



# A general dynamic theory of oceanic island biogeography

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## ABSTRACT

**Aim** MacArthur and Wilson's dynamic equilibrium model of island biogeography provides a powerful framework for understanding the ecological processes acting on insular populations. However, their model is known to be less successful when applied to systems and processes operating on evolutionary and geological timescales. Here, we present a general dynamic model (GDM) of oceanic island biogeography that aims to provide a general explanation of biodiversity patterns through describing the relationships between fundamental biogeographical processes – speciation, immigration, extinction – through time and in relation to island ontogeny.

**Location** Analyses are presented for the Azores, Canaries, Galápagos, Marquesas and Hawaii.

**Methods** We develop a theoretical argument from first principles using a series of graphical models to convey key properties and mechanisms involved in the GDM. Based on the premises (1) that emergent properties of island biotas are a function of rates of immigration, speciation and extinction, (2) that evolutionary dynamics predominate in large, remote islands, and (3) that oceanic islands are relatively short-lived landmasses showing a characteristic humped trend in carrying capacity (via island area, topographic variation, etc.) over their life span, we derive a series of predictions concerning biotic properties of oceanic islands. We test a subset of these predictions using regression analyses based largely on data sets for native species and single-island endemics (SIEs) for particular taxa from each archipelago, and using maximum island age estimates from the literature. The empirical analyses test the power of a simple model of diversity derived from the GDM: the  $\log(\text{Area}) + \text{Time} + \text{Time}^2$  model ( $\text{ATT}^2$ ), relative to other simpler time and area models, using several diversity metrics.

**Results** The  $\text{ATT}^2$  model provides a more satisfactory explanation than the alternative models evaluated (for example the standard diversity–area models) in that it fits a higher proportion of the data sets tested, although it is not always the most parsimonious solution.

**Main conclusions** The theoretical model developed herein is based on the key dynamic biological processes (migration, speciation, extinction) combined with a simple but general representation of the life cycle of oceanic islands, providing a framework for explaining patterns of biodiversity, endemism and diversification on a range of oceanic archipelagos. The properties and predictions derived from the model are shown to be broadly supported (1) by the empirical analyses presented, and (2) with reference to previous phylogenetic, ecological and geological studies.

## Keywords

Diversification, diversity theory, equilibrium theory, extinction rate, general dynamic model, island biogeography, island evolution, island life cycle, speciation.

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*To do science is to search for general patterns, not simply to accumulate facts... (R.H. MacArthur, 1972, p.1).*

## INTRODUCTION

The theory of island biogeography, first outlined by Robert H. MacArthur and Edward O. Wilson in 1963 in the journal *Evolution*, and later developed in their 1967 Princeton monograph, has a clear claim to be the most influential body of theory within ecological biogeography. It is based on fundamental dynamic processes operating on populations, and sets out to explain emergent patterns of system species richness, turnover and endemism. As they envisaged at the outset, their theory has found application to all types of insular systems, from microcosms to oceanic islands, and from ponds to habitat islands of woodland in seas of human-transformed habitat (Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007).

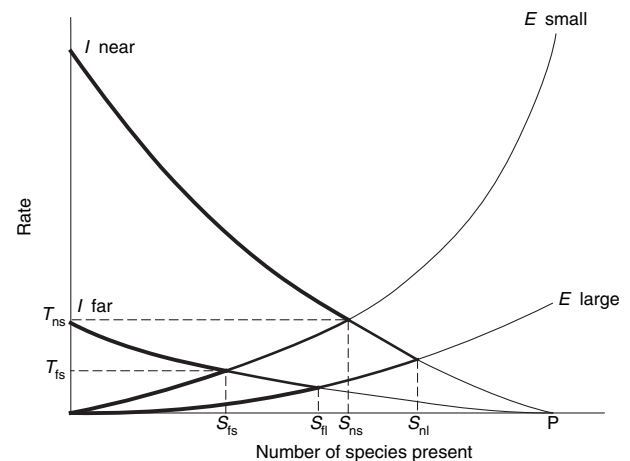
The dynamic equilibrium model detailed by MacArthur & Wilson (1967) has attracted much support (Rosenzweig, 1995) but also strong criticism in many publications, and there have been repeated calls for theoreticians to develop new models/theories (e.g. Brown & Lomolino, 2000; Lomolino, 2000; Heaney, 2007). In particular, their model has been less successful and is arguably less complete when applied to oceanic island systems operating on evolutionary timescales (e.g. Haila, 1990; Cowie, 1995; Borges & Brown, 1999; Heaney, 2000; Whittaker & Fernández-Palacios, 2007). Here, we begin to address this shortfall, by presenting a general theory of oceanic island biogeography that combines a simplified model of the life cycle of islands belonging to oceanic archipelagos with the lines of reasoning underlying the MacArthur–Wilson dynamic model.

We begin by briefly restating the central properties of the MacArthur–Wilson model. At the core of their theory is the recognition that, for a discrete and isolated biological system, the number of species at any point in time must be a function of the number previously occurring there plus those gained through immigration and/or speciation (specifically via cladogenesis<sup>1</sup>), minus those having gone locally extinct. Their model proposes that these three fundamental processes of immigration, speciation and extinction should vary in a predictable fashion in response to time since system initiation, and in relation to two principal controlling geographical/environmental influences: isolation and area. Immigration rate ( $I$ ) should decline as a function of isolation (distance), and

extinction rate ( $E$ ) should decline as a function of increasing area (a general surrogate for island carrying capacity,  $K$ ). Taking the case of a newly formed and barren island,  $I$  starts at its highest rate and declines as a hollow exponential curve as the proportion of propagules arriving on the island that represent new species declines, whilst  $E$  gradually rises as the space is occupied. In time, these rates intersect to provide a dynamic equilibrium, a condition in which  $I$  and  $E$  are in balance, with a continual turnover of species occurring thereafter (Fig. 1).

MacArthur & Wilson (1963, 1967) recognized that, on the more remote islands, the pace of immigration is so slow that increasing proportions of the biota on such islands are the result of *in situ* evolutionary change, with diversification (cladogenesis) most pronounced on larger islands towards the outer limits of the distributional reach of a taxon, an area they denoted the ‘radiation zone’. Hence, they argued that speciation increased with distance and with island area. As a simplification, their 1967 monograph focuses throughout the early chapters entirely on immigration–extinction dynamics. Perhaps in consequence of this, their argumentation regarding evolutionary dynamics is often overlooked by those commenting on and applying their theory.

Recently, Heaney (2007) called for the development of a comprehensive new model of biogeography, re-unifying ecological and evolutionary biogeography. Such a model should be based on the identification of general patterns, describe these patterns quantitatively, and capture the underlying mechanisms (Brown & Lomolino, 2000). In fact, there have been numerous attempts to link evolutionary and ecological dynamics building on the MacArthur–Wilson model (e.g.



**Figure 1** A version of MacArthur & Wilson's (1963, 1967) equilibrium model of island biogeography (EMIB), showing how immigration rates ( $I$ ) are postulated to vary as a function of distance (near,  $n$ ; far,  $f$ ), and how extinction rates ( $E$ ) are postulated to vary as a function of island area (large,  $l$ ; small,  $s$ ). The model predicts different values for  $S$  (species number), which can be read off the ordinate, and for turnover rate ( $T$ ) (i.e.  $I$  or  $E$ , as they are identical at equilibrium). Each combination of island area and isolation should produce a unique combination of  $S$  and  $T$ . To prevent clutter, only two values for  $T$  are shown.

<sup>1</sup>Anagenesis (the formation from a colonist species of a neo-endemic form via any combination of adaptive process and/or drift) does not lead to an increased number of species on an island. Thus, in so far as they were largely concerned with understanding variation in numbers of species on islands, MacArthur & Wilson (1963, 1967) focused on the contribution of cladogenesis (evolutionary change giving rise to increased numbers of species) when outlining their dynamic equilibrium model. NB. They didn't actually use the terms anagenesis and cladogenesis (Stuessy *et al.*, 1990, 2006), but these concepts neatly encapsulate the distinction made.

Wilson, 1969; Diamond, 1975; Heaney, 1986, 2000; Peck, 1990; Cowie, 1995; Peck *et al.*, 1999; Losos & Schluter, 2000; Hubbell, 2001; Price, 2004; Emerson and Kolm, 2005a,b; Heaney *et al.*, 2005), together providing helpful pointers to the ingredients required to bring about the conceptual unification Heaney (2007) has called for. Recently, Peck *et al.* (1999), and subsequently Emerson & Kolm (2005a), have drawn attention to the use of single-island endemics (SIEs) as indicators of evolutionary dynamics within oceanic archipelagos. In their analysis of SIE plants and arthropods from Hawaii and the Canaries, Emerson & Kolm (2005a,b) noted the association between high species numbers and high proportions of SIEs in both archipelagos. Their interpretation is that high diversity stimulates higher rates of speciation in a taxon (largely through competitive mechanisms) and that speciation rate and extinction rate are strongly positively related in these island systems: an interpretation that they contend is supported by the MacArthur–Wilson model. These inferences have been debated by a number of authors (Cadena *et al.*, 2005; Emerson and Kolm, 2007a,b; Kiflawi *et al.*, 2007; Pereira *et al.*, 2007; Whittaker *et al.*, 2007; Witt & Maliakal-Witt, 2007) and, as we point out above, a positive covariation between speciation and extinction rate is not in fact derivable from the MacArthur–Wilson theory (MacArthur & Wilson, 1963, 1967; and see Peck, 1990; Cowie, 1995; Peck *et al.*, 1999; Whittaker *et al.*, 2007). Nonetheless, we are in agreement with Emerson & Kolm (2005a,b) that SIE data provide a potentially valuable insight into evolutionary dynamics.

