative of its genus (Wagner, Herbst & Sohmer, 1990), but could be the last of what was once a more diverse

lineage. For many taxa/lineages undergoing cladogenesis on oceanic islands, a high proportion of cladogenetic events appear to involve inter-island population subdivision, i.e. they are archipelagic rather than island-scale cladogenesis (for slightly more complex scenarios for Galapagos finches see: Grant, Grant & Deutsch, 1996). But the most prolific radiations require a combination of both, and imply a capacity of generally poor dispersers to at least occasionally jump-disperse within the archipelago (*cf.* the intermediate dispersal hypothesis; Agnarsson, Cheng & Kuntner, 2014). The spatial configuration of islands within the archipelago is predicted to play an important role in regulating such processes, and thus the likelihood of particular lineages speciating (Cabral *et al.*, 2014).

Studies of intra-specific diversity hold promise for improving our understanding of the relative prevalence of cladogenesis/anagenesis and are allowing us to identify genetic divergence patterns expected for endemic species in the context of the GDM. For example, recent comparative analyses of island plant species that have evolved anagenetically indicate that such species typically accumulate relatively high levels of intra-specific genetic diversity and show little geographic genetic partitioning compared to cladogenetically derived species (Takayama, Sun & Stuessy, 2012; Stuessy *et al.*, 2013; Takayama *et al.*, 2015*a*). In addition, Takayama *et al.* (2015*b*) found that genetic variation within 15 plant species endemic to the Juan Fernández archipelago was higher on the older island, a pattern that was consistent for both anagenetically and cladogenetically derived species. This may suggest a more general pattern of increased genetic diversity with island age. Anagenetic lineages also often encompass a greater diversity of ecotypes and habitat adaptations. Anagenetic species are often ecological generalists: in the Canary Islands, for instance, some of the most common species and subspecies in zonal ecosystems have evolved anagenetically (*Euphorbia balsamifera, Euphorbia canariensis, Juniperus turbinata ssp. canariensis, Olea europea ssp. guanchica, Laurus novocanariensis, Morella faya, Pinus canariensis* and *Spartocytisus*

supranubius) (Fernández-Palacios, 2011). Many species from large cladogenetic radiations, on the other hand, are locally rare, and may survive in just a few (often endangered) populations (e.g. species of *Cheirolophus, Limonium* or *Helianthemum* in the Canaries) (Bañares *et al.*, 2004). Similarly, in the Hawaiian Islands, anagenetic lineages provide disproportionate numbers of species considered to be generalists and ecologically dominant (Price & Wagner, 2004), whereas rare species are disproportionately distributed in large, radiating lineages (Sakai, Wagner & Mehrhoff, 2002).

(c) The inter-island progression rule and colonization

For a young, growing island, nearby older islands in an archipelago that already have a locally adapted flora or fauna are likely source pools for potential colonizers. For instance, practically all of the plant species of El Hierro, the youngest and westernmost of the Canary Islands, stem from older nearby islands; the only three known exceptions are native non-endemic species that are not found elsewhere in the archipelago (Otto *et al.*, 2016). This process of immigration from extant to new-formed islands as they appear creates a characteristic distributional pattern known as the island progression rule (Funk & Wagner, 1995), where the most basal members of an archipelagic radiation occur on the oldest islands.

The progression rule has been well documented (Cowie & Holland, 2006). Bess, Catanach & Johnson (2013) provide evidence for the pattern for the bark louse *Ptycta* (Psocidae) in the Hawaiian Islands, by constructing molecular phylogenies based on one nuclear and three mitochondrial genes. Molecular dating indicated that the single colonization event occurred about 7.14 Ma (4.73–10.05 Ma, 95% CI), possibly on a now largely submerged island. The subsequent radiation generated two main clades and a current total of 51 species on Hawaii, the majority of which are single-island endemics. Their calibrated phylogeny indicates support for the importance of dispersal events

between adjacent islands and provides good support for the progression model. The two major clades (A and B) were dated to 2.6–3.2 Ma, a period when Oahu was the youngest island. The authors comment on the existence of a single monophyletic Kauai subclade embedded within Clade A and infer that it may be the last surviving lineage of a once larger array of *Ptycta* on this, the oldest high island, consistent with the emphasis within the GDM on the collapse of endemic radiations on old and declining islands. Further examples are provided by, e.g. Wagner & Funk (1995), Craig, Currie & Joy (2001), and Bennett & O'Grady (2013), although there are frequently exceptions to the general pattern and some taxa (perhaps mostly late-arriving lineages) fail to conform. An example of such a late-arriving and non-conforming lineage is the Afrocanarian Blue Tit (*Cyanistes teneriffae*) on the Canary Islands, for which multiple independent colonization events to different islands, and deriving from different source pools, have recently been invoked (Gohli *et al.*, 2015).

Although the progression rule thus appears commonly to be upheld, it is perhaps a necessity that the most spectacular radiations tend to involve a dominance of within-island habitat or resource switching over inter-island colonization events. Price & Wagner (2004) evaluated 52 sister-species pairs and found that parapatric (ecological) speciation, mostly occurring within a single island, was just as common as allopatric speciation. Also, in their analysis of diversification within the lobeliads (Asterales: Campanulaceae; see below) on Hawaii, Givnish *et al.* (2009) find evidence of repeated habitat-switching and for a similar partitioning of habitats and of pollinators to have occurred on each of the four largest islands, involving members of two or more clades in each instance. The early colonization of this group (possibly as early as 13 Ma on an earlier high island) allowed the members of this lineage to act as 'keystone mutualists', triggering diversification of other Hawaiian taxa,

including drosophilids, many of which use lobeliads for mating or oviposition (Givnish *et al.*, 2009).

Published shortly after the GDM paper by Whittaker *et al.* (2008), the paper by Givnish *et al.* (2009) provides perhaps the most complete (if inadvertent) evaluation of several key aspects of the GDM. Givnish *et al.* (2009) present a molecular phylogeny for the Hawaiian lobeliad clade (Campanulaceae) – possibly the largest monophyletic plant radiation found on any archipelago – consisting of six genera and 126 species, or roughly an eighth of the Hawaiian flora. The founding event is estimated to have occurred on a former high island around 13 million years ago, and all genera had diverged ecologically as well as genetically within 3.4 million years after this event. The invasion of closed-forest understorey habitat was linked to a striking acceleration in net speciation rate, and there have been repeated transitions in terms of dispersal mechanism and habitat occupancy, combined also with partitioning of pollinators (Fig. 5). These patterns have been repeated on each of the four major islands, with most inter-island colonization events being consistent with the progression rule, i.e. colonization from older to younger islands. There is evidence of saturation being reached within no more than 1.5 Myr of island formation: individual volcanic mountains younger than this age have fewer species of lobeliads than the overall species–area relationship would predict (Fig. 6). Givnish *et al.* (2009), infer high rates of extinction of all lineages on islands older than Kauai (*c.* 4.7–5.0 Ma), which they observe is "…consistent with the known history of erosion and subsidence of the north-western Hawaiian Islands and the near absence of native lobeliads below 200 m in the Hawaiian chain" (p. 414). This large monophyletic radiation appears to provide an excellent exemplar of the expectations arising from the GDM, even down to the ecological differentiation between major groups within the radiation. For example, the GDM logic predicts that more-dispersive groups will exhibit larger numbers of colonization events and thus there is a higher likelihood of multiple members of the group colonizing each island,

