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RESEARCH ARTICLE

Effects of archipelago geo-environmental dynamics on phylogenetic tree shape

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Abstract

In archipelagic environments, the successive emergence and submergence of islands induces changes in area, spatial structure and isolation. Here, we aim to understand how such geo-environmental dynamics, by altering immigration, speciation and extinction over time, may influence phylogenetic patterns. We use a neutral, stochastic, individual-based model which simulates a community evolving in an archipelago where four islands emerge and submerge consecutively. We record each birth, death and immigration event, allowing us to build the complete phylogeny at any time, from which we extract the phylogeny of extant species. We show that the rate of lineage accumulation and tree imbalance vary according to a hump-shaped curve, and we show that this is mainly due to variations in area and inter-island connectivity. We highlight that past abrupt changes, such as island emergence, may leave persistent imprints in the rate of lineage accumulation. We show that the spatial configuration of an archipelago modulates these effects: (i) enhancing inter-island connectivity leads to more frequent inter-island speciation events, resulting in a faster accumulation of lineages, and in larger evolutionary radiations, which in turn produce highly imbalanced phylogenies; (ii) increase in mainland connectivity brings ancestral lineages to the islands, which slows down the rate of lineage accumulation and increases the species turnover, allowing for more balanced phylogenies. Accounting for variations in the geo-environmental configuration of an archipelago is important to understand the shape of contemporary phylogenies. However, these effects have to be interpreted in the context of the spatial configuration of an archipelago.

Highlights

- The emergence and submergence of islands in an archipelago influences immigration, speciation and extinction rates at both island and archipelago scales
- Landscape dynamics in an archipelago drives insular species diversification rates and influences phylogenies of island species
- Inter-island dispersal favors lineage accumulation and generates imbalanced phylogenies
- Mainland connectivity increases species turnover, slows down lineage accumulation and makes phylogenies more balanced
- The establishment and size of a phylogenetic island clade may depend on the spatial configuration of the archipelago at the time of colonization

Keywords

Biogeography, connectivity, dispersal, evolutionary radiation, individual-based model, island, island ontogeny, macroevolution, spatial configuration

Introduction

The classic theory of island biogeography describes island species richness as an equilibrium resulting from the balance between immigration and extinction. This equilibrium diversity depends strongly on rates of immigration from the mainland as well as extinction rates on the

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islands, these rates varying with area and isolation, two important geographical attributes of islands (MacArthur and Wilson 1963; MacArthur and Wilson 1967; Valente et al. 2020). Speciation is also an important source of diversity beyond certain thresholds of island area and isolation (MacArthur and Wilson 1963; Losos and Schluter 2000; Valente et al. 2015; Warren et al. 2015).

Larger areas are more easily reached by immigrants due to the target area effect (Gilpin and Diamond 1976) and have an increased capacity to support diverse habitats and resources (Williams 1964), facilitating the establishment of these immigrants. In addition, larger areas reduce the probability of extinction by decreasing the effects of demographic stochasticity (Lande 1993), and increase the likelihood of speciation (Losos and Schluter 2000; Kisel et al. 2011), because more ecological niches are available and opportunities for isolation within the island are greater (MacArthur and Wilson 1967; Heaney 2000; Whittaker et al. 2008; Kisel et al. 2011). As predicted by this line of reasoning, larger islands show higher rates of immigration, lower extinction rates and host larger evolutionary radiations (Triantis et al. 2015; Valente et al. 2020; Tao et al. 2021).

Island isolation is negatively linked to immigration, as remote islands are more difficult to reach (MacArthur and Wilson 1963, 1967; Gilpin and Diamond 1976; Brown and Kodric-Brown 1977). Thus, a potential rescue effect (i.e. recolonization of a locally extinct population by the same species migrating from the mainland) diminishes and species should be more vulnerable to extinction on remote islands than on islands close to the mainland (MacArthur and Wilson 1963, 1967; Heaney 2000). Concurrently, reduced gene flow from the mainland on isolated islands may enhance opportunities for divergence that can lead to speciation (MacArthur and Wilson 1967; Heaney 2000). Also, reduced immigration decreases local competition between locally established populations and immigrants from the mainland, making it easier for local populations on islands to access resources and expand (Tao et al. 2021). As predicted by this line of reasoning, remote islands that have been colonized at lower rates show enhanced in situ speciation (Valente et al. 2020).

In archipelagos that are of volcanic origin, each island typically has its own ontogeny following a geological life cycle characterized by successive phases: growth, erosion and submersion (Price and Clague 2002). During this cycle, area, and to a lesser extent, isolation undergo dynamic changes over time. In a seminal effort to understand the role of geological processes in the community buildup on islands, Whittaker et al. (2008; but see also Whittaker et al. 2010; Valente et al. 2014; Borregaard et al. 2016; Cabral et al. 2019b; Whittaker et al. 2023) proposed the General Dynamic Model (GDM) in an attempt to incorporate the effects of these processes on biodiversity patterns. Specifically, the GDM predicts changes in immigration, extinction and speciation rates following the ontogeny of volcanic oceanic islands, leading amongst other things to a dynamically changing expected number of species. During the growth phase of an island, i.e. when area expands as elevation increases, the carrying capacity of the island (i.e. the number of species it can host) increases, and the GDM predicts maximal immigration rates during this aerial construction phase due to the availability of new space. Also, speciation rate is expected to increase as a result of new ecological niches becoming available and increased opportunities for within-island allopatry. This phase shows a rise in island species richness. During the erosion phase, i.e. when the island's area diminishes, the rate of immigration is expected to decline due to reduced habitat availability. The speciation rate reaches its maximum as erosion increases the island's topographic complexity, promoting the divergence of local populations. The early erosion phase is characterized by the island's peak in species richness. During the submergence phase, immigration and extinction rates further decline, but also the rate of speciation as opportunities for genetic divergence diminish on the shrinking island. This final phase results in a reduction in the number of species until the eventual submergence of the island. Ultimately, the GDM predicts a dynamic number of species following the hump-shaped curve that reflects the geological ontogeny of the island, and peaking when the island reaches its maximum topographic complexity.

Oceanic volcanic islands do not generally occur on their own but are usually clustered into archipelagos in which the consecutive emergence of islands creates new immigration opportunities and sources, owing to the relative proximity of islands within these archipelagos. Thus, archipelagos are the appropriate spatio-temporal units to study island biodiversity patterns (Triantis et al. 2016). The geo-environmental dynamics within an archipelago implies an ever-changing landscape, in which the degree of fragmentation, i.e. number of islands, as well as the size of the islands, are changing over time (Whittaker et al. 2008; Ali and Aitchison 2014).

Models have been developed to explore how community assembly and species diversification can be affected by archipelago structure when multiple islands emerge and submerge consecutively (Gascuel et al. 2016; Aguilée et al. 2021; Jõks et al. 2021). In an archipelagic context, inter-island dispersal and subsequent inter-island speciation can lead to the diversification of lineages (Haydon et al. 1993). As expected, evolutionary radiations emerging from inter-island dispersal are commonly observed in a wide range of taxa on different archipelagos (Emerson and Oromí 2005; Sanmartín et al. 2008; Cabral et al. 2014; Papadopoulou and Knowles 2015). A recent model (Aguilée et al. 2021) showed that the effect of inter-island connectivity on opportunities for speciation may be such that the accumulation of species is higher on an island within a geo-dynamic archipelago than on an isolated island of equivalent size. However, this effect of inter-island dispersal may be difficult to comprehend as high connectivity between islands can also erase the diversifying effect through gene flow, thus reducing opportunities for speciation.

