SPECIAL ISSUE

The general dynamic model: towards a unified theory of island biogeography?

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ABSTRACT

Aim Island biogeography focuses on understanding the processes that underlie a set of well-described patterns on islands, but it lacks a unified theoretical framework for integrating these processes. The recently proposed general dynamic model (GDM) of oceanic island biogeography offers a step towards this goal. Here, we present an analysis of causality within the GDM and investigate its potential for the further development of island biogeographical theory. Further, we extend the GDM to include subduction-based island arcs and continental fragment islands.

Location A conceptual analysis and a simulation of oceanic islands.

Methods We describe the causal relationships between evolutionary and ecological processes implied by the GDM, implement them as a computer simulation and use this to simulate two alternative geological scenarios.

Results The dynamics of species richness and rates of evolutionary processes in simulations derived from the mechanistic assumptions of the GDM corresponded broadly to those initially suggested, with the exception of trends in extinction rates. Expanding the model to incorporate different scenarios of island ontogeny and isolation revealed a sensitivity of evolutionary dynamics to attributes of island geology.

Main conclusions We argue that the GDM of oceanic island biogeography has the potential to provide a unified framework for island biogeography, integrating geological, ecological and evolutionary processes. Our simulations highlight how the geological dynamics of distinct island types are predicted to lead to markedly different evolutionary dynamics. This sets the stage for a more predictive theory incorporating the processes governing temporal dynamics of species diversity on islands.

Keywords

Carrying capacity, causal model, GDM, general dynamic theory, island biogeography, oceanic islands, simulation model, species richness, theory of ecology, volcanic islands.

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INTRODUCTION

Island biogeography has, at its core, a focus on understanding how the species diversity of islands is affected by island characteristics. The central theory of island biogeography was set out by MacArthur and Wilson in 1963, in a seminal paper that combined the effects of isolation and area on rates of immigra-tion, speciation and extinction of species on islands (MacArthur & Wilson, 1963). They expanded their theory in a monograph (MacArthur & Wilson, 1967) in which the potential for local speciation to contribute to species richness was separated from the initial description of the model, and their 'equilibrium theory of island biogeography' (ETIB) subsequently became synonymous with a largely ecological framework of processes.

This framework became paradigmatic within island biogeography, with periodic theoretical expansion and developments following (Hubbell, 2001; Whittaker & Fernández-Palacios, 2007).

In spite of the impact and heuristic success of the ETIB, a coherent understanding of the processes controlling island biodiversity has yet to emerge. This is partly because the focus of the ETIB on dynamic equilibrium has been difficult to reconcile with biogeographical evidence for the role of historical contingency and geological processes in shaping current patterns (Heaney *et al.*, 2013) and partly because the theory on ecological dynamics is not sufficiently integrated with evolutionary processes.

Whittaker *et al.* (2008) took a step towards resolving these issues and creating a coherent framework for island biogeography (Heaney *et al.*, 2013), putting forward what they termed a 'general dynamic theory' (or 'general dynamic model', henceforth GDM; Fig. S1 in Appendix S1 in Supporting Information) of oceanic island biogeography. This theory integrates the precepts of the ETIB within an evolutionary time-scale, where processes of within-island speciation and geological dynamics play increasingly dominant roles. The essence of the GDM is that geological processes drive broadly predictable changes in the area, elevation, topographical complexity, and isolation of islands over time, in turn generating predictable changes in the rates of immigration, speciation and extinction.

Although ostensibly making few assumptions, the attempted unification of biological and geological processes makes the GDM quite complex in practice. Such complex frameworks (dubbed 'constitutive theories' by Scheiner, 2010) can have considerable pedagogical and heuristic value (see also Heaney, 2000). However, the complexity of interactions may mean that straightforward inference testing is not immediately feasible, or provides inconclusive outcomes (as discussed by Borges & Hortal (2009), Bunnefeld & Phillimore (2012) and Cameron *et al.* (2013) in the context of the GDM). The challenge in working with constitutive theories is therefore to develop tractable means of testing, for example by the use of approaches such as simulation modelling.

Although Whittaker *et al.* (2008) presented a suite of predictions from the GDM, initial empirical evaluations of the GDM have focused on testing a subset of the predictions of the model that lend themselves to straightforward analytical tests: that species richness and the number and proportion of endemic species should show hump-shaped relationships to island age, when the effect of island area is controlled for. These tests have shown a reasonable (but not universal) degree of support for the model (Borges & Hortal, 2009; Bunnefeld & Phillimore, 2012; Cameron *et al.*, 2013; Steinbauer *et al.*, 2013). However, these tests alone are not conclusive evidence for the correctness of GDM dynamics.

Here, we develop the GDM by presenting a more formal analysis of the implied causal relationships of the model. We use a simulation of these causal relationships to evaluate the internal consistency of the island dynamics predicted by Whittaker *et al.* (2008). As these dynamics were based on islands formed by volcanism over mantle hotspots, we seek to expand the GDM into a more general model of evolutionary island biogeography by applying the causal model structure to alternative island ontogenies and settings.

Components of the GDM

The GDM is based on three basic premises (Whittaker *et al.*, 2008):

1. The biotas of islands are determined by the relative rates of immigration, local extinction and speciation.

2. Rates of speciation and extinction are affected by opportunities for geographical isolation and the existence of unoccupied niche space.

3. The physical geographical attributes of oceanic islands show broadly predictable dynamics over evolutionary time-scales, and this drives the ecological and evolutionary dynamics of island biotas.

The first two premises derive from MacArthur and Wilson (1967). The importance of the third in island biogeography has been suggested by several authors (e.g. Hooker in Williamson 1984; Stuessy, 2007) but the integration of the three premises into a general model was novel to Whittaker *et al.* (2008). Below we expand on the causality of each of these premises in detail.

