

RESEARCH PAPER



Assessing predicted isolation effects from the general dynamic model of island biogeography with an eco-evolutionary model for plants

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Abstract

Aims: The general dynamic model (GDM) of oceanic island biogeography predicts how biogeographical rates, species richness and endemism vary with island age, area and isolation. Here, we used a simulation model to assess whether the isolation-related predictions of the GDM may arise from low-level process at the level of individuals and populations.

Location: Hypothetical volcanic oceanic islands.

Methods: Our model considers (a) an idealized island ontogeny, (b) metabolic constraints and (c) stochastic, spatially explicit and niche-based processes at the level of individuals and populations (plant demography, dispersal, competition, mutation and speciation). Isolation scenarios involved varying the distance to mainland and the dispersal ability of the species pool.

Results: For all isolation scenarios, we obtained humped temporal trends for species richness, endemic richness, proportion of endemic species derived from within-island radiation, number of radiating lineages, number of species per radiating lineage and biogeographical rates. The proportion of endemics derived from mainland–island differentiation and of all endemics steadily increased over time. Extinction rates of endemic species peaked later than for non-endemic species. Species richness and the number of endemics derived from mainland–island differentiation decreased with isolation as did rates of colonization, mainland–island differentiation and extinction. The proportion of all endemics and of radiated endemics, the number of radiated endemics, of radiating lineages, and of species per radiating lineage and the within-island radiation rate all increased with isolation.

Main conclusions: Our results lend strong support to most of the isolation-related GDM predictions. New insights include an increasing proportion of endemics, particularly those arising from mainland–island differentiation, across isolation scenarios, as well as extinction trends of endemics differing from the overall extinction rates, with a much later peak. These results demonstrate how simulation models focusing on low ecological levels provide tools to assess biogeographical-scale predictions and to develop more detailed predictions for further empirical tests.



KEYWORDS

BioGEEM, general dynamic model, interspecific competition, island biogeography, isolation effects, metabolic theory, oceanic islands, plant endemism, process-based models, speciation rate

1 | INTRODUCTION

Geographical isolation is one of the key drivers of species diversification in both islands (Heaney, 2000; Rosindell & Phillimore, 2011; Whittaker & Fernández-Palacios, 2007) and continents (Linder, 2005; Pennington et al., 2010; Rieseberg & Willis, 2007). Mechanisms by which isolation promotes evolutionary divergence include founder effects and genetic drift (non-adaptive speciation; Rundell & Price, 2009). Evolutionary divergence is particularly promoted at species' range margins or in populations isolated by vicariance (Rosen, 1978; Wiley, 1988), including within-island geographical isolation (e.g. Malhotra & Thorpe, 2000). Such allopatric differentiation is largely dependent on dispersal barriers that limit gene flow between populations (Cowie & Holland, 2006; Wiens & Donoghue, 2004). Isolated populations may be also subject to differential selective pressures, which may trigger adaptive speciation (Rundell & Price, 2009). These mechanisms are characteristic of remote oceanic islands and are responsible for their high endemism (Steinbauer, Otto, Naranjo-Cigala, Beierkuhnlein, & Fernández-Palacios, 2012; Whittaker & Fernández-Palacios, 2007), thus providing model systems for investigating isolation effects (MacArthur & Wilson, 1967; Warren et al., 2015; Weigelt & Kreft, 2013).

Island biogeography theory holds that geographical isolation from source areas reduces colonization rates to islands and the species richness at the dynamic equilibrium between colonization, speciation and extinction, while increasing the relative contribution of within-island radiation (MacArthur & Wilson, 1967; Rosindell & Phillimore, 2011). These effects on speciation have been verbally formalized within the general dynamic model (GDM) of oceanic island biogeography, the distinguishing feature of which is to posit that diversity patterns within and across archipelagos are also influenced in a predictable fashion by the geodynamics of oceanic islands over their lifespan (Whittaker, Triantis, & Ladle, 2008, 2010). The resulting biogeographical predictions have made the GDM a powerful framework for studying islands (reviewed in Borregaard et al., 2017). However, the GDM has not yet been thoroughly assessed by niche-based, spatially and demographically explicit simulation models that focus on the processes occurring at the level of individuals and populations. Here, we use such a model to evaluate GDM-based predictions related to mainland–island isolation.

For remote volcanic islands, the GDM predicts humped trends in richness and endemism (richness and proportion) as a function of the rise and decline of island area, elevation and habitat heterogeneity over an island's lifespan (Whittaker, Triantis, & Ladle, 2008, 2010). Varying isolation is hypothesized to affect biogeographical patterns by changing the amplitude but not the shape of the temporal trends

(Whittaker, Triantis, & Ladle, 2008). More recently, Borregaard, Matthews, and Whittaker (2016) used an assemblage-level simulation model to explore GDM properties, in particular examining isolation effects, and alternative island ontogenies. Together, these simulations supported the internal logic of the GDM by revealing that more isolated islands had lower species richness, colonization and extinction rates, as well as a higher proportion of single-island endemics, number of endemic species and speciation rates (Borregaard et al., 2016). Consequently, isolation should decrease overall species numbers over ecological time-scales (MacArthur & Wilson, 1967), but increase the number and proportion of endemic species over evolutionary time-scales (Heaney, 2000; Rosindell & Phillimore, 2011). A substantial part of the increase in endemism is typically explained by radiating lineages filling niches that would be occupied by colonist species on less isolated islands (Givnish et al., 2009; Heaney, 2000; Whittaker, 1972; see also Emerson & Gillespie, 2008). An increase in endemism with isolation has been shown, however, to happen even in the absence of niche evolution (i.e. emerging from neutral evolutionary dynamics only; Rosindell & Phillimore, 2011).

Mechanistic simulation models have been identified as a promising avenue to test the GDM predictions (Borregaard et al., 2016, 2017). Such models can overcome limitations of space-for-time substitutions where islands of different ages within and across archipelagos are used as surrogates for the long-term dynamics of single islands (Borges & Brown, 1999; Borregaard et al., 2017; Leidinger & Cabral, 2017). Mechanistic models allow exploration of variations in input factors and parameters, and the control of confounding effects. The latter may include the follows: varied intra-archipelagic spatial settings (Cabral, Weigelt, Kissling, & Kreft, 2014; Weigelt, Steinbauer, Cabral, & Kreft, 2016), island hopping followed by parallel radiations (Losos & Ricklefs, 2010), rescue effects (Brown & Kodric-Brown, 1977), and the eco-evolutionary history specific to each island, archipelago and taxon (Bunnefeld & Phillimore, 2012; Whittaker & Fernández-Palacios, 2007).