In a response to Emerson & Kolm's (2005a,b) observations about patterns in SIE data from the Canaries and Hawaii, Whittaker *et al.* (2007) put forward an alternative explanatory model, the island immaturity–speciation pulse (IISP) model of island evolution, which is distinctive in incorporating the geological life cycle of islands within an evolutionary argument. In fact, the significance of the island life cycle was recognized by earlier authors (e.g. Paulay, 1994; Stuessy *et al.*, 1998), most presciently by Peck (1990, p. 375), when he wrote, 'A relationship with island age should be expected, but it would not be a straight line... Rather the relationship should be a curve which rises fast at first, reaches a peak or plateau, and then decreases as erosion destroys the island.' Herein, we expand on the IISP model, and argue that it provides the foundations of a general dynamic theory of oceanic island biogeography. First, we identify the key premises of this theoretical model, and outline the predictions it generates; second, we provide some original empirical analyses in support of this model; and third, we review relevant evidence from the island biogeographical literature.

## THEORETICAL MODEL

By naming the model the island immaturity–speciation pulse (IISP) model of island evolution in our earlier paper (Whittaker *et al.*, 2007), we focused attention on the proposition that the speciation rate will peak relatively early in the lifespan of an oceanic island, somewhat to the detriment of examining the broader properties of the model. Herein, by substantially

developing and re-framing the IISP model as a general dynamic model (GDM) of oceanic island biogeography, we attempt a more formal separation of the premises, properties and predictions of the model.

## Premises of the general dynamic model

Although the development of the model was influenced by numerous empirical and theoretical studies (as reviewed in Whittaker & Fernández-Palacios, 2007), we contend that there are only three key premises on which the GDM rests (see Table 1). The first two premises derive in large part from MacArthur & Wilson's (1967) monograph, and encapsulate both (1) their immigration/speciation–extinction dynamics, and (2) the argument that speciation and diversification in insular habitats are encouraged through the ecological opportunity signified by the concept of 'empty niche space', intertwined with the geographical opportunity provided by isolation (e.g. Lack, 1947; Peck *et al.*, 1999; Heaney, 2000; Gillespie, 2004, 2007; Levin, 2004). The final premise recognizes (3) that oceanic islands have a typical developmental life cycle from youth, to maturity, to old age and eventual loss (e.g. Nunn, 1994; Price & Clague, 2002), and crucially, that this life cycle plays itself out at a temporal scale resonant with and strongly influencing the evolutionary dynamics shaping the biota of oceanic island archipelagos and basins (Peck, 1990; Peck *et al.*, 1999; Price & Clague, 2002; Stuessy *et al.*, 2005).

Previous authors have recognized the importance of the geological dynamics of oceanic islands for the endemic biota (e.g. Peck, 1990; Peck & Kukulova-Peck, 1990; Paulay, 1994; Cowie, 1995; Stuessy *et al.*, 1998, 2005, 2006; Peck *et al.*, 1999; Gillespie & Roderick, 2002; Sakai *et al.*, 2002; Gillespie, 2004; Parent & Crespi, 2006; Gruner, 2007), but have not, to our knowledge, attempted to develop the ideas into a general model. However, we would like to draw attention to a paper by Stuessy (2007), published contemporaneously to the IISP, and presenting in outline form a rather similar model for oceanic island floras in which he postulates characteristic evolutionary responses to the ontogeny of an oceanic island, dividing the insular life cycle into arrival and establishment, early development, maturation, and senescence/extinction.

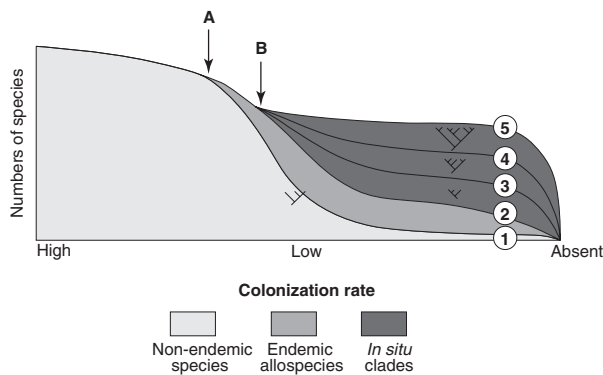
## Properties of the general dynamic model

In this section we develop general properties of the GDM through a series of graphical representations of the underlying processes, commencing with MacArthur & Wilson's (1963, 1967) familiar dynamic model (Fig. 1), described above. Their radiation zone concept can also be developed graphically, and in Fig. 2 we have selected Heaney's (2000) representation of the ideas to represent this premise. The figures show how, for a given taxon, declining frequency of colonization translates into decreasing richness combined with increased absolute and relative importance of *in situ* cladogenesis.

In Fig. 3 we set out a general representation of the life history of an oceanic island, assuming the simplest of oceanic

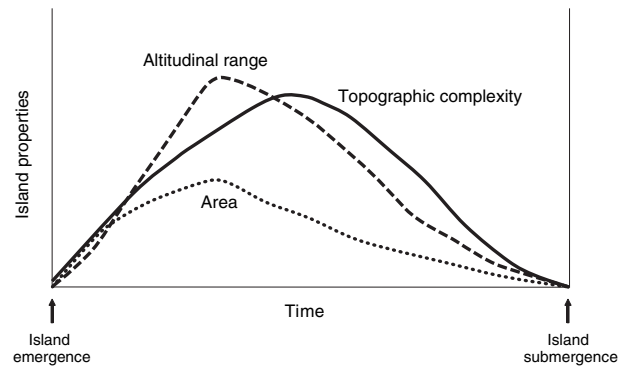
**Table 1** The three premises underlying the general dynamic model of oceanic island biogeography.

Premise	Support for the premise
<p><i>Biological processes</i></p> <p>The MacArthur–Wilson model is an essentially correct summation of the key biological processes, i.e. island biotas are a function of rates of immigration, extinction and speciation, which lead towards a biotic equilibrium broadly as they envisaged</p>	<p>A large body of literature supports the importance of these processes, but evidence of attainment of equilibrium for distant oceanic archipelagos remains equivocal as progress towards equilibrium is very slow (e.g. Cowie, 1995; Whittaker &amp; Fernández-Palacios, 2007)</p>
<p><i>Evolutionary response</i></p> <p>Diversification within island lineages is typically greatest on larger islands, where levels of interaction with closely related fellow colonists (e.g. congeners) are lowest and where lineage persistence for non-trivial periods of time is permitted</p>	<ol style="list-style-type: none"> <li>1. Island systems near the effective dispersal limits of a higher taxon, where few lineages colonize, typically show the greatest diversification per colonist lineage (the ‘radiation zone’ of MacArthur &amp; Wilson, 1967)</li> <li>2. Within oceanic island archipelagos, SIEs have a far larger minimum area threshold and increase disproportionately with increasing area relative to native species of the taxon (Peck <i>et al.</i>, 1999; Triantis <i>et al.</i>, 2008)</li> </ol>
<p><i>Geological progression</i></p> <p>Oceanic islands are formed volcanically and typically have short life spans; in the simplest scenarios, an island builds relatively speedily to maximum area and altitudinal range in its youth, next becomes increasingly dissected as it erodes, and then gradually subsides/erodes to disappear back into the sea or persist as a low-lying atoll</p>	<p>Geological dating of oceanic islands indicates much support for this, especially for the Hawaiian hotspot chain of islands (Price &amp; Clague, 2002), although not all volcanic islands follow such a simple developmental sequence (reviewed in Whittaker &amp; Fernández-Palacios, 2007)</p>



**Figure 2** Heaney’s (2000) model of the development of species richness on large islands or archipelagos that experience varying rates of colonization as a result of varying degrees of isolation. As explained by Heaney, on islands near a species-rich source initially lacking the study taxon, all species will be present through direct colonization because high rates of gene flow will inhibit speciation; thus, no endemic species will be present, but many non-endemics will be present. As the average rate of gene flow drops below approximately one individual per generation (point A), anagenesis will begin to take place, and endemic species will develop, although they will be outnumbered by non-endemic species. These endemic species (between lines 1 and 2) will have their sister taxon in the source area, not on the island/archipelago. As colonization becomes still less frequent, and as time passes, phylogenesis will produce endemic clades (represented by the branching trees) in which the endemic taxa have their sister taxon on the island/archipelago, not in the source area (species between lines 2 and 3). As more time passes, the oldest clades will become progressively more species-rich (between lines 3 and 5).

island histories: the new volcanic island emerges from the sea, builds to a high cone-shaped form, of maximal area and height, and then becomes increasingly dissected and eroded. In



**Figure 3** Idealized relationships between the age (*x*-axis, time) and area (dotted line), elevational range (dashed line), and topographic complexity (solid line) of a hypothetical oceanic island. Such a scenario is most applicable to islands with simple ontogenies, such as those found within hotspot archipelagos. Island maximum altitude and area both peak before maximum topographic complexity, but all three are expected to show a humped pattern. Note that the period of growth is typically shorter than the period of decline, such that in this and the subsequent figures the time axis should best be considered as some form of log or power function.

time, such islands typically both subside (some rapidly and substantially, e.g. Moore & Clague, 1992) and erode (aerially and through marine action), resulting in loss of both elevational range and area, until they disappear back into the sea, or persist in tropical seas as atolls – coralline islands of low elevation (Nunn, 1994; Stuessy *et al.*, 1998; Price & Clague, 2002; Whittaker & Fernández-Palacios, 2007). Maximum topographic complexity will typically occur some time after the maximal elevation and area have been reached and passed.

