1 **Original Article**

2 **Effects of time and isolation on plant diversity: testing island biogeography**

3 **theory with an eco-evolutionary model**

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ABSTRACT

Aims: The General Dynamic Model of oceanic island biogeography (GDM) predicts how biogeographical rates, species richness, and endemism vary depending on island age, area, and isolation, based on the interplay of colonization, extinction, and speciation. Here, we used a simulation model to test whether GDM predictions may arise from individual- and population-level processes.

Location: Hypothetical hotspot islands.

Methods: Our model (i) considers an idealized island ontogeny, (ii) metabolic constraints, and (iii) 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 dispersal ability and distances to mainland.

Results: Humped temporal trends were obtained for species richness, endemic richness, proportion of cladogenetic endemic species, number of radiating lineages, number of species per radiating lineage, and biogeographical rates. The proportion of anagenetic endemics 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 anagenetic endemics decreased with isolation as did rates of colonization, anagenesis, and extinction. The proportion of all endemics and of cladogenetic endemics, the number of cladogenetic endemics, of radiating lineages, and of species per radiating lineage, and the cladogenesis rate all increased with isolation.

Main conclusions: The results confirm most GDM predictions related to island ontogeny and isolation, but predict an increasing proportion of endemics throughout the experiment: a difference

42   attributable to diverging assumptions on late island ontogeny. New insights regarding the

43   extinction trends of endemics further demonstrate how simulation models focusing on low

44   ecological levels provide tools to test biogeographical-scale predictions and to develop more

45   detailed predictions for further empirical tests.

46   **Keywords**: BioGEEM, general dynamic model, interspecific competition, island biogeography,

47   isolation effects, metabolic theory, oceanic islands, plant endemism, process-based models,

48   speciation rate

49

50 **INTRODUCTION**

51 Geographical isolation is considered one of the key drivers of species diversification in both

52 insular (e.g. Heaney, 2000; Whittaker & Fernández-Palacios, 2007; Rosindell & Phillimore, 2011)

53 and continental systems (e.g. Linder, 2005; Rieseberg & Willis, 2007; Pennington *et al.*, 2010).

54 Mechanisms by which isolation operates to promote divergence and hence diversification include

55 founder effects and genetic drift via limited (or no) gene exchange with other populations (non-

56 adaptive speciation; Rundell & Price, 2009). Isolated populations may be further subject to

57 differential selective pressures compared to the source areas, triggering adaptive (e.g. ecological)

58 speciation (Rundell & Price, 2009). These mechanisms are characteristic of oceanic islands,

59 causing high numbers of endemic species (Whittaker & Fernández-Palacios, 2007; Steinbauer *et*

60 *al.*, 2012) and providing model systems for investigating isolation effects (MacArthur & Wilson,

61 1967; Weigelt & Kreft, 2013; Warren *et al.*, 2015). Island biogeography theory holds that isolation

62 reduces colonization rates and the species richness at the dynamic equilibrium between

63 colonization, speciation, and extinction, while increasing the relative contribution of speciation to

64 species richness (MacArthur & Wilson, 1967; Whittaker *et al.*, 2008). These effects on speciation

65 have been formalized within the General Dynamic Model of oceanic island biogeography (GDM),

66 the distinguishing feature of which is to posit that diversity patterns within and across archipelagos

67 are influenced in a predictable fashion by the geodynamics of oceanic islands over their lifespan

68 (i.e. their ontogeny, Whittaker *et al.*, 2008, 2010).

69 For classic hotspot islands, the GDM predicts humped trends in richness and endemism as a

70 function of the rise and decline of island area, elevation, and habitat heterogeneity over the

71 island's life span (Whittaker *et al.*, 2008, 2010). Throughout these environmental changes along

72   the island's life span, isolation affects biogeographical patterns by changing the amplitude but not

73   the shape of the temporal trends (Whittaker *et al.*, 2008). More recently, Borregaard *et al.* (2016b)

74   used a simulation model to explore GDM properties, in particular examining isolation effects, and

75   alternative island ontogenies. These simulations supported the internal logic of the GDM, and

76   provided additional island age-related predictions. For instance, more isolated islands had lower

77   colonization and extinction rates, as well as higher speciation rates (Borregaard *et al.*, 2016b).

78   Consequently, isolation should decrease overall species numbers, but increase the number and

79   proportion of endemic species. The main explanation is that on remote islands radiating lineages

80   fill niches that would be occupied by colonist species on less isolated islands (Heaney, 2000;

81   Whittaker *et al.*, 2008). In sum, the capacity to generate explicit biogeographical predictions has

82   made the GDM an important framework for many recent island studies (Borregaard *et al.*, 2016a).

83   A general limitation to testing GDM predictions is that systematic empirical data for islands

84   over their entire ontogeny cannot be obtained due to the protracted nature of volcanism and

85   erosion processes, which destroy fossils. The intractability of measuring colonization, extinction,

86   and diversification histories has justified the use of space-for-time substitutions involving analyses

87   of islands of different ages within archipelagos as surrogates for following the long-term dynamics

88   of single islands (Borregaard *et al.*, 2016a). Alternatively, the application of mechanistic

89   simulation models to investigate GDM predictions has been identified as a particularly promising

90   avenue (Borregaard *et al.*, 2016a). Such models have full control of relevant factors and processes

91   and thus exclude confounding effects. Among these are several spatial processes and factors not

92   fully described in the theory, such as island hopping followed by parallel radiations (Whittaker &

93   Fernández-Palacios, 2007; Losos & Ricklefs, 2010), rescue effects (Brown & Kodric-Brown,

94   1977), intra-archipelagic spatial settings (Cabral *et al.*, 2014, Weigelt *et al.*, 2016), and the eco-

95   evolutionary history specific to each island, archipelago, and taxon (Whittaker & Fernández-
96   Palacios, 2007; Bunnefeld & Phillimore, 2012). The variety of mechanisms contributing to
97   isolation – from distance to potential source pools to varying dispersal ability of different taxa –
98   also opens up alternative means of quantifying (Weigelt & Kreft, 2013) and simulating isolation in
99   mechanistic models. For example, assemblage-level models can simulate single islands that vary
100   only in distance to the mainland but that have identical environmental settings and geological
101   trajectory (e.g. Borregaard *et al.*, 2016b). In previous work, Cabral *et al.* (submitted), present a
102   BioGeographical Eco-Evolutionary Model (BioGEEM) consistent with and supporting GDM
103   temporal predictions of species richness and biogeographical rates via population-level processes.
104   However, only one isolation scenario was investigated by Cabral *et al.* (submitted) and thus GDM
105   predictions of isolation effects remain to be investigated in more details by such trait-based,
106   spatially-, and demographically-explicit models. This is the purpose of the present study.