Isolation is multifaceted, requiring multiple metrics for its measurement (Weigelt & Kreft, 2013) and alternative ways of simulation within models (cf. Borregaard et al., 2016). In a companion paper to the present paper, Cabral, Wiegand, and Kreft (2019) present a BioGeographical Eco-Evolutionary Model (BioGEEM) that builds on previous population- and niche-based models for species' range dynamics (Cabral et al., 2011; Sarmiento Cabral et al., 2013; Zurell et al., 2016) and for metacommunity dynamics (Cabral & Kreft, 2012). BioGEEM goes beyond these precursor models by adding evolutionary and environmental processes. This enables the exploration of how temporal and spatial patterns at population, species,



community and entire island assemblage levels emerge from population-level processes at evolutionary time-scales. Cabral et al., 2019 report that these patterns cannot be realistically generated if any of the integrated processes is switched off and that the emergent temporal trends at the island assemblage level are consistent with most GDM temporal predictions of species richness and biogeographical rates. However, they investigated only one isolation scenario, and it is thus the main aim herein to investigate isolation effects in general and to evaluate GDM predictions related to isolation in particular.

BioGEEM is designed for terrestrial seed plants and has a hierarchical structure that links ecological and evolutionary processes to local temperature and body mass via metabolic trade-offs based on the metabolic theory of ecology (Brown, Gillooly, Allen, Savage, & West, 2004). All biogeographical patterns are not imposed, but emerge from processes operating at local scales and low levels of ecological organization, for example individual dispersal, resource competition and local population dynamics. BioGEEM thus differs from previous island models that focus on geologically static islands (Hortal, Triantis, Meiri, Thébault, & Sfenthourakis, 2009; Kadmon & Allouche, 2007; Rosindell & Harmon, 2013; Rosindell & Phillimore, 2011), do not incorporate evolutionary processes (Hortal et al., 2009; Kadmon & Allouche, 2007; Rosindell & Harmon, 2013), simulate ecologically neutral processes (Borregaard et al., 2016; Rosindell & Harmon, 2013; Rosindell & Phillimore, 2011; Valente, Etienne, & Phillimore, 2014; Valente, Phillimore, & Etienne, 2015) and/or are

spatially implicit (Borregaard et al., 2016; Valente et al., 2014, 2015). The combination of properties and assumptions derived from low-level theories (e.g. metabolic, niche and coexistence theories) to obtain patterns predicted by high-level theories (e.g. island biogeography) makes BioGEEM useful to generalize insights about biodiversity dynamics across ecological levels (Cabral, Valente, & Hartig, 2017; Cabral et al., 2019; Evans et al., 2013). Here, we use BioGEEM to assess the GDM-based hypotheses for isolation effects related to eight biogeographical variables (Table 1) with a simulation experiment varying island isolation in two different ways: via distance to the mainland and via dispersal ability of the species source pool.

2 | MATERIALS AND METHODS

2.1 | Modelling approach

We summarize the BioGEEM model below. A detailed description and parameter settings can be found in Cabral et al. 2019 and in Appendix S1 (code available at <https://github.com/julianoscabral/BioGEEM>).

2.2 | State variables and scales

The model is grid-based (Figure 1a), with a cell size of 1 km². Each island cell has an elevational level, associated with a mean annual

TABLE 1 Hypothesized effects of isolation based on the GDM (Borregaard et al., 2016; Whittaker et al., 2008) for eight biogeographical variables, the model output used for their evaluation and the overall support based on trends of emergent model output

Variable	Model output	Hypothesis	Model support
Species richness	Number of species	Negative	Full
Endemic richness	Number of differentiated and radiated species	Positive	Partial; true for radiated endemics; opposite for differentiated endemics
Proportion of endemics	Percentage of all endemic, only differentiated, only radiated species richness in relation to all species	Positive	Partial; mostly for radiated endemics
Radiating lineages	Number of lineages showing within-island radiation	Positive	Partial; more evident for distance-related isolation
Radiation extent	Number of species per radiating lineage	Positive	Partial; more evident for extreme isolation in intermediate island ages
Colonization rate	Number of colonization events per time interval	Negative	Full
Extinction rate	A. Number of all extinction events per time interval	Negative	Full
	B. Number of extinction events of endemic species per time interval	Negative	Partial; more evident for extreme isolation, with a late peak. Other scenarios showed also a lower early peak
Speciation rate	Number of mainland-island differentiation and within-island radiation events per time interval	Positive	Partial; mainland-island differentiation showed a negative trend with isolation; within-island radiation showed positive effects for extreme isolation

Note: BioGEEM generates time series of all variables from eco-evolutionary dynamics under the GDM assumption of humped environmental ontogeny, but many listed hypotheses are expected from island biogeography in general. We adopted the simplest calculation of the rates to make these comparable to GDM predictions, given as the number of events occurring within arbitrary time intervals. We adopted simple hypotheses, as by the GDM logic more detailed expectations, particularly for temporal trends, would require a more detailed depiction of island ontogeny within an archipelagic setting (e.g. dispersal from and to nearby islands). We simulated two speciation modes, namely mainland-island differentiation and within-island radiation, with species emerging from these processes referred to as 'differentiated endemics' and 'radiated endemics', respectively.

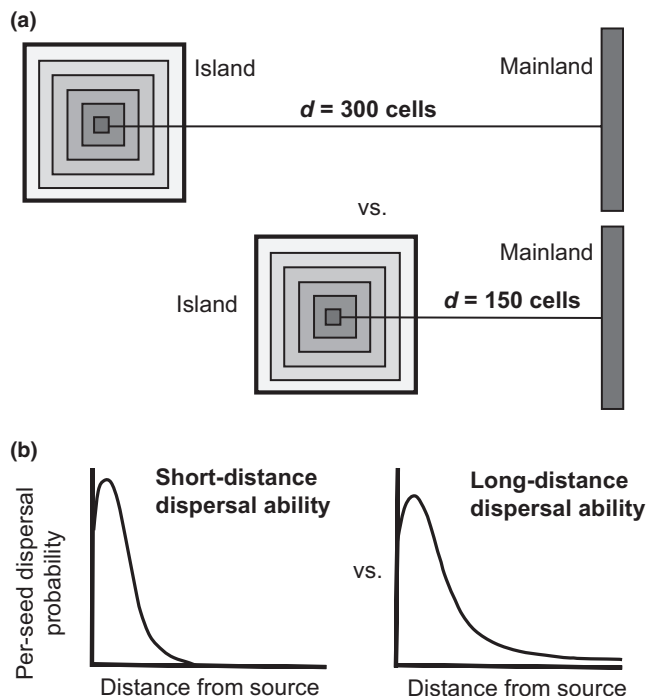


FIGURE 1 Isolation scenarios evaluated in this study. (a) Distance scenarios based on the distance d from the island centre to the mainland: $d = 300$ versus $d = 150$ cells. (b) Distance scenarios based on the dispersal ability of the mainland source pool of species: short-distance versus long-distance dispersal ability (thin and fat kernel tails, respectively).