In reality, most oceanic islands have rather more complicated histories than depicted, sometimes involving the fusion

of separate islands to become one, and often involving catastrophic episodes of volcanism (tailing off with age) and slope failures (sometimes massive) (Price & Clague, 2002; Carracedo & Tilling, 2003; Whelan & Kelletat, 2003; Hürli-mann *et al.*, 2004; Le Friant *et al.*, 2004). In addition, Pleistocene climate change and sea-level fluctuations have detectable imprints on their biogeography (e.g. Peck, 1990; Carine, 2005). Furthermore, those oceanic islands that have formed within island arcs in association with plate margins can experience yet more complex histories, involving both vertical and lateral displacement (e.g. Buskirk, 1985; Keast & Miller, 1996). Thus, as Paulay (1994, p. 135) has commented, ‘while the age, position, and physiographic evolution of hotspot islands are simple and readily predictable, those of arc islands are complex. This makes hotspot islands more attractive as model systems for the study of diversification.’ Hence, the simplified ontogenetic model presented herein is most applicable to hotspot archipelagos, and while it should, in principle, apply to other volcanic oceanic island archipelagos, some modification will be necessary to accommodate alternative and more complex geological scenarios.

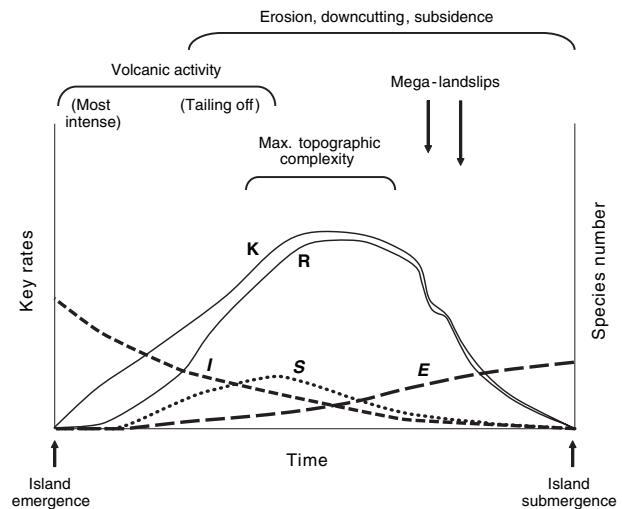
Considering the simplified scenario in Fig. 3, the model implies that (1) the maximum carrying capacity *K* of an island, in terms of biomass and number of individuals across all species, will be reached roughly coincidentally with maximum area and elevational range (Fig. 4), with (2) the maximum heterogeneity of environment, and thus maximum opportunity for within-island allopatry, occurring somewhat later, but still within the ‘middle age’ of the island (Fig. 5; and see Stuessy, 2007, fig. 5.2).

**Implications and predictions of the general dynamic model**

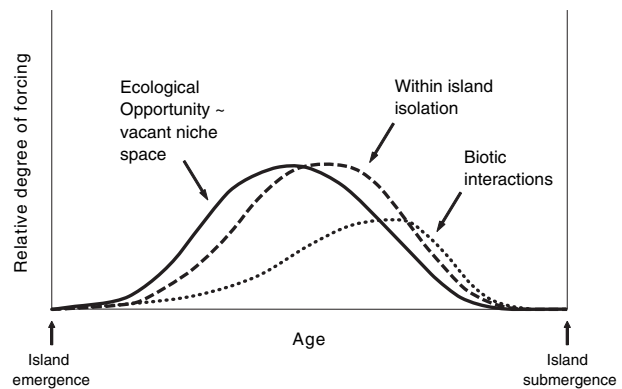
These arguments allow us to extend the MacArthur–Wilson model to incorporate the implications of both an extended pre-equilibrium phase and an extended phase in which the equilibrium point is declining and extinction exceeds species additions through immigration and speciation. Fig. 4 combines these arguments to provide a graphical model of the dynamic processes involved in the developmental cycle of an island within an oceanic archipelago. We have not attempted to fit scalars to the axes, but we suggest that the period from island emergence to maximal carrying capacity is typically far shorter than the period of decline (consider, for example, Stuessy *et al.*, 1998; Price & Clague, 2002; Carracedo & Tilling, 2003; Le Friant *et al.*, 2004), such that the time axis might best be shown as some form of log or power function.

With regard to evolutionary dynamics, the key points are as follows.

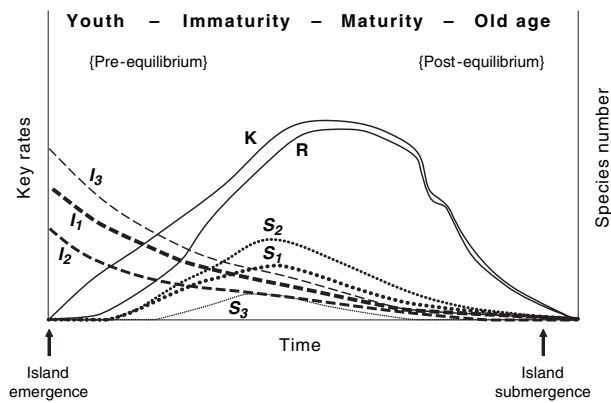
- (1) Youth – initially most species can be attributed directly to immigration, typically from older islands in the archipelago.
- (2) Immaturity – speciation rates (and rates of cladogenesis) peak relatively early on, when there are enough lineages present to ‘seed’ the process, but when there is also plenty of adaptive opportunity in the form of ‘empty niche space’.



**Figure 4** Graphical representation of the key rates and properties of the general dynamic model (GDM) of oceanic island biogeography, showing the postulated relationships between the biological characteristics and island ontogeny, where, for key rates, *I* is the immigration rate, *S* is the speciation rate, and *E* is the extinction rate; and, for species number, *K* is the potential carrying capacity, and *R* is the realised species richness. The figure has been modified from Whittaker *et al.* (2007) and Whittaker & Fernández-Palacios (2007), principally by the addition of the extinction-rate curve, which is drawn as a fairly smooth curve. For islands showing sudden extensive loss of territory resulting from landslips (as suggested by the kinks in the *K* and *R* curves), this extinction-rate curve would require modification.



**Figure 5** Schematic representation of the relative roles of various forcing factors through the life cycle of the island. Considering Figs 3 and 4, we can derive the prediction that the greatest opportunities for adaptive radiation (solid line, first peak) will occur earlier than those for non-adaptive processes linked to within-island isolation (dashed line, second peak). Biotic interactions within and across trophic levels may be expected to become more important at a later stage of the island life cycle (dotted line, third peak), past the point of maximum carrying capacity and where extinction rate is climbing with the decline of the island platform (Fig. 4). Such biotic/competitive mechanisms may produce species involved in tight mutualisms, or fine subdivisions of resources sympatrically, but not at a rate sufficient to prevent a decline in the proportion of SIE species.



**Figure 6** Modification of immigration ( $I$ ) and speciation ( $S$ ) rate curves in relation to distance between islands or mobility of the taxa concerned. The amplitude of the expected speciation rate curve will vary between archipelagos and major taxa as a function of the size of the available species pool / ease of dispersal. This variation is signified by the variation between  $I_1$ ,  $I_2$  and  $I_3$  curves, corresponding, respectively, to  $S_1$ ,  $S_2$  and  $S_3$  curves. For a given archipelago, if the system represented by the lines  $I_1$  and  $S_1$  were higher plants, then  $I_2$  and  $S_2$  might represent lizards, and  $I_3$  and  $S_3$  might represent ferns (see, for example, Tryon, 1970, on the dispersal powers and low insular endemism of ferns). Note that a suite of modified  $R$  curves should also be shown, to match the variations in the balance of rates of immigration, speciation and extinction, but have been omitted to reduce clutter.

(3) Maturity – species richness peaks, and speciation continues at a high rate partly as a result of the increasingly dissected topography that generates increased opportunities for within-island allopatry.

(4) Old age – speciation rate declines in tandem with reduced  $K$  and increased  $E$  (and thus reduced richness) as islands decline in elevation, topographic relief, area, and habitat diversity in old age.

(5) Finally, all is lost – the island founders.

Although true oceanic islands arise in varied geological circumstances, they are frequently clustered together in space, forming distinct archipelagos, within which the timing of formation of each island varies significantly (e.g. Nunn, 1994; Carracedo & Tilling, 2003; Gillespie, 2007; Whittaker & Fernández-Palacios, 2007). Thus, as each island goes through its own life cycle, an archipelago develops in which a wide array of island ages/stages is available at any given time. Hence, a young island is supplied by colonists from nearby older islands, and in time may supply colonists to the next island that forms, and, in certain island archipelagos, at least some lineages have been inferred on the grounds of molecular data to have originated on islands that have since been reduced to mere atolls or indeed have disappeared below sea level (Wagner & Funk, 1995; Price & Clague, 2002; Butaud *et al.*, 2005). Therefore, an archipelago of islands such as the Canaries or Hawaii can be conceived of as consisting of a series of terrestrial platforms each going through the sequences shown in Figs 3 and 4, but each at a different point along the time axis.

Considering a single island forming within an existing archipelago, developing to maximum size, and elevational range, then becoming increasingly dissected through erosion, and finally entering a long phase of decline in area, altitude and environmental complexity, we expect a general hump-shaped trend in potential carrying capacity, and similar trends in species richness and in speciation rate (Fig. 4). Extinction of species may occur at any stage, with high-magnitude catastrophes (large volcanic eruptions, mega-landslides) being most important – but highly unpredictable – during the building/maturity phase, and more gradual erosion and subsidence processes assuming greatest significance in the old age of the island, as the island's decline forces the extinction rate to rise above the combined processes of addition (speciation and immigration), driving the species number towards zero.