Premise 1

The first premise follows the original ETIB of MacArthur & Wilson (1963) in stating that species richness is determined by the opposing forces of immigration, speciation and extinction (Fig. S2, in Appendix S1). Although often overlooked, the ETIB explicitly stated that cladogenetic speciation would contribute to richness dynamics, but being considered a rare process except on the largest and most remote islands, it was excluded by MacArthur & Wilson (1963, 1967) from their seminal diagram. Whereas the canonical depiction (Fig. S2) conveys an intuitive understanding of the dynamic equilibrium, a clearer understanding of the causal relationships in the model may better be achieved by supplementing it with a directed graph diagram (Fig. 1a).

The causal diagram (Fig. 1a) illustrates how per-island levels of immigration and extinction are affected by the isolation and area of the island. These rates are also affected by species richness via a feedback loop, which stabilizes the model towards a dynamic equilibrium: as species richness on the island increases, the per-species extinction rate is predicted to increase due to intensification of diffuse interspecific competition for resources; and per-island immigration will decrease because more of the species that exist in the source population are likely to already be present on the island, and those that have not arrived may have lower dispersal capabilities (MacArthur & Wilson, 1967, 1967).

Premise 2

The second premise is that rates of speciation and extinction are determined by the geographical attributes of islands and by the existence of unoccupied niche space (Fig. 1b). The effect of
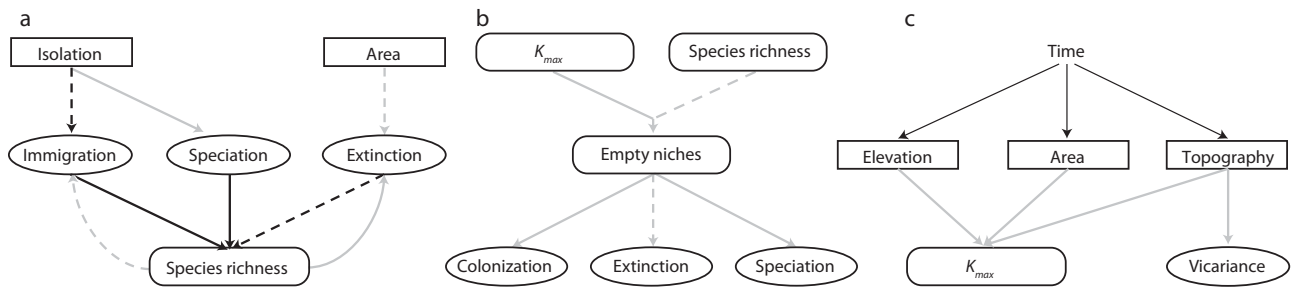
Figure 1 The causal relationships implied in the three premises of the general dynamic model (GDM). (a) Causal relationships of MacArthur and Wilson's original 1963 equilibrium theory of island biogeography, which constitute Premise 1 of the GDM. (b) Causal relationships implied by carrying capacity controlling evolutionary rates, which is Premise 2 of the GDM. (c) Causal relationships implied by the geological ontogeny of islands, which is Premise 3 of the GDM. Black arrows indicate relationships that are self-evident, for example it is clear that speciation increases species richness, whereas extinction decreases it; or theoretically uncontroversial and empirically well established, for example that island isolation decreases immigration rate. Grey arrows indicate relationships that are speculative and should be tested with empirical analyses, for example that topographic complexity affects the probability of vicariant/allopatric speciation. Dashed arrows are negative effects. Boxes indicate geological attributes, ellipses are biological processes and rounded rectangles are biological amounts.
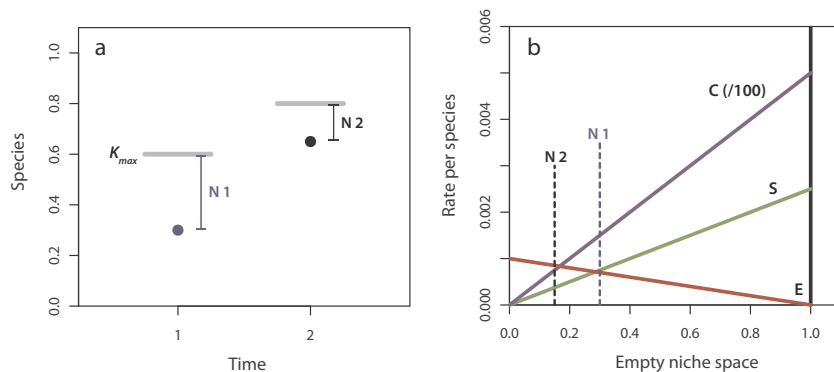

Figure 2 The assumed relationships between species richness, carrying capacity and evolutionary rates under Premise 2 of the GDM, as used in the simulation model. (a) The species richness values at two different times are shown as points and the value of K_{max} (carrying capacity) at each time are shown as grey bars. The y-axis is number of species, as a proportion of the size of the mainland source pool. The distance between K_{max} and species richness is the amount of empty niche space (N1 and N2 for the two different times). (b) The relationship between the per-species speciation rate (S), extinction rate (E) and the probability of a newly arrived immigrant colonizing successfully (C, divided by 100 to fit on the graph). Evolutionary rates vary linearly with the amount of empty niche space, expressed as a proportion of the size of the mainland source pool to be comparable among taxa of different size. Rates for times 1 and 2 are shown by dashed lines.

unoccupied niche space assumes that per-species rates of evolutionary processes exhibit diversity dependence, which is still relatively controversial – in part because the underlying mechanisms remain unclear (Benton, 1996; Jablonski, 2008; Moen & Morlon, 2014). Nonetheless, studies of evolutionary rates over deep history support a degree of diversity dependence (Rabosky & Glor, 2010; Ezard et al., 2011; Price et al., 2014). On remote islands the notion is less controversial, as support is provided by adaptive radiations involving phenotypical divergence within a single lineage (Givnish et al., 2009; Knope et al., 2012). Such adaptive radiation is usually interpreted as a diversity-dependent response to unoccupied ecological opportunity, which exists because the mainland species adapted to certain niches have not immigrated (Losos & Ricklefs, 2009).

