

1 **Original Article**

2 **Interactions between ecological, evolutionary, and environmental processes**
3 **unveil complex dynamics of island biodiversity**

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1 **ABSTRACT**

2 **Aims:** Understanding how biodiversity emerges and varies in space and time is central to
3 ecology and biogeography. Multiple processes affect biodiversity at different scales and
4 organizational levels, hence progress in understanding biodiversity dynamics requires the
5 integration of these underlying processes. Here we present BioGEEM (BioGeographical Eco-
6 Evolutionary Model), a spatially-explicit, process-based model that integrates all processes
7 hypothesized to be relevant for biodiversity dynamics and that can be used to evaluate their
8 relative roles.

9 **Location:** Hypothetical oceanic islands

10 **Methods:** The model is stochastic, grid-based, and integrates ecological (metabolic
11 constraints, demography, dispersal, and competition), evolutionary (mutation and speciation),
12 and environmental (geo-climatic dynamics) processes. Plants on oceanic islands served as
13 model system. We used the full model to test hypotheses about emergent patterns at different
14 spatio-temporal scales and organizational levels (populations, species, communities, and
15 assemblages), switching off processes to assess the importance 1) of competition for realistic
16 population and range dynamics; 2) metabolic constraints for endemism and community
17 composition; 3) environmental dynamics and 4) speciation for biogeographical patterns.

18 **Results:** The full model generated multiple patterns matching empirical and theoretical
19 expectations. For example, populations were largest on young, species-poor islands. Species,
20 particularly endemics, were better able to fill their potential range on small, species-poor
21 islands. Richness gradients peaked at mid-elevations. The proportion of endemics was highest
22 on old, large, and isolated environments within the islands. Species and trait richness showed
23 unimodal temporal trends. Switching off selected processes affected these patterns, and we
24 found most of our hypotheses supported.

1 **Main conclusions:** Integrating ecological, evolutionary, and environmental processes is
 2 essential to simultaneously generate realistic spatio-temporal dynamics at population, species,
 3 community, and assemblage level. Finally, large-scale biodiversity dynamics emerged
 4 directly from biological processes which make this mechanistic model a valuable ‘virtual
 5 long-term field station’ to study the linkages between biogeography and ecology.

6

7 **Keywords:** demography, dispersal, interspecific competition, island biogeography,
 8 mechanistic simulation model, metabolic theory, plant community, species richness, process-
 9 based niche model, speciation.

10

1 INTRODUCTION

2 Ecologists and biogeographers have a long-standing interest in explaining how species are
3 distributed in space and time, but disentangling the relative role of various potential
4 mechanisms for the generation and maintenance of biodiversity remains a challenge (Pennisi,
5 2005). Considering the complex interlinkage between eco-evolutionary processes and
6 environmental dynamics indicated to influence biodiversity, it seems crucial to account for
7 these processes simultaneously (Urban *et al.*, 2016; Cabral *et al.*, 2016). This has been
8 achieved by complex mechanistic models that simulate macro eco-evolutionary processes
9 (e.g. colonization, speciation, extinction) directly at the species and/or community ecological
10 levels to generate the biogeographical patterns of interest (e.g. Gotelli *et al.*, 2009; Colwell &
11 Rangel, 2010). Other models can simulate processes at lower ecological levels, such as
12 propagule dispersal, individual survival, or population establishment, to generate colonization
13 and extinction as emergent processes (e.g. Harfoot *et al.*, 2014; Singer *et al.*, 2016; Urban *et*
14 *al.*, 2016). This would provide insights across ecological levels and contribute to integration
15 of biogeographical and ecological theories (Evans *et al.*, 2013; Rosindell & Harmon, 2013;
16 Cabral *et al.*, 2016).

17 The major limitation of biogeographical models that simulate processes at low ecological
18 levels is high model complexity. Integrating multiple processes increases the number of
19 parameters and complicates interpretability (Dormann *et al.*, 2012). These issues can be
20 avoided by investigating multiple emergent patterns at different scales, i.e. pattern-oriented
21 modelling (Grimm & Railsback, 2012). Pattern-oriented modelling allows distinguishing
22 different parameter combinations that generate similar patterns at a given scale by evaluating
23 patterns at other scales. To counter-balance model complexity, a usefully complex model
24 should thus be able to predict patterns at multiple spatio-temporal scales and at different
25 levels of ecological organization (e.g. populations, species, communities). Likewise, a useful

1 study system should be as simple as possible, but still informative across scales and
2 ecological levels. Oceanic islands are suitable study systems because they are small and
3 isolated, have distinct boundaries, occur in large numbers worldwide, and exhibit striking
4 examples of evolutionary diversification (Losos & Ricklefs, 2010; Warren *et al.*, 2015).
5 Accordingly, island research has contributed essential information about eco-evolutionary
6 processes that shape biodiversity (e.g. Ricklefs & Bermingham, 2004; Whittaker &
7 Fernández-Palacios, 2007).

8 Different processes have been postulated to be important drivers for insular biodiversity.
9 The seminal equilibrium theory of island biogeography (ETIB) emphasizes the roles of area
10 affecting extinction and of isolation affecting colonization (MacArthur & Wilson, 1963), and
11 the importance of these factors has received ample support by many macroecological studies
12 (e.g. Kreft *et al.*, 2008; Triantis *et al.*, 2012; Weigelt & Kreft, 2013). Climate and
13 environmental heterogeneity also exert strong influence on insular biodiversity (Kreft *et al.*,
14 2008; Hortal *et al.*, 2009; Cabral *et al.*, 2014). Recently, the importance of geo-climatic
15 processes and time has been highlighted (Whittaker & Fernández-Palacios, 2007; Losos &
16 Ricklefs, 2010; Lomolino *et al.*, 2010; Weigelt *et al.*, 2016). In particular, species richness
17 and endemism depend on island age, geological ontogeny, and Pleistocene sea-level changes
18 (Whittaker *et al.*, 2008; Borregaard *et al.*, 2016; Weigelt *et al.*, 2016). Speciation is influenced
19 by speciation mode as well as island area, isolation, and environmental heterogeneity
20 (Whittaker *et al.*, 2008; Kisel & Barraclough, 2010; Rosindell & Phillimore, 2011). These
21 factors and associated processes are summarized by the General Dynamic Model of Island
22 Biogeography (GDM), which assumes a humped trajectory of area, elevation, and
23 environmental heterogeneity over a simplified life span and ontogeny typical of many oceanic
24 islands (Whittaker *et al.*, 2008). The GDM predicts humped temporal trends of species
25 richness, endemic richness, colonization, extinction, and speciation rates (predictions recently

updated by Borregaard *et al.*, 2016). Therefore, a mechanistic model focusing on insular biodiversity dynamics should generate those patterns alongside patterns at lower ecological levels, such as species-abundance distributions (Ulrich *et al.*, 2010) and species-area relationships (e.g. Triantis *et al.*, 2012).

This study aims to investigate the relative roles of ecological, evolutionary, and environmental processes for biodiversity dynamics using a process-based BioGeographical Eco-Evolutionary Model (BioGEEM). Our main hypothesis is that the integration of these three main process types is needed to accurately model biodiversity patterns. Oceanic islands served as our model systems. In our model, we extended niche models with low-level ecological processes (e.g. dispersal, population dynamics, competition, and metabolic constraints) and added evolutionary (mutation and speciation) and environmental (changes in area and environmental heterogeneity) processes. We first used the full model to evaluate emergent patterns against theoretical predictions and empirical patterns. We then assessed the relative importance of the simulated processes by switching off submodels (environmental dynamics, speciation, competition, metabolic constraints) and re-evaluating emergent patterns. We hypothesized that 1) competition is necessary to mediate population and range dynamics of competing species via competitive exclusion (Cabral & Kreft, 2012); 2) metabolic constraints are necessary to generate realistic patterns of endemism and community composition along environmental gradients and via life-history trade-offs (Brown *et al.*, 2004); 3) environmental dynamics and 4) speciation are necessary to generate biogeographical patterns as predicted by island biogeography theory (Whittaker *et al.*, 2008; Borregaard *et al.*, 2016).