temperature (25°C at the lowest elevation). The model agents are stage-structured plant populations (seeds, juveniles and adults), given in number of individuals. Populations belong to species, defined by combinations of autecological attributes (hereafter: species properties): environmental requirements (maximum cell suitability, optimum temperature, temperature tolerance, optimum island side and island side tolerance), short- and long-distance dispersal abilities, Allee threshold, body sizes (seed, juvenile and adult) and phenological ordering. Habitat requirements depict preferences associated with elevation (i.e. temperature) and with island side (as a surrogate for other environmental variables, such as wind and precipitation). Body mass and local temperature determine all demographic transitions, mutation rates, the space exploited by an individual, carrying capacity and time for speciation. These metabolic constraints account for increasing metabolism with temperature and decreasing metabolic rate with body mass (Brown et al., 2004). Demographic transitions are germination, sexual maturation, reproduction and density-independent mortality. A cell can hold one population per species, but as many species as there is space available. Due to different individual body masses and allometrically associated exploited space, metabolic constraints and local suitability (Appendix S1), the number of species within a cell can vary, but can reach the hundreds (Cabral & Kreft, 2012; Cabral et al., 2019). Consequently, species assemblages emerge from local resource competition (Cabral & Kreft, 2012; Cabral et al., 2019). The state variables comprise the spatial

distribution of seed, juvenile, and adult abundances of each species and the unoccupied area. Each time step represents one year, and a complete simulation runs over 2.21 million time steps (based on the age of Madeira Island; Appendix S1). In a companion study, which is devoted to presenting BioGEEM and assessing the necessity of its mechanistic complexity, the temporal extent has been modified in exploratory experiments, revealing little impact on the emergent patterns across ecological levels (Cabral et al., 2019).

2.3 | Initialization

Simulations are initialized with a pool of 1,000 species present in all mainland cells. The mainland has no biotic or abiotic dynamics and is composed of two rows of cells, each row with 13 cells, and thus serves only as a geographical starting point for long-distance dispersal (see Cabral et al., 2019). Species properties are randomly drawn within realistic value ranges. For example, body mass varies from a few grams to several tons, whereas mean dispersal distance varies between a few metres and a few hundred metres (details in Cabral & Kreft, 2012), whereas habitat requirements accommodate the environments present in the island. The range for long-distance dispersal ability allows for colonization events even in the most isolated islands. Hence, the value ranges are based on logical boundaries set by the experiment or by empirical evidence (Appendix S1). For example, if long-distance dispersal ability fails to allow for colonization, then the islands remain unoccupied. Moreover, species properties vary from representing specialists (e.g. narrow temperature amplitudes) to generalists (e.g. all temperatures and island sides). For each species, the habitat suitability matrix, H , is initialized based on the species' environmental requirements. A species-specific dispersal kernel D is initialized as a two-dimensional, grid-based Clark's 2Dt kernel, with two parameters, α and p , which describe short- and long-distance dispersal, respectively (Figure 1b; Clark, Silman, Kern, Macklin, & HilleRisLambers, 1999; Nathan & Muller-Landau, 2000). The stage-specific abundance matrices (seeds, juveniles and adults) and the matrix with the area occupied by all individuals are initialized empty.

2.4 | Processes

At each time step, a series of processes are executed in the following order: dispersal from mainland, population update 1, reproduction, intra-island dispersal, mutation, speciation, population update 2 and environmental dynamics. In each process, the state variables of each species are updated following the species phenological ordering as follows.

Dispersal from mainland: A random number of seeds per mainland cell from ten random mainland species are dispersed to the island according to D per time step over the entire simulation period.

Population update 1: Abundance matrices are updated by: (a) turning juveniles to adults, (b) applying density-independent mortality to remaining juveniles, (c) germinating seeds and (d) applying seed mortality.



Reproduction: The number of seeds produced by adults of each species in each cell follows the Beverton–Holt reproduction function, extended with Allee effects (Cabral & Schurr, 2010).

Intra-island dispersal: The produced seeds are dispersed within the island following D .

Mutation: As a previous step to within-island radiation (see 'Speciation'), each seed dispersed can randomly become mutant via point mutation (Rosindell & Phillimore, 2011). Mutation rates were metabolically constrained (e.g. higher for smaller plants and for higher temperatures—Brown et al., 2004) and calibrated to allow mutation events to happen almost every time step in large populations (Appendix S1). Mutant seeds received random properties according to phylogenetic constraints (values within $\pm 50\%$ of ancestral values). The H , D and abundance matrices for these mutant individuals are initialized.

Speciation: Two modes of speciation are considered: mainland–island differentiation (simulated as a neutral process) and within-island radiation (adaptive within-island diversification). These processes relate to the anagenetic and cladogenetic speciation sensu Stuessy et al. (2006), but are better described by their geography as regionally allopatric and regionally sympatric speciation, respectively (for a terminology review see Emerson & Patino, 2018a; see also Meiri, Raia, & Santos, 2018 and Emerson & Patino, 2018b). In BioGEEM, mainland–island differentiation is neutral and non-adaptive, whereas within-island radiation is non-neutral and adaptive (i.e. niche evolution). For simplicity, we refer to species emerging from these two speciation modes as 'differentiated endemics' and 'radiated endemics', respectively. The submodel checks whether enough time has passed to update mutant individuals (for within-island radiation) or colonizers (for mainland–island differentiation) as a distinct species (i.e. 'protracted speciation'—Rosindell & Phillimore, 2011). The time for speciation follows metabolic constraints to account for longer generations of larger species (Brown et al., 2004). Mainland–island differentiation is delayed by gene flow from the mainland.

Population update 2: After species status update, the submodel applies density-independent mortality to adults and updates the seed bank.

Environmental dynamics: Environmental events mimicked the geological trajectory of an idealized hotspot oceanic island (Whittaker & Fernández-Palacios, 2007; Whittaker et al., 2008), namely island growth due to volcanic activity followed by a slower erosion-dominated phase. The island grows and shrinks by gaining or losing belts of cells, respectively, and by increasing or decreasing elevation and thus local temperature accordingly. Islands grow every 0.13 Ma for the first 0.78 Ma, after which the island shrinks due to erosion every 0.26 Ma until the end of the simulation (Appendix S1). After every environmental event, H is recalculated for every species.

2.5 | Output

The model records time series of species richness (total, differentiated and radiated endemics), number of endemic lineages (species evolving from the same ancestor), number of species per endemic

lineage, and the number of colonization, speciation and extinction events.

2.6 | Study design

All intervals for drawing species properties and the scenario specifications are provided in Appendix S1. We studied a source pool with the following characteristics: (a) moderate niche conservatism and dispersal ability, (b) most potential ranges overlapped in mid-elevations, (c) biomass spanned from small herbs to big trees, (d) without intraspecific variability and (e) including annual and perennial species. Whereas these specifications can be varied in future study designs, particular situations (e.g. archipelagic dynamics, human-driven environmental and biotic change) and guilds (e.g. epiphytes, lianas, parasites and perennial semelparous species) would require further model development. To test our hypotheses (Table 1), we set up four isolation scenarios (Figure 1). The scenarios encompassed a full-factorial design, varying the shortest distance between the island at maximum size and the mainland (150 vs. 300 cells), as well as the dispersal ability of the mainland species pool (high vs. low long-distance dispersal ability). Greater long-distance dispersal ability (p_{high}) was obtained by systematically varying the dispersal parameter p for all species of the mainland source pool from the scenario with low long-distance dispersal ability (p_{low}): $p_{\text{high}} = p_{\text{low}} - 0.2$ (p_{low} values in Appendix S1). Note that although 150- or 300-cell distance might seem close to the mainland, isolation was assured by generally low long-distance dispersal ability. All islands had a maximum size of 11×11 cells. This size was arbitrary but enabled enough habitat heterogeneity (six different temperature belts), while remaining computationally feasible even for the least isolated, most species-rich islands. Larger islands were also investigated in exploratory scenarios in our companion study, yielding similar spatio-temporal trends in emergent patterns (Cabral et al., 2019).