107   BioGEEM is niche-based and integrates metabolic, demographic, dispersal, and competition
108   constraints at the local scale (and at the level of individuals and populations), with evolutionary
109   and environmental processes at biogeographical scales (Cabral *et al.*, submitted). The model is
110   specified for terrestrial seed plants and has a hierarchical structure that links ecological and
111   evolutionary processes to local temperature and body mass via metabolic trade-offs based on the
112   metabolic theory of ecology (Brown *et al.*, 2004). As a result, all biogeographical patterns emerge
113   from processes operating at local scales and low levels of ecological organization, e.g. individual
114   dispersal, resource competition, and local population dynamics. The model properties of
115   BioGEEM thus differs from previous island models, which concentrate on geologically static
116   islands (Kadmon & Allouche, 2007; Hortal *et al.*, 2009; Rosindell & Phillimore, 2011; Rosindell
117   & Harmon, 2013), do not incorporate evolutionary processes (Kadmon & Allouche, 2007; Hortal

118   *et al.*, 2009; Rosindell & Harmon, 2013), simulate ecologically neutral processes (Rosindell &

119   Phillimore, 2011; Rosindell & Harmon, 2013; Valente *et al.*, 2014, 2015; Borregaard *et al.*,

120   2016b), and/or are spatially-implicit (Valente *et al.*, 2014, 2015; Borregaard *et al.*, 2016b). In

121   short, BioGEEM includes a combination of properties and assumptions not yet applied for

122   assessing the eco-evolutionary logic of GDM predictions, which might be useful for the derivation

123   of generalizable insights (Evans *et al.*, 2013; Cabral *et al.*, 2016; see Cabral *et al.*, submitted). To

124   achieve this, we integrated into BioGEEM the GDM assumptions of geologically dynamic islands,

125   habitat heterogeneity, and niche-based adaptive radiations. In our simulation experiment, we tested

126   GDM-based hypotheses related to eight biogeographical variables (Table 1) by varying island

127   isolation in two ways: via dispersal ability of the species source pool and via distance to the

128   mainland.

129

MATERIALS AND METHODS

Modelling approach

We briefly summarize the model below. A detailed description and parameter settings can be found in Cabral *et al.* (submitted) and in Appendix S1 in Supporting Information.

State variables and scales

The model is grid-based (Fig. 1a), with a cell size of 1 km^2. Each island cell was assigned to an elevational level and mean annual temperature (the lowest elevation band was assigned 25 ˚C). 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 body sizes), and phenological ordering. Habitat requirements depict preferences associated with elevation (i.e. temperature) as well as wind and precipitation patterns in islands (i.e. island side). 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. Consequently, species assemblages emerge from local resource competition among populations (Cabral & Kreft 2012; Cabral *et al.*, submitted). The state variables comprise the spatial distribution of seed, juvenile, and adult abundances of each species

152   and the unoccupied area. Each time step represents one year and a complete simulation runs over

153   2.21 million time steps.

Initialization

155   Simulations are initialized with a species pool size of 1000 species, and the intervals for randomly

156   drawing the species properties (see Appendix S1). Species properties vary from representing

157   specialists (e.g. narrow temperature amplitudes) to generalists (e.g. all temperatures and island

158   sides). For each species, the habitat suitability matrix, *H,* is initialized based on the species'

159   environmental requirements. A species-specific dispersal kernel *D* is initialized as a two-

160   dimensional, grid-based Clark's 2Dt kernel, with two parameters, α and p, which describe short-

161   and long-distance dispersal, respectively (Fig. 1b; Clark *et al.*, 1999; Nathan & Muller-Landau,

162   2000). The stage-specific abundance matrices (seeds, juveniles, and adults) and the matrix with the

163   area occupied by all individuals are initialized empty.

Submodels

165   At each time step, a series of submodels are executed in the following order: dispersal from

166   mainland, population update 1, reproduction, intra-island dispersal, mutation, speciation,

167   population update 2, and environmental dynamics. In each submodel, the state variables of each

168   species are updated following the species phenological ordering:

169   *Dispersal from mainland*: a random number of seeds per mainland cell from ten random

170   mainland species are dispersed to the island according to *D*.

171   *Population update 1*: abundance matrices are updated by: A) turning juveniles to adults, B)

172   applying density-independent mortality to remaining juveniles, C) germinating seeds, and D)

173   applying seed mortality.

174   *Reproduction*: if adults are present, the number of seeds produced by each species in each cell

175   is given by the Beverton-Holt reproduction function, extended with Allee effects (Cabral &

176   Schurr, 2010).

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

178   *Mutation*: as a previous step to cladogenesis (see next submodel), each seed dispersed is

179   randomly assigned as mutant given a metabolic-constrained probability (Brown *et al.*, 2004) via

180   point-mutation (Rosindell & Phillimore, 2011). Mutant seeds received random properties

181   according to phylogenetic constraints (values within ±50% of ancestral values). The **H**, **D**, and

182   abundance matrices for these mutant individuals are initialized (see '*Initialization*').

183   *Speciation*: two modes of speciation are considered: anagenesis (differentiation from mainland

184   species) and cladogenesis (within-island diversification). The submodel checks whether enough

185   time has passed to update mutant individuals (cladogenesis) or colonizers (anagenesis) as a distinct

186   species (i.e. 'protracted speciation' □ Rosindell & Phillimore, 2011). The time for speciation is

187   species-specific and follows metabolic constraints to account for longer generations of larger

188   species (Brown *et al.*, 2004). Anagenesis could be delayed due to gene flow from the mainland.

189   *Population update 2*: after species status update, the submodel applies density-independent

190   mortality to adults and updates the seed bank.