A strategy to further understand how landscape dynamics influence diversification dynamics is to look at its imprints on phylogenies (Haydon et al. 1993; Valente et

al. 2014; Herrera-Alsina et al. 2021; Freitas et al. 2024). To investigate the impact of environmental dynamics on species diversification, two phylogenetic metrics are usually examined: the rate of lineage accumulation over time and tree imbalance. The rate of lineage accumulation is informative on how diversification rates vary over time through the balance between extinction and speciation events (Pybus and Harvey 2000; Ricklefs and Bermingham 2007; Rabosky and Lovette 2008). Phylogenetic imbalance is an indicator of disparities in rates of extinction and speciation among lineages, reflecting differences in their ability to diversify (Hubbell 2001; Davies et al. 2011; Gascuel et al. 2015; Herrera-Alsina et al. 2021).

While the effects of area, isolation, and the evolution of the landscape into different islands on the shape of phylogenies of island species are individually well understood, the net result of their interactions remains unclear, especially in the context of a constantly fluctuating landscape, with uneven immigration patterns, strongly influenced by the geo-environmental dynamics of archipelagos. Here, we investigate how complex landscape changes within an archipelago affect phylogenies of island species. We use a neutral, stochastic, individual-based model to simulate the evolution of an insular community within an archipelago. This archipelago experiences successive island emergence, changes in size and connectivity, until submersion of all islands. We study the shape of phylogenies by tracking the rate of lineage accumulation and imbalance of the trees.

Methods

Overview

We simulate species communities in an archipelago where four islands successively emerge and submerge, using a stochastic, individual-based and neutral model based on the Aguilée et al. (2021) model. The four islands have their own geological dynamics where they increase and then decrease in carrying capacity, following a hump-shaped curve (because of changes in area, elevation and topographic complexity, as in the General Dynamic Model, see Whittaker et al. 2008). This dynamic environment induces connectivity change between islands and with the neighboring mainland over time. To understand how communities evolve over time, we follow lineages and build their complete phylogenies, from which we extract the phylogenies of extant species. We compute from these phylogenies the rate of lineage accumulation and the phylogenetic imbalance. We link them to the emergent immigration, speciation and extinction rates to explain the effect of a dynamic environment on the shape of the phylogeny.

The model is calibrated as in Aguilée et al. (2021), for a weakly dispersing clade, such as, e.g. flowering plants or snails, whose populations can differentiate at small spatial scales (Kisel and Barraclough 2010). Thus, dispersal between islands can be considered long-distance dispersal in this model. We define a reference geographical configuration of the archipelago, the "baseline model", and we explore the effect of variations around this configuration (Fig. 1a). We also looked into different intensities of gene flow but these were always below the threshold above which inter-island or mainland dispersion inhibits speciation.

Geo-environmental dynamics

The geo-environmental dynamics of the archipelago is characterized by the emergence and submergence of four consecutive islands at regular time intervals and with identical individual geological dynamics. Each island follows the General Dynamic Model (Whittaker et al. 2008) assumptions: an island's biota is governed by speciation, extinction and immigration rates, which depend on the geological properties of the island. Here, the area of an island is expressed as the number of individuals and represents the carrying capacity. Changes in what we call "area" of an island represent, in fact, all changes in the area, elevation and topographical complexity as they all contribute to carrying capacity. The area of an island follows a hump-shaped curve as a function of time, with the growth phase being faster than the decrease in area (Fig. 1c). All islands have the same area dynamics, but they do not emerge at the same time (Fig. 1c, colored solid fill indicates each island carrying capacity dynamics). The model calibration is such that the whole archipelago's ontogeny lasts 350,000 generations.

We considered archipelagos with islands sufficiently distant from each other and from the mainland so that the effect of island area changes on inter-island distances and distance to the mainland can be ignored. In other words, we assume that all distances are constant over time. In nature, the geo-environmental dynamics of volcanic archipelagos often implies a chain of islands as they emerge consecutively following the movement of a tectonic plate over a mantle plume (Ali and Meiri 2023). Here, to better address the effect of connectivity between islands, we simplify our archipelago into a cluster of unstructured islands without such a specific spatial configuration. We assume that islands are at equal distance from each other and that they all are at the same distance from the mainland (Fig. 1a), i.e. we assume that there is no effect of the position of an island in the archipelago relative to the other islands.

Population dynamics

Population dynamics are ecologically neutral in the sense that every individual is characterized by the same ecological properties. The birth of individuals occurs at a constant rate. Mortality is density-dependent at the scale of each island community, determined by the island's carrying capacity. Thus, the probability of an individual perishing depends on the island where it occurs. Species extinction happens when all individuals that belong to the same species have died at the scale of the archipelago. Movement of individuals can occur from the mainland to each island or between

islands and we ignore back-colonization to the mainland. Individuals emigrate from a source at a constant rate per individual, resulting in a number of emigration events proportional to the size of the source population. We assume the target area effect (Gilpin and Diamond 1976) and the dispersal kernel from Clark et al. (1999): the probability that an individual immigrates increases with the increasing size of the recipient island and decreases with the increasing distance between the source and the recipient island (Suppl. material 1: appendix S2). Speciation is completed after a fixed minimum period plus a variable delay that increases with gene flow from the same species and decreases with the population size (Suppl. material 1: appendix S2). The model assumes cladogenesis following Rosindell and Phillimore (2011): each individual on the archipelago initiates a diverging lineage at constant rate. We also model anagenesis following Gascuel et al. (2016): if the species of a migrant is new to the island of destination, the migrant initiates a distinct lineage. However, if the migrant species already exist on the island of destination, it delays the speciation clock of the local population of the same species. Although all individual rates are unaffected by species identity, they depend on the population size of the island on which the individual is located, the size of the population the individual belongs to, the distance to the island of destination, as well as its size. Hence, these rates are defined by the specific time and location within the archipelago. A new-born individual inherits its mother's species identity, unless a speciation event occurs; in this case, it receives a new species identity. Individuals may belong to different species because either they are separated by a speciation event in the archipelago, or they descend from different mainland lineages resulting from different immigration events. The mainland community is described by a species pool with a constant population size distribution consistent with the neutral theory of biodiversity (Hubbell 2001) and therefore the species abundances show a log-series distribution with few very abundant species and many rare species. We assume that the mainland community does not change throughout a simulation. The same species from the mainland may send immigrants multiple times to the archipelago during a single simulation.

Experimental design: Null models

When the geographical configuration of the archipelago is calibrated with the reference parameters values (Fig. 1a configuration 1), the model described above is designated as the "baseline model".

To determine the effect of the number of islands and change in archipelago area, we build a "no geo-dynamics" null model which describes an archipelago having four islands all along the simulation, which are of constant size (equal to the maximum carrying capacity used in the baseline model) for the whole simulation.