The simulation experiment comprised 20 replicate runs per scenario, with each replicate having a different species pool. Outputs for each time step were averaged over replicates. To make results comparable to GDM predictions, we calculated colonization, speciation and extinction rates by summing up the number of colonization, speciation or extinction events within time intervals. Here, we arbitrarily chose these time intervals to be 0.01 Ma, which enabled the island to experience rare colonization events and potential speciation in small herbs (i.e. 10^4 generations—see Rosindell & Phillimore, 2011). We considered only successful colonization, that is including germination and establishment.

We focused on the general trends emerging from a mechanistic simulation experiment across hypothetical isolation scenarios with complete knowledge of assumptions, parameters and output and thus did not statistically compare the scenarios, as spurious statistical significance can be achieved simply by increasing the number of replicates or by setting more extreme scenarios (Murray & Corner, 2009; White, Rassweiler, Samhouri, Stier, & White, 2014). Therefore, our robust nonparametric comparisons provided in Appendix S3 must be interpreted with caution. Consequently,

emergent patterns can be regarded as explorative predictions from our own model. To adequately confirm these predictions, time series of the studied variables for islands with known archipelagic dynamics will be required. Here, we use standard deviation error bars to indicate the expected degree of overlap among scenarios. It is important to note that previous studies based on the same hierarchical model showed that patterns emerging across multiple ecological levels, for example population, species, community and entire insular species assemblages, generally agreed with general empirical evidence and theoretical expectations (Cabral & Kreft, 2012; Cabral et al., 2019). BioGEEEM has been shown to generate many of the temporal predictions of the GDM while producing insightful divergences (Cabral et al., 2019). Therefore, the explorative isolation scenarios shown here provide an application of a theoretically sound model whose generality has been demonstrated across ecological levels.

3 | RESULTS

The number of species and of the endemic species subset showed a humped relationship with island age (Figure 2). Richness peaks lagged behind maximum island size—a pattern that was most pronounced for more isolated islands and for radiated endemics (Figure 2). Except at the very final stages of the island, when species numbers converged, more isolated islands had lower total species (Figure 2a) and differentiated endemic richness (Figure 2b) but higher radiated endemic richness (Figure 2c). These trends were obtained when varying other isolation mechanisms (e.g. number of

species in the species pool, number of species dispersed from the mainland and smaller mainland area—Appendix S2).

The proportion of endemics increased over time and with isolation (Figure 3a). This increase was mostly driven by differentiated endemics, for which there was little difference among isolation scenarios (Figure 3b). In contrast, the proportion of radiated endemics showed either increase, stabilization or a shallow humped relationship with island age, with more isolated islands attaining higher proportions (Figure 3c). The number of radiating lineages exhibited a delayed humped temporal trend. Islands isolated by distance had the highest values (Figure 3d). The number of species per radiating lineage showed a humped relationship with island age, but varied less clearly with isolation, with only the islands isolated by both distance and dispersal having evidently higher values than the other islands (Figure 3e).

Temporal trends in colonization rates were humped for all isolation scenarios, but the maximum values strongly decreased with isolation (Figure 4a). Similar temporal trends were obtained for extinction rates, but with overall lower values during the growth phase and higher values during the erosion phase (Figure 4b). Mainland–island differentiation rates peaked at intermediate island age and monotonically decreased thereafter, with increasing isolation decreasing the maximum value (Figure 4c). Within-island radiation rates peaked at intermediate island age, with the amplitude of the curve increasing with isolation (Figure 4d). Extinction rates of endemics increased over time, showing one first small peak by the time of the first erosion step and a second higher peak by the time of the last erosion step (Figure 4e). Only the most isolated islands did not show the first small peak (Figure 4e). All islands showed a general

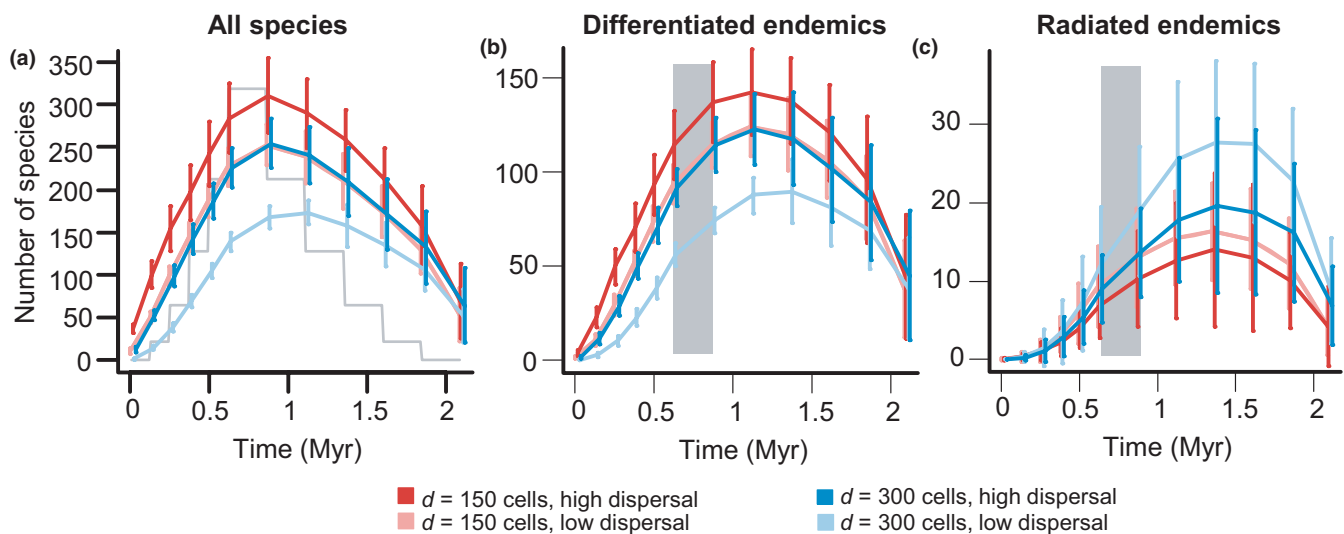


FIGURE 2 Temporal trends in species numbers of four different isolation scenarios. Time series of: (a) number of all species; (b) number of endemics derived from mainland–island differentiation and (c) number of endemics derived from within-island radiation. Isolation scenarios were given by changing the distance d from mainland and long-distance dispersal ability of the source pool. Time series were averaged within environmental time steps and over 20 replicate runs. Vertical bars indicate the standard deviation across replicates, with some jitter added to improve visualization among bars. We show the island size trajectory (minimum of one cell and maximum of 121 cells) in light grey in (a) and a shaded grey area indicating timing of maximum island size in (b and c) to display the biodiversity trends in relation to the environmental dynamics. Note in (a) that two intermediate scenarios ($d = 150$ cells, low dispersal and $d = 300$ cells, high dispersal) are barely distinguishable