We may also derive a general prediction for the trend in the proportion of single-island endemic species (pSIE) during the ontogeny of a particular, focal island. Initially, as the island ecosystems are 'seeded' from the nearby older islands in the archipelago, most species are not SIEs, although they may well include archipelago-level endemics, so the pSIE should be low. However, as the available propagule pool is relatively limited, and ecological space is initially unsaturated, speciation rate picks up, often generating significant radiations within single genera (e.g. Gillespie, 2004), thus increasing proportions of SIEs and simultaneously generating an increased species : genus ratio. As the island ages and declines, it follows that a point is reached at which  $E > (I + S)$ , and so species richness and the number of SIEs will each decline. A further prediction follows, namely that the pSIE on our focal island should also decline, for the following reasons: (1) the area threshold for SIEs is on average larger than that for multi-island endemics and non-endemic species (Triantis *et al.*, 2008), which may persist even as fairly small populations if reinforced by occasional propagule flow from other islands; (2) the loss of habitat diversity [for example upland habitats, lava tubes (P. Borges, pers. comm.)], and the corresponding increase in habitat similarity with the coastal lowlands of other islands in the group, result in the collapse of radiations of neo-endemic habitat specialists on the focal island, whereas coastal generalists persist; and (3) as the focal island supplies colonists to the next island to form, some of the SIE species of the focal island colonize the new island (in accordance with the progression rule; Funk & Wagner, 1995) and lose their status as SIEs. This latter mechanism will apply most strongly in hotspot archipelagos involving a clear age progression and may not be so evident in more complex island arc systems.

The GDM thus allows us to derive several predictions (Table 2) about the emergent properties of the biota: (1) of a single oceanic island through time; and (2) of the islands of an oceanic archipelago at a single point in time. Some of these predictions are relatively simple to derive and test, but others are likely to prove more challenging to assess. Given the extended time period (millions of years) over which data would ideally be required to explore fully the generality of the assumptions and predictions, we make use principally of



**Table 2** Predictions derivable from the general dynamic model.

1. Island species number and the number of SIEs should be a humped function of island age, and when examining snapshot data across an archipelago this will be combined with a positive linear relationship with area.
2. The amplitudes of the curves shown in Fig. 4 should vary in relation to the size of the island at maturity, with higher peak richness and SIE numbers on islands that attain greatest size (area and elevation) at maturity.
3. The relative amplitudes of the immigration and speciation rate curves should vary in relation to the effective isolation of islands, i.e. in relation either to distance between islands and their sources or to the mobility of the taxon, as shown in Fig. 6.
4. Lineage radiation (leading to multiple SIEs on individual islands) should be most prevalent after the initial colonization phase, in the period leading up to island maturity, coinciding with maximal carrying capacity (K) and the development of maximal topographic complexity.
5. Montane representatives on old, declining islands should gradually be lost because of loss of habitat, meaning that surviving montane forms are increasingly likely to be relatively old (i.e. basal) forms in relation to other members of an archipelagic radiation.
6. The proportion of SIEs should also be a humped function of island age, as islands that decline to small size and carrying capacity should lose SIEs in accordance with the second premise of the GDM (and see also prediction 8).
7. SIEs per genus should be higher on younger islands; intermediate-aged islands will have more lineages showing speciation than do young or old islands; SIEs per genus should decline on older islands so that, as islands lose SIEs, there is a tendency towards monotypic genera, preserving maximal ecological spacing in the remaining endemics.
8. As islands age, some of their SIE species should colonize a younger island, so that they become multi-island species instead. Hence, the GDM also 'predicts' that the progression rule should be a common/dominant phylogeographical pattern within an archipelago.
9. Using Stuessy *et al.*'s (1990, 2006) approach to classifying speciation modes, there should be a greater tendency to anagenesis on old, submerging islands as the dominant speciation signal. NB: this assumes that where SIEs are the only member of their genus the explanation is *in situ* speciation. In practice, we expect that on the oldest islands 'anagenesis' will often be a misnomer, as there will be a trend towards survival of single relicts from former radiations.
10. Adaptive radiation (AR) will be the dominant process on islands where the maximum elevational range occurs, as it generates the greatest richness of habitats (major ecosystem types), including novel ones that few colonists have experienced, whereas non-adaptive radiation (NAR) will become relatively more important on slightly older islands, past their peak elevation, owing to increased topographical complexity promoting intra-island allopatry. Similarly, composite islands (e.g. Tenerife, formed from three precursors), should have provided more opportunity than islands of simpler history for within-island allopatry, producing sister species that lack clear adaptive separation (e.g. Gruner, 2007). NB. AR and NAR are not always easily distinguishable (but see e.g. Price & Wagner, 2004).

predictions about 'snapshot' patterns across archipelagos in order to assess support for the GDM. This means making use of the existence of oceanic archipelagos in which a meaningful portion of the life cycle ultimately shown by a single island is available for study in the form of separate islands of widely different ages/stages. The key problem in doing so is that the islands within an archipelago do not all attain identical properties at maturity, and in particular they may vary significantly in maximum attained area and elevational range (e.g. Stuessy *et al.*, 1998; Price & Clague, 2002) – properties of key importance in regulating species diversity and patterns of speciation/extinction (Stuessy *et al.*, 2005; Stuessy, 2007). To deal with this analytically we need to include a term for island size, assuming that all islands in a group follow the same general trajectory, but that the amplitude of the curves will vary in relation to the maximum area attained.

## EMPIRICAL EVALUATION

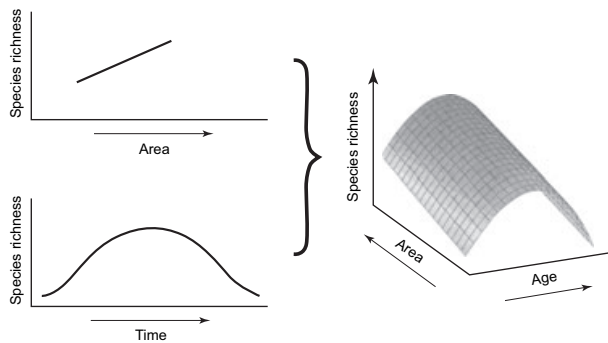
Of the 10 predictions derived from the GDM (Table 2), some may not be exclusive to the GDM (e.g. predictions 3 and 4), and some will probably be found to be hard to test (for example, obtaining data for convincing tests of predictions 3 and 10 presents considerable challenges; see Cowie, 1995;

Heaney, 2000; Fukami *et al.*, 2007). However, we consider that the postulated hump-shaped trends of particular diversity attributes in relation to island age constitute a distinguishing and testable feature of the GDM. We therefore begin the empirical evaluation of the GDM by using data from a selection of oceanic island archipelagos, each of which satisfies two criteria: (1) they provide a good span of island ages as determined by radiometric dating; and (2) fairly comprehensive survey work and compendia are available for the distribution and taxonomy of the members of particular taxa within the archipelago. The systems selected were the Canaries, Galápagos, Marquesas, Azores and the Hawaiian Islands, which are all of volcanic origin but have differing geological and palaeogeographic histories, inter-island distances and climatic regimes (Moore & Clague, 1992; Borges & Brown, 1999; Peck *et al.*, 1999; Price, 2004; Parent & Crespi, 2006; Whittaker & Fernández-Palacios, 2007).

As individual islands do not all attain the same size at maturity, tests of the GDM factoring in both space and island age are of the form

$$\text{Diversity} = a + b(\text{Time}) + c(\text{Time}^2) + d(\log \text{Area}), \quad (1)$$

where the use of a log function of area follows standard practice, empirically derived in numerous island biogeographical anal-



**Figure 7** Analytically, the GDM model is fitted to the data using a simple multiple regression approach involving a linear fit of  $\log(\text{Area})$ , and a two-parameter time model, of the form  $\text{ATT}^2$  (i.e.  $\log(\text{Area}) + \text{Time} + \text{Time}^2$ ), which is represented graphically in the figure. When fitting the  $\text{ATT}^2$  models we have not restricted the model to return a humped relationship; accordingly, we note in Tables 4 and 5 when the time relationship is not of this form.

yses. To distinguish the analytical implementations of the GDM argumentation, from the general theoretical construct, we term all models of the form shown in equation 1  $\text{ATT}^2$  models (representing  $\log(\text{Area}) + \text{Time} + \text{Time}^2$ ) (as Fig. 7).

## MATERIALS AND METHODS

### Data sources and properties

The principal data sources, number of islands, and summary geographical data are provided in Table 3. Further details on data sources follow.

#### Hawaiian Islands

Data for flowering plants (10 islands) were extracted from Price (2004). For arthropods and Coleoptera (10 islands), data were compiled from Nishida (2002). Data for land snails (10 islands)

are from Cowie (1996). In fact, data for up to 18 islands are available and were used in analyses reported in our Supplementary Material (and see e.g. Emerson & Kolm, 2005a, 2007a). However, for our main analyses we used data for only 10 islands for the following reasons. According to Peck *et al.* (1999), three Hawaiian Islands, Kahoolawe, Niihau and the Gardner Pinnacles, should be excluded from the analysis for arthropods as, for instance, Kahoolawe Island was long used as a testing ground for military explosives, and has also harboured a high population of alien ungulates, resulting in an extremely disturbed and non-representative ecosystem. We followed this approach for the two other taxonomic groups of the Hawaiian Islands, namely plants and land snails (but see below). We also excluded from the analysis all the small atolls, namely Kure, Midway, Pearl & Hermes, French Frigate Shoals, as they do not represent single islands but complexes of many small sand islets, and for the plant data set we also excluded Kaula Island, from which only a single species is reported (see Price, 2004).