To determine the imprint of past geographical changes, we use a "static" null model. As in the no geo-dynamics model, there is no geo-environmental dynamics in this static model. For each simulation of the baseline model, we simulate a series of static models. We record a snapshot of the geographical configuration of the baseline (dynamic) model every 10,000 generations, and for each snapshot we simulate a static model with the corresponding geographical configuration (Suppl. material 1: appendix S3, fig. S4). Each static model is simulated for the same duration as the age of the dynamic archipelago at the time the snapshot was taken. This allows us to examine phylogenies obtained in a static landscape with the same age as phylogenies from the dynamic archipelago (i.e. comparable branch lengths), for each geographical configuration encountered in a dynamic archipelago. The static model allows us to remove, and thus to identify, at each time in the baseline model, the potential imprint of past geographical changes in the phylogeny.

To determine the effect of the spatial structure of an archipelago with several islands on the shape of phylogenies, we use a "single-island equivalent" null model. It represents an archipelago behaving as a single island whose area varies as does the sum of the areas of the islands in the baseline model (Fig. 1a, configuration 1b). By construction, there is no inter-island dispersal in this null model, and no speciation following inter-island dispersal. We scale the target area effect of mainland dispersal such that immigration from the mainland occurs at the same rate as in the baseline model.

Experimental design: Spatial configuration of the archipelago

We explore how archipelago spatial configuration affects phylogenies of extant island species. In addition to the baseline model (Fig. 1a, configuration 1), we simulate four dynamic archipelagos with different geographical structure: they have either less or more distance between islands than in the baseline model, or they are closer or further from the mainland than in the baseline model. We consider alternately 1) a "scattered archipelago" (Fig. 1a, configuration 2) where inter-island distance is high, 2) a "compact archipelago" (Fig. 1a, configuration 3) where inter-island distance is short, 3) a "near archipelago" (Fig. 1a, configuration 4) where distance to the mainland is short, and 4) a "distant archipelago" (Fig. 1a, configuration 5) where distance to the mainland is high.

Phylogenetic simulations

With this individual-based model we are able to follow each individual on, and movement to/between, the different islands of the archipelago. The time is measured in generations. A generation time is one time unit of the simulation real time divided by the *per capita* birth rate (which equals the *per capita* death rate at the demographic equilibrium). Every 25 generations, we record the species identity

of all individuals, this allowing us to record immigration, speciation and extinction events. We plot the phylogeny every 100 generations. Because we know all population dynamics events, we know the complete phylogenies without sampling or fossilization bias (Signor and Lipps 1982). However, to be consistent with the data actually available in any empirical study on island organisms, we extract from the complete phylogeny the extant phylogeny which contains only the species that live at the "present" time on the archipelago (the "present" time being each time from the beginning of the simulation to the end, by steps of 100 generations). As simulations start with an empty archipelago, insular communities necessarily originate from mainland lineages. At the beginning of each simulation, we build a mainland phylogeny with the pool of mainland species, where the branching relationships between mainland species are defined randomly. In this mainland phylogeny, we set all inter-node distances to a small value (10^{-3}), negligible compared to the tree age. With these assumptions, the mainland tree does not influence the rate at which lineages accumulate on the archipelago, and it has a constant imbalance during the entire simulation, enabling the computation of phylogenetic statistics without bias stemming from a particular structure of the mainland phylogeny. Every 100 generations, we trace the phylogeny of the extant species on the archipelago back to the initial event of immigration from the mainland, linking each endemic species to its mainland ancestor.

Statistics

The speed of lineage accumulation over time in a phylogeny can be measured with the *γ*-statistic. We compute the *γ*-statistic from the R package Phytools (Revell 2012) which calculates the *γ*-statistic described by Pybus and Harvey (2000) (modified from Cox and Lewis 1966). The *γ*-statistic measures the relative distribution of internal nodes of a phylogeny over time:

$$\gamma = \frac{\left(\frac{1}{n-2}\sum_{i=2}^{n-1}\left(\sum_{k=2}^{i} k g_k\right)\right) - \left(\frac{\tau}{2}\right)}{\tau\sqrt{\frac{1}{12(n-2)}}} \quad (1)$$

$$\text{with } \tau = \sum_{j=2}^{n} j \cdot g_j \quad (2)$$

where *n* is the total number of species in the studied phylogeny. The numerator is given by the cumulative sum, for each internal node, indexed by *i*, of the corresponding internal-node distances *g*, weighted by its dichotomic position in the tree, indexed by *k*. The sum is divided by the number of internal nodes *n* − 2, and half the total length of the tree's branches, denoted *τ* (equation 2), is subtracted. The denominator, the product of the total branch length of the tree *τ* and the square root 1 / 12(*n* − 2), can be interpreted as the standard deviation. This scaling factor ensures that we can make comparisons across phylogenies of different sizes *n*. The interpretation of the *γ*-statistic involves a reference value *γ* = 0. This value corresponds to a phylogeny characterized by a constant and positive speciation rate along with a zero extinction rate, commonly known as the pure birth model. When the lineage accumulation decelerates compared to this constant rate pure birth model, the *γ*-statistic exhibits negative values. Conversely, when the speed of lineage accumulation accelerates, the *γ*-statistic will have positive values (Fig. 4).

Tree imbalance of a phylogeny can be measured with the Sackin index. We use the Sackin index from the R package ApTreeshape (Bortolussi et al. 2006) based on the equations of Blum and François (2005):

$$I_S = \sum_{i=1}^{n} N_i \quad (3)$$

$$I_{Yule} = \frac{I_S - 2n\sum_{j=2}^{n}\frac{1}{j}}{n} \quad (4)$$

The Sackin index, denoted I_s (equation 3), measures the sum of inter-nodes *N*, indexed by *i*, that separate each species from the root of the phylogeny, including the root itself, accumulating this sum for the total number of species in the phylogeny, denoted *n*. We use the normalized version of the Sackin index, denoted I_{Yule} (equation 4), in order to compare phylogenies with different numbers of species. This normalized index subtracts from the non-normalized Sackin index value, I_s, twice the total number of species *n* in the phylogeny multiplied by the harmonic series of the species indices (indexed by *j*), all divided by the total number of species in the phylogeny *n*. The concept of phylogenetic balance is characterized by the evenness of diversification among clades (Blum and François 2005). An imbalanced phylogeny occurs when clades exhibit different diversification rates, and those with higher rates produce more descendants (Ricklefs 2007). Consequently, when a phylogeny shows clades with different diversification rates, the highly diverse one increases the number of inter-nodes between the tips and the root of the phylogeny. The Sackin index is close to zero for a balanced phylogeny and shows higher values when the phylogeny is imbalanced (Fig. 4).

