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RESEARCH ARTICLE

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Ancient geological dynamics impact neutral biodiversity accumulation and are detectable in phylogenetic reconstructions

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Abstract

Aim: Landmasses have been continuously modified by tectonic activity, the breakup and collision of landmasses is thought to have generated or suppressed ecological opportunities, altering the rates of speciation, dispersal and extinction. However, the extent to which the signatures of past geological events are retained in modern biodiversity patterns—or obliterated by recent ecological dynamics—remains unresolved. We aim to identify the fingerprint of different scenarios of geological activity on phylogenetic trees and geographic range size distributions.

Location: Global.

Time period: Geological time.

Major taxa studied: Theoretical predictions for any taxa.

Methods: We conducted spatially explicit simulations under a neutral model of range evolution, speciation and extinction for three different geological scenarios that differed in their geological histories. We set a limit on the number of populations that locally can coexist, which, along with the geographic boundaries of landmasses, influences the rate of range expansion.

Results: Our results demonstrate regions of similar size, age and ecological limits will differ in richness and macroevolutionary patterns based solely on the geological history of landmass breakup and collision even in the absence of species' ecological differences, that is, neutrality. When landmasses collide, regional richness is higher, lineages exhibit more similar rates of speciation and phylogenetic trees are more balanced than in the geologically static scenario. Stringent local limits to coexistence yield lower regional diversity but in general do not affect our ability to distinguish geological scenarios.

Main conclusions: These findings provide an alternative explanation for existence of some hotspots of diversity in areas of high geological activity. Although a limit on the number of coexisting species largely influences regional diversity, its contribution to phylogenetic patterns is lower than variation in per-capita rates of speciation and extirpation. Importantly, these findings demonstrate the potential for inferring past geological history from distributions of phylogenies and range sizes.

KEYWORDS

biotic interchange, diversification, local species saturation, macroevolutionary dynamics, range size distribution, regional richness

1 | INTRODUCTION

The speed of plate tectonics varies across tectonic plates, ranging from 4 to 20 cm a year (Kumar et al., 2007; Torsvik et al., 1996), generating mountain ranges, dividing continents and fusing large landmasses. The importance of this geological upheaval for the distribution of life has not been overlooked (Stigall et al., 2017; Yoshida & Tokita, 2015). Its impact on the origin of new species by creating physical barriers, decreasing connectivity and limiting gene flow among populations has been verbally established (tectonics and provinciality; Valentine & Moores, 1972) and recently explored (Arteaga et al., 2012; Winston et al., 2017). However, the extent to which the signatures of past geological events are retained in modern macrodiversity patterns, or whether they are eroded by recent ecological dynamics, remains unresolved.

Two major consequences for biodiversity arise when two landmasses come into close proximity. First, species can expand their ranges into newly available land, which increases their abundance producing important changes in the community structure even under neutral ecological theory (Holland, 2018). As a consequence, the colonization of new land affects the probabilities of species extinction and speciation. The probability of extinction for a given species decreases as its geographic distribution increases (Staude et al., 2018), whereas widespread species are more likely to speciate than range-restricted species (Gaston, 1998; Rosenzweig, 1975). If geological activity does indeed influence the rates of diversification and merge different biotas, we expect an impact on the distribution of branching times in a phylogenetic tree. For instance, a phased increase in the opportunities for range expansion would foster more recent colonization, hinder recent extinction and leave a signature of increased recent diversification rates in the overall phylogenetic tree. Second, as sets of lineages from different geographic origins are brought into contact, the merged biota will reflect the outcome of two independent macroevolutionary histories. The geographic distributions and evolutionary relationships of each regional species pool result from independent processes that are specific within each biota. These recent and older processes can be reflected in phylogenetic reconstructions when fitting simple models of speciation and extinction or measuring potential shifts in diversification regime across them. If this is the case, it may be possible to detect the extent of past geological upheaval from phylogenies, but this has not yet been established.