and indeed of greater levels of inter-island gene flow: such groups should thus exhibit relatively low rates of speciation and endemism compared with less-dispersive groups. The lobeliads, being a large monophyletic radiation, allow other confounding factors to be set aside in drawing such comparisons. As described by Givnish *et al.* (2009), the lineages with minute wind-dispersed seeds (*Lobelia* section *Galeatella*, *Trematolobelia*, *Lobelia* section *Revolutella*, *Brighamia*), occupy open, windswept habitats. They are inferred to be far more effective long-distance dispersers than the 76 species of *Cyanea,* which are dispersed among (and presumably mostly within) wet-forest interiors by birds. This limited dispersal is also evidenced by the inference from the phylogeny that most inter-island dispersal events of *Cyanea* appear to have been from one older island to the next youngest in the chain (exemplifying the island progression rule). Consistent with the GDM predictions based on the differences in dispersability, the former wind-dispersed lineages on average show an island occupancy of 1.84 islands per species, whereas *Cyanea* occupy a much more restricted 1.11 islands per species.

Analogous patterns of repeated, independent specialization, rather than a classical progression rule, have been reported for *Tetragnatha* spider species. These spiders have four distinct ecotypes on each of the four high islands of Hawaii, which appear to have evolved independently on each island (Gillespie, 2004). This pattern indicates that niches and habitats are filled by local adaptation rather than by a fully developed array of specialized lineages colonizing from nearby islands, such that once different niches are filled on one island, the occupants of each niche in turn colonize the next island to emerge. The relative importance of these immigrations of habitat-adapted species from island to island *versus* the process of local diversification and adaptation is debated, and may vary among different archipelagos and taxa. In their review of archipelagic radiations, Whittaker & Fernández-Palacios (2007) label this dichotomy as clades responding primarily either to islands or to habitats: in the former

case colonization events are few, with habitat-switching common, while in the latter case, colonization events are comparatively more important in establishing diversity within a lineage, with habitat-switching less common, and thereafter habitat affinities being relatively conservative (Fig. 7). While the GDM is built on the assumption that the progression rule is a common to dominant pattern within oceanic archipelagic systems, further analysis of progression rule patterns and of associated habitat and ecological switching holds considerable potential for further refining island biogeographical models.

(3) Extending the GDM beyond oceanic hotspot archipelagos

(a) (*a*) *Plate-margin, subduction-based archipelagos*

Oceanic islands may be produced by three broad classes of processes (Nunn, 2009). Hotspot islands produced by magma plumes are discussed above; they occur widely over the world's oceans. Tectonic activity may also produce islands by uplift of ocean-floor materials (e.g. Cyprus; Panayides, 2009), especially as large land masses approach one another; much of the material that makes up the modern foothills of the Himalayas formed islands for a time, prior to being merged into the Asian continent and Indian subcontinent. Some modern oceanic islands in Wallacea (e.g. Timor and Sumba) and in the Philippines (e.g. Cebú, Bohol, and Masbate) have this type of origin (Nunn, 2009).

The third type consists of volcanic islands produced by subduction of the earth's crust, followed by production of magma that in turn produces volcanoes (Grove *et al.*, 2009). Because subduction zones have lengths of hundreds to thousands of kilometres, they typically produce archipelagos in which volcanic activity occurs simultaneously in many places, often in a sinuous, curvilinear shape; the Aleutians, Kuril, the Northern Marianas, the South Sandwich Islands and the Lesser Antilles provide examples of such volcanic arcs. Subduction zones typically persist for at least 5–10 million years, and often for many tens of millions of

years, and therefore produce islands and archipelagos that grow irregularly but progressively in area, connectivity, and height over time (Fig. 8). Some subduction zones cease their activity, causing the islands and archipelagos to disappear as erosion proceeds. Other subduction-zone-based archipelagos have an ultimate fate of merging into continental areas, as large-scale continental drift forms 'super-continents' (Hall, 2012).

Because subduction zones are large and persist over long periods of time, they tend to produce island arcs with many large, old islands. For example, Tonga, Fiji, Vanuatu and the Solomon Islands began to form along a subduction zone about 40 million years ago, followed by a complex series of tectonic movements that resulted in substantial changes to the number, size, and isolation of the islands (Colley, 2009), some of which are among the larger islands in the isolated portions of the Pacific. The largest current subduction-based island arc is the Philippine archipelago, which is officially said to contain 7,000 islands, and began to form *c.* 50 million years ago. The largest island (Luzón) is about 103,000 km^2, and has existed as a continuous dry-land area for about 30 million years (Hall, 2012; Heaney, Balete & Rickart, 2016).

Plate-margin islands begin their ontogeny in similar fashion to hotspot islands, but continue to grow during time spans within which most hotspot islands have progressed well into the decline phase or have foundered (Figs 3, 8). Some periods of quiescent subduction apparently are typical, but these are often followed by renewal of subduction and volcanic eruption. As islands grow, at times they merge, resulting in abrupt increases in area, sometimes on a very large scale.

Because of their old age, many plate-margin islands may be dominated by endemic clades that have evolved *in situ*. As an example, at least 88% of the approximately 60 species of non-flying mammals native to Luzón Island, in the Philippines, are members of two old endemic clades (Jansa, Barker & Heaney, 2006; Heaney *et al.*, 2016). One clade arrived *c.* 14

Ma, and has produced at least five genera and 14 species within Luzón (as well as some that colonized nearby smaller, younger oceanic islands), with an overall rate of one species per million years. The other clade arrived *c*. 8 Ma and has produced five genera and around 36 species on Luzón (and many elsewhere in the archipelago), with an overall rate of 4 species per million years. One sub-clade in the latter group is composed of forest mice that occur in montane regions on Luzón Island; speciation in this group has produced 11 species over a 0.5 Myr period, with a rate of *c*. 22 species per million years, largely by a process of repeated colonization of isolated mountain ranges (Justiniano *et al.*, 2015). The rate of speciation appears to have been approximately constant during the last 0.5 Myr. Sympatry of two species within the clade is common, but usually only among distantly related members of the clade. More recently arrived clades of mammals are less diverse and tend to occur in habitats that are disturbed or that have low diversity and abundance of native species: interestingly, exotic species are unsuccessful in invading natural habitats (Jansa *et al.*, 2006; Heaney *et al.*, 2013).

(b) (*b*) *Geological dynamics of short-lived islands*

Many islands of volcanic origin are small and have short lifespans; indeed, some volcanic oceanic islands last for very short periods of time, even down to just a few days, in which they emerge above the ocean surface, but do not consolidate or build further, and then disappear through erosion, sometimes before life can colonize. In many cases, these islands demonstrate the same characteristic geological ontogeny as larger islands, but on much shorter timescales, which greatly constrain the role of evolutionary processes in generating endemic species. Thus, for example, Fattorini (2009) discusses how the Aeolian Islands show a hump-shaped trajectory of island area over a time span of just 0.6 Myr, while Magnússon, Magnússon & Fridriksson (2009) comment that Surtsey, which emerged in 1963, built to its

maximum area (thus far) of 2.7 km^2 by June 1967, and by 2004 had already been reduced to 1.4 km^2. Being located in a high-latitude position, 33 km off Iceland, the species pool for colonization is poor and soil erosion processes act slowly; in the first decade of the 21st century Surtsey remained poorly vegetated and had low species richness of plants. The authors comment that they anticipate species richness increasing towards 80 to 100 species in the next few decades, after which they expect a decline driven by the continued erosion of the island and a tendency towards increasing dominance by a few species. How rapidly such islands enter and proceed through the process of erosion (and subsidence) depends on the characteristics of the volcanism involved and the resistance to erosion of the substrates.