#### Galápagos Islands

We included material from the vascular plant flora (13 islands) extracted from Lawesson *et al.* (1987) (see also Harvey, 1994). Data for smaller orders of insects (i.e. orders with small numbers of species) (13 islands) and beetles (13 islands) were extracted from Peck (2001) and Peck (2005), respectively. The data for 'insects' are from the combination of the data for beetles and small orders of insects.

#### Azorean Islands

The most recent compilation of Azorean fauna and flora (Borges *et al.*, 2005) was used for the extraction of data for plants and land snails (9 islands). We have excluded the Azorean plant data from analyses of the evolutionary dynamics metrics as SIEs were present only on two islands and the overall percentage of SIE was  $< 1.0$  (Table 4).

**Table 3** Properties of the island systems, and principal sources of species data used in the analyses. For a full list of data sources, see text.

Island group	Taxon	No. islands	Distance to mainland (km)	Range in area (km <sup>2</sup> )	Total area (km <sup>2</sup> )	Source
Canary	Arthropods	7	95	278–2058	7601	Izquierdo <i>et al.</i> (2004)
Canary	Plants	7	95	278–2058	7601	Izquierdo <i>et al.</i> (2004)
Canary	Snails	7	95	278–2058	7601	Izquierdo <i>et al.</i> (2004)
Hawaii	Arthropods	10	3660	0.2–10,433	16,397	Nishida (2002)
Hawaii	Coleoptera	10	3660	0.2–10,433	16,397	Nishida (2002)
Hawaii	Flowering plants	10	3660	0.2–10,433	16,397	Price (2004)
Hawaii	Snails	10	3660	0.2–10,433	16,397	Cowie (1996)
Galápagos	Insects	13	930	4.99–4588	7847	Peck (2001, 2005)
Galápagos	Insects (small orders)	13	930	4.99–4588	7847	Peck (2001)
Galápagos	Beetles	13	930	4.99–4588	7847	Peck (2005)
Galápagos	Plants	13	930	4.99–4588	7847	Lawesson <i>et al.</i> (1987)
Marquesas	Plants	10	4830	1.3–339	1039	F.O.M. (Flora of the Marquesas) (2007)
Azores	Plants	9	1600	17–750	2324	Borges <i>et al.</i> (2005)
Azores	Snails	9	1600	17–750	2324	Borges <i>et al.</i> (2005)



**Table 4** Percentage endemism and percentage SIEs for each taxon/archipelago combination, plus model fits for the ATT<sup>2</sup> models (equation 1) for species richness and three metrics of evolutionary dynamics, namely nSIE, number of single-island endemics; pSIE, proportion of SIEs; and DI, a diversification index (nSIE/number of genera in which SIE occur). For each model, we provide R<sup>2</sup> values, F values and P values.

Island group	Taxon	Percentage of endemism	Percentage of SIE	SR		nSIE		pSIE		DI	
				R <sup>2</sup>	F value	R <sup>2</sup>	F value	R <sup>2</sup>	F values	R <sup>2</sup>	F value
Canary	Arthropods	40	22	<b>0.93*</b>	57.18	<b>0.88*</b>	14.99	<b>0.82*</b>	47.29	<b>0.77**</b>	162
Canary	Plants	40	15	<b>0.91**</b>	155.04	<b>0.90*</b>	16.05	<b>0.90*</b>	23.13	<b>0.99**</b>	803.60
Canary	Snails	91	84	<b>0.87*</b>	32.66	<b>0.84*</b>	15.48	<b>0.88*</b>	108.35	<b>0.90*</b>	100.29
Hawaii	Arthropods	99	72	<b>0.83*</b>	17.77	<b>0.74*</b>	9.70	<b>0.71*</b>	33.10	<b>0.90*</b>	67.66
Hawaii	Coleoptera	99	83	<b>0.84*</b>	19.08	<b>0.77*</b>	11.66	<b>0.93**</b>	116.95	<b>0.93**</b>	77.93
Hawaii	Flowering plants	90	54	<b>0.94**</b>	62.84	<b>0.83*</b>	13.68	<b>0.73*</b>	11.10	<b>0.79*</b>	18.40
Hawaii	Snails	99	88	<b>0.67*</b>	7.54	<b>0.61*</b>	5.30	<b>0.96**</b>	98.93	<b>0.74*</b>	11.21
Galápagos	Insects	66	29	<b>0.80**</b>	34.67	<b>0.65*</b>	8.90	<b>0.55**</b>	27.49	<b>0.52**</b>	419.89
Galápagos	Insects (small orders)	62	30	<b>0.76**</b>	24.64	<b>0.48*</b>	4.59	<b>0.28**</b>	14.38	<b>0.34**</b>	137.43
Galápagos	Beetles	70	28	<b>0.82**</b>	42.43	<b>0.73*</b>	12.25	<b>0.70**†</b>	18.80	<b>0.47**†</b>	47.89
Galápagos	Plants	30	5	<b>0.84**</b>	49.67	<b>0.80*</b>	15.88	<b>0.73**</b>	11.87	<b>0.81**</b>	19.22
Marquesas	Plants	46	23	<b>0.95**</b>	150.18	<b>0.63*</b>	5.66	<b>0.68*</b>	7.87	<b>0.85**</b>	22.69
Azores	Plants	7.2	< 1	<b>0.83**</b>	288.30	–	–	–	–	–	–
Azores	Snails	51	31	<b>0.90**</b>	273.16	<b>0.90*†</b>	16.63	<b>0.94**†</b>	34.48	<b>0.66*</b>	5.05

†Denotes those cases for which the hump-shaped pattern is *not* observed.

\* $P < 0.05$ , \*\* $P < 0.001$ .

#### Marquesas Islands

Data for plants of the 10 largest islands in the group were extracted from the F.O.M. (Flora of the Marquesas) (2007) (for more information see Florence & Lorence, 1997; Wagner & Lorence, 1997).

#### Canary Islands

The most recent compilation of Canarian fauna and flora (Izquierdo *et al.*, 2004) was used for the extraction of data for arthropods, plants, and land snails (7 islands).

#### Data set properties

For each of the above cases we included only the number of native species, excluding introduced species. Subspecies and varieties (for plants) were also excluded. In addition, for each data set, we compiled and recorded the number and percentage of species endemic to each study island, and the numbers of genera to which the SIEs belong.

It is important to recognize that, although these may be the best available data sets, they have several shortcomings. For example, (1) despite two centuries of biological studies in the Canaries, new species have been described at a rate of approximately one species every six days over recent decades (Izquierdo *et al.*, 2004), and (2) for allopatric island taxa the application of a standardized species concept is particularly challenging (Rees *et al.*, 2001; Zink, 2002). However, because of the biological interest in oceanic islands, they are arguably better known and their phylogenies better studied than is the case for most continental areas (e.g. Wagner & Funk, 1995; Emerson, 2002; Whittaker & Fernández-Palacios, 2007). In so

far as the data are incomplete, or subject to excessive taxonomic splitting (or lumping), for the data sets used, we assume that there is not likely to be significant bias across the islands within a particular archipelago. There is some evidence that this assumption is problematic, as shown, for instance, by Cowie's (1995) path analysis of variation in species richness of Hawaiian land snails, in which the densely populated island of Oahu appears over-sampled in comparison to the big island of Hawaii. Readers are referred to the original sources for fuller accounts of such potential biases in the data.

The ages of the island complexes used were as reported in: Price (2004) for the Hawaiian Islands; Geist (1996), and Peck (2001, 2005) for the Galápagos Islands; Van Riel *et al.* (2005) for the Azores Islands; Clouard & Bonneville (2005) for the Marquesas Islands; and Carracedo *et al.* (2002) for the Canary Islands. Although the age of origin (maximum age) of each of the islands is more or less agreed upon, volcanic activity may have had a huge island-specific influence on the geomorphology and on the elements of biodiversity evaluated herein (i.e. speciation/extinction). Moreover, although the majority of the islands considered are discrete geographical entities within defined oceanic boundaries, this may change over time, with those that are separated by relatively shallow banks having been joined into larger single islands during times of lowered sea level (Whittaker & Fernández-Palacios, 2007).

Gran Canaria in the Canary Islands illustrates the problems that can arise in estimating island ages for the current purposes. Although the maximum subaerial age of Gran Canaria is *c.* 14.5 Myr (Carracedo *et al.*, 2002), some 3.5 Ma the catastrophic Roque Nublo ash flow is thought to have almost completely sterilized the island (Marrero & Francisco-Ortega, 2001; Emerson, 2003). Thus, the adoption of

*c.* 3.5 Myr (as used by Whittaker *et al.*, 2007) is arguably more appropriate in biological terms, reflecting the available time for the establishment and development of fauna and flora. Additional cases include: (1) the joining of Lanzarote and Fuerteventura (Canary Islands) into a single large island ('Mahan', *c.* 5000 km<sup>2</sup> in area) at times of low sea-level stands in the Pleistocene, and their most recent separation into discrete islands within the last 10,000 years; (2) the Maui-Nui complex in Hawaii, which similarly included the islands Molokai, Lanai, Maui and Kahoolawe (Price & Elliott-Fisk, 2004; Cowie & Holland, 2006); (3) the island of Tenerife (Canary Islands), which is composed of three Tertiary-age massifs (formed between *c.* 5 and *c.* 11.5 Ma) that were fused together by the building of the Teide massif to form a single island only within the last 2 Myr; and (4) the island of Sao Miguel (Azores), which is composed of five distinct parts varying in age from 4 to 0.29 Myr, with the present island taking shape only within the last 0.05 Myr. Finally, for most of the islands of Galápagos, although estimates of minimum and maximum age are available, it is not always clear which estimate is most appropriate in biological terms (see Geist, 1996; Peck, 2001, 2005), and indeed, in some published analyses, individual volcanoes separated by barren lava fields have been treated as separate islands (e.g. Willerslev *et al.*, 2002). Nevertheless, unless otherwise indicated and in order to establish a common first-approximation treatment of age, our results are based on the maximum age estimates for each contemporary island derived from the sources indicated.