Results

Effect of area and connectivity change on the rate of lineage accumulation

Overall the temporal dynamics of the speed of lineage accumulation display a hump-shaped curve for the baseline model (Fig. 2a). This indicates an initial acceleration followed by a deceleration in lineage accumulation in the phylogenies. The single-island equivalent null model has the same total area dynamics as the baseline model, and also shows an overall hump-shaped speed of lineage accumulation (Fig. 2a). When population size remains constant, the speed of lineage accumulation

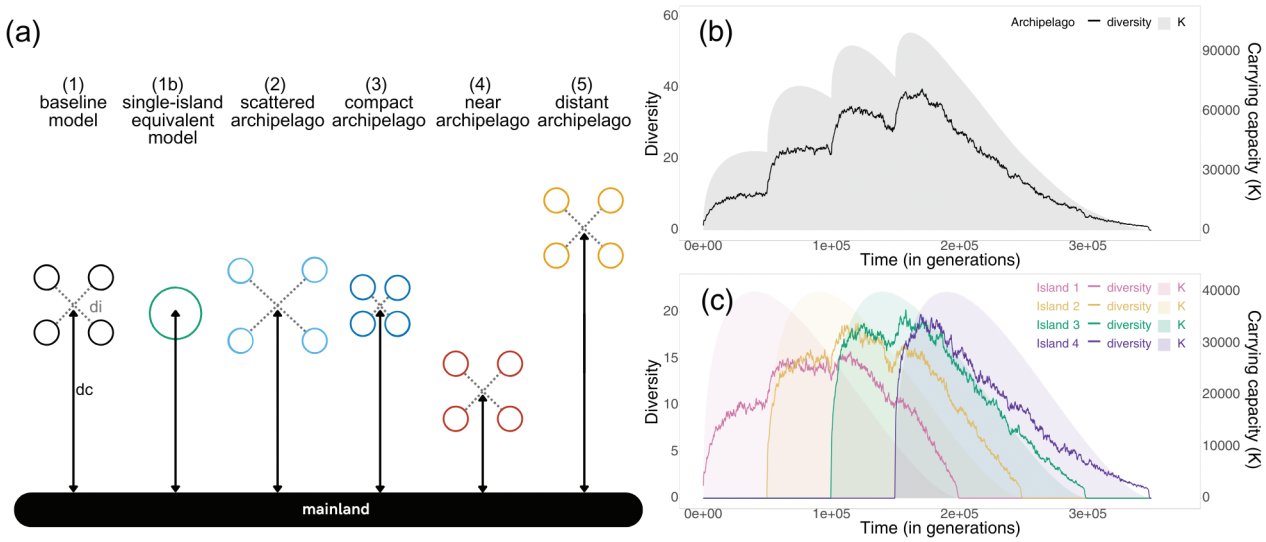

Figure 1. Model set-up (**a**) and diversity overtime in the archipelago model (**b** and **c**). The left panel (**a**) shows our framework for exploring five different geographical configurations based on two parameters: dc (distance from mainland) and di (inter-island distance). The baseline model, shown as configuration (1), serves as a reference. Configuration (1b) indicates the single-island equivalent null model. Configuration (2) represents a scattered archipelago defined by a high inter-island distance, configuration (3) depicts a compact archipelago characterized by a low inter-island distance. Configuration (4) represents a near archipelago with a short distance from the mainland, configuration (5) illustrates a distant archipelago featuring a long distance from the mainland. The right panels illustrate the average diversity in terms of species richness over thirty replicates of the archipelago model simulation (lines) and the corresponding carrying capacity (solid fill): the upper panel (**b**) presents the change in archipelago size and the total diversity which corresponds to the number of species present on the archipelago, while the lower panel (**c**) depicts the successive appearance of islands and local diversity which corresponds to the number of species present on an island, distinguished by different colors.

reaches a plateau, as we observe in an archipelago without geo-environmental dynamics (Suppl. material 1: appendix S3, fig. S2a). This indicates that the phase of acceleration of lineage accumulation mirrors the expansion of the total area, while the deceleration phase reflects its reduction in area (Fig. 2a).

Area expansion provides opportunities for more individuals to initiate divergent lineages through cladogenesis (Suppl. material 1: appendix S3, fig. S2b). When the total area is increasing, we observe an increasing total speciation rate (Suppl. material 1: appendix S3, fig. S2b), leading to an increase in diversity at the archipelago scale (Suppl. material 1: appendix S3, fig. S1d). These new lineages contribute to the accumulation of recent nodes in phylogenies, accelerating lineage accumulation over time.

When the islands of the archipelago enter their erosion phase, the total area of the archipelago starts to shrink, and the total population size decreases (Fig. 1b). This decline in population size results in a reduction in the number of speciation events (Suppl. material 1: appendix S3, fig. S2b). The proportion of recent lineages decreases, resulting in a slowdown in lineage accumulation (Fig. 2a). Additionally, the *per capita* probability of going extinct increases when the archipelago area decreases (Suppl. material 1: appendix S3, fig. S2f). Stochastic extinctions are more likely to affect smaller populations, which are mainly recent lineages (Suppl. material 1: appendix S3, fig. S3a). This leads to a slowdown of lineage accumulation as the archipelago enters the submergence phase (Fig. 2a).

The speed of lineage accumulation in the baseline model is higher than in the single-island equivalent model, as long as there are at least two islands in the archipelago (Fig. 2a). In the baseline model, each island emergence is followed by a sharp increase of the speed of lineage accumulation. In the single-island equivalent model, increases in the speed of lineage accumulation at the same time are lower (Fig. 2a). The only difference between the baseline model and the single-island equivalent is that inter-island speciation is prevented in the latter, so the faster accumulation of lineages in the baseline model is due to inter-island speciation. The growth of an archipelago by emergence of new islands sustains inter-island dispersal, leading to the splitting of populations across different islands. These geographically isolated populations may diverge from each other, enhancing the likelihood of speciation (Suppl. material 1: appendix S3, fig. S2b).

The rate of lineage accumulation in an archipelago is shaped by changes in total area which affects cladogenesis and by changes in inter-island connectivity which affects inter-island speciation (Fig. 2a).

Imprints of past geo-environmental dynamics on the rate of lineage accumulation

In the baseline model, phylogenies reflect evolutionary histories that have been influenced by past geographical changes. By contrast, the static null model generates