Here, we investigated the impact of geological histories on species diversity—and on associated signatures left in modern phylogenies—using population-based modelling. In our simulations, we modelled diversification processes under different geological scenarios with per-lineage rates of speciation and extinction that were a function of local (patch-based) processes (i.e. colonization γ, extirpation/local extinction μ, speciation λ and local species saturation K). We modelled three geological scenarios that differed in their dynamics of collision and breakup of landmasses: (a) the fusion of two equal-sized landmasses into one region in the 'Single Connection' scenario, (b) the 'Double Connection' scenario, which alternates phases of collision and breakup, and (c) the 'Unchanged' scenario, which features a single region of the same size as in the other cases but with no geological activity (Figure 1). This model was neutral in that all populations across landmasses have the same local (or per patch) ecological limits and evolutionary rates. Consequently, resulting differences in per-lineage rates and resulting biodiversity patterns were due to geological events rather than ecological differences among populations. We built phylogenetic trees using the record of lineage births, deaths and ancestor–descendant relationships to emulate those standard phylogenetic trees reconstructed by molecular methods using extant species. We report the change in the degree of phylogenetic tree imbalance, variation in reconstructed diversification rates, distribution of geographic range sizes and regional richness across geological histories under a range of model parameters (i.e. combinations of high, intermediate and low values of μ, λ and K). We demonstrate that current variation in evolutionary histories and patterns of diversity across regions and clades can be explained by tectonic dynamism even in the absence of differences in ecological features of species, clade age, region size or ecological space.

2 | METHODS

2.1 | Dynamics of the model on single landmasses

We developed a population-based simulation model based on Herrera-Alsina et al. (2018), in which populations exist in a gridded