### Metrics and analyses

The GDM predicts trends in evolutionary properties and also in properties such as species richness (SR) of native species, and carrying capacity (*K*) (e.g. Fig. 4), which set the stage within which evolutionary processes operate. We have no data for *K*, but do report patterns in SR. As metrics indicative of evolutionary dynamics we calculated three indices for each island:

- (1) nSIE – the number of single-island endemics (SIEs);
- (2) pSIE – the proportion of SIEs (nSIE/native species); and
- (3) DI – a simple diversification index, being the ratio of nSIE to the number of genera containing SIEs (note that where nSIE = 0, DI was also set to 0). To ensure normality, the pSIE data were arcsin-transformed.

All three indices are necessarily based on currently known extant distributions, and, although they might be termed speciation or diversification indices, this would arguably be an over-simplification (see discussions in Emerson & Kolm, 2005a,b, 2007a; Whittaker *et al.*, 2007). In reality (1) some current SIE species may have originated on another island (or land mass), from which they subsequently became extinct; (2) some species that evolved as SIEs may have gone extinct and so are not around to be counted; (3) some former SIE species may have colonized another island(s) to become a multi-island endemic; and (4) future inventory or taxonomic work may result in changes in designation or of known distributions – a general qualification in all such biogeographical analyses.

Although *in situ* speciation will typically be the majority driver of change in each of the three evolutionary metrics (nSIE, pSIE, DI) in the extended period leading up to the establishment of a dynamic evolutionary equilibrium (*sensu* Wilson, 1969), it is more appropriate to refer to each of these indices as being simple metrics of evolutionary dynamics, as each can be influenced by extinction (on the island in question or elsewhere) and migration, as well as by speciation. The GDM predicts that all three of these metrics should follow a broadly similar hump-shaped trend over the life cycle of an island (Table 2). For the flowering plants of Hawaii, we also make use of two additional indices of evolutionary dynamics for which data were readily available: the number of lineages (groups of species derived from a presumed founder event from outside the archipelago), and the species/lineage ratio (see Price, 2004; and see Table 2, prediction 7).

Equation 1 (above) describes the form of the ATT<sup>2</sup> models, which were fitted to the data using standard multiple regression. Model fits are described both by *R*<sup>2</sup> (variance explained) and by adjusted *R*<sup>2</sup> values (allowing comparison of models of different complexity) using a threshold significance level of *P* > 0.05 in all cases. In addition, for the comparison of the models, we applied the more general Akaike's information criterion (AIC; see Burnham & Anderson, 2002). Having undertaken these analyses for each of our diversity metrics, we test whether the ATT<sup>2</sup> model is more effective compared with four simpler models for each of our diversity metrics. The alternative models are the two standard island biogeographical species–area models (Whittaker & Fernández-Palacios, 2007), namely the semi-log model and the power model (the most commonly favoured in the literature), plus a semi-log island age model and a parabolic age model (i.e.  $D = b_1 + b_2\text{Age} + b_3\text{Age}^2$ ) to explore the fits derivable from age alone. We have applied the power model instead of the commonly used log-transformed version of it for reasons of comparison, because in the ATT<sup>2</sup> and all the other simpler models considered, the dependent variables (i.e. the number of native species and the evolutionary metrics) are untransformed. Note that the power model and the log-log model are not statistically equivalent and should be considered as different models (e.g. Ekbohm & Rydin, 1990). Note also that, when fitting the two-term age models and the ATT<sup>2</sup> models, we have not constrained the model to return a hump-shaped fit: accordingly, we note below when the models were not humped. For reasons of space limitation, some of these analyses are relegated to the online Supplementary Material (Tables S1–S3).

### RESULTS

The ATT<sup>2</sup> models describing species richness were statistically significant in each of the 14 cases tested from the five island groups (Table 4). The *R*<sup>2</sup> values ranged from 0.67 to 0.95, with a mean value of  $0.85 \pm 0.08$  (SD), and in each case the relationship with island age was humped in form. Similar findings pertain for each of the evolutionary dynamics metrics, with ranges of *R*<sup>2</sup> values as follows: nSIE, 0.48–0.90; pSIE,

**Table 5** Adjusted  $R^2$  values for the five alternative models fitted to the data for (a) SR and nSIE, and (b) pSIE and DI. The adjusted  $R^2$  values adjust for the complexity of the models. The  $ATT^2$  models (equation 1) are compared with models of the form indicated in the column headers, where D is the relevant diversity metric, A is the area, and T is time (i.e. island age). These models provide the two most common species–area models (semi-log and power models) plus two time models (semi-log and parabolic models), the latter to demonstrate the relationship with time when not included in a combined area/time model. All regression models are significant at  $P > 0.05$  unless indicated (NS). Data properties are as given in Tables 3 and 4.

Island group	Taxon	SR (Species richness of native species)					nSIE (Number of single-island endemics)				
		$ATT^2$	D–LogA	D–A	D–LogT	T+T <sup>2</sup>	$ATT^2$	D–LogA	D–A	D–LogT	T+T <sup>2</sup>
<b>(a)</b>											
Canary	Arthropods	<b>0.86</b>	NS	0.28	NS	0.09	<b>0.64</b>	NS	0.37	NS	NS
Canary	Plants	<b>0.82</b>	NS	0.22	NS	0.24	<b>0.70</b>	NS	0.30	NS	0.44
Canary	Snails	<b>0.74</b>	NS	0.02	NS	0.49	<b>0.52</b>	NS	0.04	NS	0.42
Hawaii	Arthropods	<b>0.75</b>	0.77	0.79	0.51	0.50	<b>0.53</b>	0.63	0.67	0.35	0.31†
Hawaii	Coleoptera	<b>0.76</b>	0.77	0.75	0.49	0.51	<b>0.59</b>	0.65	0.62	0.33	0.33†
Hawaii	Flowering plants	<b>0.91</b>	0.88	0.78	0.53	0.61	<b>0.69</b>	0.42	0.39	NS	NS
Hawaii	Snails	<b>0.51</b>	0.58	0.43	NS	0.33	<b>0.30</b>	0.48	0.43	NS	0.20†
Galápagos	Insects	<b>0.73</b>	0.61	0.61	NS	–0.16	<b>0.53</b>	0.41	0.40	NS	NS
Galápagos	Insects (small orders)	<b>0.68</b>	0.57	0.56	NS	–0.16	<b>0.31</b>	NS	0.16	NS	NS
Galápagos	Beetles	<b>0.76</b>	0.62	0.64	NS	–0.16	<b>0.64</b>	0.57	0.62	NS	NS
Galápagos	Plants	<b>0.79</b>	0.72	0.76	NS	–0.12	<b>0.73</b>	0.42	0.32	NS	NS
Marquesas	Plants	<b>0.93</b>	0.83	0.87	NS	–0.14	<b>0.33</b>	0.50	0.78	NS	NS
Azores	Plants	<b>0.73</b>	0.74	0.74	NS	0.07	–	–	–	–	–
Azores	Snails	<b>0.84</b>	0.54	0.52	NS	0.36	<b>0.80†</b>	NS	NS	0.71	0.92†
		pSIE (Proportion of SIE)					DI (Diversification index)				
		$ATT^2$	D–LogA	D–A	D–LogT	T+T <sup>2</sup>	$ATT^2$	D–LogA	D–A	D–LogT	T+T <sup>2</sup>
<b>(b)</b>											
Canary	Arthropods	<b>0.64</b>	NS	0.18	NS	0.30	<b>0.54</b>	NS	–0.04	NS	0.36
Canary	Plants	<b>0.80</b>	NS	0.17	NS	0.33	<b>0.98</b>	NS	0	NS	0.51
Canary	Snails	<b>0.76</b>	NS	–0.02	NS	0.82	<b>0.80</b>	NS	–0.10	NS	0.81
Hawaii	Arthropods	<b>0.57</b>	NS	0.34	NS	0.44†	<b>0.85</b>	0.83	0.86	0.55	0.56†
Hawaii	Coleoptera	<b>0.90</b>	NS	0.31	0.37	0.81†	<b>0.90</b>	0.82	0.84	0.63	0.65†
Hawaii	Flowering plants	<b>0.60</b>	0.33	0.34	NS	0.10†	<b>0.69</b>	0.60	0.56	NS	0.27†
Hawaii	Snails	<b>0.94</b>	0.83	0.73	0.83	0.38†	<b>0.61</b>	0.66	0.57	0.33	0.37†
Galápagos	Insects	<b>0.40</b>	0.34	0.35	NS	–0.13†	<b>0.36</b>	NS	0.22	NS	–0.08†
Galápagos	Insects (small orders)	<b>0.04</b>	NS	–0.07	NS	0.08†	<b>0.12</b>	NS	–0.01	NS	0.02†
Galápagos	Beetles	<b>0.60</b>	0.41	0.42	NS	0.09†	<b>0.29</b>	0.39	0.34	NS	–0.10†
Galápagos	Plants	<b>0.64</b>	0.29	0.23	NS	0.09†	<b>0.75</b>	0.38	0.29	NS	0.18†
Marquesas	Plants	<b>0.01</b>	0.53	0.72	NS	NS	<b>0.78</b>	0.66	0.63	NS	–0.08†
Azores	Plants	–	–	–	–	–	–	–	–	–	–
Azores	Snails	<b>0.90†</b>	NS	NS	0.69	0.90†	0.46	NS	NS	0.57	0.50†

†Denotes those cases where the hump-shaped pattern is *not* observed.