191   *Environmental dynamics*: environmental events occur that mimicked the geological trajectory

192   of a typical oceanic island (Whittaker & Fernández-Palacios, 2007; Whittaker *et al.*, 2008),

193   namely island growth due to volcanic activity followed by a slower erosion-dominated phase. The

194   island grows and shrinks by gaining or losing belts of cells, respectively, and by increasing or

195   decreasing elevation and thus local temperature accordingly. Islands grow every 0.13 Ma, whereas

196   erosion takes place every 0.26 Ma (see Appendix S1). After every environmental change event, $\boldsymbol{H}$

197   is recalculated for every species.

Output

199   The model records time-series of species richness (total, anagenetic, and cladogenetic endemics),

200   number of endemic lineages (including species that evolved from the same ancestor), and number

201   of species per endemic lineage, as well as the number of colonization, speciation, and extinction

202   events.

Study design

204   All intervals for drawing species properties, the model, and the scenario specifications are

205   provided in Appendix S1. To test our hypotheses (Table 1), we set up four isolation scenarios (Fig.

206   1). The scenarios encompassed a full-factorial design, varying the shortest distance between the

207   island at maximum size and the mainland (150 vs. 300 cells), as well as the dispersal ability of the

208   mainland species pool (high vs. low long-distance dispersal ability). Greater long-distance

209   dispersal ability (p_{high}) was obtained by systematically varying the dispersal parameter p for all

210   species of the mainland source pool from the scenario with low long-distance dispersal ability

211   (p_{low}): $p_{high} = p_{low} - 0.2$ (p_{low} values in Appendix S1). Note that although 150- or 300-cells distance

212   might seem close to the mainland, isolation was assured by generally low long-distance dispersal

213 ability. Nevertheless, we calibrated the dispersal ability so that even the most isolated islands

214 could receive at least one species during time steps with minimum island size. All islands had a

215 maximum size of 11×11 cells.

216 The simulation experiment comprised 20 replicate runs per isolation scenario, with each

217 replicate having a different species pool to represent different mainland species compositions.

218 Outputs for each time step were averaged over replicates (only averaged time-series are shown for

219 visual clarity, but see Figure S1 of the Appendix S2 for examples of 95% standard deviation

220 envelopes around average time-series). To make results comparable to GDM predictions,

221 colonization, speciation, and extinction rates were calculated by summing the number of

222 colonization, speciation, or extinction events within time intervals of 0.01 Myr. Only successful

223 colonization, i.e. germination and establishment, was considered.

224

RESULTS

225

226 Total species richness and endemic richness showed a clear humped relationship with island age

227 (Fig. 2). Richness peaks lagged behind maximum island size – a pattern that was most pronounced

228 for more isolated islands (Fig. 2) and for cladogenetic endemics (Fig. 2b). Except at the very final

229 island stages where species numbers converged, more isolated islands had the lower total species

230 and anagenetic endemic richness and the higher cladogenetic endemic richness (Fig. 2).

231   The proportion of endemics increased over time and with isolation (Fig. 3a). This increase was

232 mostly driven by anagenetic endemics and there was little difference among isolation scenarios

233 (Fig. 3b). In contrast, the proportion of cladogenetic endemics showed a shallow, humped

234 relationship with island age and more isolated islands attained higher proportions (Fig. 3b). The

235 number of radiating lineages also exhibited a humped relationship with island age. More isolated

236 islands had higher values, and there was a strong difference between isolation scenarios at

237 advanced island age (Fig. 3c). The number of species per radiating lineage showed a general

238 humped relationship with island age, and varied less clearly with isolation, with only the islands

239 isolated by both distance and dispersal having evidently higher values than the other islands (Fig.

240 3d).

241   Temporal trends in colonization rates were humped for all isolation scenarios, but the

242 maximum values strongly decreased with isolation (Fig. 4a). Similar temporal trends but overall

243 lower values were obtained for extinction rates (Fig. 4b). Anagenesis rates peaked at intermediate

244 island age and monotonically decreased thereafter, with increasing isolation decreasing the

245 maximum value (Fig. 4c). Cladogenesis rates were also humped and peaked at intermediate island

246 age, with the amplitude of the curve increasing with isolation (Fig. 4d). Extinction rates of

247   endemics increased over time and dropped sharply in the last thousand years (Fig. 4e). All islands

248   showed a general positive net change rate (colonization rate + speciation rate - extinction rate)

249   throughout the simulation (Fig. 4f), despite decreases in species richness during short-term peaks

250   in extinction right after erosion events (averaged out across time steps in Fig. 4, but visible at

251   higher temporal resolution as shown in Figure S2 of the Appendix S2). In our simulations, this

252   increase was led by colonization rates, which were orders of magnitude higher than speciation

253   rates.

254

255   **DISCUSSION**

256   **Species richness**

257   The simulation results for species richness patterns supported the GDM-derived hypotheses

258   concerning temporal trends and isolation effects (Table 1). All isolation scenarios showed similar

259   humped temporal trends in species richness, as predicted by the GDM based on the environmental

260   dynamics of hotspot oceanic islands (Fig. 2a; Whittaker *et al.*, 2008; Borregaard *et al.*, 2016b;

261   Cabral *et al.*, submitted) and from empirically well-supported, positive relationships between

262   species richness and island area, elevation, and habitat heterogeneity (e.g. Kreft *et al.*, 2008; Hortal

263   *et al.*, 2010). These three environmental factors positively affect species carrying capacity, a key

264   concept in the GDM (Whittaker *et al.*, 2008). In our results, species richness seemed to approach

265   carrying capacity only after area started to decrease. This was indicated by higher species richness

266   during the erosion phase compared to the growth phase (Fig. 2a). This result is in line with the

267   spatially-implicit model of Borregaard *et al.*, (2016b) but contrasts with indications for an early

268   peak during island ontogeny (e.g. Steinbauer *et al.*, 2013; Lenzner *et al.*, 2016). Simulation

269   experiments and empirical correlations must be compared with caution, as empirical estimations of

270   carrying capacity entail shortcomings arising from the space-for-time substitution. For example, if

271   the growth phase is several times shorter than the erosion phase, species richness is expected to

272   peak relatively early. This should be particularly true if the island is within an archipelago, as

273   immigration may be comparatively rapid in the youth of the island, due to colonization from the

274   local (constrained) source pool provided by nearby islands. Here, BioGEEM simulates single

275   islands and carrying capacity is an island property emerging from the environmental dynamics (in

276   contrast of being a model parameter in Borregaard *et al.*, 2016b). These model features assure that

277   how the carrying capacity changes and is filled does not depend on archipelagic effects but

278   directly on available resources, environments, species properties, and on eco-evolutionary

279   processes. This an advantage over spatially-implicit, neutral approaches, which often constrain

280   carrying capacity via a parameter for the maximum number of individuals or species without

281   considering individuals' traits (Cabral *et al.*, 2016).

