The effects of archipelago spatial structure on island diversity and endemism: predictions from a spatially-structured neutral model

Fanny Gascuel,1,2,3,4,5 Fabien Laroche,1,6,7 Anne-Sophie Bonnet-Lebrun,1,8 and Ana S. L. Rodrigues1

1Centre d’Ecologie Fonctionnelle et Evolutive, UMR 5175, Montpellier, France
2Center for Interdisciplinary Research in Biology, CNRS UMR 7241, Collège de France, Paris, France
3Sorbonne Universités, UPMC Univ Paris 06, CNRS UMR 7625, Paris, France
4Institut de Biologie de l’Ecole Normale Supérieure, CNRS UMR 8197, Ecole Normale Supérieure, Paris, France
5E-mail: fanny.gascuel@college-de-france.fr
6AgroParistech ENGREF, Paris, France
7Irstea, UR EFNO, F-45290 Nogent-sur-Vernisson, France
8Department of Zoology, University of Cambridge, Cambridge, United Kingdom

Received November 5, 2014
Accepted September 6, 2016

Islands are particularly suited to testing hypotheses about the ecological and evolutionary mechanisms underpinning community assembly. Yet the complex spatial arrangements of real island systems have received little attention from both empirical studies and theoretical models. Here, we investigate the extent to which the spatial structure of archipelagos affects species diversity and endemism. We start by proposing a new spatially structured neutral model that explicitly considers archipelago structure, and then investigate its predictions under a diversity of scenarios. Our results suggest that considering the spatial structure of archipelagos is crucial to understanding their diversity and endemism, with structured island systems acting both as “museums” and “cradles” of biodiversity. These dynamics of diversification may change the traditionally expected pattern of decrease in species richness with distance from the mainland, even potentially leading to increasing patterns for taxa with high speciation rates in archipelagos off species-poor continental areas. Our results also predict that, within spatially structured archipelagos, metapopulation dynamics and evolutionary processes can generate higher diversity on islands more centrally placed than at the periphery. We derive from our results a set of theoretical predictions, potentially testable with empirical data.

KEY WORDS: Biodiversity, biogeography, neutral model, protracted speciation, spatially explicit model, species richness.
(e.g., Rey 1981; Heaney 1984; Milne and Forman 1986; Kadmon and Pulliam 1993; Hecnar et al. 2002; Ren et al. 2009). Several (nonmutually exclusive) explanations have been proposed for the lack of consistency, including: biodiversity on islands may not be at equilibrium (due to young island age, strong isolation reducing immigration rates, or abiotic disturbances; e.g., MacArthur 1972; Wilcox 1978; Whittaker et al. 2008); other island characteristics affect their carrying capacity (e.g., elevation, habitat composition, and heterogeneity; Dueser and Brown 1980; Milne and Forman 1986; Peck et al. 1999; Kallimanis et al. 2009; Carstensen et al. 2011); colonization rates may vary across islands (e.g., because of ocean currents or winds; Gill 1976; Rey 1981) and among species (because of differences in dispersal abilities; e.g., Wenner and Johnson 1980; King 1988); and interspecific interactions affect extinction rates and islands’ carrying capacity (e.g., Moulton and Pimm 1983; Loumolo 1984; Hecnar et al. 2002; Gravel et al. 2011).

However, even after taking into account the above factors, ETIB may still fail to predict empirical island diversity by overlooking the long-term contribution of evolutionary processes to community assembly in archipelagos. Speciation has long been known to contribute to shape diversity patterns on islands (MacArthur and Wilson 1963, 1967; Lack 1976), and is now incorporated in island-centric models, which assess the role of colonization, extinction, and speciation in community assembly and diversification patterns (e.g., Valente et al. 2014, 2015; Triantis et al. 2015). Accordingly, it was taken into account in the Unified Neutral Theory of Biodiversity and Biogeography (“UNTB”; Hubbell 2001), which built from the hypotheses of migration-drift introduced by the ETIB to propose a mechanistic framework generating quantitative predictions of macroecological diversity patterns. In the original version of UNTB (Hubbell 2001), speciation was restricted to the metacommunity (analogous to the mainland in the ETIB), with the diversity of local communities (analogous to islands in the ETIB) determined solely by colonization and demographic stochasticity. However, empirical studies have shown that rapid speciation within islands may explain an important part of present species diversity in archipelagos (Schluter 2000; Price et al. 2010).