Within the GDM, the action of diversity dependence is operationalized using the notion of 'environmental carrying capacity', K_{max}, which is the number of species that could coexist on an island if the ecological niche space were completely filled (Figs 2 & S1; see also Walker & Valentine, 1984). This concept of species carrying capacity is distinct from the concept of individual carrying capacity known in population biology, often expressed as the parameter K from the logistic growth equation. The concept of species richness being limited by a set carrying capacity has been challenged, because it seems to assume that island communities are fully saturated. Ecological saturation seems especially unlikely on remote oceanic islands, which are generally considered to be characterized by lower species numbers than islands close to the continent (Johnson &

Simberloff, 1974; Kreft *et al.*, 2008). Etienne *et al.* (2012) recently demonstrated that taxa evolving under evolutionary diversity dependence with a constant K_{max} will generally not approach full saturation of niche space. This is because extinction continuously removes species, whereas speciation rates decrease towards zero as full saturation is approached. This observation reconciles the notions of diversity dependence and equilibrium, by positing that species richness is controlled by an equilibrium between diversity-dependent rates. This is essentially a trivariate equilibrium model as envisioned by Heaney (2000).

In the graphical depiction of the GDM by Whittaker *et al.* (2008), the species richness of young islands is shown to lag in its increase towards K (i.e. K_{max}), and then to follow K closely as it decreases on older islands undergoing erosion and submergence (Fig. S1). However, complete community saturation is not an integral element of the model, and an expression of Premise 2 that is consistent with Etienne *et al.*'s (2012) findings is shown in Fig. 2. As the realized species richness approaches K, the extinction rate increases and the speciation rate decreases (Fig. 2a). It is also possible that the amount of empty niche space will affect the probability of successful colonization of immigrating species (as depicted in Fig. 2b). Because we include an effect of niche space on colonization success, which was not explicitly considered by Whittaker *et al.* (2008), we distinguish between immigration, which is the number of new species arriving on an island, and colonization, which is the number of those species that successfully establish populations.

Premise 3

The third premise is that islands are geologically dynamic, and that the geological life cycle of an island is an important driver of ecological and evolutionary processes. Whittaker *et al.* (2008) focused on volcanic hotspot islands in the open ocean, and suggested that these islands follow a predictable geological trajectory throughout their life cycle, driven mainly by processes of volcanic island activity, tectonic subsidence and erosion. This life cycle is characterized by an initial phase of island building followed by a protracted phase of erosion and submergence, and can be approximated as a roughly hump-shaped relationship, in which the area and elevation of an island reach their peak at an early age and then decline. They also suggested that the complexity of an island's topography should peak at intermediate age, though somewhat later than area and elevation (Fig. S3 in Appendix S1).

The idea that island development should play a role in determining species diversity is not new (e.g. Hooker in Williamson, 1984; Borges & Brown, 1999), but is only now starting to receive focused attention. The geological ontogeny of islands is predicted to affect evolutionary rates via two mechanisms: (1) the area, elevation and topographic complexity of the island determine K_{max} by influencing the overall size of the resource base (controlling the rate and total of primary and secondary productivity); and (2) the topographical complexity of the island should also affect the probability of species populations achieving reproductive isolation within the island, for example two islands may have the same number of major habitat types but one may have a more complex mosaic of isolated patches due to its greater topographic complexity, thus stimulating micro-allopatric speciation (Fig. 1c). In this context, we refer to this latter type of speciation as 'non-adaptive' cladogenesis.

The causal model of island biogeography

By combining the causal relationships derived from the individual premises, we can depict the total implied causality of the GDM (Fig. 3). This representation can be used as a basis for computer simulation of GDM dynamics, and as a tool to investigate emergent patterns from islands operating under the GDM. We used the directed graph model to implement a basic unitless simulation model, which mimicked the behaviour of a system operating under the GDM. We then used this simulation model to answer a number of key questions about the GDM:

1. Are the temporal trajectories of species richness and evolutionary rates suggested by Whittaker *et al.* (2008) consistent with their verbal model of causal relationships?

2. What is the expected relationship between K_{max} and species richness under increasing levels of island isolation?

3. What are the expected temporal trajectories of evolutionary rates for islands that follow common geological ontogenies other than the iconic hump-shape of volcanic hotspot islands?

We then discuss how the GDM forms a coherent framework that can be used to form the basis of a constitutive theory of island biogeography.

MATERIALS AND METHODS

Simulation model

The simulation model was implemented as a basic discrete time function in R 3.0, running over 5000 time steps, which means that each time step might realistically represent 1–5 kyr. The model itself is in arbitrary units. We parameterized the model to be as simple as possible, while still consistent with the full causal complexity of the GDM. All causal relationships were assumed to be linear where this was consistent with theory, because linear relationships require just one parameter (the slope). The only exception was the influence of native species richness on the probability that a new immigrant would belong to an already established species. Because some species in the source population are presumed to immigrate more often (MacArthur & Wilson, 1967), this relationship was assumed to follow a saturation curve with exponent Msa. The parameter values (e.g. slopes) of each causal relationship were balanced so that any variable was affected approximately equally by all arrows leading to that variable, under the philosophy that only relationships with a strong effect should be represented in the model. The functional relationships are shown as arrows in Fig. 3.