(c) (*c*) *A more general theory of dynamic islands?*

The GDM was firmly rooted in a consideration of classic oceanic island archipelagos, emphasizing a simple hotspot island ontogeny. As discussed herein, analysis of island ontogeny may, however, be profitably downscaled to volcanos or massifs within a single island (e.g. Otto *et al.*, 2016), extended to analyses of multiple archipelagos simultaneously (e.g. Cameron *et al.*, 2013), or modified to apply to sea-mounts, short-lived near-shore islands, or persistent plate-margin islands. A hierarchical expansion of the model to encompass these islands and other contexts (e.g. mainland sky islands) would be a challenging but useful theoretical advance, especially if it were able to generate further testable predictions. Such a hierarchical expansion should take account of the dynamics of the spatial connectivity among islands, the role of archipelagic dynamics in the process of speciation, and how the evolution of the archipelagic species pool affects processes of island colonization, adaptation and extinction, the operation of taxon cycles (Economo & Sarnat, 2012) and the directionality of trait changes within the context of distinct island ontogenies.

IV.   DEVELOPING THE GDM FRAMEWORK OF ECOLOGY AND EVOLUTION ON ISLANDS

The macroecological tests reviewed herein confirm that large-scale patterns of island diversity are reasonably consistent with GDM predictions, but are not sufficient to demonstrate that the specific causality invoked by the GDM (Fig. 2) accurately describes insular diversity dynamics. The mechanics of the GDM posit that changes in diversity are caused by a complex interplay between habitat diversity, ecological opportunity, geological dynamics and area. It is not feasible to include all these explanatory variables in statistical analyses. Instead, evidence may come from detailed case studies, by simulation modelling (e.g. Borregaard *et al.*, 2015), or by investigating the individual assumptions and premises of the model.

Here, we develop alternative lines of evidence for testing the GDM framework, and lay out the consequences of a dynamic framework for ecological and evolutionary aspects of island biogeography. Our goal is to identify and highlight particular facets of island biogeography for which new insights may be gained, by interpreting them through the perspective of the GDM. While this exercise may help us build a more general picture of eco-evolutionary processes on oceanic islands, we do not aim to expand the GDM into a 'theory of everything'. The strength and robustness of the model may gain from an interaction with a variety of sub-disciplines, but many fundamental processes that underlie the topics discussed below lie outside the scope of what can and should be explained under the GDM's remit. Our hope is to stimulate discussion on 'core' island biogeography topics within the wider field of ecology and evolution, so as to inspire further research on biodiversity on islands.

(1) Patterns of lineage diversification

Central to the GDM is the idea that early in the lifespan of isolated oceanic islands, unusual levels of ecological opportunity, i.e. vacant niche space, generate enhanced rates of speciation and diversification. Perhaps the most direct way to assess this proposition is by analysis of diversification within lineages. This is complicated by the fact that there is typically a strongly skewed pattern of diversification (Price & Wagner, 2004; Domínguez Lozano *et al.*, 2010): most island colonists, even on the most remote islands, fail to diversify, generating zero or only one endemic species *via* anagenesis (Papadopulos *et al.*, 2011; Igea *et al.*, 2014), while a few radiate spectacularly. These few prolifically radiating groups are typically those that attract analysis by molecular biologists; hence some caution is required in reviewing such data for comparative purposes. However, there is evidence that speciation rates in islands are generally much higher than in mainland regions under similar climatic conditions. Analysing the radiation of 19 species and eight subspecies of Hawaiian *Bidens* (Asteraceae), Knope *et al.* (2012) noted that diversification rates for flowering plants as a whole have been estimated to fall within the range 0.078–0.091 net speciation events per million years. They estimated a rate of 0.3–2.3 for Hawaiian *Bidens,* which is comparable with the fastest continental radiations, such as the 'sky-island' Andean *Lupinus* (2.5–3.7; Hughes & Eastwood, 2006). These numbers become even more striking considering that the radiation of *Bidens* has occurred in a much smaller area. Expressed on a per unit area basis, Knope *et al.* (2012) found that the radiations of *Bidens* and another classic insular plant radiation, the Macaronesian genus *Echium*, were 1–4 orders of magnitude faster than celebrated continental groups, such as *Lupinus* or Eurasian *Dianthus* (Valente, Savolainen & Vargas, 2010).

(a) (*a*) *Temporal changes in net diversification on islands*

Evidence for the key prediction—that rates of per-species speciation and extinction peak on younger islands—can be gathered from molecular analysis of individual radiations on islands. Analyses of the increasingly available molecular phylogenies for oceanic island lineages provide a powerful means to compare the current diversification rates on islands of different ages within an archipelago (e.g. Bennett & O'Grady, 2013). Over the last decade, several statistical methods have been developed to draw inferences about diversification patterns and diversity dynamics from reconstructed phylogenetic hypotheses (Morlon, 2014). Such changes in diversification rate are not immediately transferable to the GDM because radiating clades may be younger than the islands on which they appear (or older, in cases like Hawaii where some of the archipelagic biota originally colonized islands that are no longer extant; Price & Clague, 2002). Even so, such highly resolved studies provide valuable information for addressing the predictions of the GDM, and may be valuable sources of evidence in developing the GDM framework. These methods may be able to distinguish between equilibrium and non-equilibrium systems and to infer changes in diversification rate and the underlying speciation/extinction ratio (Valente, Phillimore & Etienne, 2015). Here we rely largely on evidence from phylogenetic analyses of individual clades, published since Whittaker *et al.* (2008).

Analyses of two genera of Canarian spiders, *Dysdera* and *Pholcus,* both of which peak in richness on intermediate-aged islands, support the notion that diversification rates are lower on older islands (Cardoso *et al.*, 2010). For *Dysdera,* a genus of woodlouse-hunting spiders, diversification-rate analysis restricted to species occurring within the eastern Canary Islands indicates a significant deceleration in diversification within the last few million years on Lanzarote and Fuerteventura, the two oldest Canary islands (*c.* 16–20 Ma). This result is compatible with increasing extinction rates (or decelerating speciation

rates, or both) due to ecological changes driven by climatic and geological changes in the eastern Canaries (Macías-Hernández, Oromí & Arnedo, 2008). *Pholcus* appears to have had a long evolutionary history within the Canaries, with evidence of deceleration in species accumulation between 3.5 and 1 Ma, but most current species are the result of rapid, recent speciation from around 0.7 Ma, possibly driven by sexual selection. Species richness peaks on the intermediate-aged islands of Tenerife and Gran Canaria (Dimitrov, Arnedo & Ribera, 2008; Cardoso *et al.*, 2010).