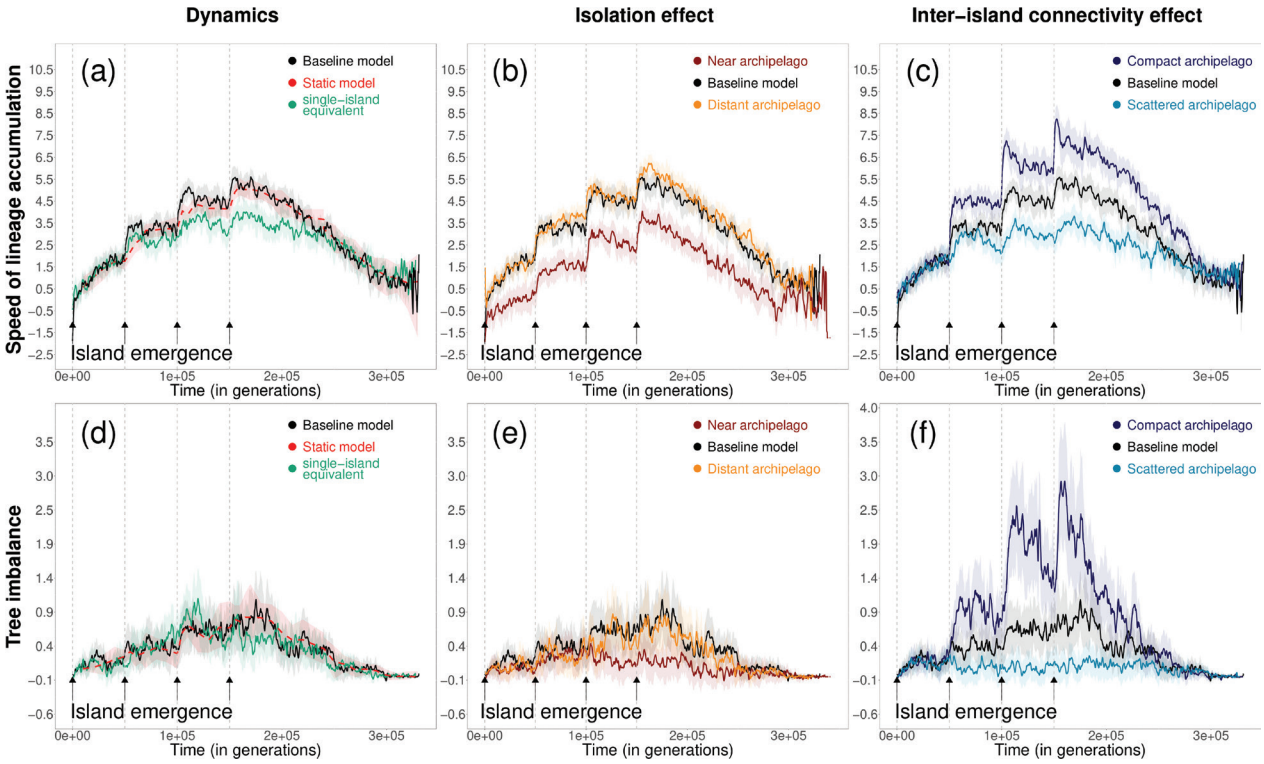

Figure 2. Comparison of the speed of lineage accumulation (measured by the γ-statistic, top panels), and tree imbalance (measured by the Sackin index, bottom panels). In the left panels (**a, d**) we compare the baseline model, where four islands emerge and submerge consecutively (black), with the static model (red) and the single-island equivalent model (green). In the middle panels (**b, e**), we compare the baseline model with different levels of archipelago isolation (near the mainland in red and distant in orange) and in the right panels (**c, f**), we compare the baseline model with different levels of inter-island connectivity (a compact archipelago in dark blue and a scattered archipelago in light blue). The four black arrows indicate the times of island emergence. Each curve is the mean over 30 replicates for each model, and shaded regions represent 95% confidence intervals.

phylogenies at each point in time based on the same geographical configuration as the baseline model, but with no past geographical changes. The overall dynamics of the speed of lineage accumulation is the same in both models (Fig. 2a), indicating that the rate of lineage accumulation is mainly influenced by the current area and inter-island connectivity of the archipelago. However, in the static model, we observe a delay in the rate of lineage accumulation at island emergence (Fig. 2a). The sharp increase of the speciation rate at this moment, due to islands rapidly reaching their maximum carrying capacity after emergence (Fig. 1c), leaves a distinct imprint of geographical changes on the rate of lineage accumulation. The difference between the baseline model and the static model rapidly erodes after island emergence (Fig. 2a), which suggests that past geographical dynamics leaves an imprint in the speed of lineage accumulation only when abrupt changes occur.

Effect of area and connectivity variations on tree imbalance

The baseline and single-island equivalent models share identical area dynamics over time and consistently show hump-shaped dynamics of tree imbalance (Fig. 2d). By contrast, tree imbalance is stationary when population size remains constant over time (Suppl. material 1: appendix S3, fig. S2d). This shows that an increase in the archipelago's area intensifies tree imbalance, while a decrease in area leads to more balanced phylogenies.

Area expansion of the archipelago allows for more cladogenetic speciation events (Suppl. material 1: appendix S, fig. S2b). Older lineages have on average higher abundances (Suppl. material 1: appendix S3, fig. S3b), and have a higher chance of experiencing these cladogenetic speciation events. New species tend to accumulate in the same older branches of the phylogeny, resulting in more imbalanced trees. As the archipelago shrinks, species with small population size are more likely to disappear stochastically. These species are mainly the newest ones (Suppl. material 1: appendix S3, fig. S3b), those who have previously accentuated tree imbalance. Their extinction reduces tree imbalance (Fig. 2d).

The baseline and single-island equivalent models show the same tree imbalance dynamics (Fig. 2d), i.e. changes in inter-island connectivity do not seem to impact phylogeny imbalance. However, as will be described below, we detect an effect of inter-island connectivity in tree imbalance by considering alternative spatial configurations, and this was particularly obvious in the case of a compact archipelago (Fig. 2f).

Imprints of past geo-environmental dynamics in tree imbalance

We do not observe any differences between the baseline model and the static null model in the dynamics of tree imbalance (Fig. 2d). This indicates that we do not detect any imprint of past geographical changes in tree imbalance.

Effect of the spatial configuration on the geo-environmental signal in phylogenies

We observe that a compact archipelago (Fig. 1a, configuration 3), with abundant inter-island dispersal compared to the baseline model, shows increased signal of geo-environmental dynamics in lineage accumulation (Fig. 2c) and allows for the detection of connectivity dynamics in the tree imbalance dynamics (Fig. 2f). In a compact archipelago, speciation rates exceed those of the baseline model (Fig. 3a), while extinction rate and the number of successful immigration events from the mainland, i.e. the number of mainland species that reached the archipelago and actually diverged into insular lineages, remain comparable (Fig. 3b and Fig. 3c). Each immigration event from the mainland leads to larger evolutionary radiations (Fig. 3d), demonstrated by an increase of the rate of lineage accumulation compared to the baseline model (Fig. 2c). The distribution of diversity among the colonist lineages (i.e. lineages originating from the immigration of a mainland species) is uneven (Fig. 3d), resulting in highly imbalanced phylogenies (Fig. 2f). The phylogeny of a compact archipelago is characterized by a dominant colonist lineage that has recently performed large evolutionary radiations alongside less diverse colonist lineages. (Fig. 4a).