The model is defined to be scalable, i.e. it applies equally to a study of moths and to all arthropods, under the neutral assumption that species are roughly equivalent. The actual richness
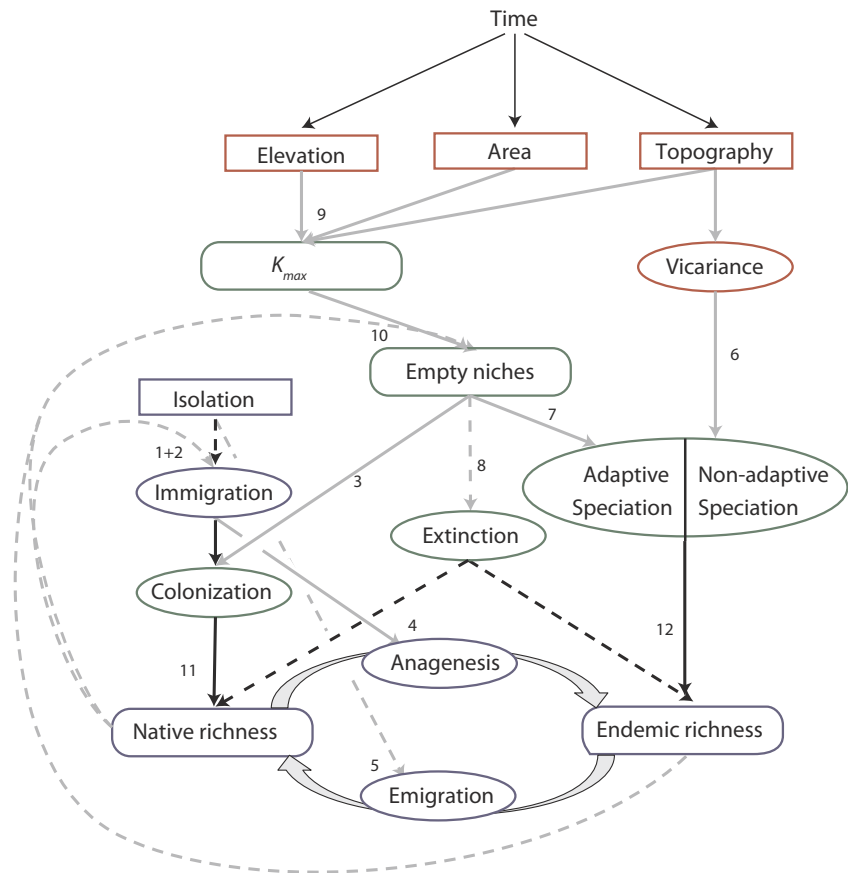
Figure 3 The causal relationships of the combined GDM. Thin arrows indicate causality (similar to Fig. 1), whereas block arrows indicate the movement of species between categories. The numbers correspond to equation numbers in Appendix S2 (in Supporting Information). In the context of this simulation, 'native species' refer to the group of native non-endemics, i.e., native species that also exist in the mainland. K_{max} is the theoretical maximum number of species that can be supported on the island.

Table 1 The parameters used in simulations of GDM dynamics herein. The values were chosen to have realistic relative sizes and lead to realistic turnover rates. As the simulation is on an arbitrary scale, no conclusions are drawn based on absolute numbers. The results of multiplying all evolutionary rates by 10 are shown in Fig. S1 in Appendix S1.

Parameter	Meaning	Value
Vs	Probability of a vicariance event when topography equals 1	0.0005
Vsp	Probability that a vicariance event will lead to speciation	0.075
S_0	The per-species probability of adaptive speciation at maximum empty niche space	0.0025
E_0	The per-species probability of extinction when richness equals K_{max}	0.001
Ms	The species richness of the mainland source pool	500
Iso	A descriptor of island isolation in arbitrary units	(0.3, 1, 3)
Imm	The probability of one species arriving from the mainland per time step	0.002
C_0	The per-species probability of successful colonization at full empty niche space	0.5
Ana	The per-species probability of anagenesis per time step	0.002
Emi	The per-species probability of recolonization of the source area per time step	0.0002
Z	The exponent of the species–area relationship between the island and the source area	0.25
Ma	The realized size of the source area that provides new species	1000
Msa	A power exponent controlling the species abundance distribution of the source area	0.3

values are scaled by varying the size of the mainland source pool (Ms), and the central values of K_{max} and empty niche space are defined as a proportion of Ms. The value of K_{max} at each time step is found by summarizing island geology (G) as the mean of area, elevation and topographical complexity, and then calculated from the size of the metacommunity by the formula $(G/Ma)^Z \times Ms$ (see Table 1 for parameters), which is the standard power-law

relationship between species richness and area (Arrhenius, 1921). For the results presented, we use a mainland source pool of 500 species but calculate all amounts as continuous numbers. All equations of the models are listed in Appendix S2.

As a result of the regulating effect of the environmental carrying capacity, the absolute values of parameters are not predicted to have a strong influence on the qualitative results

presented. However, higher evolutionary rates are predicted to lead to a higher turnover of species. The realized turnover of species on oceanic islands has been a source of vigorous debate, largely because of the practical measurement difficulties (Whittaker & Fernández-Palacios, 2007). To estimate the sensitivity of results to our chosen parameter values, we also conducted an analysis where rates of speciation, extinction and immigration were multiplied by 10. Below, we present results based on varying parameters in accordance with realistic scenarios of different island isolation and geological ontogenies, rather than automatically scanning over a certain area of parameter space, as we consider this to be more informative about the possible evolutionary trajectories on islands.