0.28–0.96; and DI, 0.34–0.99. The island age component was humped except in four cases, namely nSIE and pSIE for Azorean snails, and pSIE and DI for Galápagos beetles.

Table 5 provides a direct comparison between the performance of the  $ATT^2$  model and four alternative models for all diversity metrics, SR, nSIE, pSIE and DI, using the adjusted  $R^2$  values. The  $ATT^2$  model provides the most effective model according to the adjusted  $R^2$  values in between 8 and 10 cases for each metric. The four alternative models are each simpler than the  $ATT^2$  models, being two-parameter (T+T<sup>2</sup>) or one-parameter models. The two conventional area models each provide higher adjusted  $R^2$  values than the  $ATT^2$  model for particular data sets (between one and four cases, depending on

the metric used), but, unlike this model, neither provides significant fits to all data sets, with non-significant fits most evident for the three Canarian taxa. The time models generally perform poorly in comparison with the  $ATT^2$  models, with one exception, namely the Azorean snail data, for which, contrary to the expectations of the GDM, the relationship with time is not humped. Undertaking the same comparisons but using AIC values rather than adjusted  $R^2$  values for model comparisons, the results remain the same, with the  $ATT^2$  model being the best model (lowest AIC value) in most of the cases (Tables S1 & S2).

Table S3 provides additional results for three of the archipelagos using different data sets and/or assumptions.

For the Canaries, we switched the relative positions of Tenerife (11.6 Myr) and Gran Canaria (14.5 Myr) by adopting an intermediate age of 8 Myr for the three proto-islands of Tenerife, and an age of 3.5 Myr (after the Roque Nublo ash flow) for Gran Canaria (see Whittaker *et al.*, 2007). For the Galápagos, we used minimum and mean island age estimates. Finally, for Hawaii, we included additional islands that were excluded from our main analyses on the basis of concerns over validity of data. Unsurprisingly, these decisions do influence the statistical fits ( $R^2$ ) of the models, but the overall pattern appears robust, with the ATT<sup>2</sup> models generally providing significant fits. Exceptions include the model for Hawaiian flowering plants, for which the inclusion of 18 islands and atolls in place of 10 resulted in a poor fit for the ATT<sup>2</sup> nSIE model (consistent with Emerson & Kolm's (2007a) analyses, which were based on 16 Hawaiian islands and showed an apparently erratic relationship between pSIE and island age). On the other hand, the use of mean island age in the case of the Galápagos Islands led to increased fit of the ATT<sup>2</sup> model.

Finally, we were also able to test the fit of the ATT<sup>2</sup> model for Hawaiian flowering plants using two additional diversification metrics (from Price, 2004): the number of lineages, and the species/lineage ratio. In both cases, good fits were obtained, and the hump-shaped pattern was observed (Table S3). For the number of distinct lineages present on each island,  $R^2 = 0.97$ , and adjusted  $R^2 = 0.96$  ( $F = 135.45$ ,  $P < 0.0001$ ), and for the species/lineage ratio,  $R^2 = 0.94$ , and adjusted  $R^2 = 0.91$  ( $F = 135.25$ ,  $P < 0.0001$ ). In both cases, the ATT<sup>2</sup> model was more effective according to the adjusted  $R^2$  values (and the AIC values; not shown) compared with all four simpler models. The highest adjusted  $R^2$  values from among these competing models were exhibited by the semi-log model: 0.94 and 0.85 for the number of lineages and the species/lineage ratio, respectively.

## DISCUSSION

### Empirical findings from fitting the ATT<sup>2</sup> models

The foregoing analyses demonstrate that the ATT<sup>2</sup> model provides a generally good fit with data from a range of plant and animal taxa from five oceanic island archipelagos, both for numbers of native species (SR) and for metrics more directly indicative of evolutionary dynamics (nSIE, pSIE, DI). The effectiveness of the ATT<sup>2</sup> model in fitting data for particular archipelagos is expected to depend on the extent to which the archipelago provides a full range of island developmental stages. So, for example, for archipelagos providing only young islands, it would be consistent with the GDM for a simpler 'area + time' model to provide a better fit than the full ATT<sup>2</sup> model. However, across the data sets evaluated herein, comparison with the alternative models provides confirmation that the ATT<sup>2</sup> model, although not the simplest model (and not necessary in all cases), has greater generality than the traditional diversity–area models, or time-only models.

There are, as outlined earlier, several important limitations to these tests: first, the effective ages of the islands cannot be

determined with certainty, given the complexities of island histories and the limitations of the dating methods; second, the quality of the taxonomic and distributional data suffers from the same limitations as all such data sets (in particular, see Cowie, 1995); and third, the small number of islands per archipelago means that we are close to the threshold at which the fit of a three-parameter model in any particular case might be deemed trivial. We have minimized the taxonomic problem by ignoring subspecies designations and counting only endemic species in the DI and SIE metrics. We have also addressed the dating and survey quality problem by running a number of alternative models (above, Table S3). Overall, we take encouragement from the fact that the ATT<sup>2</sup> models appear able to capture a significant proportion of the variance in the data from these rather different archipelagos, and that the general form of the relationships is, as predicted by the GDM (Table 2, for example predictions 1, 6, and 7), a linear relationship with  $\log(\text{Area})$ , combined with a humped relationship with island age.

### General evaluation of the general dynamic model

Consideration of the literature for the study systems we have examined herein provides further support for the GDM. For example, Silvertown (2004) notes that large endemic taxa within the Canarian endemic flora are typically monophyletic (e.g. 63 species of Crassulaceae, and 37 species of *Echium*); that is, they typically derive from single colonization events. Silvertown suggests that this may be indicative of the operation of niche pre-emption by early colonizing lineages, which, once having colonized, may have both inhibited the success of later-arriving mainland relatives and spread out across the archipelago as new islands formed, frequently radiating into new habitats. This interpretation has been the subject of some debate (Saunders & Gibson, 2005; Silvertown *et al.*, 2005), but has been supported by further work (Carine *et al.*, 2004) and is consistent with the GDM, and particularly the prediction of most rapid lineage radiation occurring on relatively young islands. An analogous mechanism is tentatively supported by Cowie (1995) in his analysis of Hawaiian land snails.

Phylogenetic analyses also provide support for the notion that younger islands are more active arenas for speciation. On the Hawaiian Islands, the estimated speciation rate for plants is a negative function of island age, varying from 0.20 species per lineage per million years on Kauai (island age: 5.7 Myr) to 2.1 species per lineage per million years on Hawaii (island age: 0.5 Myr) (Levin, 2004). Perhaps the best-resolved example of this within a taxon is that of the Hawaiian silverswords, for which Levin (2004) argues that the majority of the speciation events occurred early in the history of the group when the flora was not saturated (for phylogenetic analyses, see Baldwin & Robichaux, 1995; Baldwin & Sanderson, 1998). Studies from the flora of the Juan Fernández Islands also support the idea of high *initial* rates of radiation, with faster rates evident on the younger island: 0.33 species per lineage per million years on Mastierra (island age: 4 Myr) vs. 0.96 species per lineage per

million years on Masafuera (island age: 1–2 Myr) (Levin, 2000; cited in Levin, 2004). Electrophoretic data for the endemic genus *Robinsonia* (Asteraceae) suggest that the founding population arrived early in the 4.0-million-year history of Masatierra Island, radiating and speciating rapidly after colonization (Crawford *et al.*, 1992). Similarly, Kaneshiro *et al.* (1995, p. 71), in their analysis of species groups within the picture-wing *Drosophila* of Hawaii, make the following observation: ‘Most of these species, like many other extant terrestrial endemic fauna, show a very strong but by no means exclusive tendency to single-island endemism. Most species thus appear to evolve on an island early in its history and thereafter remain confined to that island...’.

Evidence for the loss of species as a result of island erosion and subsidence (prediction 5, Table 2) can be invoked from first principles but is likely to be extremely hard to demonstrate unequivocally as the likelihood of finding fossil evidence is negligible in such circumstances. However, there are numerous cases in which island phylogenies point to the existence of earlier forms on islands (or in upland habitats) that no longer exist (e.g. Wagner & Funk, 1995; Keast & Miller, 1996; Butaud *et al.*, 2005; Pulvers & Colgan, 2007). Similarly, Emerson & Oromí (2005), in their discussion of the distribution of Canarian *Tarphius*, explain the absence of these beetles from the two oldest Canarian Islands (the eastern islands of Fuerteventura, and Lanzarote) as a result of the loss of their cloud forest habitat, prior to which presumably *Tarphius* did occur. Arnedo *et al.* (2000) use similar logic to explain a hump-shaped relationship between island age and number of endemic species of the aranid genus *Dysdera* in the Canaries, arguing that erosion of the mountains on these islands to below 800 m prevents the formation of the trade-wind inversion that supplies moisture to the mesic habitats found on the younger islands: ‘The low number of endemics in the eastern islands could therefore be explained by extinction mainly related to the major environmental change that took place on these islands. The distribution of the eastern endemic specimens seems to support this hypothesis. Most of the specimens were collected from sites located on the northern slopes of massifs over 400 m high. These places represent the wettest parts of these islands’ (Arnedo *et al.*, 2000, p. 289).