In the first analysis accounting for local speciation in UNTB, Rosindell and Phillimore (2011) introduced a neutral model consisting of a mainland and an island connected by limited dispersal, where restricted gene flow results in local speciation (i.e., island endemics). This study provided quantitative predictions on the effects of island size and isolation on biodiversity patterns. However, it did not account for the spatial structure of island systems, that is, the subdivision of archipelagos into multiple islands linked by dispersal (only discussing its impact on the overall rate of insular cladogenesis). Yet, the latter is often strong in empirical systems, and known to affect not only migration and drift through stepping-stone effects and metapopulation dynamics (e.g., Rey 1981; Milne and Forman 1986; King 1988; Hanski 1998), but also gene flow among islands, and therefore local speciation (Coyne and Orr 2004). This effect was emphasized by other advances in neutral models, which considered communities as networks of spatial patches interlinked by limited dispersal and explored the relationships between speciation and isolation (e.g., Economo and Keitt 2008; Munepeerakul et al. 2008; Warren et al. 2010; Desjardins-Proulx and Gravel 2012). However, by not accounting for an external source of propagules (i.e., a mainland) those works have not generated explicit feedback toward the ETIB, despite being highly relevant to true island systems.

Here, we build from these advances in community ecology (e.g., Hubbell 2001; Economo and Keitt 2008; Rosindell et al. 2008; Rosindell and Phillimore 2011) to investigate how the interaction between the spatial structure of archipelagos and the process of speciation limited by gene flow within islands can impact diversity patterns. First, we introduce a “spatially structured” neutral model: this new model explicitly considers how island communities might assemble when archipelagos, receiving propagules from the mainland, are structured into multiple islands. We examine the case of an archipelago encompassing aligned islands, comparing its diversity, and endemism to those obtained through a similar but unstructured model (a “null hypothesis” model). From these comparisons we derive predictions for: the effects of spatial structure on the overall diversity and endemism of archipelagos; the effects of belonging to an archipelago on the diversity and endemism of individual islands; and the extent to which these predictions are affected by mainland diversity and by speciation rates on islands. To investigate the contribution of speciation to these effects, we also look at the predictions of the two models above without island speciation (i.e., considering that speciation only occurs in the mainland, as in Hubbell 2001).

**Methods**

**MODELS**

The spatially structured model

In our spatially structured model, an archipelago is a set of islands receiving migrants from a mainland and exchanging migrants among themselves. The mainland is modeled as a large pool of individuals with a predefined species-abundance distribution consistent with UNTB (see online S1; Hubbell 2001). Islands are defined as points in space, each containing a set of individuals. The metacommunity dynamics is modeled through death-replacement cycles, so that the number of individuals remains constant. All individuals have the same probabilities of birth, death, migration, and speciation, irrespective of their species (the neutral assumptions; Hubbell 2001). The death of an individual in an island opens a gap that is instantaneously colonized by a newly born propagule.
This propagule may come from the same island, or be a migrant, either from another island, or from the mainland. Its origin is chosen following a lottery game, with probabilities determined by a matrix of connectivity between all landmasses (all islands in the archipelago and the mainland), M. The matrix M establishes, for each pair of landmasses \((i, j)\), the probability \(M[i,j]\) for a vacant site in landmass \(i\) to be colonized by a propagule coming from landmass \(j\). To obtain these probabilities, we combined the matrix of geographic distances between all landmasses, their carrying capacity, and a fat-tailed dispersal kernel (Clark et al. 1999; Chave and Leigh 2002), such that closer and/or larger landmasses provide more propagules (see S2).