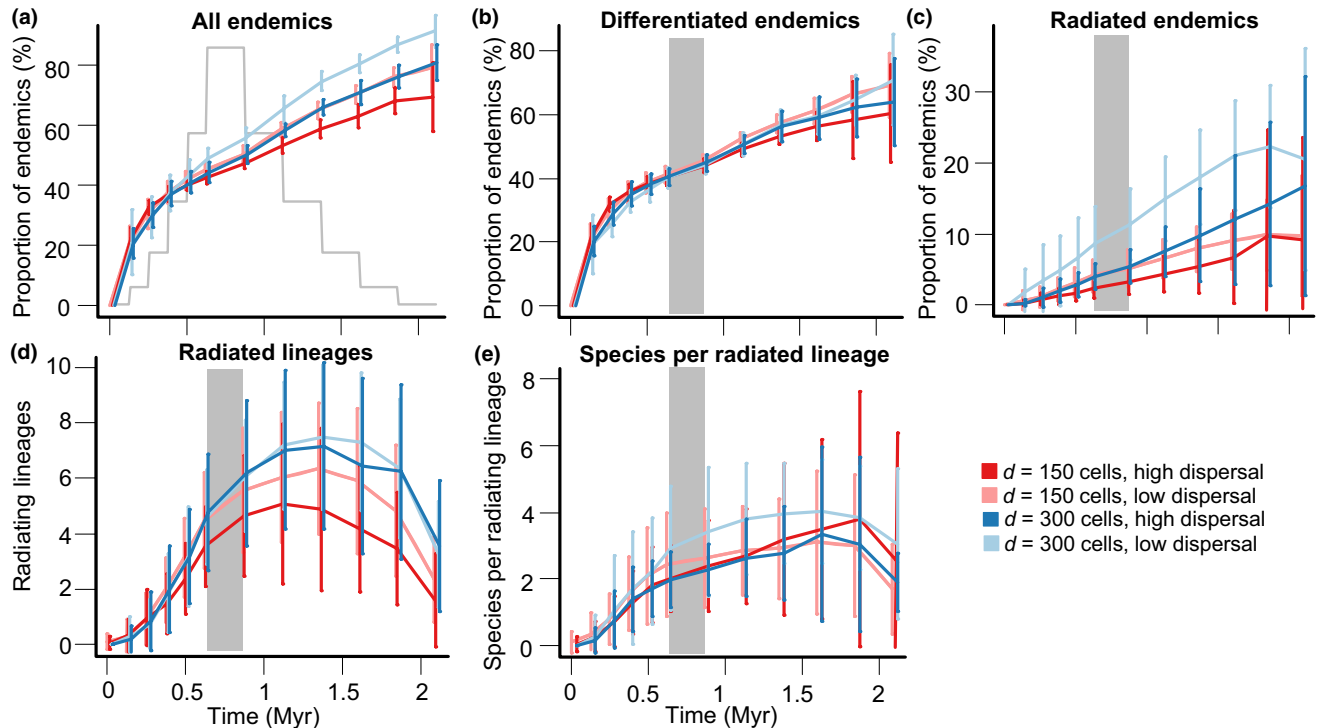


FIGURE 3 Speciation-related trends of four different isolation scenarios. Proportion of (a) all endemics, (b) differentiated and (c) radiated endemics (in each case as a function of all species). (d) Number of radiating lineages. (e) Number of species per radiating lineage. Note the steady increase in proportion of endemics in (a), mostly due to endemics differentiated from mainland populations (b), despite overall humped richness trends shown in Figure 2. Isolation scenarios were given by changing the distance d from mainland and long-distance dispersal ability of the source pool. Time series were averaged within environmental time steps and over 20 replicate runs. Vertical bars indicate the SD across replicates, with some jitter added to improve visualization among bars. We show the island size trajectory (minimum of one cell and maximum of 121 cells) in light grey in (a) and a shaded grey area indicating timing of maximum island size in (b–e) to display the biodiversity trends in relation to the environmental dynamics

positive net change in species richness during the growth phase and a general negative net change during the erosion phase, with isolation decreasing the amplitude of the temporal dynamics (Figure 4f). The increase in species richness during the growth phase was led by colonization rates, which were higher than speciation rates.

4 | DISCUSSION

4.1 | Species richness

The results for species richness supported the expected pattern of negative relationships with isolation (Table 1, Figure 2a). Moreover, all isolation scenarios showed similar humped temporal trends in species richness, as predicted by the GDM (Figure 2a; Borregaard et al., 2016; Cabral et al., 2019; Whittaker et al., 2008) and expected based on empirically well-supported, positive relationships between species richness and island area, elevation and habitat heterogeneity (e.g. Hortal, Roura-Pascual, Sanders, & Rahbek, 2010; Kreft, Jetz, Mutke, Kier, & Barthlott, 2008). These findings are consistent with the spatially implicit model of Borregaard et al. (2016), but the obtained delayed peaks contrast with early peaks during island ontogeny empirically shown by, for example, Steinbauer, Dolos, Field, Reineking, and Beierkuhnlein

(2013) and Lenzner, Weigelt, Kreft, Beierkuhnlein, and Steinbauer (2017). Simulation experiments and empirical patterns must be compared with caution, as empirical estimations of species carrying capacity (a central component of the GDM—Whittaker et al., 2008) entail shortcomings arising from the space-for-time substitution. For example, if the growth phase is several times shorter than the erosion phase, species richness is expected to peak relatively early. This would happen for two main reasons. First, different habitats would be available earlier for colonization (e.g. lower environmental filtering). Secondly, early colonization should be particularly true within archipelagos, as colonization from the local source pool provided by nearby islands may be comparatively rapid. Further simulation experiments may tackle these issues by comparing scenarios with different relative lengths of growth phase compared to the erosion phase and considering a second, more closely located species source pool to mimic nearby older islands. BioGEEM focuses on single islands, and species carrying capacity is an island property emerging from the environmental dynamics. These model features assure that how the species carrying capacity changes and is filled does not depend on archipelago effects but directly on available resources, environments, species properties and on eco-evolutionary processes. This is an advantage over spatially implicit, neutral approaches, which often