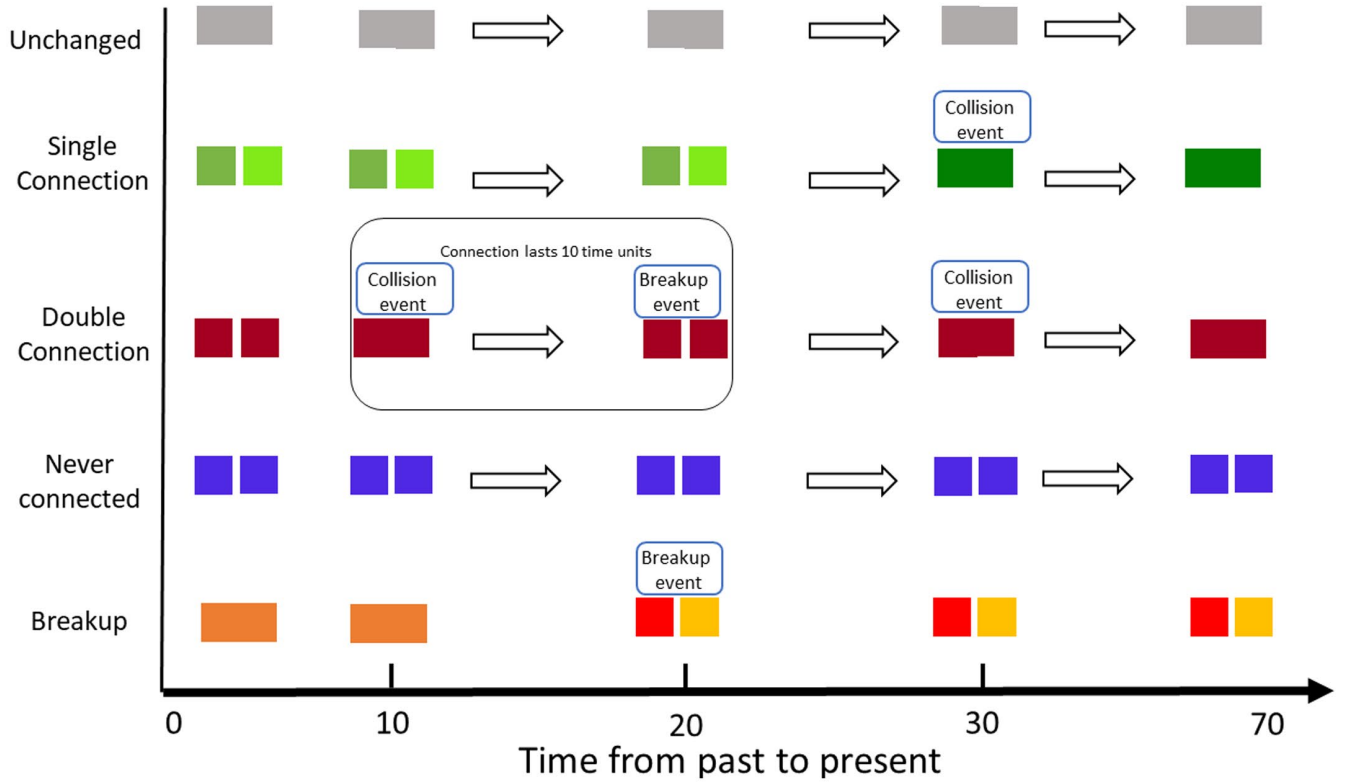

FIGURE 1 Five modelled geological scenarios for the development of a geographic region over time. In the Unchanged scenario, the region does not change over time. In the Single Connection scenario, we modelled a region that is formed by the union (i.e. collision) of two landmasses of the same size at some point in time. In the Double Connection scenario, the geological history of a region is highly dynamic and includes collision followed by breakup and re-collision of two landmasses. In the Never-connected scenario, two independent landmasses are considered as a single unit and there is no change in landmass configuration. The Breakup scenario shows a region formed by two landmasses that drift apart

domain. Each cell may contain a number of species (one population per species) equal to the cell carrying capacity (K); thus, we assume that there is a limit on the number of species that can coexist in a cell. Every cell of the domain has the same K. Species' range expansion takes place through colonization of neighbouring cells (four adjacent cells in the cardinal directions) at rate γ and range contraction happens by removing a population from a cell at rate μ (local extinction, extirpation hereafter). Species identity does not influence the likelihood of successful colonization of a species into a cell; a cell can be colonized by any species as long as the cell's carrying capacity has not been reached. The range expansion of species is, therefore, limited by local saturation and the rigid geographic boundaries of the landmass. Early on in the simulation, species range expansion is not restricted, as most of the domain is empty and all attempts to colonize adjacent cells will be successful. Later on, when cells start being saturated with species, expanding species will encounter cells that are not available for further expansion, which leads to unsuccessful colonization events. In other words, although per-capita rates of colonization are constant over time, the probability of successful colonization is a function of the saturation degree of the system. Speciation happens when a population of a given species transforms into a new one at rate λ, which is equivalent to point-mutation speciation (Hubbell, 2001). Populations across species are ecologically equivalent to one another: they have the same rates of colonization, extirpation and speciation regardless of their species identity. Note that because the overall rate of these processes at the species level depends on the number of cells occupied by the species (range size), the per-lineage rates of speciation, extirpation and speciation will be different across species that differ in range size. Thus, species diversification rates are neutral with respect to population-level processes but are strongly influenced by differences among lineages in biogeographic histories, which influence range size.

The dynamics of this model are fully described in Herrera-Alsina et al. (2018). Briefly: (a) the simulation starts with one population of a single species randomly placed within the domain; (b) species first expand their range size to occupy most of the domain; (c) as speciation events take place, new species appear and expand their range, increasing local species richness; (d) clade diversification rate increases as all species continue range expansion and (v) eventually, most of the cells reach K, which causes range expansion to slow, but regional richness continues to increase, due to species turnover, until the system reaches a dynamic equilibrium (Supporting Information Figure S4). We applied this model to examine the consequences of geographic integration (see next section) of two independent areas that are already at steady state.