1 MATERIALS AND METHODS

2 General model description

3 We extended a spatially-explicit multi-species model for range dynamics of plants (Cabral &
4 Kreft, 2012) with relevant evolutionary and environmental processes. We implemented
5 environmental dynamics that reflect the growth and erosion phases of oceanic islands (Fig.
6 1b; Whittaker & Fernández-Palacios, 2007; Whittaker *et al.*, 2008). Ecological and
7 evolutionary processes were controlled by metabolic constraints in a hierarchical structure
8 (Fig. 1a). Specifically, processes were linked to environmental variables (local temperature)
9 and species properties (body mass, Brown *et al.*, 2004). Metabolic constraints generated
10 spatial (via local temperature) and interspecific (via body mass) variation in eco-evolutionary
11 processes and accounted for life-history trade-offs, and thus precluded super-organisms (e.g.
12 minimal resource requirement and maximum reproduction). We focused on terrestrial seed
13 plants, but these metabolic constraints are ubiquitous (Brown *et al.*, 2004). Below, we
14 summarize the model. A detailed description following the Overview, Design concepts, and
15 Details protocol (ODD, Grimm *et al.*, 2010) is provided in Appendix S1 in Supporting
16 Information.

17 State variables and scales

18 The model was grid-based (Fig. 1c) with a cell size of 1 km², which was large enough to
19 sustain viable tree populations yet small enough to distinguish between short-distance (<< 1
20 km) and long-distance dispersal (Cabral & Kreft, 2012). Each island cell was assigned to an
21 elevational level with an associated mean temperature. The model agents were populations,
22 which were stage-structured (seeds, juveniles, adults) and measured in number of individuals.
23 Populations belonged to species, which were conceptualized as specific combinations of
24 autecological attributes, such as environmental requirements, dispersal ability parameters, and

1 demographic traits (hereafter: species properties). Body mass and local temperature
2 determined demographic transitions, mutation rates, the space exploited by an individual,
3 carrying capacity, and time for speciation (see Appendix S1). These metabolic constraints
4 accounted for the increase of metabolic rates with temperatures and their decrease with body
5 mass (Brown *et al.*, 2004). The application of metabolic theory accounts for metabolic trade-
6 offs related to energy allocation (e.g. survival vs. growth). Demographic transitions were
7 germination, sexual maturation, reproduction, and density-independent mortality.

8 Unoccupied cell area was used as the interaction currency (Kissling *et al.*, 2012), for which
9 populations competed. A cell could hold one population per species, but as many populations,
10 and thus species, as there was area available. Consequently, species coexistence in a cell and
11 on the island, and thus meta-communities and species assemblages, directly emerged from
12 local resource competition (Cabral & Kreft, 2012). The state variables comprised the spatial
13 distribution of seed, juvenile, and adult abundances of each species and the unoccupied area.
14 Each time step was one year and a complete simulation ran over millions of years (Fig. 1d and
15 'Study design'). Eco-evolutionary processes took place every time step, whereas
16 environmental events happened at longer intervals (Fig. 1e).

17 **Initialization**

18 The model was initialized by reading in the simulation grid (Fig. 1c) and run specifications:
19 mean annual air temperature at sea level (298 K, or 25 °C), size of the species pool (1000
20 species), and intervals for randomly drawing the species properties from a uniform
21 distribution (see Appendix S1 for the list of parameters, interval values, and the justification
22 of the values).

23 For each species, we randomly assigned the following properties: maximum cell
24 suitability, optimum temperature, temperature amplitude, optimum island side, island side

1 amplitude (environmental requirements), life form, mean dispersal distance, dispersal kernel
 2 thinness, strength of Allee effects, stage-specific body masses, and phenological ordering
 3 related to other species. Environmental requirements determined the distribution and quality
 4 of suitable habitat for each species. Optimum island side and island side amplitude
 5 represented requirements other than temperature affecting species distributions on islands,
 6 such as sunlight exposure or windward/leeward differences in precipitation (Whittaker &
 7 Fernández-Palacios, 2007). Temporal variation of island side and local temperature
 8 combinations accounted for changes in environmental heterogeneity, with maximum
 9 heterogeneity occurring at maximum island size. Depending on these environmental
 10 requirements, each species received a habitat suitability matrix, \mathbf{H} (see Appendix S1). Seeds
 11 could only germinate in suitable cells.

12 A dispersal kernel \mathbf{D} was initialized for each species by generating a two-dimensional,
 13 grid-based Clark's 2Dt kernel, with two parameters (mean dispersal distance and dispersal
 14 kernel shape parameter) that described short- and long-distance dispersal, respectively (Clark
 15 *et al.*, 1999). The explicit consideration of long-distance dispersal is an advantage of Clark's
 16 2Dt (Clark *et al.*, 1999; Nathan & Muller-Landau, 2000) because it allows the simulation of
 17 both within-island and mainland–island dispersal processes.

18 On the island, the abundance matrices for adults, N_a , juveniles, N_y , and seeds, N_s , of each
 19 species as well as the matrix with the area occupied by all individuals, \mathbf{A}_t , were initialized
 20 empty.

21 **Dispersal from mainland**

1 At each time step, ten random species from each mainland cell f dispersed to the island. The
 2 seed bank for each species at island cell i was incremented by $\text{Poisson}(\sum_f D_{(i,f)})$
 3 $\text{Uniform}(1,10000)$), where $D_{(i,f)}$ gives the dispersal probability per seed from cell f to cell i .

4 **Population update 1**

5 Following the phenological ordering, we first calculated the area used by all individuals.
 6 Subsequently, abundances were sequentially updated by: i) turning juveniles to adults, ii)
 7 applying density-independent mortality to remaining juveniles, iii) germinating seeds, and iv)
 8 applying seed mortality (see Appendix S1 for equations). If germinating and maturing
 9 individuals in a cell surpassed the space available, excess individuals died. This accounted for
 10 density-dependent mortality through self-thinning, which is a difficult process to model
 11 (Reynolds & Ford, 2005; Wiegand *et al.*, 2008) but emerged in our simulations from space
 12 competition.

13 **Reproduction**

14 The number of seeds produced by species j in cell i ($S_{p(i,j)}$) was given by $N_{a(i,j)} R(N_{a(i,j)})$, where
 15 $N_{a(i,j)}$ is the number of adults of species j in cell i and R a function describing per-capita
 16 density-dependent reproduction.

17 **Intra-island dispersal**

18 Seeds of species j received in cell z and from source cell i , ($S_{d(z,j)}$), were given by \sum_z
 19 $D_{(z,i)} S_{p(i,j)}$.

20 **Mutation**

1 We implemented a point-mutation process, which is a simple but efficient way to model
 2 cladogenesis (i.e. *in situ* speciation where two or more species evolve from a common
 3 ancestor, Rosindell & Phillimore, 2011). The number of mutated seeds was a Poisson random
 4 variate, whose probability was given by multiplying $S_{d(z,j)}$ with a metabolic mutation rate
 5 (Appendix S1). These genetically diverging individuals were initialized with random
 6 maximum cell suitability, optimum temperature, temperature amplitude, optimum island size,
 7 and island size amplitude (see '*Initialization*'). The remaining species properties were
 8 randomly drawn within the $\pm 50\%$ intervals around the values of the ancestral species to
 9 account for phylogenetic constraints. These evolving species properties allowed spatial and
 10 attribute divergence, which is commonly observed on islands.

11 **Speciation**

12 We checked whether the time for genetically diverging individuals becoming a distinct
 13 species was reached (i.e. 'protracted speciation', Rosindell & Phillimore, 2011). We also
 14 included anagenesis (i.e. colonizers becoming distinct from the mainland form without *in situ*
 15 cladogenesis occurring). Both speciation modes depended on metabolic constraints to account
 16 for longer generations for larger body mass (Brown *et al.*, 2004). For anagenesis, the
 17 speciation time was counted from the island colonization event (no mutation required).
 18 However, every time mainland immigrants became adults, completion of anagenesis was
 19 delayed due to gene flow. The delay was arbitrary but varied metabolically and could re-start
 20 the speciation countdown (see Appendix S1). For cladogenesis, the speciation time was
 21 counted from the time step of the mutation event. Mutants surviving until their speciation
 22 time was completed were updated as cladogenetic endemics. The colonizer species giving
 23 origin to cladogenetic endemics remain either non-endemic under continuous gene flow or
 24 become anagenetic endemic.

1 **Population update 2**

2 Abundance matrices were updated sequentially by applying density-independent mortality to
3 adults and updating the seed bank after dispersal and mutation. These stochastic transitions
4 followed respective metabolic transition rates (Appendix S1).