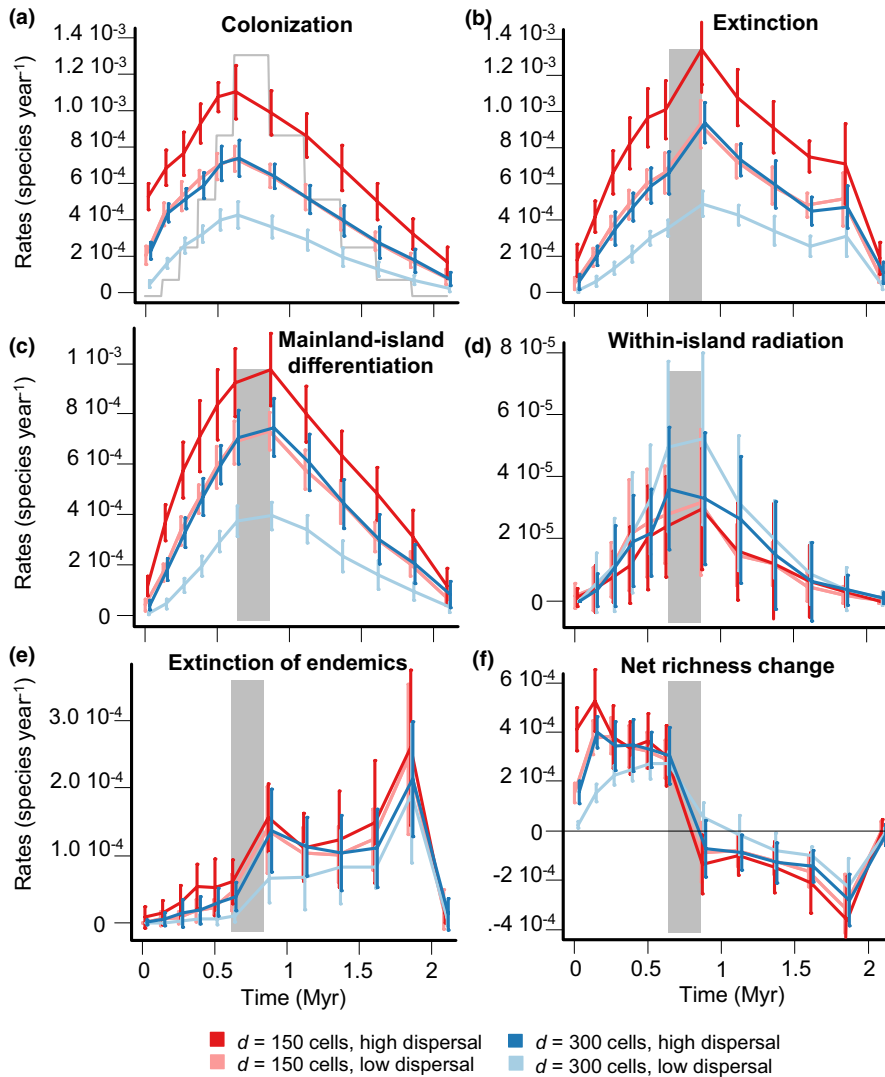


FIGURE 4 Biogeographical rates of four different isolation scenarios. (a) Colonization rates. (b) Extinction rates. (c) Mainland–island differentiation rates. (d) Within-island radiation rates. (e) Extinction rate of endemics. (f) Net richness change: colonization + speciation–extinction rates. Isolation scenarios were simulated by changing the distance d from mainland and long-distance dispersal ability of the source pool. Rates are given in species per year, averaged within environmental time steps and over 20 replicate runs. Vertical bars indicate the standard deviation across replicates, with some jitter added to improve visualization among bars. We show the island size trajectory (minimum of one cell and maximum of 121 cells) in light grey in (a) and a shaded grey area indicating timing of maximum island size in (b–f) to display the biodiversity trends in relation to the environmental dynamics

constrain species carrying capacity via an imposed parameter for the maximum number of individuals or species (e.g. in Borregaard et al., 2016) and without considering individual traits (Leidinger & Cabral, 2017).

Both mechanisms of isolation (by distance and by dispersal ability) seemed interchangeable, as the scenarios with either isolation mechanism revealed very similar, intermediate values. Simpler island simulation models have also supported the negative effects of isolation on species richness, despite accounting for isolation only indirectly by imposing variation in colonization rates or in island occupation at model initialization without explicitly considering geographic distances or species traits (Borregaard et al., 2016; Chen & He, 2009; Rosindell & Harmon, 2013; Rosindell & Phillimore, 2011). These simpler approaches impose isolation effects, limiting insight into the underlying eco-evolutionary processes. Here, we have shown that BioGEEM can also generate lower species richness in exploratory scenarios considering alternative isolation mechanisms, namely fewer mainland cells, dispersing species per time step and species in the source pool (Appendix S2). Whereas we have limited these analyses to explore isolation effects of single islands without

considering intra-archipelagic dynamics, the approach can potentially be used to assess processes at the intra-archipelagic level, including island hopping, parallel radiations, taxon cycles and island merging (cf. Cabral et al., 2014; Weigelt et al., 2016). The largely unappreciated complexity of isolation and related eco-evolutionary mechanisms highlights that we should be cautious in interpreting results from correlative studies, as islands might be under the influence of different isolation mechanisms over time. The development and use of more sophisticated, dynamic models of isolation offers a promising research avenue as most simulation models and correlative studies assume simplified isolation mechanisms (but see, e.g., Weigelt & Kreft, 2013).

4.2 | Endemic richness

Endemic richness was humped in all isolation scenarios and had a delayed peak compared to species richness (Figure 2b,c; Borregaard et al., 2016; Cabral et al., 2019; Steinbauer et al., 2013), as predicted by the GDM (Whittaker et al., 2008). Our results for endemic richness supported the hypothesis of positive isolation effects for



radiated endemics only (Table 1). The opposing effects of isolation on differentiated and radiated endemic species richness (negative and positive, respectively) support previous findings of neutral models considering islands that are already isolated (as anagenetic and cladogenetic species, respectively—Rosindell & Phillimore, 2011). For weakly isolated islands, these neutral models demonstrated that intense gene flow from the mainland prevents both speciation modes (Rosindell & Phillimore, 2011). As isolation increases, reduced gene flow facilitates mainland–island differentiation. On already isolated islands, the further increasing isolation leads to a lower number of colonizing species, and thus, a lower number of potentially endemic species differentiated from mainland populations. Simultaneously, radiating species start to fill empty niche space (Rosindell & Phillimore, 2011). This switch in predominant speciation mode emerges in neutral models simply by lowering colonization rates (Rosindell & Phillimore, 2011). While also capturing this switch, niche-based models explicitly integrate adaptive radiation and trait evolution (Cabral et al., 2019). Such evolutionary dynamics can be further assessed along environmental gradients (Cabral et al., 2019), an advantage over most previous island models, which are generally spatially implicit besides being neutral (see Leidinger & Cabral, 2017 for a review of island models). Therefore, future experiments comparing niche- and neutral-based models could shed more light on the relationship between habitat heterogeneity and trait evolution. This is important for assessing GDM predictions, including that adaptive radiations occupy 'empty niches'. However, it should also be noted that the GDM also accepts a role for non-adaptive radiation by intra-island isolation mechanisms, that is bottlenecks and genetic drift in small isolated habitats, especially during the phase of maximum topographic complexity (see fig. 5 in Whittaker et al., 2008). Further simulation experiments could include such intra-island isolation mechanisms and could assess GDM assumptions related to eco-evolutionary trait and niche patterns by varying, for example, the trait composition of species pool, the within-island environmental dynamics and extreme isolation scenarios (e.g. including islands initially connected with the mainland—Rosindell & Harmon, 2013). Nevertheless, Cabral et al. (2019) already showed that diverging species tend to be ecologically distinct from co-occurring species, thus better occupying the niche space, as assumed by the GDM.