282   The fact that isolation consistently led to lower species richness over the entire island's life

283   span confirmed the GDM-based hypothesis (Table 1, Fig. 2a). Interestingly, both mechanisms of

284   isolation (by distance and by dispersal ability) seemed interchangeable, as the scenarios with either

285   isolation mechanism revealed very similar, intermediate values. Certain island models have also

286   confirmed the negative effects of isolation on species richness, despite accounting for isolation

287   only indirectly by varying colonization rates or island occupation at model initialization without

288   explicitly considering geographic distances or species traits (Chen & He 2009; Rosindell &

289   Phillimore, 2011; Rosindell & Harmon, 2013; Borregaard *et al.*, 2016b). These simpler approaches

290   can simulate isolation effects, but provide limited interpretation of underlying ecological

291   processes. In exploratory scenarios with alternative isolation mechanisms, BioGEEM also

292   produced lower species richness with fewer mainland cells, dispersing species per time step, and

293   species in the source pool (Figure S3 of the Appendix S2). Further modifications that remain to be

294   tested involve processes at the intra-archipelagic level, including island hopping, parallel

295   radiations, taxon cycles, and island merging (Cabral *et al.*, 2014; Weigelt *et al.*, 2016). This

296   complexity in isolation and other eco-evolutionary mechanisms indicates that caution must be

297   taken when interpreting results from correlations, as islands might be under the influence of

298   different isolation mechanisms. It also offers a promising research avenue as most simulation

299   models and correlative studies assume simplified isolation mechanisms (but see Weigelt & Kreft,

300   2013).

Endemic richness

302   Our results for endemic richness supported the hypotheses on temporal trends for both anagenetic

303   and cladogenetic endemics as well as isolation effects for cladogenetic endemics (Table 1).

304   Endemic richness was humped and had a delayed peak compared to species richness (Fig. 2b;

305   Steinbauer *et al.*, 2013; Borregaard *et al.*, 2016b; Cabral *et al.*, submitted). The opposing effects of

306   isolation on anagenetic and cladogenetic richness (negative and positive, respectively) support

307   previous findings of neutral models where considering islands that are already isolated (Rosindell

308   & Phillimore, 2011). For weakly isolated islands, these neutral models demonstrated that intense

309   gene flow from the mainland prevents both speciation modes (Rosindell & Phillimore, 2011). As

310   isolation increases, reduced gene flow facilitates anagenesis. On already isolated islands, the

311   further increasing isolation leads to a lower number of colonizing species, and thus a lower

312   number of potentially anagenetic species. Simultaneously, radiating species start to fill empty

313   niche space (Rosindell & Phillimore, 2011). This switch in predominant speciation mode emerges

314   in neutral models simply by lowering colonization rates (Rosindell & Phillimore, 2011). While

315   also capturing this switch, niche-based models explicitly integrate adaptive radiation and trait

316   evolution (Cabral *et al.*, submitted). This is important for testing GDM predictions, as the GDM

317   assumes that adaptive radiations occupy 'empty niches' (Whittaker *et al.*, 2008). In this sense,

318   Cabral *et al.* (submitted) showed that radiating species tend to be ecologically distinct from co-

319   occurring species, better occupying the niche space, as assumed by the GDM.

Proportion of endemic species

321 Proportion of endemic species varied depending on speciation mode (Fig. 3), supporting the

322 hypothesized isolation effects for all endemics and cladogenetic endemics as well as the temporal

323 humped-trend only for cladogenetic endemics (Table 1). In our simulations, the overall endemism

324 was mostly driven by anagenesis, which consistently increased over time but did not vary between

325 isolation scenarios (Fig. 3b). The fact that the proportion of anagenetic endemics does not decrease

326 indicates that anagenetic endemics are more likely to survive at the final island stage than

327 cladogenetic endemics. This could arise because many anagenetic endemics evolved from

328 colonizer species that were able to colonize and survive in such small islands and that did not

329 establish radiating lineages. Thus, these anagenetic endemics have fewer close-competitors than

330 species from cladogenetic lineages. Interestingly, Whittaker et al. (2008) also predict that the

331 relative proportion of single-endemic lineages compared to multi-endemic lineages should

332 increase over the final stages of an island's existence, with one additional reason being the

333 collapse of some multi-endemic lineages, ultimately to single representatives as the other members

334 of former radiations become extinct.

335 In the final stages of island ontogeny, it is nevertheless expected within the GDM that

336 proportion of single-island endemics drops (Whittaker *et al.*, 2008). This was based on two

337 considerations. First it was argued that over time, some of these species colonize younger islands

338 in an archipelago. Second, as islands become very old and low-lying islands (e.g. atolls), they may

339 be increasingly characterized by disturbed, open, and strand-line habitats. These habitats facilitate

340 the dominance of a few non-endemic, widespread, and disturbance-tolerant species, which make

341 old islands with these habitats more akin to biologically "young" islands (see Dickinson 2009).

342 BioGEEM does not simulate such conditions and it is thus unsurprising that anagenetic endemism

343 did not decrease in our simulations. Nevertheless, the proportion of cladogenetic endemism

344   showed the humped trend predicted by the GDM, but with a very delayed peak (Fig. 3b; Whittaker

345   *et al.*, 2008). In real-world systems, the proportion of single-island endemics peaks at the same

346   time as endemic richness (Steinbauer *et al.*, 2013). However, dispersal of single-island endemics

347   to younger neighboring islands may contribute to earlier peaks, as some species lose their status as

348   single-island endemics (see Borregaard *et al.*, 2016b).