The simulation is completely deterministic and structured as a dynamic coupled system. Thus, the model was run only once for each parameter combination. This type of model is useful for assessing the effect of causal dynamics, and the internal consistency of predicted patterns. The model could easily be made stochastic by adding an arbitrary random error term to each relationship and/or by modelling parameters as random variables, which may affect the overall dynamics when species numbers are small. Stochastic models are useful when attempting to fit complex models to empirical data, but the added complexity makes them less suited for our purpose of assessing the consistency of causal dynamics. To evaluate the effect of varying immigration, the isolation factor of the model was varied between simulations (Table 1).

Generalizing the geological ontogeny

We based the trajectories of area, elevation and topography on Whittaker *et al.* (2008; their Fig. 3, reproduced here as Fig. S3 in Appendix S1). Whittaker *et al.* (2008) noted that these trajectories were schematic and may differ from actual island trajectories. Moreover, they suggested that the earlier phases might be faster than later phases (consistent with a logarithmic time axis), a suggestion which was supported in an empirical analysis by Steinbauer *et al.* (2013). However, for comparability and consistency with the graphs presented by Whittaker *et al.* (2008), we use their original trajectories. We also extended the model by replacing the geological progression with appropriate trajectories for two other major types of islands: subduction-based island arcs and continental fragment islands.

Island arcs are formed in areas where one continental plate is continually subducted under another. The lower plate melts as it undergoes subduction, creating constant volcanic activity along the edge of the upper plate (Grove *et al.*, 2009). Such islands make up a great majority of the world's volcanic islands, including archipelagos such as the South Sandwich Islands and the Philippines (Ringwood, 1974). In contrast to hotspot islands, this class of islands may continue to gain area by volcanic activity and by merging with nearby islands, thus avoiding the downward erosive phase of the hump-shaped curve. The area and topographical complexity of such islands will, however, fluctuate over time, as volcanic activity and erosion affect the islands.

Continental fragment islands are bits of continents that have broken off and become isolated in the open ocean; examples include Madagascar and New Zealand. Continental fragments differ from other oceanic islands in that they start with a full complement of continental species. These islands often exist for very long periods of time (e.g. New Zealand is estimated to have split from Gondwana *c.* 80 Ma; McDowall, 2007), and become gradually more isolated as time passes. Some continental fragments also undergo gradual submergence (Whittaker & Fernández-Palacios, 2007).

For island arcs and continental fragments we sketched out generalized ontogenies for area, elevation and topographical complexity. These ontogenies of course represent a substantial simplification. In the case of New Zealand, for instance, it has been suggested that the islands may have been largely or completely submerged at some point in the recent past (Trewick *et al.*, 2006), with their subsequent growth then creating extensive opportunities for the nearby Australasian fauna and flora to colonize. There is also evidence that much of New Zealand comprises allochthonous terranes that have accreted after the split from Gondwana (Heads, 2008). More generally, sea-level changes caused by cycles of polar glaciation through the Pleistocene have changed the area and relative isolation of islands repeatedly over the last 2.6 Myr, possibly profoundly influencing dynamics of diversity (Wallace, 1881; Ali & Aitchison, 2014). However, we view the general division of island ontogenies into hotspot, subduction arc and continental fragments as a useful starting point in extending the GDM to a wider array of oceanic islands.

RESULTS

For the parameter values used to generate the main results (Table 1), the total turnover of species on the island over the 5000 time steps was *c.* 250, where the maximal number of species on the island was *c.* 80. By contrast, in the sensitivity analysis in which rates of speciation, extinction and immigration were multiplied by 10, the total turnover reached *c.* 2500 species (Fig. S4 in Appendix S1), which seems unrealistically high for most taxa and islands.

In our main simulation, the rates of evolutionary processes (Fig. 4) roughly followed the trajectory suggested by Whittaker *et al.* (2008). Species richness followed a humped trajectory and approached K_{max} more closely as the island aged, so that the amount of empty niche space peaks relatively early in an island's life. The rate of colonization generally decreased over time and speciation peaked at intermediate age, with adaptive speciation peaking earlier than non-adaptive allopatric speciation. However, there were also differences between our results and the graphical models of Whittaker *et al.* (2008). First, K_{max} rose and declined more rapidly than originally suggested, which is attributable to our assumption of a power-law relationship between K_{max} and area. Another notable difference, which follows from our implementation of Premise 2, was the continued existence of empty niche space throughout most of island life, so that the
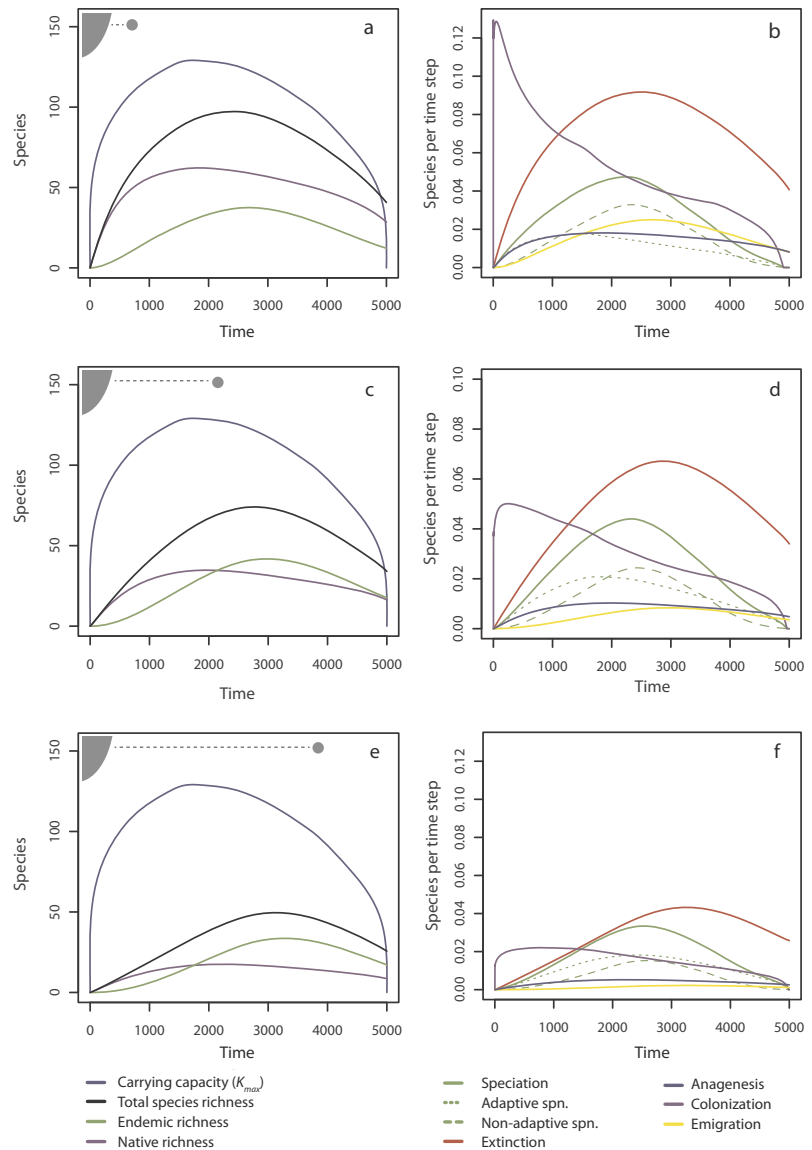
Figure 4 Temporal dynamics of species richness and evolutionary rates, as predicted by the GDM, under varying levels of island isolation. (a), (c), (e) The dynamics of K_{max}, and the endemic, native non-endemic and total species richness, as predicted by a causal model of the GDM. (b), (d), (f) The dynamics of per-island evolutionary rates as predicted by the causal model. Speciation rates are shown as total (solid line) and separated into adaptive (dotted line) and non-adaptive (dashed line). Results are shown for very little (0.3; a, b), intermediate (1; c, d) and very high (3; e, f) degrees of isolation. The ontogeny corresponds to a single volcanic hotspot island, such as the islands of Hawai'i.