Speciation is assumed to be “protracted,” meaning it takes time and is delayed by gene flow (Rosindell et al. 2010; Rosindell and Phillimore 2011). It is modeled as population-scale phenomenon: when the individuals of a given species within a given island (i.e., a population) have differentiated long enough, they all switch from their ancestral to a new species (never seen before either in the mainland or the archipelago). We define \(T_{spc}[i] = T_{spc} + \text{delay}[i]\) the expected time (measured in number of birth–death cycles) needed to complete speciation on island \(i\) for the population of any species. \(T_{spc}\) is the baseline time needed to complete speciation, and \(\text{delay}[i]\) is a random delay due to gene flow slowing down genetic divergence, which increases linearly with the proportion of external propagules received by island \(i\) (see details in S3). Hence, each individual migrating onto an island where no conspecific is already present establishes a new population that starts to differentiate. When a population undergoes speciation, the new species starts to differentiate again. Unlike Rosindell and Phillimore (2011), we opted not to model cladogenesis within islands through point speciation to consider only one explicit speciation process, and examine how this process interacts with archipelago spatial structure to shape diversity patterns.

For computing efficiency, our algorithm uses a coalescent approach (Rosindell et al. 2008, 2010), working backward in time to reconstruct the genealogy of a sample of the individuals at present time. This imposes approximations on the times needed to complete speciation, but these approximations do not impact our results and conclusions (see S3 and S4).

In our analyses, we focused on a simple one-dimensional geographic configuration, where the archipelago consists of eight islands at progressively larger distances to the mainland (Fig. 1A). The islands are equal-sized, with 6000 individuals each, of which 10% are sampled. The mainland is considered much larger than the islands, with a carrying capacity of 1,000,000 individuals. Its diversity is determined by the fundamental biodiversity number, \(\Theta\) (a constant governing the species richness of the metacommunity in UNTB; Hubbell 2001), set at 60 (see S1). The baseline expected time to protracted speciation within archipelagos is set at

Figure 1. Effects of archipelago spatial structure on predicted diversity and endemism. Schematic representations of two archipelagos of same overall carrying capacity and same average distance to the mainland: (A) structured archipelago consisting of eight islands; (B) unstructured archipelago. Variation in the numbers of species in structured versus unstructured archipelagos, for increasing distance to the mainland: (C) variation in total species richness in scenarios without speciation; (D) variation in total species richness in scenarios with protracted speciation; and (E) variation in the number of island endemics in scenarios with protracted speciation. The archipelagos were modeled as having 48,000 individuals (6000 per island in A), 10% of which were sampled. Fundamental biodiversity number on the mainland \(\Theta = 60.\) Expected time to protracted speciation (in D and E), \(T_{spc} = 25\) million birth-death cycles. Boxplots, calculated over 100 simulation replicates, represent the first, second, and third quartiles, with whiskers giving the maximum and minimum values.
Tspc = 25 million birth–death cycles (corresponding to about 520 generations in an isolated metacommunity of 48,000 individuals).

We investigated how distance between the mainland and (the centroid of) the archipelago affects island communities. Distance was measured relatively to the dispersal ability of the individuals, modeled as the width $c$ of the fat-tailed dispersal kernel (given in S2); we rescaled geographic distances by dividing them by the value of $c$ (maintained constant at $c = 55$). Distances are thus expressed in units of width of the dispersal kernel, $c$. We considered eight scenarios of archipelago distance from the mainland (Fig. 1): 5, 14, 23, 32, 41, 50, 59, or 68 distance units. Adjacent islands within an archipelago were separated by one distance unit (e.g., in the archipelago whose centroid is at 68 distance units, islands were at 64.5, 65.5, 66.5, 67.5, 68.5, 69.5, 70.5, and 71.5 distance units from the mainland).

We also tested the influence of the carrying capacity of archipelagos, by comparing our main results with those obtained with archipelagos of smaller carrying capacities (9600 individuals; S5).

For each set of parameters, we created 100 replicates, and then obtained: average total species richness; average number of species endemic to the archipelago (E); and average number of single-island endemics (SIE). Analyses on the simulated data were done in R (“R Development Core Team” 2012). Our spatially structured model was coded in Java language, and is available on a Dryad repository at http://dx.doi.org/10.5061/dryad.n49qg.

**The null model: The unstructured archipelago**

We created a null model equal in all to the structured model described above but without an internal archipelago spatial structure. This unstructured archipelago was modeled as a point in space, containing the same number of individuals as the structured archipelago. Here, the matrix of connectivity $M$ only includes the fraction of propagules coming from within the archipelago versus from the mainland. To ensure differences between both models derive solely from the effect of spatial structure, we set the fraction of mainland propagules as equal to that arriving to the corresponding structured archipelago (different for each scenario of distance to mainland).