349   Isolation effects varied the two different speciation modes, with no evident effect on the

350   proportion of anagenetic endemics (also found by Stuessy *et al.*, 2006), but increasing the

351   proportion of cladogenetic endemics (Fig. 3b). Hence, the observed higher proportion of all

352   endemics on more isolated islands was largely driven by cladogenesis (Fig. 3a-b), confirming the

353   important role of cladogenesis in filling empty niches on isolated islands, as assumed by the GDM

354   premises (Whittaker *et al.*, 2008). In these premises, the higher prevalence of cladogenesis on

355   remote, high-elevation islands seems more likely due to limited gene flow and greater ecological

356   opportunities (Heaney, 2000; Stuessy *et al.*, 2006; Whittaker & Fernández-Palacios, 2007; Price &

357   Wagner, 2011). Moreover, in their neutral and environmentally-static simulation analysis,

358   Rosindell and Phillimore (2011) indicated a gradual replacement of anagenetic by cladogenetic

359   endemics with increasing isolation. However, we did not obtain any replacement despite an

360   increase in cladogenetic endemics (Fig. 3b). Instead, within the simulations, cladogenetic

361   endemics seem to prevent colonization of non-endemics by being better adapted to local

362   environments and communities than these naturally recurrent colonizers (Cabral *et al.*, submitted).

363   Furthermore, only a minority of colonizing plant lineages on isolated islands are prone to

364   diversification, while the majority of lineages only produce anagenetic endemics (compare Figs.

365   2b and 3c; Stuessy *et al.*, 2006; Price & Wagner, 2011). Such complex relationships between

366   speciation modes can thus be addressed by integrating ecological, evolutionary, and environmental

367   processes and by acknowledging species differences.

368   **Number of radiating lineages**

369   Results for the number of radiating lineages supported the hypotheses on temporal trends and

370   isolation effects (Table 1). Humped temporal trends were found in all scenarios as predicted by the

371   GDM (Fig. 3c, Whittaker *et al.*, 2008), whereas isolation showed positive effects (Fig. 3c). Such

372   results indicate that some lineages only radiate under low competition/colonization conditions. In

373   fact, a few genera and families have been shown to be particularly radiation-prone wherever

374   arriving in remote archipelagos, such as Hawaiian, Society, and Marquesa Islands (Price &

375   Wagner, 2004; Price & Wagner, 2011; Lenzner *et al.*, 2016). Therefore, while knowledge about

376   speciation on islands is constantly improving (e.g. Igea *et al.*, 2015), future simulation studies

377   could investigate to what extent radiation-proneness is lineage-specific (e.g. mediated by common

378   traits).

379   **Number of species per radiating lineage**

380   Results for the number of species per radiating lineage were complex, supporting the hypothesis of

381   an overall humped temporal trend (Fig. 3d; Whittaker *et al.*, 2008), but only partially supporting

382   isolation effects, with an unexpected interaction between temporal and isolation effects (Table 1).

383   Here, the isolation mechanism influenced the amplitude of the temporal trends, with an increase in

384   species radiations becoming evident only for the most isolated islands (Fig. 3d). That is because

385   islands isolated by just one isolation mechanism may still receive enough colonizers that occupy

386   available niches. In contrast, islands isolated by both distance and dispersal can foster larger

387   radiations than other islands due to less competition and greater ecological opportunities (e.g.

388 empty niches; Whittaker & Fernández-Palacios, 2007). Therefore, large radiations may be more

389 common where multiple isolation mechanisms are combined.

Colonization rate

391 Results for the colonization rates supported the predicted negative isolation effects and predictions

392 of humped temporal trends in all four isolation scenarios (Fig. 4a, Table 1). A decrease in

393 colonization rates with isolation agrees with the predictions of both the equilibrium theory of

394 island biogeography (MacArthur & Wilson, 1967) and the updated GDM (Borregaard *et al.*,

395 2016b). A higher rate of colonization on growing islands is consistent with an alleviated

396 environmental filtering due to higher habitat heterogeneity and with a higher chance of a dispersal

397 unit hitting the island (i.e. the target area effect - Lomolino, 1990). Environmental filtering and the

398 target area effect are not explicitly considered by the GDM (Whittaker *et al.*, 2008). However, a

399 simplified environmental filtering was considered by Borregaard *et al.* (2016b) by correlating

400 colonization rates with carrying capacity.

Extinction rate

402 Results for the extinction rates followed those of colonization rates, supporting hypothesized

403 temporal and isolation effects (Fig. 4b, Table 1). When assessing only the extinction rates of

404 endemic species, the hypotheses were also supported, but with a later peak and less difference

405 between isolation scenarios (Fig. 4e, Table 1). The distinction between types of extinction is

406 important. While endemic species can go globally extinct, non-endemics can (potentially) have

407 their local extinction on an island reversed by re-colonization. In this sense, if colonization rates

408 are much higher than speciation rates, extinction rates represent the extinction of non-endemics

409 and reflect mostly colonization rate trends (Fig. 4a-b). If speciation rates have values comparable

410   to or higher than colonization rates, such as in Borregaard *et al.* (2016b), extinction rates should

411   reflect speciation rate trends. Furthermore, the overall positive net change rates (Fig. 4f; but see

412   Figure S2 of the Appendix S2 for short, extinction-dominated net rate periods) indicate that a

413   dynamic equilibrium cannot be achieved by the extinction rate that emerges in our experiments,

414   namely from demographic stochasticity and environmental dynamics. In accordance, islands might

415   steadily accumulate species if environmental dynamics are excluded (Cabral *et al.*, submitted).

416   Future model developments might explore how extinction rates and the dynamic equilibrium vary

417   with processes not implemented here, such as disturbances.

418   **Speciation rate**

419   Results for speciation rates supported the hypotheses of temporal trends for both anagenesis and

420   cladogenesis, but supported isolation effects only for cladogenetic endemics (Fig. 4c-d, Table 1).