A similar analysis by Havran, Sytsma & Ballard (2009) determined evolutionary relationships among Hawaiian violets based on nuclear rDNA data. This lineage most probably established on the Maui Nui complex within the last 1.2–2 Myr, subsequently diversifying adaptively into clades with dry- (dry forest and cliffs) and wet- (higher habitats including cloud forests and bogs) adapted species. Species colonized both the older islands of Oahu and Kauai from this origin on Maui Nui, and subsequently colonized the newly emerged island of Hawaii. Estimates of molecular evolution rate indicate that species on the younger islands (those of the Maui Nui complex and Hawaii) are diverging more rapidly than are their analogues on Kauai. As also found for the larger radiation of Hawaiian lobeliads (see Section III.2*c*), there has been a greater propensity for species of open habitats (bog or dry forest) to disperse between islands than for species of the wet-habitat clade.

(b) (*b*) *Changes in diversification rate within clades*

For very well-described radiations, molecular substitution models make it possible to assess changes in diversification rate of individual clades explicitly, instead of comparing diversification rates on different islands (Liow, Quental & Marshall, 2010). Bennett & O'Grady (2012, 2013) analysed changing rates of diversification over time using a six-gene

molecular data set for 191 species of leafhoppers in the genus *Nesophrosyne* (Cicadellidae) from the six largest Hawaiian Islands. They used a time-calibrated maximum clade credibility tree within a 'relaxed Bayesian' framework and rejected the hypothesis of a constant rate of diversification. Their reconstructions indicate an origin on the oldest high island Kauai (<5.0 Ma) and support an initial high rate of diversification, associated with host-plant transitions involving Urticaceae and Rubiaceae, and with the establishment of the lineage on slightly younger, multi-volcano islands, as they emerged and developed in turn (Bennett & O'Grady, 2013). They further reported that "[n]et diversification rates exhibit a diversity-dependent decline, corresponding to the end phase of island formation" (Bennett & O'Grady, 2013, p. 1512), and in particular a recent slowdown at 0.16 Ma following the end of the formation of the Mauna Loa massif *c*. 0.2 Ma. Their work thus supports an opportunity-driven model of diversification for these host-plant-specific leafhoppers, in which the geological dynamics of the island system are interwoven with the arrival times of their host plants and with inferred roles for competitive interactions with other insects. In particular, they emphasised that…

"[t]he repeated pattern of host–plant transitions on both old and young islands, and especially across large evolutionary distances between hosts, indicates that this pattern is a continually operating driver of diversification in *Nesophrosyne*" (Bennett & O'Grady, 2012, p. 715), with an important role also found for allopatric speciation within islands connected to high topographic complexity. They thus noted that their data support three predictions from the GDM: (*i*) high early rates of speciation on newly emerged and unsaturated islands, (*ii*) a transition to greater importance of non-adaptive mechanisms as topography and other features of the island become more variegated, and (*iii*) a decrease in diversification linked to the finite resources of older islands.

(c) *(c) Are speciation patterns driven by a subset of taxa of intermediate dispersability?*

Although oceanic islands are known for their high endemism, typically the histogram of the number of endemic species per endemic lineage is strongly skewed, with very few lineages speciating profusely and with most lineages that contain endemics producing just one or two species (Price & Wagner, 2004, 2011; Whittaker & Fernández-Palacios, 2007; Papadopulos *et al.*, 2011; Igea *et al.*, 2014). Thus the cladogenetic response that drives the hump-shaped trajectory of species richness can be attributed to a relatively small number of extensively (and often rapidly) radiating lineages (*cf*. Givnish *et al.*, 2009; Section III.2*c*). This has been demonstrated indirectly in analyses of species densities for several Hawaiian clades by Gillespie & Baldwin (2010), who found that the richest clades peak in density on intermediate-aged islands (although this result must be interpreted with some caution, as these islands are also the most geologically complex in Hawai'i). It is also evident in the family-level ATT^2 regression models for Hawaiian snails reported by Cameron *et al.* (2013), in which the richest families demonstrated the clearest ATT^2 pattern.

In general, we would expect, on theoretical grounds, that lineage radiation should be favoured in taxa with limited levels of dispersability. Similar to MacArthur & Wilson's (1967) concept of the radiation zone, the greatest amount of radiation is predicted to occur when dispersal events are possible but infrequent, thus allowing reproductive isolation to be maintained while adaptive processes or non-adaptive drift cause differentiation to occur (*cf*. the intermediate dispersal hypothesis; Agnarsson *et al.*, 2014). Within flowering plants, there is great variation in dispersal ability, and genetic analyses reveal that lineages that have spread to several islands without producing multiple endemics typically show elevated genetic mixing between islands (e.g. García-Verdugo *et al.*, 2010; Takayama *et al.*, 2012, 2015*b*; Pérez de Paz & Caujapé-Castells, 2013). Lineages that radiate extensively, by contrast, are more likely to feature small-ranged single-island endemic

species that possess limited dispersal powers. These species exhibit reproductive isolation over short geographic distances, thus permitting high rates of within-island cladogenesis. Although such hypotheses are well founded in theory, formal tests of them would require high-resolution distributional data, alongside analyses of genetic distance and gene flow among populations.

The standard logic for remote-island colonists is that they must possess exceptional dispersal ability, but that once having colonized many taxa/ecological groups undergo strong selection pressure for loss of dispersal ability (Whittaker & Fernández-Palacios, 2007). There is some evidence for this and for differential dispersal capacities within radiating lineages to be related to the rate of differentiation (Section III.2*c*). However, a naïve analysis of dispersal syndromes may fail to predict how some species actually colonized a remote archipelago, as very rare non-standard means of arrival may account for the colonization of poorly dispersing species, which means that post-colonization loss of dispersal ability cannot always be inferred (e.g. Heleno & Vargas, 2015). Hence, the analysis of dispersal-trait evolution within radiating lineages should prove a productive but at times challenging line for further research. Part of the challenge will come from other confounding factors that need to be considered alongside dispersal traits. For example, there is also evidence that, for species arriving early, the absence of closely related species could be particularly conducive to *in situ* radiation in oceanic island plants (Heaney, 2000; Silvertown, Francisco-Ortega & Carine, 2005). Analyses of multiple systems is therefore necessary to permit robust tests of such hypotheses.

(2) Temporal patterns of empty niche space

The GDM postulates that the diversity dependence of speciation and extinction on islands results from changes in the availability of empty niche space: this can be conceptualized as

volumes within the hyper-dimensional niche space that are unoccupied, creating directional selection on populations and possibly stimulating the formation of reproductive isolation. Empty niche space is predicted by the GDM to be most available during the early stages of the developmental history of an island's biota and landscapes (stage 1 to 2), but then diminish over time as the species richness of the island approaches K_{max}, and to almost disappear late in island life as extinctions come to dominate. Here we expand on this line of thinking.

(a) (*a*) *Empty niche space and the diversity of functional traits*

Although empty niche space is a fuzzy concept, it may be possible to test the GDM predictions by analysing the occupancy of functional trait space by taxonomic group (e.g. spiders, or all arthropods) in relation to the developmental stage of an island within an archipelago. While such a test has yet to be performed, Whittaker *et al.* (2014) illustrate a general approach of quantifying functional trait space occupancy for beetles and spiders of the Azores. Their analyses demonstrate how endemic, native non-endemic, and exotic species contribute to the functional space occupancy in Azorean native forests. Interestingly, the results provide no support for saturation of trait space at the island level.