Protracted speciation occurs under the same process as in islands of a structured archipelago, with Tspc = 25 million birth–death cycles for 48,000 individuals. Here, panmixia however prevents endemic lineages from undergoing speciation.

**Model variants without speciation within archipelagos**

For both structured and unstructured models, we implemented a variant without speciation within the archipelago, to understand the extent to which the effects of spatial structure on diversity are determined by speciation vs. by migration and drift. Here, the species identities of the sampled individuals are defined by simple succession from their mainland ancestor (which is akin to an infinite time to protracted speciation). In the unstructured model, this process corresponds to the original neutral model (Hubbell 2001).

**EXPERIMENTAL DESIGN**

To investigate how spatial structure can shape diversity patterns in archipelagos, we applied the above-described models to three in silico experiments.

First, we investigated how accounting for the internal spatial structure of an archipelago affects model predictions about its overall diversity and endemism (Fig. 1), by comparing results from our spatially structured model (Fig. 1A) with those of the equivalent unstructured (null) model (Fig. 1B). This experiment was performed for the eight scenarios of distance to mainland described above.

Second, we investigated how belonging to an archipelago affects predictions of diversity and endemism in individual islands (Fig. 2), by comparing results for each island in our spatially structured archipelago (Fig. 2A) to those predicted with this island alone, that is considering that propagules can only come from the same island or from the mainland (Fig. 2B). We considered 64 scenarios of distance to mainland (corresponding to eight archipelagos of eight islands each, with island distances ranging from 1.5 to 71.5 distance units).

Third, we investigated the sensitivity of the predictions made by our spatially structured model to mainland diversity and to speciation rates within islands. We compared predictions of total archipelago diversity for the structured and equivalent unstructured null model, for $\Theta$ values of 20, 60, or 100 and for Tspc values of 20, 25, or 30 million birth–death cycles.

**Results and Discussion**

**EFFECTS OF SPATIAL STRUCTURE ON PREDICTIONS OF ARCHIPELAGO DIVERSITY AND ENDEMISM**

At intermediate to long distances from the mainland, our spatially structured model predicted higher species diversity in archipelagos than the null, unstructured model, resulting in a much slower decline in species richness with distance from the mainland (Fig. 1D). There could a priori be two (nonmutually exclusive) explanations: spatial structure may affect the migration and drift within archipelagos, or it may affect speciation. We address these in turn.

The comparison between structured and unstructured models in the absence of speciation (Fig. 1C) reveals that we can discard the former hypothesis, as both models predicted very similar species richness in archipelagos. This suggests that the positive effects of archipelago spatial structure on species diversity
Figure 2. Effects of belonging to an archipelago on predicted island diversity and endemism. Schematic representations of two islands of same carrying capacity and same distance to the mainland: (A) island belonging to a structured archipelago of eight islands; (B) single island. Variation in the numbers of species per island, on islands within archipelagos versus single islands, for increasing distance to the mainland: (C) variation in total species richness, in scenarios without speciation; (D) variation in the total species richness, in scenarios with protracted speciation; and (E) variation in the number of endemics, in scenarios with protracted speciation. For islands within archipelagos, we distinguish between single-island endemics (SIE; less abundant) and overall endemics (E; most abundant). Modeling parameters as in Figure 1. Boxplots, calculated over 100 simulation replicates, represent the first, second, and third quartiles, with whiskers giving the maximum and minimum values.

The differences between the predictions by the spatially structured and unstructured models (Fig. 1D) must therefore result from the interaction between space and the speciation process. When considering protracted speciation, substantially larger numbers of endemic species were generated in structured than in unstructured archipelagos (Fig. 1E, for distances above 5 distance units). Two mechanisms contribute to this result. First, in the spatially structured model, a species from the mainland can undergo distinct anagenesis events in distinct islands. Second, endemic lineages can further radiate in the structured archipelago (i.e., generate several new endemic species from one endemic species; cladogenesis), because their migration between islands generates further opportunities for speciation. This is prevented in unstructured archipelagos by constant genetic homogenization.