5 **Environmental dynamics**

6 We considered the geo-climatic changes assumed on oceanic hotspot islands (Fig. 1b;
7 Whittaker & Fernández-Palacios, 2007). To mimic volcanic island growth, each simulation
8 started with a single cell that grew regularly by adding concentric belts of cells around the
9 margins and by uplifting the interior belts. Thereafter, island size remained temporarily stable,
10 followed by an erosion phase. At each erosion step, one belt of cells disappeared from the
11 island margin, and the elevation of remaining cells decreased (Fig. 1b). Temperature
12 decreased by 1 K for each elevational belt following uplift and increased by 1 K following
13 erosion. We assumed an arbitrary length for each growth time step of 0.13 Myr (based on
14 estimates for Madeira, see Appendix S1). We doubled this time length for the stable phase
15 and erosion time steps to account for a slower erosion phase compared to the volcanic growth
16 phase (Whittaker & Fernández-Palacios, 2007). Each simulation spanned 2.21 Myr. After
17 every environmental event, H was recalculated for every species.

18 **Output**

19 Output variables were N_a , N_y , and N_s . Additionally, we recorded for every time step and cell
20 species richness (total, non-endemics, and anagenetic as well as cladogenetic endemics),
21 radiating lineages (species showing cladogenesis on the island) and species per radiating
22 lineage. For the entire island, we counted colonization, speciation, and extinction events per
23 time step.

1 Study design

2 We designed two simulation experiments. First, we simulated the full model including all key
3 processes. For each ecological level, we assessed multiple patterns and compared them to
4 empirical data and theoretical predictions whenever possible. At maximum size, the simulated
5 islands were 300 cells away from the mainland. The maximum island size was 11×11 cells
6 and the mainland species pool comprised 1000 species. For this experiment, we simulated 20
7 replicate runs, each with a different mainland source pool.

8 The second experiment simulated exploratory scenarios in which we switched off
9 processes to assess their relative role. Three replicate model runs were performed for each
10 exploratory scenario. This replicate number allowed us to explore all scenarios, while still
11 producing variability in the resulting time series. We simulated four scenarios: 1) without
12 competition; 2) without metabolic constraints; 3) without environmental dynamics; 4) without
13 speciation. Except for the scenario without metabolic constraints, replicate runs were based on
14 the same source pool, thereby controlling for source pool-related variability. For the scenario
15 without competition, we excluded competition with other source pool species by simulating
16 each of 500 random species from the source pool in separate. However, competition was kept
17 between evolving species. Otherwise, endemic richness would have increase exponentially.
18 For the scenario without metabolic constraints, we switched off the body mass and local
19 temperature control on demographic and evolutionary rates, which were then drawn
20 independently (e.g. no trade-offs between reproduction and survival rates; Appendix S1). For
21 the scenario without environmental dynamics, the island had a constant size of 7×7 cells. For
22 the scenario without speciation, we switched off anagenesis, mutation, and cladogenesis.
23 Given our focus on general trends and causal effects, we depicted variability of model
24 simulations (e.g. 95% confidence envelopes) but we did not perform statistical tests when

- 1 comparing scenarios because significance for minor differences emerges simply by increasing
- 2 replicates (White *et al.*, 2014).
- 3

1 RESULTS

2 The first simulation experiment generated temporally and spatially-explicit patterns spanning
 3 four different ecological levels. At the population level, the dynamics of population structure
 4 and species abundance at local scale and for the entire island emerged from the simulations
 5 (Fig. 2 a-f). Population structure (proportion of seeds, juveniles, and adults within the
 6 population) varied from mostly stable (Fig. 2d) to episodically changing due to island growth
 7 or erosion events (Fig. 2e-f) to ever changing (mostly due to declining adult abundances, Fig.
 8 2c). Native non-endemics (from now simply non-endemics) tended to decrease in mean
 9 abundance (Fig. 2g), whereas anagenetic (Fig. 2h) and cladogenetic (Fig. 2i) endemics had
 10 more stable abundances over time.

11 At the species level, the spatial distribution of abundance and realized range changed over
 12 time and could strongly deviate from the distribution of potential habitat, with some species
 13 being able to survive only in sub-optimal environments (Fig. 3a). The species tended to have
 14 lower levels of range filling at intermediate to advanced island age, with cladogenetic
 15 endemics retaining higher range filling than anagenetic endemics and non-endemics (Fig. 3b).

16 At the local community level, rank-abundance distributions followed a lognormal
 17 distribution (Fig. 4a). Local species richness, richness of cladogenetic endemics, and
 18 proportion of cladogenetic endemics increased over time (Fig. 4b-d, respectively). Species
 19 richness and cladogenetic endemic richness peaked at intermediate elevations (Fig. 4b-c,
 20 respectively), whereas the proportion of cladogenetic endemics was highest at low elevations
 21 (Fig. 4d).

22 At the level of the island-wide meta-community (from now on termed as assemblage),
 23 species–area relationships (SARs) were steeper during the growth phase than during the
 24 erosion phase (Fig. 5a-b). Species richness showed a humped trend and peaked at

1 intermediate to advanced age (Fig. 5c), whereas the peaks for anagenetic and cladogenetic
2 endemics lagged slightly behind (Fig. 5c). Colonization and extinction rates were humped and
3 peaked at intermediate island ages (fig. 5d). This trend was also obtained for rates of
4 anagenesis and cladogenesis, but it was two orders of magnitude lower than for immigration
5 (Fig. 5e). Extinction of endemics was also humped, but with a very late peak (Fig. 5e). The
6 number of radiating lineages, the number of species per radiating lineage, and trait richness all
7 peaked at advanced island ages (Fig. 5f, g). However, species packing showed an initial steep
8 decrease followed by a humped trend over time (Fig. 5h). For the cladogenetic endemics, the
9 mean pairwise trait distance to their ancestral species showed a very shallow humped trend
10 over time, whereas the distance to all species increased almost for the entire island lifespan,
11 decreasing only at very advanced island age (Fig 5i).

12 The second simulation experiment, namely switching off main processes, revealed patterns
13 diverging from the first, full model experiment (Fig. 6). At the population level, population
14 structure was generally stable in the scenario without competition (Fig. 6a vs. Fig. 2b),
15 whereas population structure was highly oscillatory without metabolic constraints (Fig. 6b).
16 Without environmental dynamics, species colonized earlier, but were subjected to extinction
17 as in the full model (Fig. 6c). Without speciation, colonizers decreased in abundances over
18 time, but survived the entire simulation (Fig. 6d). Without competition, range filling was
19 lower at intermediate island age and for cladogenetic species (Fig. 6e vs. Fig. 3b), whereas
20 without metabolic constraints, range filling was variable, with non-endemics going extinct at
21 advanced island age (Fig. 6f). Without environmental dynamics, range filling was highest for
22 cladogenetic endemics, but showed stable dynamics after the initial colonization period (Fig.
23 6g). Without speciation, species maintained high levels of range filling (Fig. 6h). In the
24 scenario without competition, the proportion of cladogenetic endemics was extremely high at
25 advanced island age, particularly in the lowlands (Fig. 6i vs. Fig. 4d right panel). In the

1 scenario without metabolic constraints, the proportion of cladogenetic endemics was also
2 high, but without spatial structure (Fig. 6j). Moreover, without environmental dynamics, the
3 proportion of cladogenetic species peaked at low and high elevations (Fig. 6k), whereas
4 endemics were understandably absent without speciation (Fig. 6l). At the assemblage level,
5 species richness showed a humped trend over time and was dominated by endemics, with
6 very high values without competition (Fig. 6m vs. Fig. 5c) and very low values without
7 metabolic constraints (Fig. 6n). Without environmental dynamics, total species richness on
8 the island tended towards equilibrium but the number of cladogenetic species continued to
9 increase (Fig. 6o), whereas without speciation, species richness showed a humped trend
10 similar to, but with lower values and less variation than, the full model (Fig. 6p vs. Fig. 5c).