We observe that a scattered archipelago (Fig. 1a, configuration 2), with reduced inter-island dispersal compared to the baseline model, shows softened changes over time of the speed of lineage accumulation, and that those of tree imbalance become undetectable (Fig. 2c and Fig. 2f). Compared

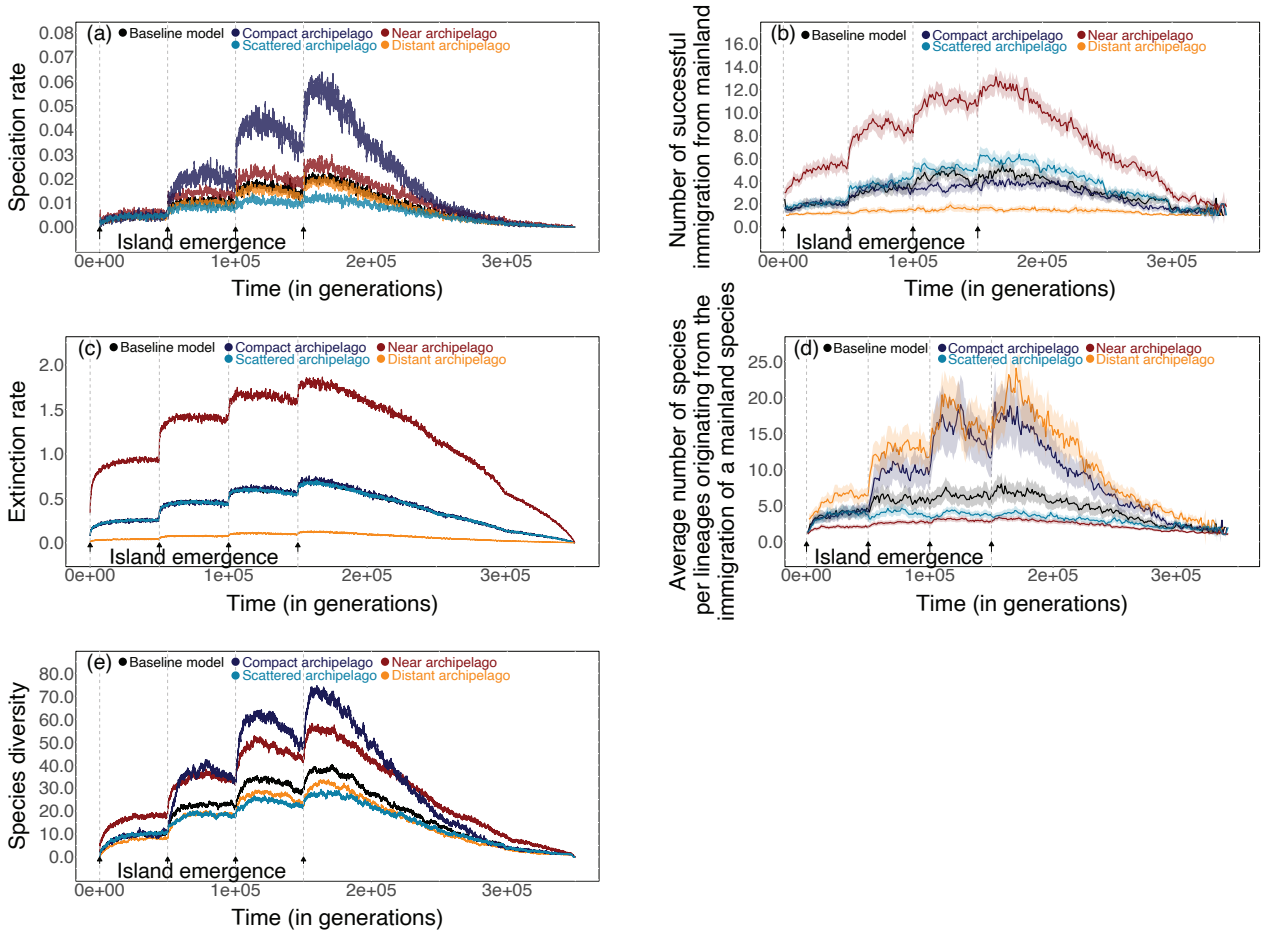

Figure 3. Behavior of various summary statistics over time and between models. Left panels show the speciation (**a**) and extinction (**c**) rates, and (**e**) the number of species over time. Each curve is the mean over 30 replicates for each model. Right panels show the number of successful immigrations from mainland (**b**), i.e. the number of mainland lineages that migrated to the archipelago and actually diverge into insular lineages, and the average number of species per colonist lineages (**d**), i.e. the average number of species descendants of an immigration event from the mainland for each immigration event, each curve is the mean over 30 replicates for each model and shaded regions are 95% confidence intervals. The four black arrows indicate the times of island emergence in the archipelagos. All plots are done for the baseline model (black) and for archipelagos with different spatial configurations: a compact archipelago (dark blue), a scattered archipelago (light blue), a near archipelago (red) and a distant archipelago (orange).

to the baseline model, the scattered archipelago shows lower speciation rates (Fig. 3a) and similar extinction and number of successful immigration events from the mainland (Fig. 3b and Fig. 3c). Each immigration from the mainland gives rise to a few species (Fig. 3d). This type of archipelago inhibits inter-island dispersal, resulting in a dynamics of the speed of lineage accumulation with an imprint of area change without the cumulative effect of island emergence dynamics, the speed of lineage accumulation is lower than the baseline model (Fig. 2c). We observe the loss of inter-island connectivity in tree imbalance which does not show any signal of island emergence (Fig. 2f), indicating a balanced distribution of diversity in the phylogenies (Fig. 4c).

A near archipelago (Fig. 1a, configuration 4), with abundant mainland dispersal compared to the baseline model, diminishes the values of the speed of lineage accumulation without impacting its dynamics (Fig. 2b). However, the effect of geo-environmental dynamics becomes undetectable in the tree imbalance (Fig. 2e). A near archipelago shows slightly higher speciation rates than the baseline model (Fig. 3a), while the rates of extinction and the number of successful immigration events from the mainland are substantially higher (Fig. 3b and Fig. 3c). Phylogenies are composed of a high number of colonist lineages, i.e. connected to ancestral branches in the phylogenies, reducing the speed of lineage accumulation values (Fig. 2b). Each of these colonist lineages diversifies into only a limited number of species (Fig. 3d), inducing balanced phylogenies, and erasing the geo-environmental signal in tree imbalance dynamics (Fig. 2e).

We observe that a distant archipelago (Fig. 1a, configuration 5), with lower mainland dispersal than in the baseline model, has the same signal of geo-environmental dynamics in lineage accumulation and tree imbalance as the one of the baseline model (Fig. 2b and Fig. 2e). In a distant archipelago, the speciation rate is similar to the baseline model (Fig. 3a) but the extinction rate and the number of successful immigration events from the mainland are substantially reduced (Fig. 3b and Fig. 3c). Phylogenies display few successful immigration events from the mainland but large evolutionary radiations (Fig. 3d). Combined with low levels of dispersal from the mainland, the phylogeny results in a unique colonist lineage representing the diversity of the archipelago (Fig. 3b). We do not see any effect on tree imbalance, which varies only with area, similarly to the dynamics of tree imbalance in the baseline model (Fig. 2e).

Discussion

We show that temporal changes in two important features of an archipelago, area and inter-island connectivity, have a positive effect on the speed of lineage accumulation and tree imbalance. Our results strongly suggest that the geo-environmental dynamics of an archipelago likely affect phylogenetic patterns in present-day island species communities. Past environmental dynamics may leave imprints in phylogenies, particularly during substantial and rapid environmental changes, such as island emergence, which abruptly increases the archipelago carrying capacity. Our results indicate that the effects of an archipelago geo-environmental dynamics on phylogenetic patterns depend on the geographical configuration of the archipelago. Overall, our results underscore the importance of considering historical environmental influences when interpreting phylogenetic patterns as past geological and environmental histories leave predictable imprints on phylogenies.