These effects of spatial structure do not occur at short distance to the mainland (5 distance units), where diversity was similar between structured versus unstructured models (Fig. 1D) and between models with and without speciation within islands (compare Figs. 1C and D). This is because high levels of gene flow from the mainland (high $T_{spc}$) prevent anagenesis and cladogenesis, and thus the generation of endemic species (Fig. 1E). In these simulations, archipelagos behave as if they were a sample from the mainland, their diversity being only driven by colonization and extinction.

In unstructured archipelagos, the number of endemics had a hump-shaped relationship with distance (Fig. 1E), reproducing the predictions made for anagenetic species by Rosindell and Phillimore (2011) although with different modeling choices. This reflects a trade-off between the positive and the negative effects of immigration from the mainland on speciation: in archipelagos too close to the mainland, high gene flow delays speciation, preventing anagenesis; in remote archipelagos, the lower propagule influx produces fewer opportunities for anagenesis. At very far distances from the mainland, we expect only one endemic species in the unstructured archipelago, because of limited anagenesis and of the absence of cladogenesis. In the structured archipelago, however, the decline in anagenesis with distance from the mainland was more than compensated by cladogenesis (Fig. 1E), maintaining the number of endemic species high even under extremely rare migration from the mainland (parallel to what was found by Rosindell and Phillimore 2011 for cladogenetic species generated by point speciation).

**EFFECTS OF BELONGING TO AN ARCHIPELAGO ON ISLAND DIVERSITY AND ENDEMISM**

Islands modeled as being part of a spatially structured archipelago had not only consistently higher species diversity than single
islands of equal size and at equal distance, but the patterns of variation in species diversity with distance to mainland also differed (Fig. 2D). Whereas the single-island model predicted a monotonic decrease of the overall species richness with distance, islands within a spatially structured model had a hump-shaped profile of species richness with respect to the position of the island. Again, there are two possible explanations: demographic (due to migration and drift) and evolutionary (changes in speciation rates).

Consistently with the ETIB (MacArthur and Wilson 1967), islands within an archipelago should have higher diversity than isolated islands because rescue effects reduce local extinction rates. Our results without speciation support this prediction (Fig. 2C), both because islands’ diversity was systematically higher if they were within an archipelago, but also because islands in the centre of each archipelago had higher diversity than those at the edges, as expected from their better connectivity to other islands (Economo and Keitt 2010; Desjardins-Proulx and Gravel 2012). The resulting hump-shaped pattern within each archipelago shows that even without accounting for speciation the spatial structure of archipelagos may create distortions to one of the main patterns predicted by the ETIB: that island diversity declines monotonically with distance to the mainland.

Furthermore, the results with protracted speciation (Figs. 2D and E) show that the positive effects of belonging to an archipelago were also due to a major impact on island speciation rates. Indeed, for distances from the mainland large enough for speciation to occur, the number of endemics on islands was much higher if they belonged to an archipelago than if they were alone (Fig. 2E). As in the first experiment, this was due to increases in both anagenesis and cladogenesis in the structured archipelago. These processes accentuated the hump-shaped pattern of variation in island species richness with distance to the mainland (compare Figs. 2C and D), because islands at the centre of each archipelago received more and more diverse propagules.

**SENSIBILTY TO MAINLAND DIVERSITY AND ISLAND SPECIATION RATE**

Our results were sensitive both to diversity in the mainland and to the speciation rates within island (Fig. 3). A lower time to speciation Tspc (i.e., faster speciation dynamics) magnified the difference between structured and unstructured archipelagos, by substantially increasing species diversity in structured archipelagos (when sufficiently far from the mainland for speciation to occur; Fig. 3). As above, this resulted from more endemic species (Fig. S1.6–1 in S6), due to both faster anagenesis and cladogenesis.

Mainland diversity (i.e. Θ, and so the diversity of mainland propagules) had an important effect on the shape of the relationship between archipelago diversity and distance to the mainland, particularly for structured archipelagos. For unstructured archipelagos, we generally obtained the familiar monotonic decline in species richness with distance to the mainland predicted by the ETIB. It was only for low mainland diversity (Θ = 20), for which archipelago diversity is more dominated by endemic species, that the monotony of this pattern was slightly disturbed (at 23 distance units; Fig. 3), reflecting the hump in the relationship between the number of endemic species and the distance to the mainland (Fig. 1E).