11

1 **DISCUSSION**

2 **Population level**

3 In the full model, population structure varied according to local environment, species
 4 evolutionary origin (non-endemic, anagenetic, or cladogenetic), and island age (Fig. 2). The
 5 high relative abundances, particularly of non-endemics (Fig. 2g), on young islands can be
 6 explained by lower competition due to low species number. Population establishment
 7 decreases with island age, a pattern which has been observed for biological invasions on
 8 islands worldwide (Kueffer *et al.*, 2010). Interestingly, endemics were better able to sustain
 9 stable or increasing populations compared to non-endemics (Fig. 2g-i). Empirical data
 10 comparing abundances of endemic and non-endemic plant species are rare, but evidence from
 11 pollination networks on oceanic islands suggests that endemics tend to be generalists and to
 12 have higher relative abundances than non-endemics (Olesen *et al.*, 2002). Moreover, endemic
 13 arthropods in the Azores also tended to show higher densities and occupancy than native non-
 14 endemic species (Gaston *et al.*, 2006). Strikingly, without competition, species could sustain
 15 high and stable abundances (Fig. 6a), whereas without speciation, populations decreased over
 16 time, but could survive longer than in the full model (Fig. 6d). These results confirm our first
 17 hypothesis that competition regulates populations, particularly considering the colonization
 18 and evolution of competitors.

19 **Species level**

20 Under the full model experiment, the sharp decrease in normalized abundances after the initial
 21 island growth phase (Fig. 2g - i) translated into a general decrease in range filling at the
 22 species level at intermediate to advanced island ages (Fig. 3). Even if species could fill their
 23 entire potential range, the realized abundance distribution could diverge from the distribution
 24 of habitat suitability, particularly at intermediate island age (Fig. 3a). Such divergence can be

1 explained by interspecific competition, which decreases abundances and may shift abundance
2 peaks to sub-optimal environmental conditions, as reported for plants and animals (McGill,
3 2012; Wisz *et al.*, 2013). With decreasing island size, extinction of poorer competitors
4 increased range filling of surviving species (Fig. 3b). Remarkably, cladogenetic endemics
5 were better able to fill their potential range compared to non-endemics and anagenetic
6 endemics, which indicates high selective pressure on species to cope with competition.
7 Because anagenetic endemics did not change their niche upon speciation, their range filling
8 dynamics were coherently comparable to non-endemics.

9 The scenario without competition revealed similar trends, but with higher range filling
10 compared to the full model, with cladogenetic endemics showing the lowest values (compare
11 Fig. 6e with Fig. 3b). The lowest values for cladogenetic endemics reflected the persistence of
12 competition between endemics in this scenario (see Materials and Methods) and that the
13 number of endemics was very high (Fig. 6m). Hence, the lower range filling of cladogenetic
14 endemics can be explained by an almost unconstrained diversification. Accordingly, in the
15 scenario without speciation, and thus without competition with endemics, non-endemics
16 achieved high range filling throughout the simulation (Fig. 6h). In contrast, without metabolic
17 constraints, super-dominant species evolved, leading to low range filling followed by
18 extinction of non-endemics (Fig. 6f). Together, these results confirmed our first hypothesis
19 that competition is necessary to regulate range dynamics (see also Singer *et al.*, 2016; Urban
20 *et al.*, 2016), mostly via competition between non-endemic and endemic species.

21 **Community level**

22 The full model produced realistic rank abundance distributions with only few dominant
23 species (Fig. 4a). The general lognormal shape of the rank abundance plots were consistent
24 with a recent meta-analysis (Ulrich *et al.*, 2010). Moreover, species abundance distributions

1 could be described by the recently introduced gambin distribution (Appendix S2; Matthews *et*
2 *al.*, 2014). When assessing the spatial distribution of local species richness, the mid-elevation
3 peaks (Fig. 4b-c) reflected the random distribution of temperature niches of the source pool,
4 with most ranges overlapping in mid-elevations due to mid-domain effects (Colwell & Lees,
5 2000; Cabral & Kreft, 2012). Accordingly, cells between island sides had higher richness
6 reflecting ecotones caused by overlapping of ranges of island side specialists. Remarkably,
7 the percentage of cladogenetic endemics was highest at lower elevations (Fig. 4d). On real
8 islands, species richness often peaks at low or mid-elevations (Sanders & Rahbek, 2012;
9 Seipel *et al.*, 2012). The percentage of single-island endemics, in contrast, tends to peak at
10 high elevations (Steinbauer *et al.*, 2012), which might be due to higher isolation, lower
11 competition, and lower gene flow in high-elevation environments (Steinbauer *et al.*, 2012). In
12 our simulations, intermediate elevations were the least isolated environments due to the
13 random assignment of temperature niches, which resulted in more species overlapping their
14 ranges at these elevations. Therefore, the higher proportion of cladogenetic endemics in the
15 lowlands in the full model supports the isolation effects because these elevations were
16 suitable for a lower number of species compared to intermediate elevations. The low
17 endemism at high elevations can then be explained by time and area effects, considering that
18 high elevations had the smallest area and had less time to accumulate species. In fact, the
19 scenario without environmental dynamics showed a high proportion of cladogenetic endemics
20 at both low and high elevations (Fig. 6k).

21 Beyond area, time, and isolation, environmental variables also affected endemism via
22 increasing mutation and speciation rates with temperature (Allen *et al.*, 2006). Very high
23 values and no evident spatial structure of cladogenetic endemism in the scenario without
24 metabolic constraints (Fig. 6j) confirmed that these constraints influence the spatial structure
25 of speciation and local communities, supporting our second hypothesis. These constraints

1 prevent super-dominant species (e.g. species with high reproductive and survival rates
2 combined with low resource requirements □ Brown *et al.*, 2004). Moreover, metabolic
3 constraints interact with competition to regulate optimal environments for speciation,
4 indicated by the mid-elevation peaks in endemic richness in the full model. This happens
5 because higher speciation rates in the lowlands can be prevented by higher resource
6 requirements (Brown *et al.*, 2004) and thus stronger interspecific competition, despite higher
7 mutation rates (Allen *et al.*, 2006) as well as higher resource availability (i.e. larger area).
8 Consequently, mid-elevations represent the best balance between higher mutation rates and
9 resource availability in the lowlands vs. lower competition pressure in the highlands.

10 **Assemblage level**

11 Species richness of entire islands closely tracked environmental dynamics (Fig. 5a-b). Slope
12 values of power-law SARs considering the entire island life-span matched remarkably well
13 with real-world SARs of oceanic islands (mean $z = 0.39$ in Fig. 5b compared to $z = 0.38$ in
14 Triantis *et al.*, 2012). Moreover, the SAR intercepts reflecting the average species density
15 (mean $c = 1.4$, Fig. 5b) were also comparable to intercepts reported for plants ($c = 1.6$ in
16 Triantis *et al.*, 2012), but larger than intercepts reported for oceanic islands ($c = 0.6$; Triantis
17 *et al.*, 2012). Such low reported intercepts are, however, closer to the intercepts obtained
18 when considering only the growth phase ($c = 0.55$; Fig. 5b), when the islands start devoid of
19 life. In real world, low intercepts (i.e. low richness per unit area) are found for area-
20 demanding taxa (e.g. vertebrates and trees) and on very small, low-lying islands, such as
21 atolls. These islands are also subject to frequent disturbances (Morrison, 2010), which are not
22 simulated. Nevertheless, the obtained differences in SARs indicate that future studies should
23 account for the geological phase of the islands.

1 Species richness and endemic richness (Fig. 5c) followed the humped trend over time
 2 predicted by the GDM (Whittaker *et al.*, 2008; Hortal *et al.*, 2010; Borregaard *et al.*, 2016).
 3 This hump was absent in the scenario without environmental dynamics (Fig. 6o), confirming
 4 our third hypothesis that the environmental processes drive the temporal dynamics of species
 5 richness. Without environment processes, the seemingly stable species richness (ca. 160
 6 species, Fig. 6o) is in line with the ETIB assumption of static islands (MacArthur & Wilson,
 7 1963). However, whereas the species richness stabilizes through a dynamic equilibrium
 8 between colonization and extinction in ETIB, our results represent a dynamic balance
 9 between colonization, speciation, and extinction with a almost constant disequilibrium caused
 10 by environmental dynamics. Remarkably, without ecological and evolutionary processes the
 11 humped trend was retained but richness values were affected (Fig. 6m-n, p). In particular,
 12 species richness reached high values without competition (Fig. 6m), whereas it was very low
 13 without metabolic constraints (Fig. 6n). In both scenarios, island floras were dominated by
 14 endemics, suggesting that competition and metabolic constraints affect evolutionary processes
 15 and species assemblage composition, although their impacts are assumed to mostly affect
 16 richness locally (but see Waters *et al.*, 2013; Pedersen *et al.*, 2014).