Effect of area and connectivity changes on phylogenetic tree shape

We demonstrated that, in an archipelago where total area follows a hump shape, the speed of lineage accumulation also follows a hump shape. This indicates that larger area accelerates the accumulation of recent lineages, which is in agreement with one of the predictions of the island biogeography theory that the probability of extinction is reduced and the probability of speciation is increased on larger areas (MacArthur and Wilson 1967; Whittaker et al. 2008; Valente et al. 2020; Tao et al. 2021). This result also corroborates the view that larger archipelagos, in terms of total area, are more likely to exhibit larger evolutionary radiations, which is a trend observed in many studies (Losos and Schluter 2000; Valente et al. 2020).

Tree imbalance positively changes with area and consequently follows a hump-shaped function of time. This reflects a positive effect of increasing area on the heterogeneity in speciation and extinction probabilities between colonist lineages. The increasing uneven distribution of species abundances between colonist lineages may be explained by a priority effect, i.e. the first species to colonize an empty island has an abundance advantage over later-arriving competitors by monopolizing local resources (Chase 2003; Fukami et al. 2007; Urban and De Meester 2009; Fukami 2015; De Meester et al. 2016). Because mainland species do not all colonize at the same time, each population does not reach the same level of abundance depending on the order and timing of arrival and demographic stochasticity. The reduction of the tree imbalance that we found in archipelagos close to the mainland supports this hypothesis, as high dispersal reduces the time lag between the first colonizer and the later ones, and increases the frequency at which mainland species arrive on the archipelago (De Meester et al. 2016). Besides, high levels of tree imbalance were reached under strong levels of inter-island dispersal only. Thus, inter-island dispersal might amplify the priority effect at the archipelago scale. As inter-island dispersal favors immigration from a neighboring island, it increases insular population abundances at the archipelago scale. The first arriving lineages monopolize the resources of the archipelago and hinder the expansion of newly arriving lineages from the mainland, as they face competition with dominant insular lineages. Phylogenies of island communities in archipelagos with high levels of inter-island dispersal can be highly imbalanced. However, because our model is ecologically neutral,

priority effects encountered in our simulations are not due to ecological differences between species, and hence cannot explain systems where such differences are the main driver of community assembly (Fukami et al. 2015; Shaw and Gillespie 2016), a situation that might be common in nature (see e.g. Fernández-Palacios et al. 2021).

Effect of past geo-environmental changes on phylogenetic tree shape

We demonstrated that both the rate of lineage accumulation and tree imbalance are mainly affected by the current geographical configuration of the archipelago. The rate of lineage accumulation depends on past geo-environmental changes when abrupt changes occur, such as island emergence, while tree imbalance is determined by current geographical configuration only. These results support the contention that the growth phase of island ontogeny is a crucial moment that promotes evolutionary opportunities (Carson et al. 1990; Whittaker et al. 2008; Whittaker et al. 2010), in our context by leaving an imprint in phylogenies due to evolutionary radiations. However, in our model, time between island emergences is relatively short and constant. This geological setting is not the general rule for most archipelagos in nature. Typically in hotspot archipelagos, the lag time between island emergence depends on the speed of the tectonic plate which carries an island away from the mantle plume head and induces the ontogeny of the next island. The plate speed variation may cause changes in an archipelago geo-environmental dynamics by varying the duration of the volcanic phase (Ali and Meiri 2023). Thus, islands of similar age can be at different ontogenic stage when occurring in different archipelagos with different geological dynamics (Triantis et al. 2016). This suggests that the total area of an archipelago does not necessarily vary according to a hump-shaped curve, as assumed in our model. Therefore, the speed of lineage accumulation may depict different dynamics depending on the geological regime of the archipelago and different phylogenetic imprints may be observable if the dynamics of an archipelago are different from our model.

Effect of the spatial configuration on phylogenetic tree shape

We demonstrated that the spatial configuration of the archipelago influences the effects of the geo-environmental dynamics on the shape of phylogenies. Higher inter-island dispersal (i.e. islands closer to each other) enhances the effect of archipelago geo-environmental dynamics on the rate of lineage accumulation. Emergence of islands exerts a positive and cumulative effect on the rate of lineage accumulation, because islands do accumulate rapidly more species at the beginning of their ontogeny, and because connectivity with neighboring islands induces inter-island speciation. Higher

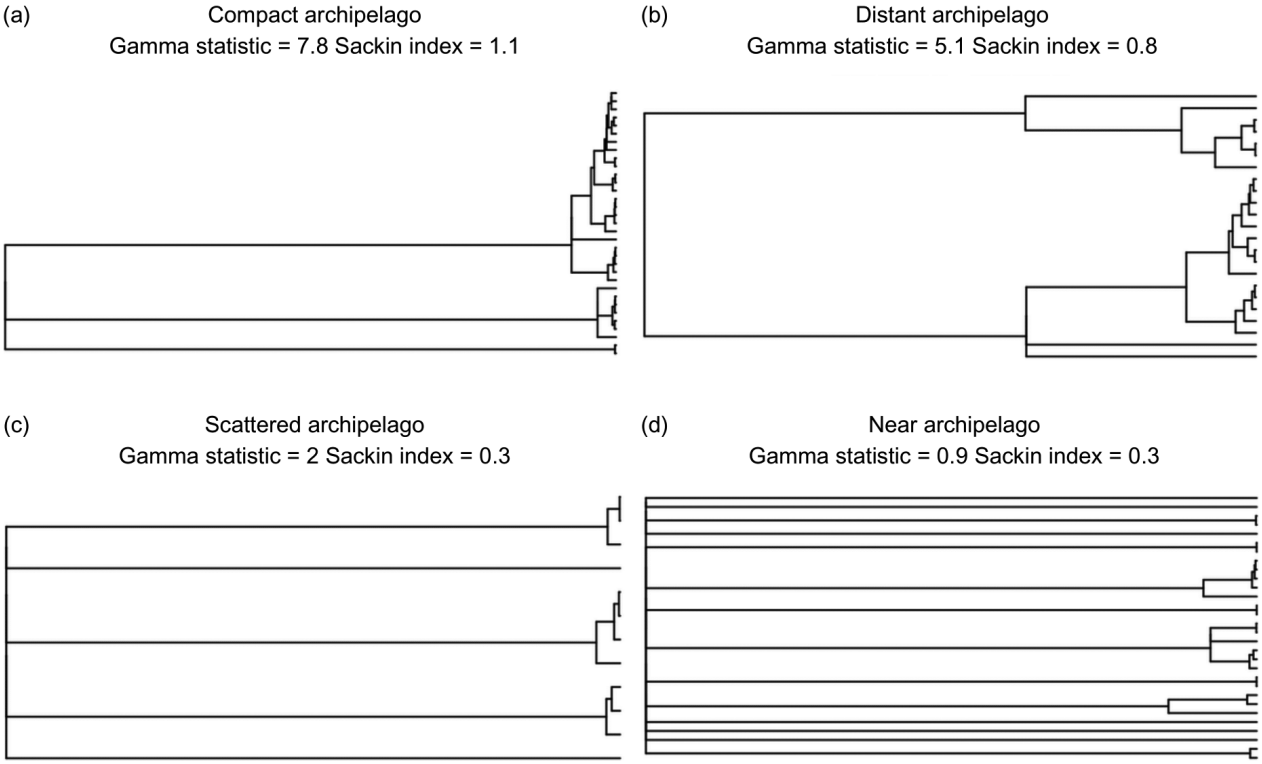

Figure 4. Example of phylogenies obtained for different spatial configurations of archipelagos with their corresponding speed of lineage accumulation (measured by the γ-statistic) and tree imbalance (measured by the Sackin index). The upper panels describe a compact archipelago (**a**) and a distant archipelago (**b**). The lower panels describe a scattered archipelago (**c**) and a near archipelago (**d**). These phylogenies are extracted from a simulation replicate. All four phylogenies are approximately the same age (around 200,000 generations, which in our model corresponds to an archipelago whose four islands have emerged).