421   The differential effect of isolation on anagenesis and cladogenesis has not been the focus of the

422   GDM, which focused predictions on species radiations, and thus cladogenesis (Whittaker *et al.*,

423   2008; Borregaard *et al.*, 2016b). In this sense, the increase in cladogenesis rates with isolation

424   (Fig. 4d) was in accordance with empirical and modelling evidence (Heaney, 2000; Whittaker *et*

425   *al.*, 2008; Rosindell & Phillimore, 2011; Borregaard *et al.*, 2016b). For the anagenesis rate, the

426   negative isolation effect has been previously obtained by neutral models for islands that are

427   already isolated enough to foster radiations (Rosindell & Phillimore, 2011). In BioGEEM, these

428   differences between anagenesis and cladogenesis emerged within a niche-based approach, which

429   indicates that disentangling the relative importance of neutral and non-neutral dynamics in real

430   islands might not be trivial.

431   **Limitations and perspectives**

432 The main limitation of BioGEEM is its complexity and data requirements for validation or

433 parameterization (cf. Dormann *et al.*, 2012). Nevertheless, Cabral *et al.* (submitted) demonstrated

434 that the model matches empirical and theoretical evidence at multiple ecological levels and that all

435 simulated processes are necessary to simultaneously generate realistic patterns (i.e. 'pattern-

436 oriented' modelling, *sensu* Grimm & Railsback, 2012). Therefore, scenario-based simulation

437 experiments, such as presented here, have the potential to increase our understanding of process

438 interactions and to generate simulation-driven hypotheses to be tested when appropriate data

439 become available. Here, important differences compared to previous, simpler models are the

440 explicit simulation of population-based processes (e.g. resource competition, stage transitions,

441 individual dispersal) and species differences. These model features align with current trend in

442 improving structural realism in ecological modelling (Cabral *et al.*, 2016; Grimm & Berger, 2016)

443 and assure that biogeographical patterns are emergent system properties and not directly simulated

444 via processes with biogeographical parameters (i.e. colonization, extinction, speciation rates as

445 model parameters, not as emergent variables).

446 Another limitation is associated with the study design, namely that isolation did not vary over

447 time. Isolation dynamics are not considered in the environmental dynamics assumed by the GDM

448 and thus not accounted for in the present study. However, isolation changes at various time scales,

449 from recently increased source pools via human-induced activities and dispersal (i.e. alien species;

450 Kueffer *et al.*, 2010), over climate-mediated changes in sea levels over glaciation cycles

451 (Fernández-Palacios *et al.*, 2015; Weigelt *et al.*, 2016), to deep-time scales of plate tectonics,

452 archipelagic dynamics, and evolutionary changes in the source pool. Moreover, beyond the

453 isolation mechanisms simulated in this study, intra-archipelagic isolation may play an important

454 role for trends of single-island endemics (Cabral *et al.*, 2014; Borregaard *et al.*, 2016b), and, thus,

455   further insights might be gained by disentangling intra-archipelagic isolation and connectivity and

456   distance to different source pools. Integrative process-based frameworks, such as ours, provide

457   excellent means to assess isolation dynamics explicitly, opening ground for future studies on

458   theoretical developments and conservation assessments (e.g. due to human-induced sea level

459   changes and alien species).

460   **Conclusions**

461   In this simulation experiment, emergent patterns largely confirmed theoretical predictions of

462   temporal trends and isolation effects on biogeographical patterns. However, noteworthy

463   divergences that emerged included the steady increase in proportion of all endemics, as well as

464   new insights regarding the extinction trends of endemics and the differential trends in proportion

465   of endemics depending on speciation mode. Mechanistic simulation models like BioGEEM can

466   thus contribute greatly to the theoretical understanding of the dynamics of complex systems. In

467   fact, we demonstrated that dynamics of richness, endemism, colonization, speciation, and

468   extinction emerge from individual- and population-level processes interacting with different

469   isolation mechanisms. In the real-world, the dynamics of the insular environments, isolation, and

470   area at the evolutionary time scale means that those ecological processes may never – or rarely –

471   reach an equilibrium, which is reflected in our findings. Therefore, the adequate representation of

472   persistent non-equilibrium conditions and the relevant processes affecting individuals and

473   populations seems crucial to improving our understanding of biodiversity dynamics.

474

475   **ACKNOWLEDGEMENTS**

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484   **REFERENCES**

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606   **SUPPORTING INFORMATION**

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

608   **Appendix S1** Detailed model description.

609   **Appendix S2** Supporting figures.

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617 **BIOSKETCH**

618 **Juliano Sarmento Cabral** is interested in processes and factors influencing species and

619 biodiversity dynamics across spatio-temporal scales. His research includes processes determining

620 spatial and temporal distribution of tropical epiphytes, species ranges, island plant diversity as well

621 as global species richness and endemism patterns.

622 Author contributions: J.S.C. and H.K. designed the study, with input from K.W.; J.S.C.

623 implemented and simulated the model; J.S.C. led the analyses and writing, with input from all co-

624 authors.

1   **Table 1.** Hypotheses based on the GDM (Whittaker *et al.*, 2008; Borregaard *et al.*, 2016b) for

2   eight biogeographical variables and the model output used for their evaluation. The

3   BioGEEM generates time-series of all variables covering the entire lifespan of islands. We

4   adopted the simplest method for calculating the rates to make these comparable to GDM

5   predictions, given as the number of events occurring within arbitrary time intervals.

| Variable	Model output	Hypotheses	
		Temporal trend	**Isolation effects**
1. Species richness	Number of species	humped	negative
2. Endemic richness	Number of anagenetic and cladogenetic species	humped	positive
3. Proportion of endemics	Percentage of all endemic, only anagenetic, only cladogenetic species richness in relation to all species	humped	positive
4. Radiating lineages	Number of lineages showing cladogenesis	humped	positive
5. Radiation extent	Number of species per radiating lineage	humped	positive
6. Colonization rate	Number of colonization events per time interval	humped	negative
7. Extinction rate	A. Number of all extinction events per time interval	humped	negative
	B. Number of extinction events of endemic species per time interval	humped	negative
8. Speciation rate	Number of anagenetic and cladogenetic speciation events per time interval	humped	positive