17 The humped distribution of species richness over time in the scenario without speciation
 18 rejected our forth hypothesis that speciation is necessary to generate this pattern. Our results
 19 indicate that the humped richness can emerge through colonization and extinction rates alone
 20 and without involving speciation rate. In the full model, colonization and cladogenesis rates
 21 indeed followed the theoretical predictions of decreasing colonization and humped speciation
 22 rates for a hotspot geological trajectory (Fig. 5d-e; Whittaker *et al.*, 2008; Borregaard *et al.*,
 23 2016). Moreover, within cladogenesis, the numbers of radiating lineages and species per
 24 radiating lineage over time (Fig. 5f) were also consistent with theoretical predictions
 25 (Whittaker *et al.*, 2008; see also Cabral *et al.*, submitted). This indicates that diversification

continues after volcanic activity has ceased and area has decreased (Whittaker & Fernández-Palacios, 2007). Furthermore, the humped extinction (Fig. 5d) and anagenesis (Fig. 5e) rates were consistent with GDM predictions (Borregaard *et al.*, 2016). Overall extinction rates followed the expected humped colonization trends (Fig. 5e; Borregaard *et al.*, 2016) and reached a dynamic equilibrium only on very old islands akin to ETIB predictions (similar extinction and immigration rates in Fig. 5d; MacArthur & Wilson, 1963). Interestingly, the much delayed peak extinction of all compared to that only of endemic species (compare Figs 5d-e) indicates that endemic species might be less susceptible to extinction (i.e. better adapted to in situ conditions) than non-endemic species during early stages of island erosion.

Trait richness followed the humped trend of species richness, consistent with the positive relationship between trait richness and species richness (Fig. 5c,g; Petchey & Gaston, 2002; Carnicer *et al.*, 2012). We found initially high values in species packing followed by a sharp decrease (Fig. 5h), possibly reflecting strong environmental filtering, indicating that only species with similar trait syndromes (e.g. lowland-adapted, good dispersing herbs) might be able to colonize young islands. As islands gain in environmental heterogeneity, new colonizers and evolving endemics increased the trait space, causing the sharp decrease in species packing (Fig. 5h). Thereafter, species start to fill the trait space, closely tracking island area. However, species packing was not random, as cladogenetic endemics were selected to fill the environmental space away from the co-occurring species thereby avoiding niche overlap and competitive exclusion (e.g. trait dispersion or character displacement; Mizera & Meszéna, 2003), while their trait distance to the ancestor was phylogenetically constrained (Fig. 5i). This indicates complex interactions between trait, demographic, and diversification dynamics (see Carnicer *et al.*, 2012 for a review) and a strong influence of competition on trait selection and evolution.

Model properties, limitations and potentials

1 The ability of the model to simultaneously generate multiple patterns across different
2 ecological levels provides opportunities for cross-scale validation (Grimm & Railsback,
3 2012). Other process-based island models (Kadmon & Allouche, 2007; Hortal *et al.*, 2009;
4 Rosindell & Phillimore, 2011; Rosindell & Harmon, 2013; Valente *et al.*, 2014, 2015;
5 Borregaard *et al.*, 2016) have fewer parameters and thus lower complexity. However, these
6 models tend to simulate biogeographical processes directly (e.g. colonization, extinction, and
7 speciation) and are spatially-implicit. Our approach, in contrast, describes the same
8 biogeographical patterns emerging from population-level processes in a spatially-explicit
9 context. The unrealistic patterns we obtained when switching off core processes support the
10 importance of these processes and justify model complexity. Additionally, the explicit
11 representation of space and environmental heterogeneity of our approach facilitates a niche-
12 based framework, which is fundamental for testing island biogeography theory given the role
13 of habitat heterogeneity and niche opportunities for speciation (Whittaker *et al.*, 2008).

14 Limited availability of empirical data generally hampers model validation,
15 parameterization, and quantification of model uncertainty (Jeltsch *et al.*, 2008; Dormann *et*
16 *al.*, 2012). The hierarchical structure of our model allows the use of different data types of to
17 calibrate the model and to evaluate different emergent patterns (Wiegand *et al.*, 2003). For
18 example, estimates of demographic rates can be used to fit metabolic functions (Schurr *et al.*,
19 2012) and abundance distributions to fit demographic functions (Cabral & Schurr, 2010).
20 Simulating large and species-rich islands might be computationally unfeasible, but within
21 feasible computational scenarios data scarcity can be overcome with pattern-oriented
22 modelling by using emergent patterns to calibrate unknown parameters and preventing error
23 propagation (Wiegand *et al.*, 2003; Grimm & Railsback, 2012).

24 We used theoretical predictions and empirical data for evaluation of model structure and
25 validation of the full model. A range of emergent patterns followed well-documented

1 empirical trends and relationships. Namely, these were rank-abundance distributions (Ulrich
2 *et al.*, 2010), relationship between proportions of endemic species and environmental isolation
3 (Steinbauer *et al.*, 2012), species–area relationships (Triantis *et al.*, 2012), species richness
4 and endemism over time (Whittaker *et al.*, 2008; Cameron *et al.*, 2013). Such cross-scale and
5 cross-ecological level validation suggests that our model produces generalizable predictions
6 over a wide range of systems (see Evans *et al.*, 2013 for a review on generality of complex
7 models). Some of the patterns generated currently lack empirical data for evaluation and thus
8 constitute predictions to be tested in future studies (e.g. humped trait diversity over time, Fig.
9 5g). Additionally, in all predictions (with and without available comparable empirical data),
10 our model inherently integrates variability by considering demographic, colonization,
11 extinction and speciation stochasticity via multiple replicate runs. Finally, parameter and
12 model uncertainties can be addressed by varying scenarios (e.g. different isolation scenarios,
13 Cabral *et al.*, submitted) and model structure (Fig. 6). Therefore, data limitation should not
14 prevent the exploration of relevant processes in simulation models (Evans *et al.*, 2013).

15

16 **Model implications and conclusions**

17 Our modelling results show that understanding biodiversity dynamics requires the
18 consideration of many different ecological, evolutionary, and environmental processes. In an
19 island biogeography-related context, the novelty of our approach is that it simulates processes
20 at the level of the individuals and populations in a stochastic, niche-, and metabolism-based
21 framework. This framework leads to biogeographical dynamics emerging at large spatio-
22 temporal scales. Our approach thus unifies mechanistically multiple ecological and
23 evolutionary theories with island biogeography theory. Besides confirming several predictions
24 of island biogeography theory, the integration of eco-evolutionary and environmental

processes pinpointed interesting divergences and provided insights into less studied patterns and process interactions. We therefore argue that process-based models hold a great potential to serve as ‘virtual, long-term field stations’ in biogeography.

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17 **SUPPORTING INFORMATION**

18 Additional supporting information may be found in the online version of this article:

19 **Appendix S1** Detailed model description.

20 **Appendix S2** Gambin fit to species abundance distributions.

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1 BIOSKETCH

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

6 **Kerstin Wiegand** is interested in the role of space for population dynamics, interspecific
7 interactions, and biodiversity. The methodological emphasis of her research is on (spatially
8 explicit, agent-based) simulation models and spatial statistics.

9 **Holger Kreft** has a broad interest in biogeographical and macroecological patterns,
10 particularly gradients in species richness and endemism. His research includes analyses of
11 plant and vertebrate diversity, island and conservation biogeography.