community only reached saturation at the end of the island's life span.

The extinction rate, which was shown by Whittaker *et al.* (2008) to peak at the end of an island's life, instead peaked at an intermediate age, where species richness was highest. The explanation is that while the per-species extinction rate rises towards the end of the island's life span, the fewer species existing at this time means that the per-island extinction rate (which is what is at issue here) must decline. Hence, in practice, the extinction rate trajectory shown in Fig. 4 of Whittaker *et al.* (2008) was a product of an error in reasoning, and the difference between our simulation results and the original graphic thus demonstrates the power of combining causal analysis with an explicit simulation model. In the present case, R.J.W. did previously realize that the trajectory of the extinction curve was in error and has presented a version of the GDM with a declining extinction rate at several public talks. The rate of colonization decreased slowly, and maintained a minimum level throughout island history,

because extinction continued to create opportunities for repeated colonization events. As species richness drops, the probability that a new immigrant will already be represented on the island also decreases. In the model, anagenesis occurs at a constant per-species rate, and the trajectory thus followed the richness of native species on the island. The relative magnitude of anagenesis and cladogenesis is likely to vary among island systems and taxa.

When varying the level of island isolation, species richness decreased markedly at high levels of isolation, even though the trajectory of K_{max} was identical in the different scenarios (Fig. 4e). As suggested by Heaney (2000) and by Whittaker *et al.* (2008; see their Fig. 6), the resultant lower levels of species richness stimulated an increased rate of local adaptive speciation, leading to an assemblage with a high preponderance of endemic species. The increase in local speciation, however, was insufficient to compensate for reduced immigration, keeping the total species richness low.
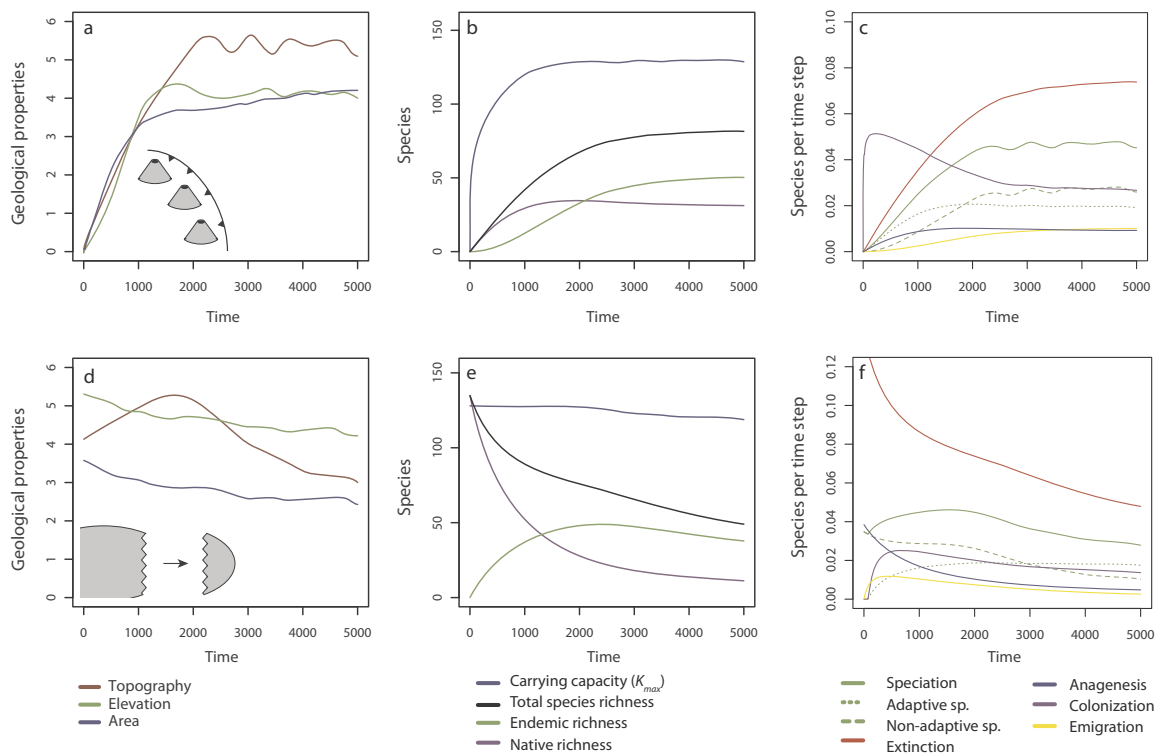
Figure 5 The trajectory of island dynamics on islands with varying geological ontogenies. The panels show generalized ontogenies (a, d), richness dynamics (b, e) and per-island evolutionary rates (c, f) of subduction-based arc islands (a, b, c) and continental fragment islands (d, e, f). Time steps are *c.* 1000 years; the geological properties of area, elevation and topographical complexity are shown on the arbitrary scale employed in the model.