2.2 | Geological scenarios

With the model outlined above, we simulated the evolution of clades in two landmasses (Landmass 1 and Landmass 2) under different geological histories (Figure 1). Landmass 1 and Landmass 2 have the same area (same number of cells), shape and the same local carrying capacity *K*. Species on both landmasses have the same rates of colonization (γ), extirpation (μ) and per-population speciation (λ). We considered three geological scenarios of landmass shifts: 'Single Connection', 'Double connection' and 'Unchanged'. Under the 'Single Connection' scenario Landmass 1 and Landmass 2, having independently reached a regional dynamic equilibrium, come together to form Landmass 1 + 2. Lineages from Landmass 1 can then start to spread onto Landmass 2 and vice versa. This will only be possible when extirpation of a population opens a spot for colonization. The shape of the phylogenetic tree (see next section) in each landmass is tracked from the beginning of the simulation until they collide. After collision, we combined the lineages into one phylogenetic tree (as we are interested in the patterns of the entire clade) and tracked its shape until the end of simulation.

In the 'Double Connection scenario', Landmass 1 and Landmass 2 start independently, collide and continue together for some time until they separate again. This means that, after the breakup, Landmass 1 and Landmass 2 are independent, but they now have a shared legacy. Both landmasses evolve independently until a second collision event takes place, after which they remain as a single landmass until the end of the simulation. Before landmass collision or breakup, we ensure the system had reached an equilibrium in regional richness (Supporting Information Figure S5). Finally, in the 'Unchanged' scenario, a clade evolves in a single, large region of the same size as Landmass 1 + 2, without any shift in its geological configuration. In all scenarios Landmasses were rectangle-shaped, and they collided or broke up along their widest side. Because simulations in Single and Double Connection models start with one species in each landmass (two in total), whereas simulations in the Unchanged scenario start with a single species, we tested whether this initial condition might have an effect. Supporting Information Figure S2 shows that this initial condition does not influence the model behaviour as both cases rapidly become equal.

2.3 | Shape of phylogenies and parameter combinations

For each scenario, we built phylogenetic trees using the information tracked during the simulations: date of birth of each species and its parental species. The ancestor–descendant relationships along with the timing of speciation events become the topology and branch lengths of the phylogenetic tree (L2phylo function in DDD R package; Etienne et al., 2012). We did not include extinct species, in order to resemble the reconstructed phylogenies that are usually obtained using molecular information from extant species. We used the ΔR metric to measure the variation in diversification rate over time, which compares the rate of diversification between the first and the second halves of a tree (Pigot et al., 2010). Positive values of ΔR point to an increase in diversification, whereas negative values suggest a slowdown. We also measured tree imbalance using the Sackin index (Blum & Francois, 2005), which quantifies the departure of a reconstructed tree from a hypothetical tree produced by a pure birth process where all lineages have the same chance of speciating. Finally, we used a maximum likelihood approach to fit a standard birth–death process (Etienne et al., 2012) to the reconstructed trees to estimate the per-lineage speciation and extinction rates. We tracked species' range size through the simulation.

We ran simulations with combinations of high, intermediate and low values of λ, μ and *K* (27 different parameter combinations in total; Supporting Information Table S1); we report the results of 50 replicates for each parameter set and geological scenario. The rate of range evolution is the difference between colonization and local extinction (γ − μ). The model ran in continuous time where waiting times between events were taken from an exponential distribution with a mean equal to the sum of all population rates (Gillespie algorithm). Simulated time is, therefore, expressed in plain time units rather than in thousands or millions of years. The simulated time was chosen to ensure the system would reach an dynamic equilibrium given the parameter values. Parameter values were arbitrarily chosen but selected to cover a broad range of parameter combinations which yield to important variation in the response variables (see Results). Altering the magnitude of the parameters leads to changes in the total simulated time required to reach equilibrium. Colonization rate = 2 indicates that two colonization events are to take place per-population within one time unit. For instance, in the first time unit of the simulation, the first population in the grid will colonize two more cells and these two new populations could each colonize another two. Parameters are not bounded between 0 and 1 because they are not probabilities but unitless rates whose magnitude should be compared with one another. Significant differences between geological histories are calculated through comparison of the medians over the 50 replicate simulations.