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

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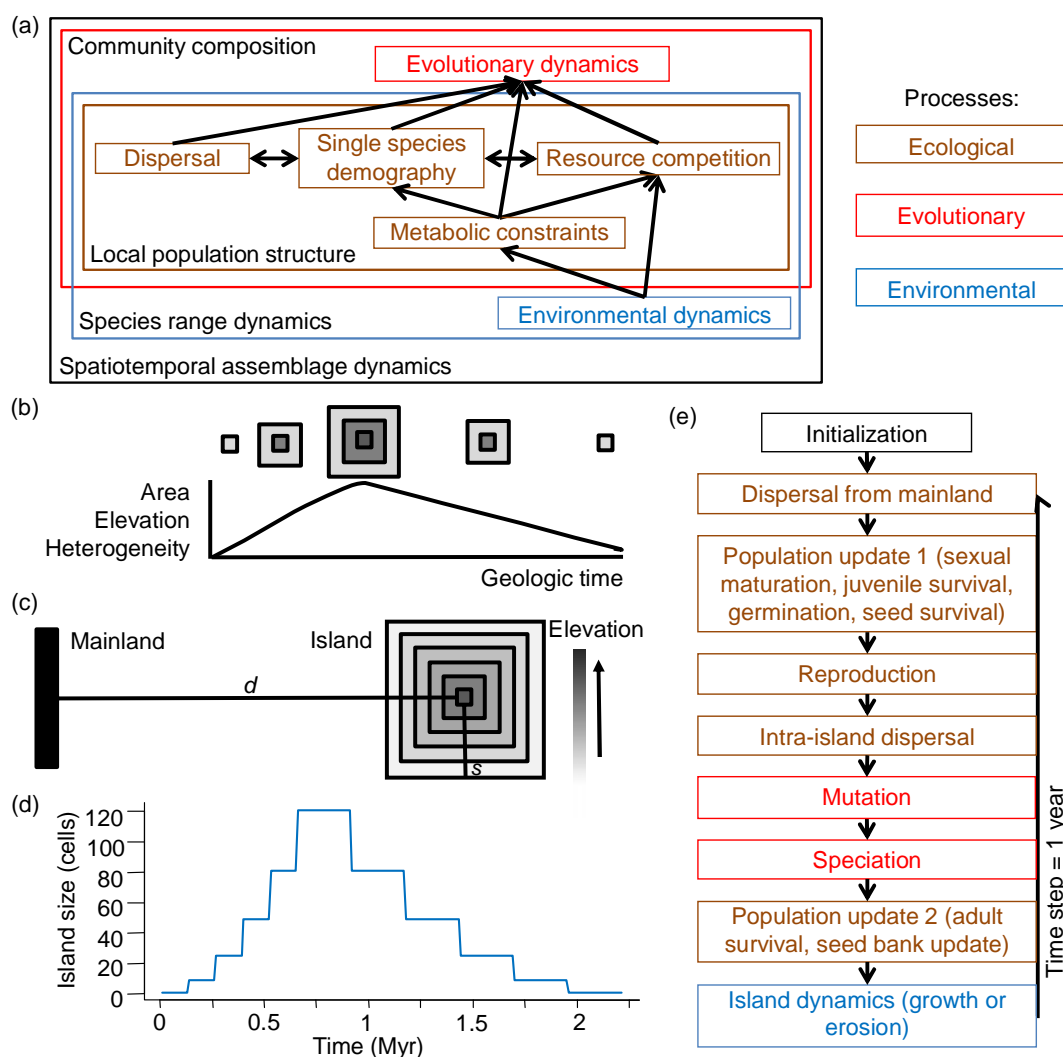


Figure 1 Model framework. (a) Hierarchical structure of simulated processes and emergent patterns. (b) Growth and erosion of hypothetical volcanic islands over geological time. Elevation and environmental heterogeneity are expected to correlate positively with island size and thus to be a humped function of island age. (c) Simulation grid at maximum island size, where s is the maximum distance between island centre and edge ($s = 5$ cells). Grid dimensions are described by s and distance d from the island centre to the mainland: $(2s+3)(s+d+4)$ cells. The island is initially a single cell at $s+1$ cells from the left, top, and bottom borders of the grid, and the mainland is at the right grid margin with two columns of cells. (d) Island size over time (in Myr). (e) Flow chart illustrating the sequence of simulated processes. Note that ecological and evolutionary processes were performed every time step, but island dynamics took place at much greater intervals (see panel d and 'Study design').

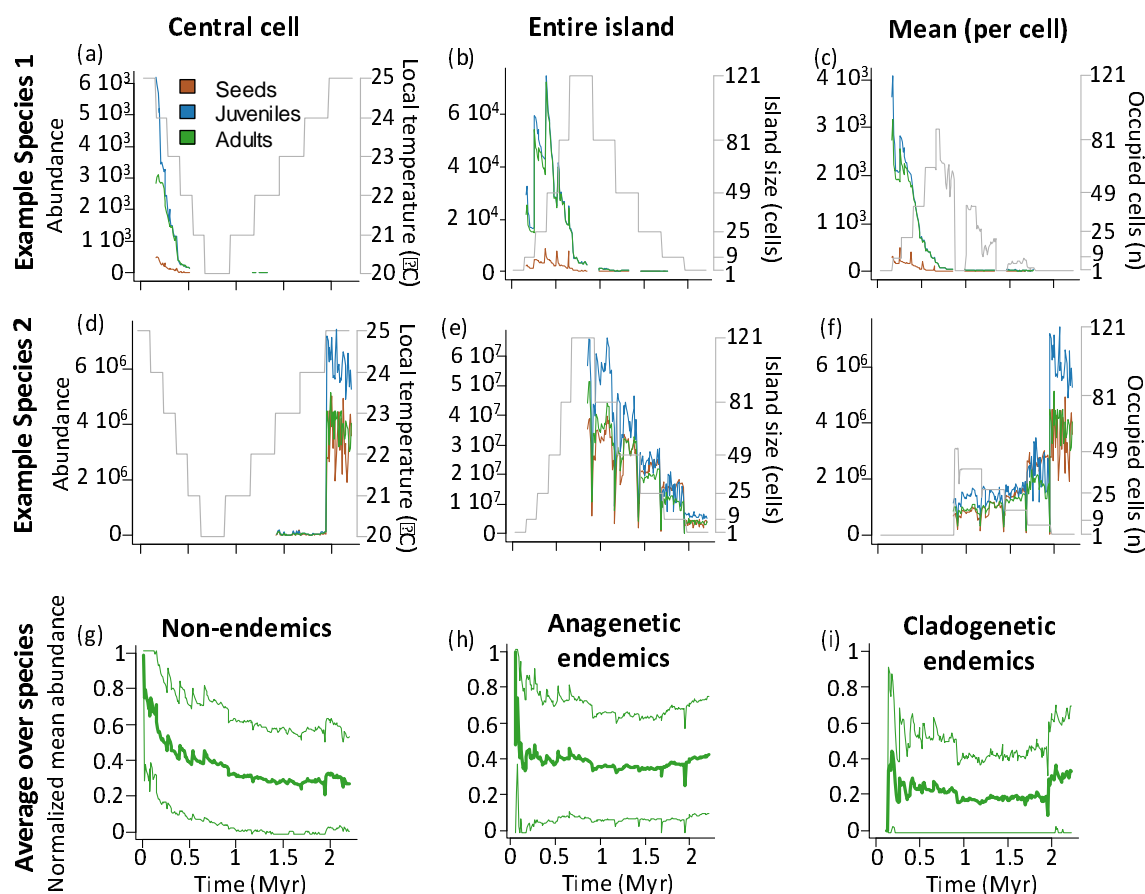


Figure 2 Population level temporal patterns. The top and intermediate rows show one exemplary species each, whereas the bottom row describes the abundance of adults normalized by dividing the time-series by the maximum abundance. (a-c) Seed, juvenile, and adult abundances (legend in a) in number of individuals of a non-endemic tree species adapted to lowlands and (d-f) of an endemic herb species adapted to lowlands (see Appendix S1 for detailed species properties). Panels (a) and (d) give local abundances in the central cell, (b) and (e) total island abundances, and (c) and (f) mean abundances (per occupied cell). The grey lines in (a-f) refer to the right y-axis: local temperature of the central cell (a, d), number of island grid cells (b, e), and occupied island grid cells (c, f). (g-i) Normalized mean cell abundances of (g) non-endemics, (h) anagenetic endemics (i) and cladogenetic endemics. Mean cell adult abundances were normalized by the highest value in the time-series per species. Thick lines in g-i indicated the average over replicates ($n = 20$) and species (n varies with replicate and time step), whereas thin lines indicate 95% CI (truncated at 0 and 1). The time-series were additionally averaged within time classes of 0.01 Myr.