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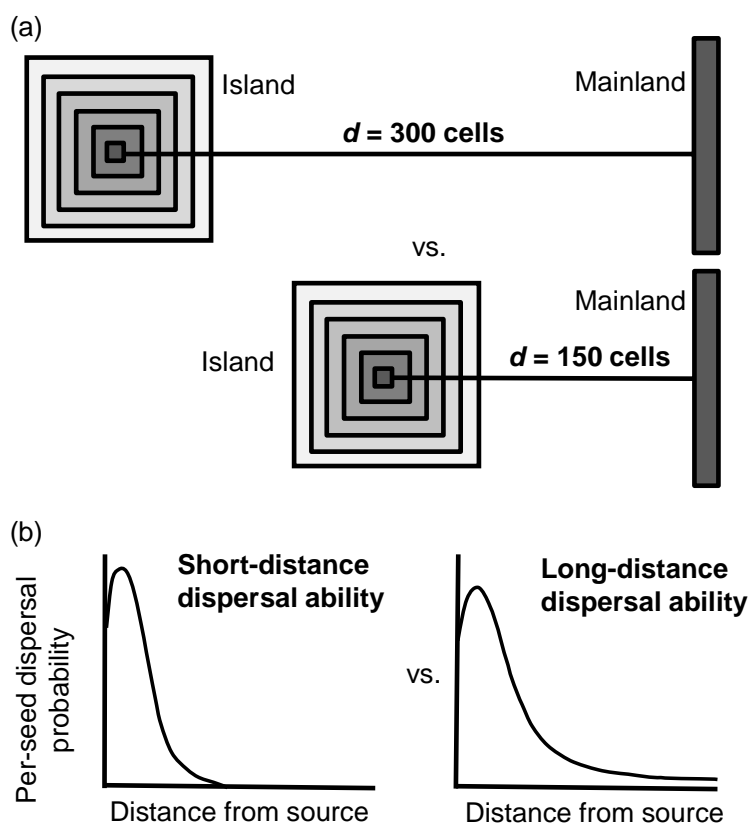
Figure 1 Isolation scenarios. (a) Distance scenarios based on the distance d from the island centre to the mainland: d=300 vs. d=150 cells. (b) Distance scenarios based on the dispersal ability of the mainland source pool of species: short-distance vs. long-distance dispersal ability (thin and fat kernel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

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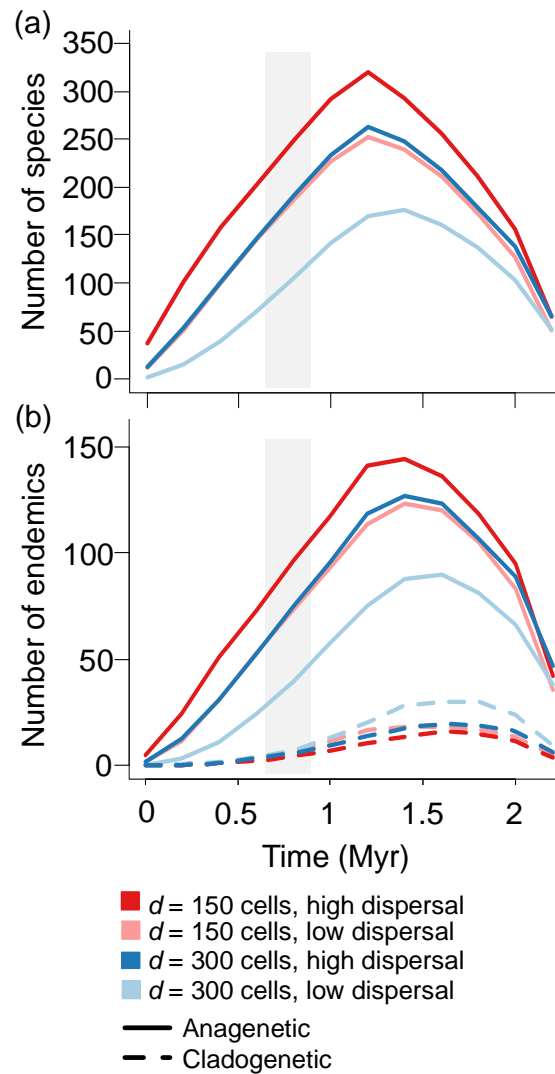
Figure 2 Temporal trends in species numbers of four different isolation scenarios. Time-series of: (a) number of all species; and (b) number of anagenetic and cladogenetic endemics. Isolation scenarios were given by changing the distance *d* from mainland and long-distance dispersal ability of the source pool. Time-series were averaged within environmental time steps and over 20 replicate runs. The shaded area indicates the period with maximum island size. Note in (a) that two intermediate scenarios (*d* = 150 cells, low dispersal and *d* = 300 cells, high dispersal) are barely distinguishable.