While richness should, according to the GDM, exhibit a hump-shaped relationship with island age that should be reflected in functional diversity, we may also predict tighter, more regular packing of functional trait space over time. At the outset, islands are likely to be colonized by a strongly dispersive subset of species, providing a relatively limited array of traits. This array will increase with the arrival of further colonists, and with new species generated by adaptive cladogenesis. When an island is in transition between stages 2 and 3, we would anticipate considerable opportunities for allopatric populations of congeners, including those arising from seemingly non-adaptive cladogenesis: such species may be relatively little differentiated in functional traits. However, as opportunities for allopatry

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diminish and extinction rates rise in stage 4, there should be a decrease in richness, filtering out species specialized to habitats that are being lost and increasing competitive exclusion among those with similar functional traits. This suggests both a decrease in overall volume of the trait space, concordant with decreases in richness, but also a more regular spacing of traits within that trait volume. It should, in principle, be possible to test these predictions, although this requires both the availability of appropriate trait data and of metrics that can distinguish between the alternative scenarios.

(3) Local-scale processes and biotic interactions

While the GDM focuses on emergent diversity properties of islands, a more mechanistic understanding of the underlying processes would require forging an explicit link to local population dynamics. While much recent attention has been given to the problem of linking patterns and process across different scales, it remains challenging to do so in empirical analyses for several reasons, e.g. (*i*) in local-scale analyses it can be difficult to ensure that all relevant confounding variables have been eliminated or held constant, and (*ii*) it is unclear to what degree patterns are consistent across scales (Srivastava, 1999; Gaston, 2000). Hence, it would seem necessary to establish scaling relationships by means of multiple hierarchical nested data series for well-specified systems before attempting to interpret tests made in isolation at a particular, fine scale of analysis.

The main focus of the GDM framework is the interaction between the geological dynamics of islands and the evolutionary and ecological processes that shape island biota. Some of these processes are abiotic in nature, and relate to the complexity of island topography and meso-climate. As biota gradually build up, interactions between species become increasingly important in determining the success of colonization and speciation, and the selective regime for local adaptations (Thompson, 2013). This is intuitively apparent on

volcanic islands, which start out as sterile environments lacking organic material but, being subject to an array of inputs (e.g. deposition of flotsam, fallout of live and dead insects and seeds, deposition of guano, etc.), quickly develop functioning ecosystems. Indeed, they can develop limited detritus-based food webs prior to the first plant colonization (Whittaker & Fernández-Palacios, 2007). The initial stages of ecosystem spin-up typically involve feedbacks between species of plants and animals, such as those based around key plant-dispersal mutualisms (e.g. as shown for Krakatau; Whittaker & Fernández-Palacios, 2007). Later, new untapped resource space for a lineage can open up, by adaptive shifts or by the arrival of a 'keystone mutualist', a pollinator, food plant, etc., that may stimulate the diversification of a particular lineage (e.g. Givnish *et al.*, 2009). Thus, the local biotic interaction structure, i.e. the local ecological network composed of all species and their interactions, builds up slowly and has a profound impact on the adaptive evolution of species.

As hotspot islands go through their life cycle, the topographic complexity of the island is also predicted to increase, and then decrease relatively late in the island life cycle. This topographical complexity of the abiotic environment may also lead to a complex spatial distribution of the biotic interaction network, creating fractal patterns of e.g. vegetation and distribution of habitat (e.g. Alados *et al.*, 2005; Kéfi *et al.*, 2007; Scanlon *et al.*, 2007). Higher topographical complexity, habitat diversity, fractality of the environment and overall species richness should also lead to an increase in the diversity of trophic relationships. Understanding the latter is the domain of trophic island biogeography, a synthesis of food web theory and island biogeography (Holt, 2010; Gravel *et al.*, 2011). This theory moves the focus to 'vertical' ecosystem processes that cross trophic levels, such as predation, and away from the 'horizontal' processes of competition and extinction, on which the ETIB was founded.

The 'exploitation ecosystems hypothesis' (Oksanen & Oksanen, 2000) describes how the trophic layers of an ecosystem are added successively, e.g. at a certain prey richness, predators begin to arrive, etc. (Terborgh, 2009). As new layers are added, frequency-dependent predation reduces prey populations, which relaxes interspecific competition among prey, and opens new ecological opportunities at lower trophic levels (Schluter, 2000). Thus, the trophic network itself is predicted to stimulate the processes of adaptive speciation, as formulated by Thompson (2005) in his coevolutionary alternation hypothesis.

Like trophic networks, mutualistic interaction networks may also augment speciation. Interacting communities of species act as each other's selection regimes: e.g. plants interact with their pollinators and select for specific traits in pollinator species, and *vice versa*, i.e. pollinators select for certain plant traits. This reciprocal process may be seen as a co-evolutionary vortex, which involves more and more species as the network grows. New interactions become established between species with complementary traits, causing trait convergence among species of the same community. Because of the benefits of mutualistic interactions, the involved species may become more abundant; this again facilitates the formation of additional links, and as a consequence the network grows in size. At some point in the GDM cycle, the interaction networks become so species rich and complex that strong unidirectional selection can no longer operate (see Thompson, 2013). Thus the co-evolutionary effect weakens, and adaptation and speciation are expected to slow down. Biodiversity has its own internal network dynamics, acting as a self-augmenting process, which is accelerated or decelerated by biodiversity itself (Thompson, 2005; Bascompte & Olesen, 2015), in addition to the effects of the abiotic environment.

(a) (*a*) *Ecological network complexity*

Trøjelsgaard *et al.* (2013) developed the argument that changes in richness and species composition over the life cycle of islands should be reflected in the complexity of inter-specific interaction networks at the local scale. Using five of the Canary Islands as a case study system, they investigated the relationship between various properties of insect pollination networks and the age and area of islands. Their analysis was based on field data from 12 sites selected to include sizeable populations of the shrub *Euphorbia balsamifera,* in order to provide a degree of standardization of habitat type. Two of these sites were located within massifs of differing ages within Tenerife, and because of their differing evolutionary and geological histories, they were allocated different ages in the analyses. The richness of plant–pollinator interactions and the average degree of pollinator specialization showed hump-shaped relationships with island age, as did plant species richness. Pollinator richness largely matched overall invertebrate richness, but intriguingly, the proportion of single-island interactions showed a U-shaped relationship with age. (Single-island interactions are those only observed on single islands, although the species involved may be found on other islands.) This unexpected result may reflect differences in the patterns of development of specialization with island age between plants and their pollinators.

Other types of ecological networks, such as the interaction between plant species and herbivorous insects, host–parasitoid interaction networks and decomposition food webs are also predicted to increase and then reduce in complexity with island age. For example, a study of arthropod communities from grasslands on the Azores found that the oldest island, Santa Maria, had more specialized herbivores and a greater ratio of herbivores to predators than the rest of the archipelago (Borges & Brown, 1999). Island communities generally tend to have high proportions of generalist parasitoids (Santos *et al.*, 2011), but the link between this pattern and island age has not been clarified, and is a promising avenue for future study.