3 | RESULTS

We found that two geographic regions with different geological histories show important differences in biodiversity patterns even if they are of the same size and their populations are subject to the same rates of ecological and evolutionary processes (Figures 2, 3 and 4). The scenarios differ in geographic range size frequency, probabilities of speciation across lineages, patterns of diversification and species richness.

The Single Connection scenario produces geographic range size distributions that are less skewed (i.e. asymmetry in distribution frequency) than the Unchanged scenario, which means: (a) a

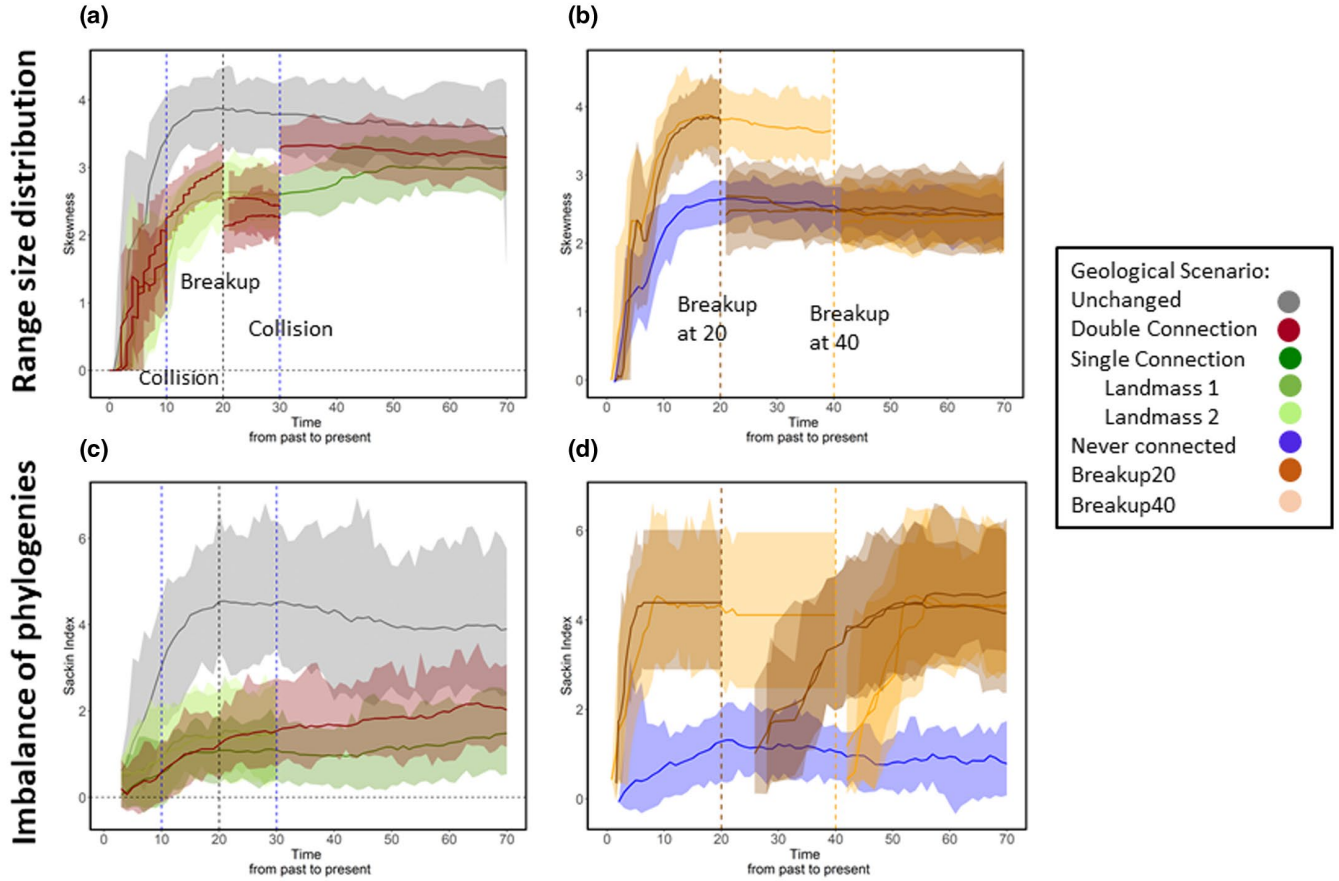

FIGURE 2 Changes in the species' range size distribution (skewness of distribution) and in the shape of reconstructed phylogenies (Sackin index of tree imbalance with greater value indicating higher imbalance) over evolutionary time and across geological scenarios. Panels (a) and (c) display the evolution of regions whose present-day configuration is a single, large landmass. Panels (b) and (d) show regions that are formed by two small and independent landmasses in the present time. The figure shows 50 replicate simulations (solid line shows the mean, shaded area the 95% intervals of confidence) with intermediate rates of per-population speciation, range evolution and local carrying capacity (see Supporting Information Table S1)

smaller number of range-restricted species, and (b) more species attaining medium- and large-sized ranges. This pattern appeared at an early stage in the simulation time, prior to landmass collision (Figure 2a), indicating that the difference in size between Landmass 1 (or Landmass 2) and an area of Landmass 1 + 2 is responsible for the increased homogeneity in range size. In addition, this early onset suggests that range size distributions are determined primarily during the period that preceded the landmasses colliding and remained relatively stable afterwards. Moreover, when Landmasses 1 and 2 collided to form