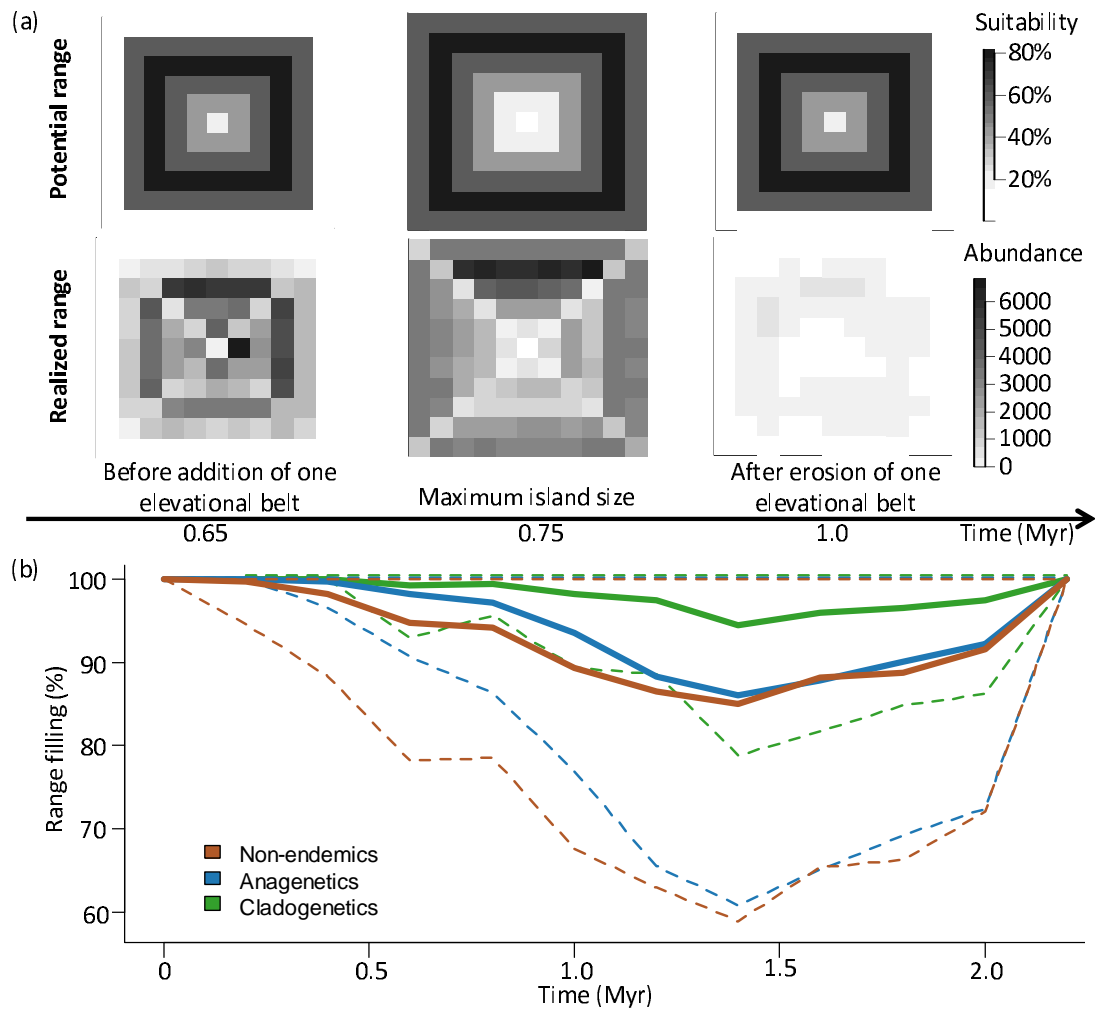


Figure 3 Temporal and spatial patterns at the species level. (a) Potential (top row) and realized (bottom row) range of a shrub species adapted to lowlands ($T_o = 24^{\circ}\text{C}$, $T_a = 4$) at three different time steps: before (left column), during (middle column), and after (right column) the island has reached maximum size (see Appendix S1 for detailed species properties). (b) Range filling time series of range non-endemic species, anagenetic endemics, and cladogenetic endemics ($n = 20$; thick lines indicate means, thin dashed lines 95% CI). Time-series in (b) were averaged within each geological time step.

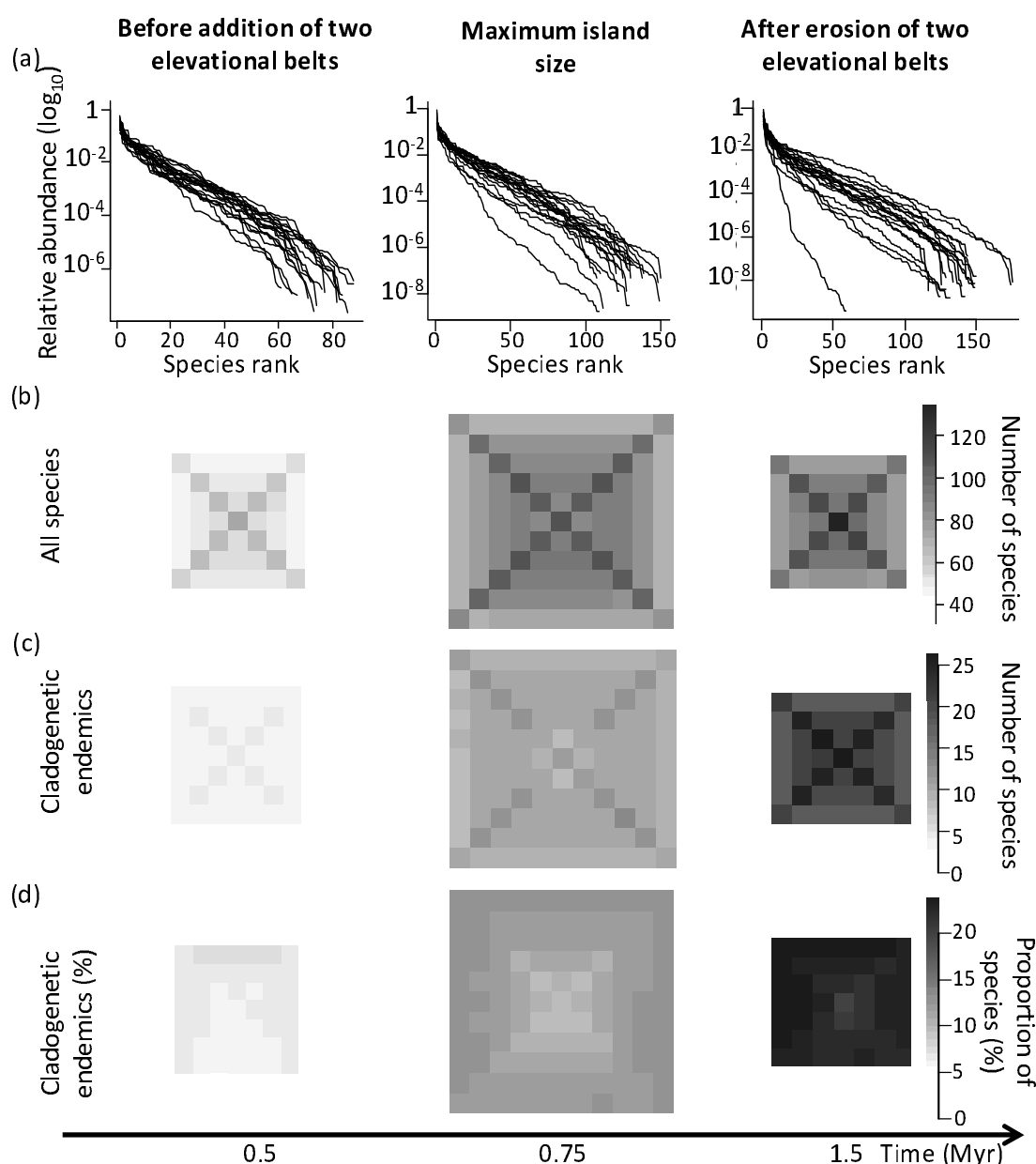


Figure 4 Temporal and spatial patterns at the community level. (a) Rank abundance plots of the central cell, (b) spatially-explicit species richness considering all species and (c) cladogenetic endemics, as well as (d) proportion of cladogenetic endemics at three different times steps: before (left panels), during (middle panels), and after (right panels) the island has reached maximum size. Rank abundances of each replicate are given by single lines in (a) and all of them fitted the lognormal distribution best when comparing AIC values for fitted logseries, lognormal and power law distributions to the abundance data (R package 'sads'). Species richness and proportion of cladogenetic endemics were averaged over the 20 replicate runs.