(b) (*b*) *The interaction of habitat diversity and local species richness*

How habitat diversity interacts with local-scale species diversity patterns to determine emergent island-scale patterns remains poorly understood. One line of argument based on the GDM would be that local species richness should be expected to increase in the early stages of island diversity increase, as the processes of immigration and ecological speciation add species to the species pool. Species density within habitats should increase as the island matures, but as the island declines in old age (stages 3 and 4) it may be anticipated to decline again, because the island's pool of species around the patch decreases. The loss of island area means that there will be fewer 'sink' species around to supply transient/ephemeral members to local communities (see also Matthews, Borges & Whittaker, 2014*a*). A few recent studies have explicitly tested the response of local species diversity to island age using the GDM's ATT^2 model (e.g. Keppel, Buckley & Possingham, 2010; Gillespie *et al.*, 2013). These studies took a subtly different line in arguing that there should be proportionality between plot-level and whole-island-level diversity if other factors (e.g. habitat type, elevation, disturbance, etc.) are controlled for, i.e. that diversity of small plots within islands should scale with the overall diversity of each island across an archipelago. While such analyses are challenging to conduct in practice, further analyses of local–regional richness relationships for oceanic islands should prove productive (Ricklefs, 1987; Srivastava, 1999; Borges & Brown, 2004; Gruner, 2007; Karger *et al.*, 2014).

(c) *(c) Species abundance distributions*

As communities build up and erode over the island life cycle, the relative abundance of species at local and regional scales should also undergo major changes. The abundance of species within each ecological community is commonly described by a species abundance distribution (SAD; McGill *et al.*, 2007), typically categorized in terms of how well they resemble a geometric, log-series or log-normal distribution, although multi-modal patterns can also occur (Matthews & Whittaker, 2014; Matthews *et al.*, 2014*a*). Whereas poor communities, dominated by few abundant species, follow a geometric series, communities dominated by mostly rare species follow a log-series, and communities with many common, intermediate and rare species follow a log-normal distribution (i.e. a distribution where the maximum occurs for intermediate abundance classes). Unfortunately, very few studies are available in which communities were sampled in a standardized fashion for islands of different geological age, thus we are as yet unable to analyse SADs formally in relation to the GDM [but see Borges & Brown (1999) and Matthews *et al.* (2014*b*) for a potentially promising approach using data from the Azores].

In the early stages of island formation few species may dominate the communities, generating a right-skewed distribution as observed for Terceira Island, Azores. As islands grow in complexity and new niches are created, early bursts of species formation (cladogenesis) may create a disproportionate number of rare species, pushing the SADs towards the log-series. These rare species may support new functions in the island ecosystems and eventually may become more abundant, adding to the intermediate mode of species abundance. More mature and complex islands can support more habitat types and thus more species. They can also support more replicated patches of the same habitat types, which may contain different species, generated by within-island reproductive isolation. Thus, we may expect a log-normal distribution at the whole-island scale. The late stages of island ontogeny

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are characterized by loss of habitats, biotic impoverishment and a tendency towards increasing dominance by a few species. This might induce a gradual shift from log-normal towards log-series SADs (i.e. increasing right skew).

A slightly different approach is to deconstruct entire island assemblages into different biogeographical subsets (SIEs, archipelagic endemics, and native non-endemics), analysing each subset for particular patterns individually. In such an analysis, for Azorean arthropods, Fattorini *et al.* (2016) found that the slopes of regression lines in rank–abundance plots fitted by the geometric series were highest for SIEs, which indicates a relative predominance of few highly abundant SIE species that may be assumed to be well adapted to their islands.

(4) Recent introductions and invasive species

Most populated oceanic islands are inhabited by large numbers of species that have been introduced by the actions of humans, in many cases outnumbering the species native to islands. For example, on the Azores about 80% of the current flora (Silva & Smith, 2004; Carine & Schaefer, 2010) and 58% of arthropod species are exotic (Borges *et al.*, 2009). In some islands, the introduction of non-native species has led to profound changes in the ecological dynamics, and to the extinction/endangerment of many native and endemic species (Whittaker & Fernández-Palacios, 2007; Cardoso *et al.*, 2010; Kueffer *et al.*, 2010; Triantis *et al.*, 2010; Helmus, Mahler & Losos, 2014; Terzopoulou *et al.*, 2015). This complicates the interpretation of presently observed species numbers in the context of island biogeographical theories such as the GDM. It also raises the question of what predictions may be derived from the GDM for the species richness of non-native species across oceanic archipelagos.

Given that the richness of non-native species is not determined by *in-situ* speciation, the mechanisms invoked by the GDM (Fig. 1) do not apply directly to these species. Their realised richness on oceanic islands might therefore be expected to be a function of island

area, habitat diversity, human population size, or some measure of connectivity of human societies with remote source regions (Blackburn *et al.*, 2015), rather than showing a strong (or independent) relationship with island age (see analysis by Borges *et al.*, 2006). However, given that non-native species may interact directly with the existing native species pool on the island (Florencio *et al.*, 2013; Rigal *et al.*, 2013), a strong relationship between native species richness and non-native species richness may also be anticipated (Blackburn *et al.*, 2015). Indeed, analysis of island species–area relationships (ISARs) across several oceanic island archipelagos suggests that native and non-native species ISARs often have very similar forms and slopes (e.g. Sax, Gaines & Brown, 2002; Whittaker & Matthews, 2014; Whittaker *et al.,* 2014) and thus that non-native patterns at the island scale echo those of the native biota.

The great success of non-native and invasive species on oceanic islands and the consequent net increase often observed in island species richness (Sax & Gaines, 2008), appears to indicate that indigenous island biota are far from ecological saturation. This may seem to contradict the notion that most old oceanic islands (stages 3–4) have biota close to an inherent carrying capacity or dynamic equilibrium. However, human introductions of species to islands usually occur in the context of massive habitat alteration, changes to nutrient levels and modified disturbance regimes. For example, the Azores were almost completely covered by quite homogenous sclerophyllous laurel forest at the time of human colonization in the 15th century, but today this type of forest only takes up 2.5% of the area of the islands, which are now predominantly covered by a mixture of open pastures and plantations of exotic *Cryptomeria* and *Eucalyptus* (Borges *et al.*, 2009; Cardoso *et al.*, 2009; Triantis *et al.*, 2010). The introduced arthropod fauna on the Azores, which constitutes 58% of the total (Borges *et al.*, 2009), is largely associated with these novel habitat types, whereas the native fauna still dominates the remnants of original laurel forest (Borges *et al.*, 2006). In the Azores, exotic arthropod species are already integrated into the indigenous communities (Rigal *et al.*, 2013;

Whittaker *et al.*, 2014), promoting assemblage homogenization (Florencio *et al.*, 2013). Consistent with this, most exotics appear able to build up high abundances only in anthropogenic habitats (Borges *et al.*, 2008; Meijer, Whittaker & Borges, 2010), although there are important exceptions. In the Philippines, exotic rats are able to invade natural habitats when these have species-poor native rodent communities, but are unable to do so when the native communities are species rich (Rickart *et al.*, 2011), indicating that an intact local biota can withstand invasion by exotics. However, it is too early to say if these patterns may be generalized to other oceanic archipelagos.