4.3 | Proportion of endemic species

The proportion of endemic species varied depending on speciation mode (Figure 3), supporting the hypothesized effect of increased endemism with isolation mostly for radiated endemics and to a lesser extent for all endemics (Table 1). In our experiments, the overall endemism was mostly driven by mainland–island differentiation, which consistently increased over time (see also Cabral et al., 2019), but did not conspicuously vary between isolation scenarios (Figure 3b). Empirical evidence also suggests no isolation effects on the proportion of differentiated endemics (Stuessy et al., 2006). These differences between isolation effects depending on speciation mode have not been explicitly stated by the GDM (Whittaker et al., 2008),

although by the GDM logic the endemism in more isolated islands is increasingly more related to within-island radiation (see also Heaney, 2000), while the relative contribution of mainland–island differentiation should indeed increase slightly in the final phase of the island lifespan (prediction 9 of the GDM; Whittaker et al., 2008). Moreover, the higher proportion of all endemics obtained with increasing isolation was mostly driven by within-island radiation (Figure 3a–c), supporting the important role of within-island radiation in filling empty niches on isolated islands (Whittaker et al., 2008). The higher prevalence of within-island radiation on remote, high-elevation islands is assumed to be driven by limited gene flow and greater ecological opportunities (Heaney, 2000; Stuessy et al., 2006; Whittaker & Fernández-Palacios, 2007; Price & Wagner, 2011). Also, in their neutral and environmentally static simulation analysis, Rosindell and Phillimore (2011) indicated a gradual replacement of endemics differentiated from mainland populations by endemics derived from within-island radiation with increasing isolation. Indeed, Cabral et al. (2019) have shown that radiated endemics seem to prevent colonization of non-endemics (i.e. potential differentiated endemics) by being better adapted to local environments and communities than these naturally recurrent colonizers. Evidence of this was given by the explorative scenarios manipulating the underpinning low-level processes (e.g. switching off speciation or competition—Cabral et al., 2019). Experiments varying isolation mechanism under different competition scenarios could provide insights about the increase with isolation in endemism derived from within-island radiation.

4.4 | Number and extent of radiating lineages

Results for the number of radiating lineages supported the hypothesis of positive isolation effects, particularly for distance-related isolation (Table 1, Figure 3d). Only a minority of colonizing plant lineages on isolated islands are prone to diversification, while most lineages do not diversify and only produce differentiated endemics (compare Figures 2a and 3b,c; Price & Wagner, 2011; Stuessy et al., 2006). In the companion paper, we showed that some lineages only radiate under low competition/colonization conditions (Cabral et al., 2019). In fact, a few genera and families have been shown to be radiation-prone wherever arriving in remote archipelagos, such as the Hawaiian, Society and Marquesas Islands (Lenzner et al., 2017; Price & Wagner, 2004, 2011). Therefore, while knowledge about speciation on islands is constantly improving (e.g. Igea, Bogarin, Papadopulos, & Savolainen, 2015), future studies could investigate to what extent radiation-proneness is lineage-specific and mediated by traits. Potential scenarios that could be simulated to address this question are simulating each lineage separately to control for competition effects and in multiple environmental settings to control for niche availability. In all these scenarios, the complex relationships between speciation modes can thus be addressed by integrating ecological, evolutionary and environmental processes and by acknowledging species differences.

Results for the number of species per radiating lineage were complex, with an overall humped temporal trend (as Whittaker et al.,

2008), but only partially supporting positive isolation effects, with an unexpected interaction between temporal and isolation effects (Figure 3e; Table 1). Here, the isolation mechanism influenced the amplitude of the temporal trends, with an increase in species radiations becoming evident only for the most isolated islands (Figure 3e). That is because islands isolated by just one isolation mechanism may still receive enough colonizers that occupy available niches. In contrast, islands isolated by both distance and dispersal can foster larger radiations than other islands due to less competition and greater ecological opportunities (e.g. empty niches; Whittaker & Fernández-Palacios, 2007). Therefore, large radiations may be evidence of multiple isolation mechanisms combined.

4.5 | Biogeographical rates

Emergent colonization rates supported the predicted negative isolation effects (Figure 4a, Table 1). A decrease in colonization rates with isolation agrees with the predictions of both the equilibrium theory of island biogeography (MacArthur & Wilson, 1967) and the GDM (Borregaard et al., 2016; Whittaker et al., 2008). Higher colonization rates on growing islands are consistent with reduced environmental filtering due to higher habitat heterogeneity and with a higher chance of a dispersal unit hitting the island (i.e. the target area effect—Lomolino, 1990), whereas a decrease in colonization rate in the erosion phase reflects the prior occupancy of the island, including by island-adapted endemics (Cabral et al., 2019). Environmental filtering and the target area effects are not explicitly considered by the GDM (Whittaker et al., 2008). However, Borregaard et al. (2016) considered a simplified environmental filtering by correlating colonization rates with species carrying capacity. To further disentangle habitat heterogeneity and target area effects, follow-up simulation experiments could compare different scenarios of environmental heterogeneity versus area.

Extinction rates followed colonization rates, also supporting hypothesized negative isolation effects (Figure 4b, Table 1). When assessing only the extinction rates of endemic species, the hypotheses were generally supported, but with unanticipated peculiarities. These were the presence of two peaks, with the highest being the second one at very advanced island age, and overall less difference between scenarios, except for the fact that the most isolated islands did not show the first peak but had the most evident negative isolation effect (Figure 4e, Table 1). Potential explanation for the late peak may be that the surviving radiated endemics are those that cope best with the island environment (e.g. small size, limited environmental heterogeneity), and thus, their extinction would mostly happen under critical levels of those environmental features (see also Cabral et al., 2019). This is further supported by the fact that extinction of endemics in the most isolated scenario did not show the first small peak after the first erosion step (Figure 4e) even though it had the highest number of radiated endemics (Figure 2c). Additionally, the overall lower species richness of this scenario (Figure 2a) may also contribute for a low competitive pressure (e.g. no species saturation), ultimately

allowing endemics to better survive in isolated islands. Hence, the distinction between types of extinction and isolation mechanisms is important. While endemic species can go globally extinct, particularly in less isolated islands, non-endemics may go locally extinct but then re-colonize the island. Where colonization rates are much higher than speciation rates, overall extinction rates mostly reflect the extinction of non-endemics and thus follow colonization rate trends. Our simulations mostly follow these conditions of higher colonization, as overall extinction rates more closely followed the colonization trend than the trend of extinction of endemics (Figure 4a,b,e). If speciation rates have values comparable to or higher than colonization rates, such as in Borregaard et al. (2016), overall extinction rates reflect trends of speciation rate and extinction of endemics. Furthermore, the overall non-zero rate of net richness change (Figure 4f) indicates that a dynamic equilibrium cannot be achieved in our ever-changing island. Even if environmental dynamics are excluded, islands might steadily accumulate species due to speciation (Cabral et al., 2019). Future model developments might explore how the different biogeographical rates and the dynamic equilibrium vary with processes not implemented here, such as disturbances.