a larger area, the distribution of range sizes remained more homogeneous than expected for an area of the same size that experienced no geological change (Figures 2a and 3). The difference between the unchanged and the Double Connection scenarios was similar to the difference between the Unchanged and Single Connection scenarios. However, range size distributions produced under the Double Connection scenario were associated with higher values of skewness compared to the single connection scenario (Figure 3). This is due to an earlier collision of landmasses in the Double Connection scenario, which increases geographic space availability so that early born species can attain large range sizes. This increases the heterogeneity in range sizes across species and, in turn, makes the Double Connection scenario become more similar to the Unchanged scenario than to the Single Connection case. When the regional richness is low due to a combination of low per-capita rate of speciation and intermediate/high extirpation, species have more homogeneous range sizes, with a tendency towards large ones. Importantly, this is the only case where range size distributions do not inform on the past geological history of a region.

Our model featured an emergent positive relationship between geographic range size and diversification, such that heterogeneity in range size caused a differential probability of speciation events among species—a process reflected in the tree imbalance (i.e. the distribution of taxa among the different clades of a tree, measured with the Sackin index; Blum & Francois, 2005). The Sackin index indicated that phylogenetic trees under the Single and Double Connection scenarios were more balanced than under the Unchanged scenario (i.e. lineages produced a more similar number of descendants; Figures 2c and 4a). This difference was seen from an early stage in the simulations (Figure 2c), indicating that the size of the region has a substantial early impact on tree shape that is not eroded over time.