Another hypothesis for the success of non-native species in colonizing and spreading within oceanic island systems has been that island interaction networks may be disproportionately easy to add species to and specifically that some high-abundance endemics are super-generalized and thus 'pre-adapted' to include exotics as new interaction partners (Olesen, Eskildsen & Venkatasamy, 2002). Yet it is also the case that many non-native species form entirely new networks of mutualists, for example, with exotic birds or mammals acting as seed-dispersal agents for exotic plants (Whittaker & Fernández-Palacios, 2007).

From this very brief review, it appears clear that our understanding of patterns and processes for non-native species diversity within and among oceanic islands remains limited. The distribution of exotic species is primarily determined by historical anthropogenic contingencies and mostly falls in the realm of invasion biology. However, in the context of the GDM, it remains an interesting question whether the age and ontogenetic stage of the island system has any explanatory power for the degree of invasibility of native ecosystems by non-native species, e.g., through an effect on community saturation level. Also, in itself the application of island biogeography models to conservation and management of oceanic islands is an essential future step for island biologists; however, this discussion falls outside the scope of the current manuscript.

(5) Model extensions: simulation models and mathematical development

Process-based simulation models provide a means to move towards a more mechanistic understanding of island diversity. They also provide a means of investigating interactions between island characteristics and species characteristics (e.g. body size, dispersal ability and/or gene flow; Kisel & Barraclough, 2010) in determining emergent diversity patterns of remote islands.

Chen & He (2009) modelled the effects of immigration, extinction and speciation on species richness under scenarios of different sizes of the mainland species pool. In their models, immigration rates decreased, whereas speciation rates increased, over time. Moreover, they showed that the positive relationship between percentage of endemic species and species richness may be influenced by both speciation and extinction rates. Rosindell & Phillimore (2011) simulated diversity dynamics over time on islands varying in area and isolation by implementing immigration, reproduction and speciation within a neutral framework, differentiating between cladogenetic and anagenetic speciation. Cladogenetic speciation was initiated by the random emergence of variant individuals in the community, which would become new species if they had any living descendants after a certain number of time steps ('protracted speciation'; Rosindell *et al.*, 2010). Anagenetic speciation, on the other hand, was initiated automatically as an individual from a new species immigrated to the island. This would also in time become a new species, but the speciation event would be delayed each time a conspecific individual arrived on the island. A strong effect of island isolation on speciation emerged from this simulation model: near islands were dominated by immigrant species (i.e. no speciation), anagenetic speciation predominated at intermediate distances, and the most distant islands were characterized by cladogenesis, consistent with MacArthur & Wilson's (1967) 'radiation zone'.

Rosindell & Harmon (2013) presented a neutral simulation model, addressing two alternative scenarios of island origin: empty (e.g. oceanic) and fully colonized (e.g. land-bridge) islands. They demonstrated that the immigration and extinction curves took rather unintuitive forms when they were far from the dynamic equilibrium, arising from the fact that extinction probabilities depended on SAD form, as extinction rates are predicted to increase when there are many rare species. Their simulation generated a positive correlation between immigration and extinction curves when immigrants became unable to increase their abundance and thus went extinct (Rosindell & Harmon, 2013). While their model did not consider a role for island ontogeny as set out in the GDM, it demonstrated a means to develop mechanistic linkages between the form of SADs and emergent whole-island properties, and thus suggests a promising line for future work.

The above models are not immediately comparable to the GDM, as they assume constant area and carrying capacity. Two recent efforts, however, have developed analogous approaches designed explicitly to incorporate the geological dynamics of islands. Valente *et al.* (2014) used differential equations of the central processes within the GDM to model the consequences of varying isolation and diversification rates under a greatly simplified island ontogeny, and Borregaard *et al.* (2015) used a computer simulation with a greater number of processes to simulate the consequences of different realistic scenarios of island ontogeny. These models have led to conceptual clarifications about the interaction between species carrying capacity and species richness, and may in principle be used to estimate evolutionary rates by comparing model expectations to observed data.

Although the GDM and related simulation models explicitly invoke spatial processes such as dispersal, elevational shifts and local isolation, existing models are spatially implicit (but see Gavrilets & Vose, 2005). In the future, more spatially explicit approaches may be

developed, that set out to capture variation in SADs across landscapes, as both dispersal and population dynamics can be affected by the shape, topography and arrangement of the habitat (Dormann *et al.*, 2007). Additionally, the explicit geological dynamics and timescale considered by the GDM requires that both changes in environmental factors (e.g. area and habitat heterogeneity) and speciation are simulated together. The explicit consideration of habitat heterogeneity and of the role of empty niches on island radiations (Heaney, 2000; Whittaker *et al.*, 2008) thus requires testing of niche-based models (including differences in dispersal ability) in contrast to neutral ones.

Among the processes that might improve simulation models are demographic and dispersal processes (Cabral & Kreft, 2012), from which immigration and extinction naturally emerge and which directly determine abundance distributions. In this sense, a sound theoretical appraisal of individual-based fecundities and population reproductive rate is essential (see also Cabral & Schurr, 2010). Furthermore, as highlighted above, considering the large spatiotemporal scales involved, non-standard, rare long-distance dispersal events became important for immigration (Nathan, 2006; Heleno & Vargas, 2015). It therefore becomes important to select appropriate dispersal functions to calculate dispersal probabilities for island biogeography, accounting for different scales and mechanisms of dispersal (e.g. within island/archipelago; between mainland and island) (Nathan & Muller-Landau, 2000; Heleno & Vargas, 2015).

The essential link between demographic processes and the GDM concept of carrying capacity is in how the species exploit the available resources and compete with other species. So far, the simulation models on islands have applied neutral resource competition (e.g. Rosindell & Harmon, 2013), which in practice is unlikely to be the case. Whereas these models may act usefully as null models, metabolic theories can provide more general frameworks for e.g. body size and resource exploitation [e.g. dynamic energy

budgets: Kooijman (2009); the metabolic theory of ecology (Brown *et al.*, 2004)].

Metabolic theories explicitly consider species characteristics (e.g. body mass) and

environmental variables (e.g. temperature) to describe physiological constraints on

biological functions, including resource exploitation and demographic transitions (e.g.

Savage *et al.*, 2004) as well as mutation and speciation (Allen & Gillooly, 2006; Gillooly

& Allen, 2007). The consideration of metabolic constraints in this context would help in

dissecting the role that environmental variables, such as temperature, play in regulating

species diversity (Kreft *et al.*, 2008; Cabral *et al.*, 2014).

The incorporation of too many processes into a model may increase equifinality,

which is when multiple parameter combinations generate similar results (Dormann *et al.*,

2012). Indeed, a model may become so complex that it ceases to be useful for explaining

observed patterns, and the appropriate level of model complexity depends on the question

being asked. For complex models, the issue of equifinality can be addressed if the models

are able to produce multiple patterns, ideally across ecological levels (Grimm *et al.,* 2005),

such as patterns of individuals, populations, species and community. This allows the

effects of different parameter combinations to be disentangled. For example, incorporating

changes in abundance meant that Rosindell & Harmon (2013) were able to generate

predicted SADs in addition to predictions for species richness. Including abundances

increased model complexity, but also produced a pattern at a different level, making it

possible to cross-check patterns across different scenarios. However, the main limitation

for validating complex models such as these remains the limited availability of appropriate

empirical data at several levels. In particular, field efforts to gather distribution and

abundance data for island species are essential.