By applying the causal model to the outline trajectories shown in Fig. 5(a) and (d), we were able to predict the results from GDM dynamics for other types of oceanic islands. For our island arc simulation, the total species richness increased with increasing island area (Fig. 5b). However, after a certain point, the number of native species remained constant and the increase in richness derived from continual speciation forming new endemics. This is probably due to a depletion of the source population: most of the species that were likely to spread to the island already existed there. The immigration probability of the remaining species in the source population was so low that the effects of immigration were counteracted by island extinctions. Our model of continental fragment islands indicated that the number of species declines as the island gradually loses area to submergence (Fig. 5e). As the island becomes increasingly isolated, the complement of continental species is slowly replaced by local endemics, leading to a very high proportion of endemism for old islands.

DISCUSSION

We used a simulation approach to clarify the causality inherent in the GDM, to assess the consistency of GDM predictions and to expand GDM dynamics more generally to the most common remote island ontogenies. The simulation analysis largely confirmed the descriptive account of the GDM from the original

papers (Whittaker & Fernández-Palacios, 2007; Whittaker *et al.*, 2007, 2008, 2010), but has also led to clarifications. A revised version of the canonical figure from Whittaker *et al.* (2008; their Fig. 4) is shown in Fig. 6. By implementing the model as a dynamic system, we get a much clearer appreciation of the expected relationships within the models, and can frame predictions more explicitly. This is facilitated by the R code (see Appendix S3), which can be used to generate predictions over a wide range of scenarios.

A constitutive theory of island biogeography

The focus on dynamic equilibrium in the ETIB has been difficult to reconcile with biogeographical evidence for the role of historical processes in shaping current patterns, especially on the more remote oceanic islands (Whittaker & Fernández-Palacios, 2007; Sax & Gaines, 2011). Studies that focus on the biogeography of individual clades have found clear associations between the distribution of species and the geological processes that have shaped islands and archipelagos (Rosen, 1978; Macías-Hernández *et al.*, 2013; Ali & Aitchison, 2014). The apparent contradiction between these views has led to a long-running controversy (Heaney, 2007). Our analysis highlights the potential for the GDM to act as a basis for a theoretical unification of these contrasting views in island biogeography.
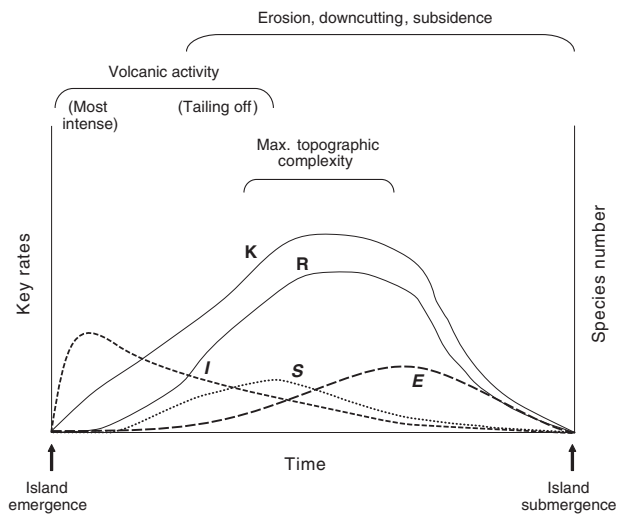
Figure 6 A revised version of Fig. 4 from Whittaker *et al.* (2008) that reflects the results from the current paper. Note that for consistency with Whittaker *et al.* (2008), the abbreviations differ from those used elsewhere in the present paper. The extinction curve (marked '*E*') now has a humped trajectory, with a higher peak. The species richness curve (marked '*R*') is lowered, giving more empty niche space, shown as the difference between the species richness curve and the carrying capacity curve (marked '*K*'). The colonization curve (marked '*I*') is changed to reflect that total colonization rates are low in the first stages of island life. The curve marked '*S*' details speciation. We have removed the 'mega-landslips' for consistency with the smooth extinction curve. All rates are shown per-island. The curves shown are based on the simulation results shown in Fig. 4.

At the same time, our analysis underlines the difficulty of testing island models conclusively. This difficulty stems from several causes. Firstly, rates of extinction and immigration are difficult to estimate except at very short time-scales (e.g. Simberloff & Wilson, 1970), and it is unclear how the processes scale up to larger island systems and geological time-scales. At larger scales, analyses of the GDM to date have focused on comparing islands within archipelagos, but this approach suffers from low statistical power because most hotspot archipelagos consist of too few islands (Bunnefeld & Phillimore, 2012).