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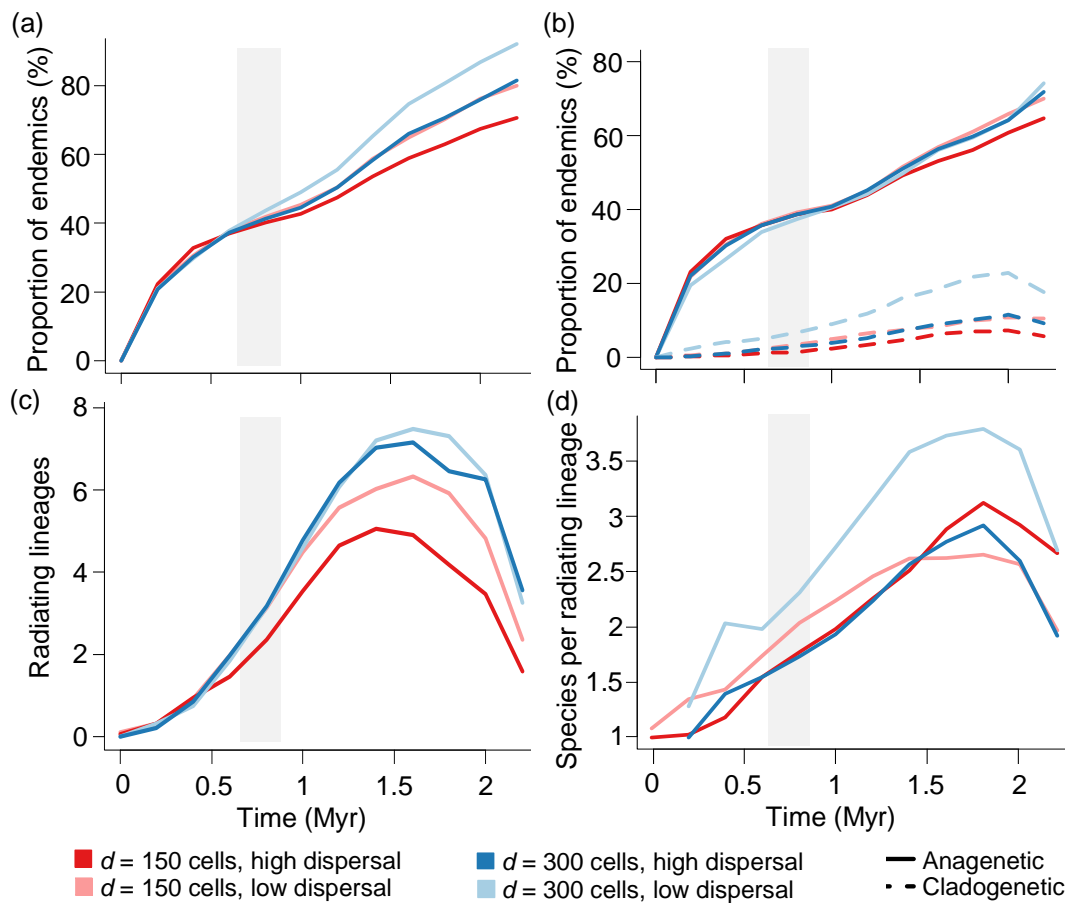
Figure 3 Speciation-related trends. (a) Proportion of all endemics. (b) Proportion of anagenetic and cladogenetic endemics (in each case as a function of all species). (c) Number of radiating lineages. (d) Number of species per radiating lineage. Note the steady increase in proportion of endemics in (a), mostly due to anagenetic endemics (b), despite overall humped richness trends shown in Fig. 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. The shaded area indicates the period with maximum island size.
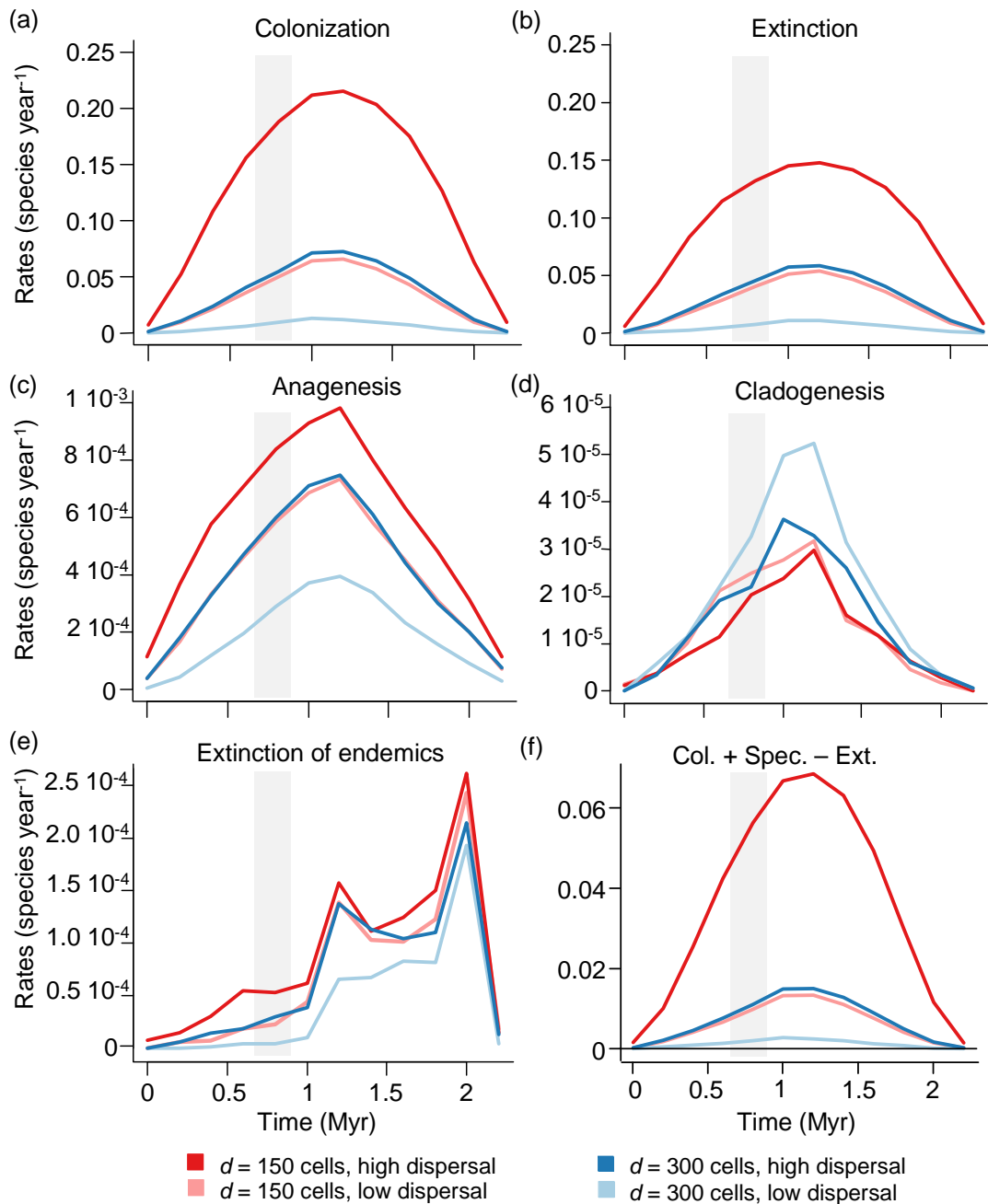
Figure 4 Biogeographical rates. (a) Colonization rates. (b) Extinction rates. (c) Anagenetic speciation rates. (d) Cladogenetic speciation rates. (e) Extinction rate of endemics. (f) Net rate: colonization + speciation - extinction rates. Isolation scenarios were simulated by changing the distance d 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. The shaded area indicates the period with maximum island size.