V.   CONCLUSIONS

(1) The General Dynamic Model (GDM) of oceanic island biogeography has already played a valuable role as a driver of a renewed focus on island biogeography. By combining ecology, evolution and geological dynamics, it forms the core of a comprehensive framework for island biogeography, in part because of its strength in identifying areas in need of further theoretical and empirical work. The emerging research agenda falls into several major themes, each addressing a distinct set of questions with appropriate data.

(2) Macroecological analyses using the ATT^2 model (Area + Time - Time^2) initially served as the main framework to test predictions arising from the GDM, and to generate additional insights into the ecology and evolutionary dynamics of oceanic island biota. Although the level of support for the GDM is arguably mixed, its explanatory power has withstood testing and it has proved to be generative of both ideas and technical developments in data analysis.

(3) The GDM emphasized the importance of geological dynamics in driving island evolution, but employed a simplified representation of island ontogeny, primarily suitable for oceanic hotspot archipelagos. The complex geological dynamics of real-world islands include island merging and splitting, indefinite growth patterns, and an archipelagic context with highly dynamic levels of inter-island connectivity. Most of these processes have predictable, if complex, impacts on dynamics of species diversity, and it appears possible to incorporate their effects to specify more sophisticated predictions for island biota.

(4) Although the GDM, and indeed most of island biogeography, focuses on dynamics at the scale of whole islands, the island-scale dynamics driving the evolution of diversity are also predicted to have an impact at the local, ecological scale, generating a signal that may

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be detected *via* the analysis of e.g. species abundance distributions, local habitat diversity, and the fractal pattern of species distribution.

(5) In addition to driving diversity dynamics across scales, the island dynamics considered by the GDM are expected to affect a wide range of properties of island biota. This includes functional diversity and the packing of functional trait space, the complexity of ecological interaction networks, and the susceptibility to degradation from the direct and indirect influences of anthropogenic activity.

(6) The GDM and related models of island diversity make explicit hypotheses about island evolution that lead to specific predictions concerning the topology of phylogenies of radiating clades. Reviewing a range of phylogenetic studies, which have not previously been discussed in the context of island-scale models of diversity, reveals a general good support for the predictions of the GDM.

(7) An obvious next step is to express complex island theory in the form of explicit simulation models, and this approach has already led to some promising results and conceptual clarifications.

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Figure legends

Fig. 1. Graphical representations of the General Dynamic Model (GDM) of oceanic island biogeography. (A) A conceptual depiction of the temporal trajectory of key aspects of diversity, modified by Borregaard *et al.* (2015) from Whittaker *et al.* (2007, 2008). Note that the extinction and immigration curves have been modified from those originally shown by Whittaker *et al.* (2008): to correct the trajectory of the extinction curve at the end of the sequence (originally incorrectly shown to continue increasing) and to incorporate the likelihood of immigration rate initially increasing during the early phases of island-building, a phase intentionally simplified in the original model. (B) A depiction of the same diversity aspects derived from a simulation model that is explicitly based on the causal relationships suggested by Whittaker *et al.* (2008; modified from Borregaard *et al.*, 2015; see also Fig. 2). Although there are some discrepancies, mainly in the relative contributions of processes, the overall trajectory is consistent with the original model. *I*, immigration rate; *S*, speciation rate; *E*, extinction rate; *K*, carrying capacity; *R*, species richness. *I*, *S* and *E* are island-level rates and expressed in species per unit time (right axis); *K* and *R* are in absolute species numbers (left axis).

Fig. 2. Causal relationships within the General Dynamic Model (GDM) as set out by Borregaard *et al.* (2015). The colours of boxes indicate which premise of the GDM they derive from (see Section I): blue for premise 1, green for premise 2, and red for premise 3. Thin arrows indicate causality: black arrows represent relationships that are either self-evident (e.g. speciation increases species richness and extinction decreases it) or theoretically uncontroversial and empirically well-established (e.g. island isolation decreases immigration rate); grey arrows indicate relationships that are more speculative and should be empirically tested. Dashed arrows are negative effects. Thick arrows depict the movement of species between categories. K_{max}, maximum carrying capacity.

Fig. 3. Area and elevation for eight oceanic archipelagos. Area and elevation of islands, plotted as a function of island age. Axes are the same for all plots. Lines show the fit of the first- or second-order polynomial (T or $T + T^2$) with the lowest Akaike Information Criterion value. Island ages, areas and elevations are taken from Cameron *et al.* (2013).

Fig. 4. Dates of origin and present sizes of the major islands of eight archipelagos drawn to the same scale. The figure illustrates how island ontogenies compare across archipelagos, and also how lifespan and maximum size vary within archipelagos. Note that the ages of islands follow the geological literature in giving the age of sediments or volcanic material, which is not necessarily the time an island emerged from the sea surface, and does not reveal whether an island has been submerged at a later stage. This complexity makes it difficult to assess their ages in terms of the evolutionary dynamics of the General Dynamic Model (GDM).

Fig. 5. Trait and habitat evolution among the Hawaiian lobeliads and close relatives (with *L. erinus* and *Pratia borneensis* grafted to the bottom of the in-group tree). The overlays of inferred ancestral traits illustrate the evolution of (A) fruit type), (B) inflorescence position, (C) habit, (D) pollination syndrome, and (E) habitat. From Givnish *et al.* (2009).

Fig. 6. Species–area relationship of lobeliad species for individual volcanic mountains [with approximate age from Clague (1996) shown through colour variation]. Species occurrences are from Price *et al.* (2012) and represent the presence of species on individual volcanic mountains (which are somewhat separate units that have their own local endemics). Areas represent mesic and wet climate zones within each given volcano (as derived from Price *et al.,* 2012), to account for the fact that nearly all lobelioids are confined to these habitats. The overall trend is that volcanoes older than 1 Ma align linearly with respect to the species–area relationship, whereas younger volcanoes have fewer species than area alone would predict (an exception is the smallest volcano, Niʻihau, whose lobeliad habitat is marginal and degraded).

Fig. 7. Schematic illustrating two ends of the spectrum of how radiating lineages respond to the habitat as they follow the island progression rule, dispersing from old to young islands within a hot-spot archipelago. In the upper sequence, the clade diverges into different species/ecotypes on the oldest island, and each of these then colonizes the next oldest island,

whereas in the lower sequence, the clade colonizes each island once and then repeats a similar divergence into different species or ecotypes. The end result could be similar numbers of species on each island but with a very different shape of phylogeny.

Fig. 8. Conceptual model of the history of a plate-margin oceanic island (grey and dotted lines) compared to that of a hot-spot island. Hot-spot islands typically build up in size and elevation for a relatively short period of time, then erode down and eventually disappear (Whittaker *et al.*, 2008). Plate-margin islands grow irregularly due to volcanism produced by subduction zones, which may become inactive for a time or permanently, but which usually remain active for many millions of years. The many small islands produced along the subduction zone, which often occur in a roughly linear array, often gradually merge into progressively larger and more topographically diverse islands of varied geological age. Modified from Heaney *et al.* (2016).