inter-island connectivity leads to more imbalanced phylogenies, likely reflecting the fact that a small number of colonist lineages give rise to a substantial portion of the archipelago's biodiversity. Thus, the order of immigration events from the mainland strongly influences the probability that a colonist lineage undergoes speciation on the islands, because the priority effect is strongly enhanced by higher inter-island connectivity. In the particular case of a scattered archipelago (islands far from each other), we find that variations of archipelago area have no detectable effect on tree imbalance and the signal of geo-environmental dynamics in the rate of lineage accumulation is significantly decreased. This is consistent with our hypothesis that the phylogenetic patterns observed in an archipelago strongly depend on variations in area and connectivity between islands.

If islands are close to the mainland, higher dispersal opportunities lead to more frequent immigration from the mainland which may induce higher competition for space (Tao et al. 2021). Thus high connectivity between mainland and islands implies a high probability for recent lineages to go extinct, resulting in a high turnover of species on the archipelago. Since species do not persist for a long time on the archipelago, newly arriving clades can establish. Thus, a stronger turnover of ancestral mainland lineages diminishes the rate of lineage accumulation.

Also, high connectivity between mainland and islands decreases the effect of landscape dynamics in tree imbalance. As stated before, higher dispersal reduces the time lag between the first colonizer and the late ones (De Meester et al. 2016). This effect decreases the disparities of abundances between colonist lineages and reduces the imbalance of phylogenies. By contrast, when mainland connectivity decreases, we detect a substantial decrease in the extinction rate due to a low competition for space between colonist lineages. This results in phylogenies with few successful immigration events from the mainland with large evolutionary radiations, similarly to previous models investigating the positive effect of isolation on endemic radiation (Rosindell and Phillimore 2011; Cabral et al. 2019a). Consequently, the effect of landscape dynamics on the rate of lineage accumulation is maintained when isolation increases. However, we do not detect any changes in the tree imbalance signal compared to the baseline model when the archipelago is isolated, probably due to phylogenies having a unique colonist lineage. Overall, although we explored different intensities of dispersal, the values used in our simulations never exceeded the threshold above which inter-island or mainland dispersion inhibits speciation according to the Intermediate Dispersal Hypothesis (see Yamaguchi 2022 for a review).

Limitations of this study and perspectives

Several models and empirical studies have shown that, in addition to the overall spatial configuration of the archipelago, explicit position of islands relative to one another in an archipelago also plays a role in the buildup of island biodiversity (Cabral et al. 2014; Gascuel et al. 2016; Aguilée et al. 2021; Jõks et al. 2021) and that it can also depend on island age (Emerson and Gillespie 2008; Bunnefeld and Phillimore 2012; Ávila et al. 2019). Our results show that these spatially explicit effects could be difficult to interpret if based on phylogenies only, as the lineage accumulation and tree imbalance dynamics are strongly influenced by inter-island connectivity and archipelago isolation. For example, a scattered archipelago, whose diversity is mainly driven by single island in situ speciation, would be more likely to show a correlation between island age (and relative spatial position) and phylogenetic diversity than a compact archipelago, which would rather show a relationship with the archipelago's age as few colonist lineages monopolize most of the archipelago surface independently of the island order of emergence. Yet, our results are in line with archipelago scale studies that link area, spatial structure and isolation and the size of evolutionary radiations (Haydon et al. 1993; Gillespie 2004; Helmus and Ives 2012; Valente et al. 2020; Tao et al. 2021). This highlights the importance of integrating geo-environmental dynamics and geographic structure when interpreting phylogenies, and of accounting for both archipelago-level and island-level spatial scale.

Empirical phylogenies usually show a slowdown of diversification (Phillimore and Price 2008; McPeek et al. 2008; Rabosky and Lovette 2008; Etienne and Rosindell 2012), which corresponds to a negative γ-statistic value. In contrast, γ-statistic is always positive in our results, indicating an acceleration of the speed of lineage accumulation, even when the archipelago declines in area. This is because we assume that mainland species appear all at the same time at the beginning of the simulation. Dispersal from the mainland leads to the introduction of ancient lineages in the phylogenies of the archipelago, pulling the γ-statistic towards positive values. This effect is indeed reversed at the very end of the archipelago's life where there are very few species remaining on the archipelago: phylogenies contain almost only ancestral nodes, pulling the γ-statistic to negative values as it mimics an extreme deceleration of lineage accumulation in the present. However, this does not impact our conclusions, which are all based on the dynamics of the γ-statistic and its relative value when comparing different geographical settings. Nevertheless, the neutrality of our model constrains our results. It would be useful to develop our hypotheses further by including species-specific effects based on non-neutral models (Cabral et al. 2019b).

We found that geological factors can influence diversification patterns by isolating populations on the different islands of an archipelago and they are reflected in phylogeny shape. We demonstrated that changes in area and number of islands over time leave detectable imprints on the shape of phylogenies, and that the geographical configuration of the archipelago can further modulate these imprints. Thus, it is difficult to disentangle the temporal and spatial effects of geographical structure from the lineage accumulation or tree imbalance patterns based solely on the study of phylogenetic topologies. This confounding effect of the archipelago's geography could substantially impact the interpretation of phylogenies in dynamic contexts, especially in the context of

islands. As islands are surrounded by water, sea-level variation is another important factor having geographical consequences which alters island area and connectivity between islands over time (Rijsdijk et al. 2014; Fernández-Palacios et al. 2016; Borregaard et al. 2017; Norder et al. 2018, 2019). Because sea-level fluctuations occur on a faster timescale than geological changes and because we found that rapid past geo-environmental changes may have a substantial imprint on phylogeny structure, we expect climatic factors and associated sea level fluctuations to introduce additional complexity when attempting to reconstruct the biogeographic history of a community based on its phylogenetic patterns.

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Author contributions

Robin Aguilée conceived the study design and setting, and supervised the project. Amandine Vidal-Hosteng developed the analytical methods and performed the simulations and data analysis. All authors discussed the results. Amandine Vidal-Hosteng wrote the manuscript with support and critical review from Robin Aguilée, Rampal S. Etienne and Christophe Thébaud.

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Supplementary materials

Supplementary material 1

appendix S1: Geo-environmental dynamics; appendix S2: Population dynamics; appendix S3: Supplementary tables and figures (figures S1–S4, table S1) (.pdf)
Link: https://doi.org/10.21425/fob.18.146650.suppl1