Emergent speciation rates supported the hypothesis of positive isolation effects only for radiated endemics, particularly for the most isolated islands (Figure 4c,d, Table 1). These simulation outputs permitted these different modes of speciation to be followed explicitly and thus allowed mainland–island differentiation to be more fully unpacked and scrutinized than hitherto possible from either the simple graphical depictions within the original paper or previous high-level simulations (Borregaard et al., 2016; Whittaker et al., 2008). In this sense, the increase in within-island radiation rates with isolation (Figure 4d) was in accordance with empirical and modelling evidence (Borregaard et al., 2016; Heaney, 2000; Whittaker et al., 2008; Rosindell & Phillimore, 2011). For the mainland–island differentiation rate, the negative isolation effect has been previously obtained by neutral models for islands that are already isolated enough to foster radiations (Rosindell & Phillimore, 2011). Moreover, once the island is in the final phases, opportunities for within-island radiation (i.e. habitat heterogeneity) decline, whereas the steady accumulation of endemics by mainland–island differentiation can continue a bit longer, meaning that it should contribute relatively more to endemism during this phase (Whittaker et al., 2008). In BioGEEM, the emergence of these differences between mainland–island differentiation and within-island radiation (simulated as neutral and non-neutral processes, respectively) indicates that the relative contribution of neutral and non-neutral dynamics in real islands might indeed vary over time and isolation mechanism.

4.6 | Limitations and perspectives

The main limitation of BioGEEM is its complexity and data requirements for parameterization and validation (cf. Dormann et al., 2012). Nevertheless, Cabral et al. (2019) demonstrated that the model matches empirical evidence and theoretical predictions at multiple



ecological levels and that all simulated processes are necessary to simultaneously generate realistic patterns (i.e. 'pattern-oriented' modelling, sensu Grimm & Railsback, 2012). Therefore, scenario-based simulation experiments with a realistic model, such as presented here, can increase our understanding of how multiple processes and drivers interact. They also generate hypotheses to be assessed when appropriate data become available. For these tasks, important properties of BioGEEM compared to previous, simpler models are species differences and the spatially explicit simulation of population-based processes (e.g. resource competition, stage transitions, individual dispersal).

The advantage of simulating processes at lower ecological levels is exemplified by the explicit separation of isolation factors—the abiotic component of physical distance and the biotic component of dispersal ability. In BioGEEM, island colonization becomes a high-level process emerging from multiplying the geographical distance from mainland with the individual dispersal ability. This made the biogeographical process of colonization more explicit regarding the underlying mechanisms than previous models, which impose rates for colonization and thus are more phenomenological than mechanistic. Whereas these different isolation mechanisms seem interchangeable for the higher level emergent patterns (e.g. total species richness), they can show differences for patterns depicting particular subsets, such as the number of radiating lineages and species per radiating lineage (Figure 3). These model features align with current trends towards improving structural realism in ecological modelling (Cabral et al., 2017; Grimm & Berger, 2016) and ensure that biogeographical patterns are emergent system properties and not imposed via biogeographical parameters (i.e. colonization, extinction, speciation rates as model parameters instead of emergent variables). Models imposing biogeographical parameters tend to be neutral (for all processes, including dispersal), and thus, future experiments with BioGEEM could add scenarios with neutral within-island radiation to compare emergent patterns with previous island models.

Another possibility in the future would be to vary isolation over time. Isolation dynamics are not explicitly assumed by the GDM and thus not accounted for in the present study. However, isolation changes at various time-scales, from recently increased source pools via human-induced activities and dispersal (i.e. alien species; Kueffer et al., 2010), over climate-mediated changes in sea levels (Fernández-Palacios et al., 2015; Weigelt et al., 2016), to deep time-scales of plate tectonics, archipelagic dynamics and eco-evolutionary changes in the source pool. Moreover, intra-archipelagic isolation may play an important role for trends of single-island endemics (Borregaard et al., 2016; Cabral et al., 2014), and thus, further insights might be gained by disentangling isolation in relation to intra-archipelagic versus mainland source pools. Inter-island dispersal within archipelagos has rarely been considered (Leidinger & Cabral, 2017), but we anticipate that its explicit consideration should contribute to earlier colonization in young islands and associated decrease in single-island endemism for older islands (Borregaard et al., 2016; Whittaker et al., 2008). Extending

integrative process-based frameworks, such as ours, to include archipelagic dynamics should enable scrutiny of inter-island isolation dynamics, opening ground for theoretical developments and conservation assessments (e.g. due to human-induced sea-level changes and alien species).

5 | CONCLUSIONS

The emergent patterns generally supported the temporal trends of and isolation effects on island floras as predicted by the GDM. However, noteworthy details that emerged included an unexpected steady increase in the proportion of endemic species, particularly endemics differentiated from mainland populations, and different extinction trends of endemics compared to those of non-endemic species. The divergences from expectations (summarized in Table 1) provide insights about isolation mechanisms and bring up new questions that can be investigated in future simulation experiments. For example, future scenarios can focus on disturbances and disturbance-adapted widespread species in the final stages of island ontogeny as well as dispersal from and to nearby large islands (as originally envisaged in the GDM) to explicitly investigate their role in shaping the very initial and final stages of speciation, colonization and extinction.

The dynamic nature of insular environments, isolation and area at evolutionary time-scales causes the theoretical dynamic equilibrium to change continuously, and consequently, those ecological processes may only crudely, or rarely reach an equilibrium, and this is also reflected by our findings. Therefore, an adequate representation of persistent non-equilibrium conditions and the relevant processes affecting individuals and populations seems crucial to improving our understanding of biodiversity dynamics on islands and beyond.

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BIOSKETCH

Juliano Sarmiento Cabral is interested in processes and factors influencing species and biodiversity dynamics across spatio-temporal scales. His research includes processes determining spatial and temporal distribution of tropical epiphytes, species ranges, island plant diversity as well as global species richness and endemism patterns.

Author contributions: J.S.C. and H.K. designed the study, with input from K.W.; J.S.C. implemented and simulated the model; J.S.C. led the analyses and writing, with input from all co-authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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