For structured archipelagos, the effect of mainland diversity on patterns of variation in archipelago species richness with distance to the mainland was quite dramatic. Indeed, whereas for high values of Θ we found the familiar monotonic decline in species richness with distance, for low values of Θ we obtained the counter-intuitive result that archipelago richness increased at first with distance, before slowly stabilizing or declining. These results reflect the interplay between the three processes generating diversity in structured archipelagos: (i) migration from the mainland, which is stronger close to it and a more dominant process when mainland diversity is higher; (ii) anagenesis from lineages originating from the mainland, which has a hump-shape distribution with distance to the mainland (Fig. 1E); (iii) and cladogenesis within archipelagos, which is stronger further from the mainland and whose role becomes dominant when mainland diversity is low and the archipelago speciation dynamics is fast (i.e. low Tspc; Fig. 3).

Our sensitivity analyses show that these results are robust to the carrying capacity of archipelagos (S5).

**Predictions and Implications**

Our results from the null, unstructured archipelago model (or when considering single islands; Figs. 1B and 2B), support previous model predictions for mainland–island systems: a decrease in species richness with distance to the mainland (Figs. 1D and 2D; MacArthur and Wilson 1967; Rosindell and Phillimore 2011; Rosindell et al. 2011) and a peak in endemic (anagenetic) species at intermediate distances from the mainland (Figs. 1E and 2E; Rosindell and Phillimore 2011). However, our spatially structured model made substantially different predictions about the diversity and endemism on archipelagos: spatial structure not only increased the total number of species and the number of endemic species predicted in archipelagos (Fig. 1), but in some cases it also changed the pattern of variation in diversity with distance to the mainland, generating hump-shaped (Figs. 2D and 3) or increasing patterns of species richness variation with distance (Fig. 3).

A number of theoretical predictions can be derived from these results, potentially testable with empirical data. First, at distances sufficiently far from the mainland for island speciation
to occur, archipelagos composed of a higher number of islands are expected to have higher diversity than archipelagos of similar overall carrying capacity composed of fewer islands. This higher diversity should come along with a higher proportion of endemic species (Figs. 1D-E and 2D-E). In agreement with this prediction, Cabral et al. (2014) found that across 23 oceanic archipelagos, island number had a positive effect on vascular plant diversity, after controlling for other geographic and climatic variables. However, in an analysis of 14 archipelagos, Triantis et al. (2015) found a negative effect of island number on both overall richness and number of endemic species (of birds, plants, snails, and spiders), reflecting an increase in extinction risk with fragmentation. This discrepancy may reflect limitations in the general statistical approach employed by Triantis et al. (2015), for example by not taking into account the interaction between spatial structure and other variables, as demonstrated by our model. But it may also reflect limitations in our model, such as the rigid zero-sum assumption that forces communities to always remain at carrying

Figure 3. Sensitivity of the predicted effects of spatial structure of archipelagos to variations in the diversity of the mainland (higher for higher values of the fundamental biodiversity number $\Theta$) and in the speciation rates on archipelagos (higher for lower values of time to speciation $T_{spc}$, in million birth–death cycles). Other modeling parameters as in Figure 1D. Structured archipelagos are represented in dark gray, unstructured in light gray. Boxplots, calculated over 100 simulation replicates, represent the first, second, and third quartiles, with whiskers giving the maximum and minimum values.
capacity. In real islands, populations can go extinct following environmental perturbations, which may result in a decrease in species richness with archipelago fragmentation. In addition, the effect of spatial structure should be reduced if communities are not at equilibrium (e.g., MacArthur 1972; Wilcox 1978; Whittaker et al. 2008). Models accounting for island geological dynamics (distinguishing in particular continental vs. oceanic islands, which often undergo island cycles; Whittaker et al. 2008) could provide further insight on this question.

Second, our results suggest that the lower the diversity of mainland propagules, the stronger the relative importance of cladogenesis to archipelago diversity (Fig. 3). So we predict that patterns of increase in archipelago diversity with distance to the mainland are likely to be found off continental areas hosting few species or few species prone to dispersal (e.g., forest compared to open habitats), especially when considering taxa with high speciation rates. Such patterns are not expected off species-rich continental areas.