Although there is therefore some support for increased rates of speciation and adaptive radiation on younger islands, these findings may at least in part be the outcome of the effects of erosion and subsidence on older islands reducing the persistence of neo-endemic lineages within these islands (Stuessy, 2007). As Peck *et al.* (1999, p. 535) write in relation to Hawaiian insect taxa: ‘Thus, it appears that the younger main islands display higher species/genus ratios, not just as a result of increased rates of speciation or explosive radiation but also because their varied habitats and relaxed competition allow for continued speciation *as well as the retention of the products of such speciation.*’ [our emphasis]. It is intrinsically difficult to obtain evidence of changes in rates of the vital processes (migration/immigration, extinction, and speciation) through time and in relation to other island attributes (spacing, overall

archipelago isolation, Quaternary climate change), and this is especially the case for the biotas of remote oceanic islands, many of which can be attributed to natural colonization rates expressed in units of time of thousands of years (e.g. Wagner & Funk, 1995; Peck *et al.*, 1999). Similarly, attributing evolutionary outcomes to ‘non-adaptive’ vs. ‘adaptive’ process is challenging (but see Price & Wagner, 2004). Claims for non-adaptive radiation have been most convincingly made for land snails on deeply dissected oceanic islands such as Porto Santo (Madeira) (Cameron *et al.*, 1996), although, for example, Barrett (1996) has suggested that the term may be applied to particular plant lineages within Aegean islands.

The three indices of evolutionary dynamics that we present in Tables 4 and 5 are each based (wholly or partly) on the number of single-island endemic species, and it might be argued that they therefore only capture a small part of the outcome of evolutionary dynamics ongoing not only across whole oceanic island archipelagos such as the Galápagos, but also across island regions such as Macaronesia (comprising the Canaries, Azores, Madeira, Salvage Islands, Cape Verde Islands, and source areas in Africa and southern Europe). However, we follow other recent authors (e.g. Peck *et al.*, 1999; Emerson & Kolm, 2005a) in adopting the rationale that SIE data are likely to be indicative of trends and patterns in other metrics of evolutionary dynamics. For example, tallies of data for the overall number of Canarian endemic plants across the seven main islands of the archipelago (reproduced in Whittaker & Fernández-Palacios, 2007) show that, at least in this case, the pattern for the number of Canarian endemics is strongly correlated with the nSIE and again shows a humped relationship with island age. Moreover, those endemics found on two islands (only) are all shared by island pairs in close proximity to one another, such that species are shared between Lanzarote and Fuerteventura; Gran Canaria and Tenerife; Tenerife and La Palma; Tenerife and La Gomera; and each pairing of La Gomera, La Palma and El Hierro. These data are consistent with the idea that, once a species has formed, it may in time colonize another island within the archipelago, with the probability of colonization being an inverse function of distance. In the Canarian archipelago, this pattern of shared endemism between adjacent islands also largely conforms to the developmental history of the archipelago (reviewed in Whittaker & Fernández-Palacios, 2007), as does the pattern in Hawaii (e.g. Wagner & Funk, 1995). However, not all patterns of shared endemics necessarily relate to a pattern of speciation followed by over-water colonization. In the case of Lanzarote and Fuerteventura, the islands were fused prior to the Holocene transgression, and so it cannot be determined where within the two islands the approximately 17 plant species currently shared only by them originated. Indeed, more generally, we have to allow that species may have occurred in the past on one or more other islands from which they have subsequently gone extinct by natural (e.g. Butaud *et al.*, 2005) or indeed by anthropogenic (e.g. Paulay, 1994; Borges & Brown, 1999; Whittaker & Fernández-Palacios, 2007; Blondel, 2008) drivers.

Phylogeographic analyses of island lineages provide further lines of evidence for the pattern of movement and evolution across archipelagos. One commonly supported pattern involves taxa showing a pattern of dispersal from older to younger islands within an archipelago, with speciation occurring on newly colonized islands. This progression-rule pattern (Funk & Wagner, 1995) is particularly evident in archipelagos showing a clear linear age sequence of islands. Examples drawn from the many that provide support for this rule include: from Hawaii, *Drosophila*, *Hesperomannia*, *Hibiscadelphus*, *Kokia*, *Remya*, *Tetragnatha* (Funk & Wagner, 1995; Gillespie, 2004; Pons & Gillespie, 2004), and *Orsonwelles* spiders (Hormiga *et al.*, 2003); from Macaronesia, *Olea*, *Gallotia*, *Hegeter*, *Gonopteryx* (cited in Whittaker & Fernández-Palacios, 2007), *Pimellia* and *Hegeter* (cited in Gillespie & Roderick, 2002) and possibly *Dysdera* (Arnedo *et al.*, 2000); from Galápagos, scarabs and weevils (cited in Gillespie & Roderick, 2002); and from the Austral Islands, *Misumenops rapaensis* (Garb & Gillespie, 2006). Various other patterns (or no resolvable pattern) have been detected from these and other oceanic archipelagos. In some cases, for example Galápagos birds, evolutionary scenarios involve multiple phases of island-hopping and of alternating periods of allopatry and sympatry within a single radiation (Lack, 1947; Grant & Grant, 1996). In contradiction to the progression rule, data for some taxa are most parsimoniously explained by a sequence of colonization from a young to an older island. For example, mtDNA data suggest that the Canarian blue tit first colonized Tenerife (in the middle of the island-age gradient), and that this was followed by subsequent spread both to older and to younger islands (Kvist *et al.*, 2005); and for Canarian plants, see Sanmartín *et al.* (2008). It should therefore be understood that the progression rule is merely a general tendency (as Funk & Wagner, 1995; Gillespie & Roderick, 2002), but it is one that based on the GDM should be expected to be a dominant pattern, followed by many taxa in archipelagos that show a strong island age sequence, and especially so in taxa that happen to colonize early in the developmental history of an archipelago, but that also exhibit sufficient dispersal limitation to speciate within the islands of that archipelago.

We are under no illusions that the GDM, as described herein, provides a complete model of island biogeography and evolution. Modification will be necessary for those classes of island that conform poorly to the ontogenetic model proposed here, including many island arc archipelagos and islands of continental origins showing complex histories of horizontal and vertical movement, erosion and re-building (e.g. Buskirk, 1985; Keast & Miller, 1996; McDowall, 2008). For those oceanic islands that do conform to the simple ontogenetic model, perhaps one of the most important omissions from the framework is the role of Quaternary climate change and the accompanying variation in the configuration of islands (e.g. Williams, 1972; Peck, 1990; Nunn, 1994; Carine, 2005; Whittaker & Fernández-Palacios, 2007; Ávila *et al.*, 2008). This not only altered the number, area and elevational range of islands in these archipelagos, but also their relationship with source pools. For instance, Carine (2005) argues that the evolutionary pattern in Macaronesian *Convolvulus*

*ulus* is suggestive of there having been discrete waves of colonization of this island region, which he explains through a mechanism he labels the 'colonization window' hypothesis. This postulates that colonization opportunities vary through time in relation both to the geo-tectonic mechanisms discussed herein (island formation, island sterilization/disturbance) and to periods of climate change. Linked to the latter, low sea-level stands during the Pleistocene saw the emergence of stepping-stone islands, aiding dispersal among the more persistent islands of Macaronesia, and between them and the mainland (Whittaker & Fernández-Palacios, 2007). Similar arguments have been invoked elsewhere, and the notions that dispersal distances and directionality of dispersal related to major current systems can change through time provide additional components that require integration into a comprehensive general theory of oceanic island biogeography (Cook & Crisp, 2005; Cowie & Holland, 2006).

Finally, no consideration of oceanic island biogeography is complete without some reference to the impact of humans on the biodiversity of oceanic island archipelagos (e.g. Gillespie, 2007; Whittaker & Fernández-Palacios, 2007). In the historical period of island exploration (roughly the last 400 years), approximately 60% of recorded extinctions have been of island species, with Pacific island birds particularly badly depleted (e.g. Steadman, 2006). The application of the ideas discussed herein to particular oceanic islands and taxa is therefore subject to the potential disruption of biogeographical patterns following from the impact of anthropogenic habitat conversion, introductions, and extinctions.

## CONCLUSION

In this paper we have outlined a general dynamic theory for the biogeography of oceanic islands that explicitly places MacArthur & Wilson's (1963, 1967) dynamic equilibrium model into the geological and evolutionary context of oceanic archipelagos. The GDM is a deliberately simplified representation of diversity dynamics on oceanic islands. Our aim was to 'capture' the few major factors that drive diversity patterns on oceanic islands of different sizes and ages, rather than to produce a precise predictive model. In doing this we are following a long tradition in ecology and biogeography. Indeed, MacArthur & Wilson (1967, pp. 5–6) explicitly intended their model to have similar properties, stating 'A theory attempts to identify the factors that determine a class of phenomena and to state the permissible relationships among the factors ... substituting one theory for many facts. A good theory points to possible factors and relationships in the real world that would otherwise remain hidden and thus stimulates new forms of empirical research ... If it can also account for, say, 85% of the variation in some phenomenon of interest, it will have served its purpose well.'

We argue that the main advantage of the GDM is not the better fit of the ATT<sup>2</sup> models over the other simple models tested herein, as other higher-order models can have this property too (an ecological example being Kalmar & Currie's (2006) models of bird species richness on islands), but the fact



that it offers an improved theoretical framework for describing and understanding the evolutionary biogeography of oceanic islands (as called for by Heaney, 2007). Thus, although a more complete, formal treatment awaits further development, we hope that the GDM can offer the foundation for a newly expanded theory of island biogeography, unifying ecological and evolutionary biogeography.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

**Table S1** AIC values for the five alternative models fitted to the data for two metrics: SR and nSIE.

**Table S2** AIC values for the five alternative models fitted to the data for two metrics: pSIE and DI.

**Table S3** Model fits for the ATT<sup>2</sup> models (equation 1) varying the assumptions made about the archipelagos, for species richness of native species, nSIE, pSIE and DI.

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## BIOSKETCHES

**Robert J. Whittaker** has a long-term fascination with the biogeography of islands, and has worked for many years on the recolonization and island ecology of the Krakatau Islands, Indonesia. His other research interests include diversity theory, scale effects, and conservation biogeography.

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