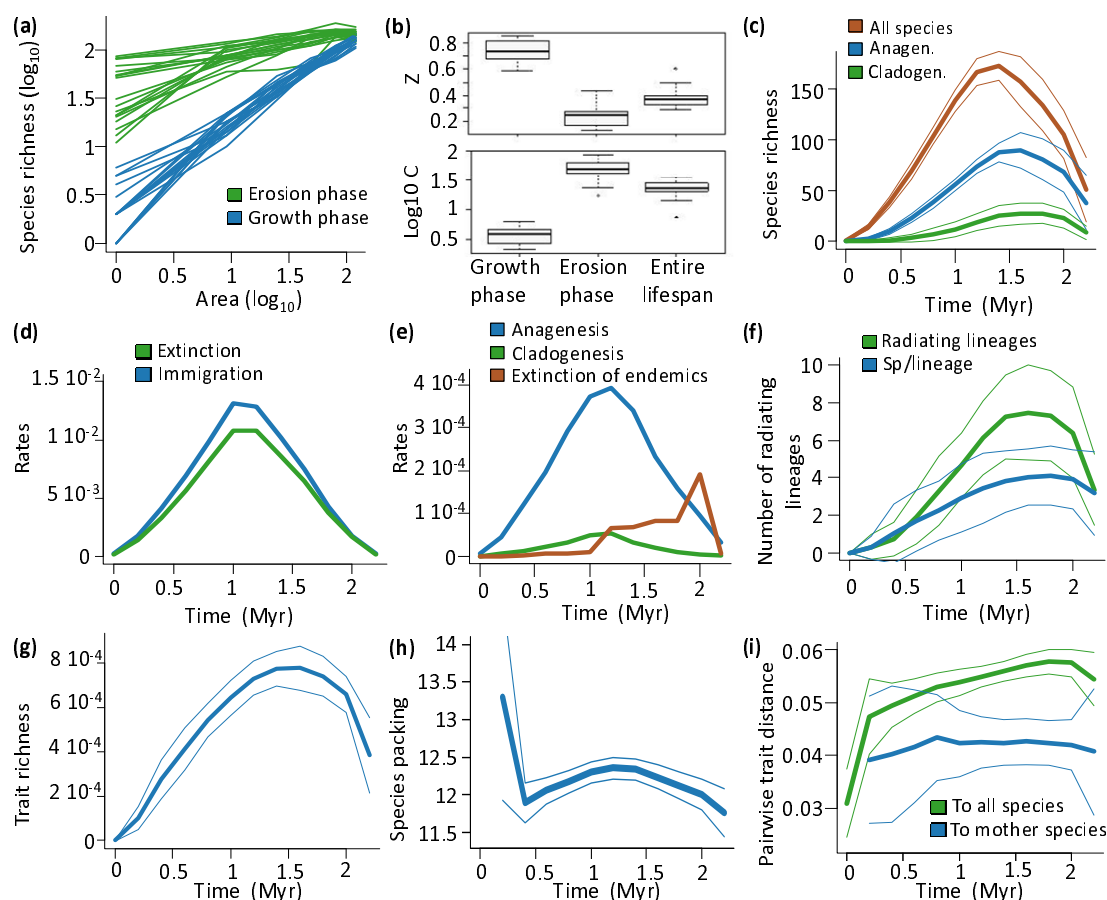


Figure 5 Temporal patterns at the assemblage level. (a) Log-log species-area relationships (SARs) for growth and erosion phases (lines represent replicates), (b) slope z and intercept $\log C$ of estimated power-law SARs for growth and erosion phases as well as the entire island geological lifespan, (c) species richness over time, (d) colonization and extinction rates over time, (e) anagenesis, cladogenesis, and extinction rates of endemics over time, (f) number of radiating lineages and species per radiating lineage over time, (g) trait richness (volume of the convex hull of the multivariate space considering all species properties) over time, (h) species packing (number of species per trait richness unit) over time, (i) pairwise trait distance of cladogenetic endemics to their mother species and to all other species over time, averaged per trait and per species pair. Thick lines in (c-i) indicate average within each environmental time step (see ‘environmental dynamics’ in the methods) and over 20 replicates, with 95% CI (thin lines, omitted in panels d and e for visual clarity).

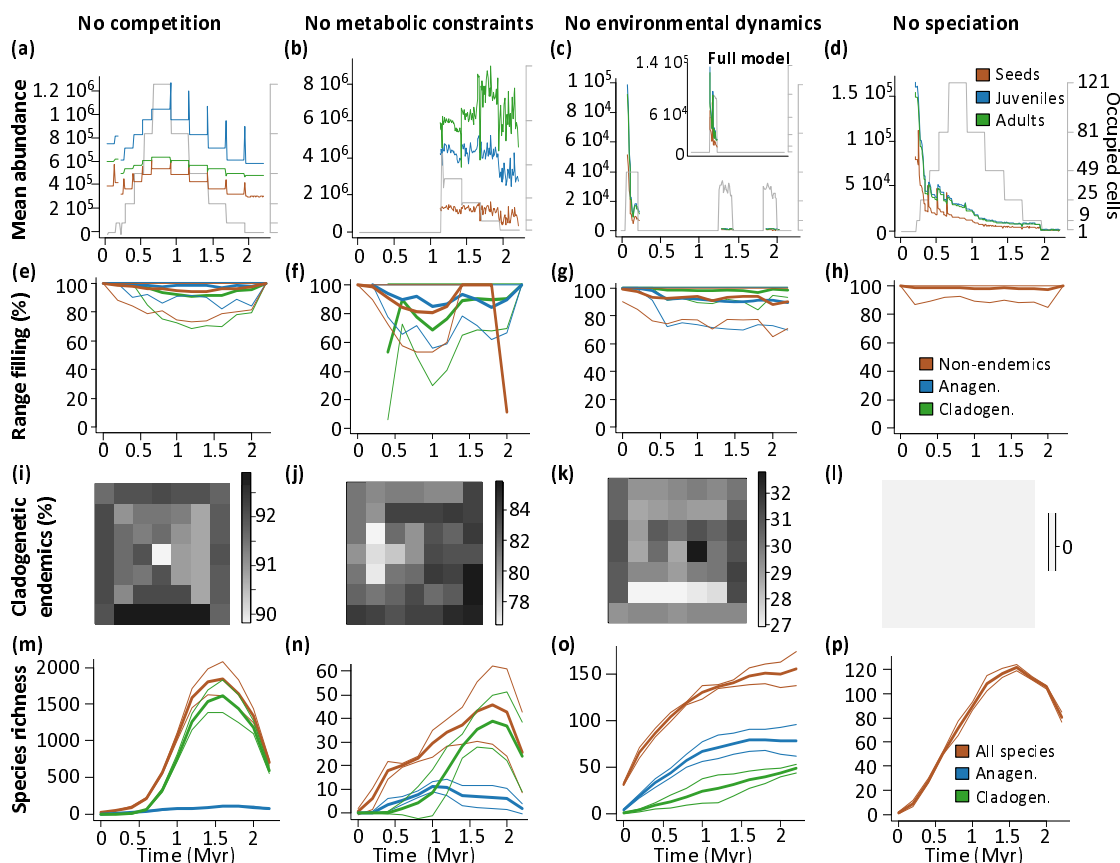


Figure 6 Evaluation of the model structure across patterns at different ecological levels (rows) by switching off key processes (columns). (a-d) Population dynamics of an example species, given by mean abundances (per occupied cell). (e-h) Overall range filling dynamics. (i-l) Proportion of cladogenetic endemics at advanced island age, 1.5 Myr. (m-p) Total species richness dynamics of exploratory scenarios with no competition (left column), no metabolic constraints (middle left column), no environmental dynamics (middle right column) and no speciation (right column). Colour legends differ between rows: legends in (c) for population dynamics, in (h) for range filling dynamics, and in (p) for total richness dynamics. The panels (a), (c), and (d) illustrate the population dynamics of one example non-endemic shrub species adapted to intermediate elevations that survived in these three scenarios and in the full model (inset in c). Panel (b) illustrates the population dynamics of one example cladogenetic endemic herb species adapted to lowlands (see Appendix S1 for detailed species properties). Grey lines and right y-axis in (a-d) indicate the number of occupied cells. The other panels illustrate values averaged over replicates ($n = 3$) and within each geological time step (95% CI given as thin lines for range filling and total species richness dynamics).