Third, we predict higher diversity (including higher numbers of endemics) on islands within archipelagos than on similarly sized and isolated single islands, especially far from the continent (Figs. 2D–E). Moreover we predict, in agreement with previous models (Econo and Keitt 2008; Desjardins-Proulx and Gravel 2012), higher diversity on islands more centrally placed within archipelagos than on islands at the periphery (everything else being equal; Fig. 2D). This pattern was previously observed in empirical data, but explained in terms of chronology of archipelago formation (e.g., Simberloff and Wilson 1969; Gillespie 2004; Cameron et al. 2013; Valente et al. 2014): islands of intermediate age may allow higher diversity due to reduced species density (linked to recent colonization events) or to increased area (associated with their ontogenetic trajectory). Here, we present an alternative explanation.

More generally, we investigated the effect of distance to mainland (while keeping the dispersal abilities of organisms constant), but our results are also interpretable in terms of decreasing dispersal ability of organisms (while keeping distance to the mainland constant). From a modeling perspective, the two are equivalent. Consequently, ours and Rosindell and Phillimore’s (2011) prediction of maximum anagenesis at intermediate distance from the mainland is supported by observations of increased species richness among lineages of intermediate dispersal ability (Claminunt et al. 2012; Agnarsson et al. 2014). We also predict that spatial structure will have a stronger effect on archipelago diversity for taxonomic groups with relatively low dispersal ability (e.g., amphibians compared to birds), given similar speciation rates and population sizes.

Here, we have applied our model to theoretical systems with very simple spatial configurations (treating landmasses as points, with islands aligned along a one-dimensional axis) to generate predictions for the broad effects of spatial structure on island diversity and endemism. However, our spatially structured model can easily be applied to other spatial configurations, by simply changing the matrix of connectivity between landmasses. It notably allows investigating the influence of island internal structure, by considering islands as composed of sets of adjacent spatial units connected by limited dispersal. Predictions are expected to depend on the relationship between the spatial grain and species’ dispersal abilities (Kisel and Barraclough 2010; and on disturbances if the latter are included).

Spatial structure has largely been overlooked from both empirical analyses of diversity and endemism (e.g., Heyne 1981; Heaney 1984; Milne and Forman 1986; Kadmon and Pulliam 1993; Hecnar et al. 2002; Ren et al. 2009) and from previous neutral community models (e.g., Hubbell 2001; Rosindell and Phillimore 2011) but our results suggest that taking it into account is important to understanding spatial biodiversity patterns in certain biogeographic contexts (archipelagos with high spatial structure, off species-poor continental areas, or far from the mainland), particularly for taxonomic groups with high diversification rates or low dispersal ability. Indeed, archipelagos can work both as “museums” (by delaying rates of extinction within islands) and as “cradles” (by increasing rates of speciation) of diversity (Gaston and Blackburn 1996). These results reinforce the importance of islands, and spatially structured landscape in general (“key landscapes”; Givnish 1997), as centers of diversity and of endemism (e.g., WWF and IUCN 1994; Stattersfield et al. 1998). Future work testing and refining the above predictions (under different spatial configurations, out-of-equilibrium, and in the presence of environmental perturbations, but also combining macroecological to macroevolutionary patterns of biodiversity) should therefore shed an important light into the mechanisms underpinning diversity patterns.

**ACKNOWLEDGMENTS**

We are grateful to Marie-Claude Quiodoz, Christian Ciangura, and Cyril Bernard for technical support. Philippe Jarne, François Massol, and Christophe Thébaud provided very helpful comments on a previous version of this manuscript, subsequently substantially improved following reviews by James Rosindell, Rampal Etienne, Eva Kisdi, Albert Phillimore, and an anonymous reviewer.

**DATA ARCHIVING**

The doi for our data is 10.5061/dryad.n49qg.

**LITERATURE CITED**


Associate Editor: E. Kisdi
Handling Editor: M. Servedio

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher’s website:

Figure S1. Modelling the mainland.
Figure S2. Connectivity matrix of structured archipelagos.
Figure S3. Algorithm of the spatially-structured neutral model.
Figure S4. Sensitivity analysis to approximations on the times needed to complete speciation, using the forward-in-time algorithm.
Figure S5. Sensitivity to the carrying capacity of archipelagos.
Figure S6. Sensitivity of the patterns of variation in number of endemic species with distance to mainland to mainland diversity and archipelago speciation rates.