Secondly, perhaps the central difficulty with regard to conceptual and simulation analyses is the relatively high complexity of such models, giving them a high degree of flexibility and making it difficult to test them in practice. Valente *et al.* (2014) recently implemented a simplified simulation model that was inspired by GDM dynamics, and also demonstrated that a great diversity of trajectories could be produced by broadly varying model parameters between high and low extremes. It should be possible to make some progress towards more accurate predictions by using, for example, phylogenetic methods to estimate realized rates of speciation, immigration and possibly even extinction (Whittaker *et al.*, 2010; Morlon, 2014; Valente *et al.*, 2014), and by implementing analyses in a Bayesian framework. Nonetheless, the causal complexity of the model itself, the difficulty in quantifying the evolutionary rates that form the basis

of the model and the constraints of existing island biogeographical data all mean that a single solid test that would conclusively validate the GDM is difficult to design. We consider this to be a reflection of the nature of ecological systems rather than a flaw of the model.

Simulation analysis

One of the main clarifications to emerge from the simulation analysis concerns the relationships between island isolation, carrying capacity and species richness. An interesting aspect is the observation that species richness tended to slightly exceed K_{max} towards the end of an island's life. This pattern highlights a distinction between evolutionary and ecological species carrying capacity. The evolutionary species carrying capacity refers, in this context, to the hypothetical situation in which speciation can no longer occur because niche space is fully saturated (Rabosky & Glor, 2010), removing the selective pressure for adaptive divergence of populations and potentially intensifying competitive exclusion of incipient species. After a period of loss of habitat or niche space, an island might sustain species richness in excess of this carrying capacity for extended periods. The ecological carrying capacity, on the other hand, refers to an environmental limit on the amount of biomass at a given trophic level (Levinton, 1979), which translates to a limit on the number of species that can uphold a sustainable population size (MacArthur & Wilson, 1967). This is predicted to incur a rapid extinction response if the environmental carrying capacity is reduced, although exactly how rapid remains a subject of debate (e.g. Triantis *et al.*, 2010).

The causal diagram (Fig. 3) uses grey arrows to highlight relationships that have still not been conclusively established, and which represent key areas for further analysis. For instance, anagenesis is represented as a constant rate per species, but other studies (e.g. Rosindell & Phillimore, 2011) have suggested that anagenesis is counteracted by repeated re-immigration of the same species from the source population, so that the per-species rate of anagenesis should be related to immigration and, in turn, island isolation. Additionally, anagenesis may be affected by empty niche space, because unoccupied niches may lead to character release (Yoder *et al.*, 2010) and cause morphological divergence from the source population (Gillespie, 2004; Givnish *et al.*, 2009).

There are a number of additional avenues to explore in order to make the GDM a truly general theory. One is the incorporation of spatial variation in the factors that determine the basic processes, such as differences in geological composition and climate among islands (e.g. Kalmar & Currie, 2006). Another complication relates to the role of isolation. Most oceanic islands occur as part of archipelagos, and their isolation can be measured at several scales (Weigelt & Kreft, 2013). Moreover, the degree of isolation varies over time, for example due to ocean basin spread, terrane movement, in situ island formation and loss, and eustatic adjustments leading to the repeated appearance and disappearance of stepping-stone land masses (Fernández-Palacios *et al.*, 2011; Ali & Aitchison, 2014). The

archipelagic setting means that most of the species that immigrate to an island will be species from nearby islands, i.e. the archipelagic species pool. This archipelagic species pool also undergoes changes, as processes of immigration, speciation and extinction on other islands introduce or remove species. Much of the speciation in archipelagos is thought to happen when populations become reproductively isolated and undergo divergence on different islands in an archipelago (Grant *et al.*, 1996). In the GDM this process is represented as anagenetic speciation and subsequent emigration/immigration, but this representation does not take into account that the process changes the archipelagic species pool.

Here, we have presented a way of extending GDM dynamics more broadly to two of the most important classes of islands in oceans, and to generate testable hypotheses about the patterns expected on these island types. This could be strengthened by more geographically explicit models of the empirical geological ontogenies of individual islands, based on analyses of substrate composition and age, ocean current patterns and the timing of volcanic events (e.g. Llanes *et al.*, 2009). Potentially, this approach opens up the possibility for applying the model much more generally, maybe even within mainland systems.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Supplementary figures.

Figure S1 Reproduction of the predicted dynamics of the GDM from Whittaker *et al.* (2008).

Figure S2 The 1963 ETIB of MacArthur and Wilson as reproduced by Whittaker *et al.* (2008).

Figure S3 Reproduction of the ontogeny of hotspots islands from Whittaker *et al.* (2008).

Figure S4 Predicted trajectories from the simulation model, given evolutionary rates that are 10 times higher than in the main text.

Appendix S2 Formulae. The equations used to calculate relationships in Fig. 3.

Appendix S3 Simulation code. R source files containing the source code used to generate all results in the paper.

BIOSKETCHES

Michael Krabbe Borregaard was a post-doctoral researcher at the University of Oxford while doing this work, and is now an assistant professor at the Center for Macroecology, Evolution and Climate, University of Copenhagen. His research interests span island biogeography and macroecology and the factors driving species richness and turnover across spatial scales.

Thomas J. Matthews was a DPhil student at the University of Oxford while working on this paper, and focuses on species abundance distributions, species–area relationships and the applicability of island biogeography to terrestrial habitat islands.

Robert J. Whittaker is a Professor of Biogeography at the University of Oxford, who has a thing about islands. He is editor-in-chief of the *Journal of Biogeography* and a past president of the *International Biogeography Society*.

Author contributions: M.K.B. and R.J.W. conceived of and designed the study, M.K.B. conducted the simulations, and M.K.B. and R.J.W. wrote the paper with significant input from T.J.M.

Editor: Richard Field