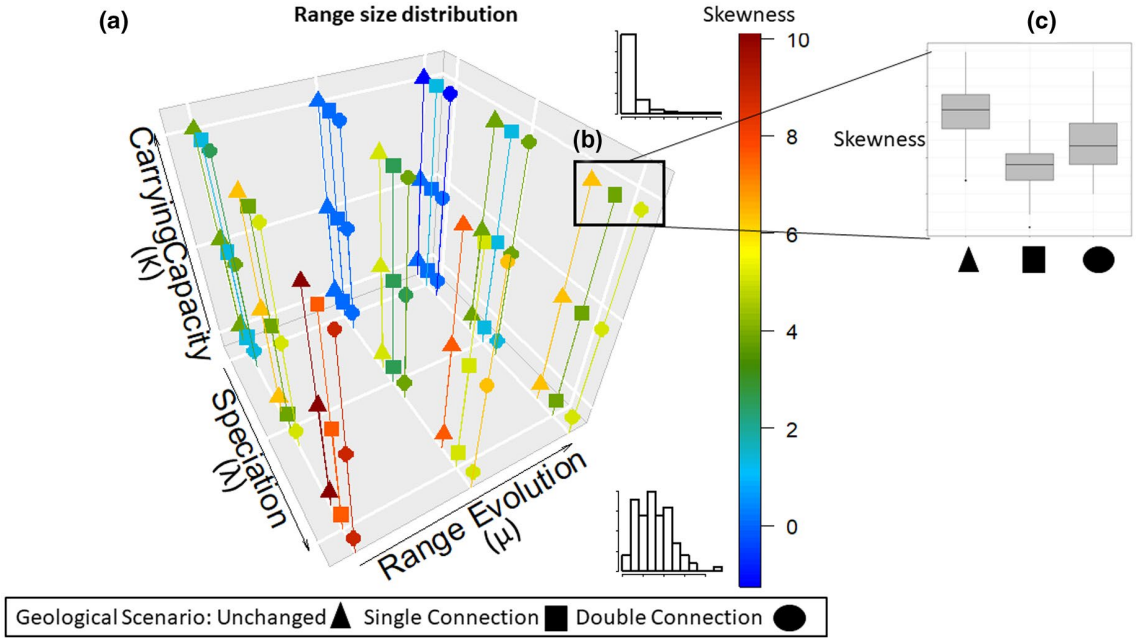

FIGURE 3 The distribution of species' geographic range size depends on (1) the combination of local limits to coexistence (carrying capacity) and per-population rates of speciation and range evolution (i.e. colonization–extirpation), and (2) the geological history of the region. We simulated clades with low, intermediate and high rates of speciation and range evolution along with three levels of local carrying capacity for a total of 27 parameter combinations. The 3-D plot (a) shows values of the skewness of range size distributions, ranging from low (cold colours) to high (warm colours) across the parameter space. Each parameter combination contains a cluster of geometric shapes (b) that represents the three different geological scenarios. For instance, the cluster shown in (b) is the outcome of high carrying capacity, high per-population speciation and high range evolution, and shows that with these parameters, the unchanged scenario (triangle) has higher skewness than the other two scenarios. Different colours of the geometric shapes indicate significant differences between geological histories, calculated through comparison of the median skewness over 50 replicate simulations [as in (c)]

However, in simulations with low per-population speciation rate (λ), or with the combination of intermediate λ and high extirpation rate (μ), the Unchanged and Single Connection scenarios produced similarly low Sackin values (i.e. balanced trees; Figure 4a), suggesting that the signatures of geological history on clades with very low net diversification rates were more difficult to detect. The Double Connection scenario produced trees that were more unbalanced than the Single Connection scenario, except when low λ or when intermediate λ is combined with high extirpation rate (Figure 4a).

Despite equal per-population rates across scenarios, the Single Connection scenario showed higher regional species richness (i.e. the total number of species in the entire area) than the Unchanged scenario. This difference in regional richness, however, faded when the rates of per-population speciation λ were intermediate or high (Figure 4c), and thus rates of species turnover were high enough to erase historical legacies of ancestral range dynamics in species richness, but *not* in phylogenetic patterns (see above paragraphs). We found that Single Connection scenario showed higher regional richness than Double Connection scenario only when λ was low (Figure 4c).

To explore whether the difference in richness and evolutionary patterns between Unchanged and Single Connection scenarios were due to area availability early in the simulation, we ran an extra scenario where a region was defined by two landmasses, representing the same total area as our other scenarios, but which never exchanged species (Figure 1). We found that this scenario holds similar regional richness to the Single Connection scenario. Figure 2b shows, on the one hand, that the reduction in size of a region leads to range size distributions that are identical to those in a region that has kept its [small] size over time. On the other hand, the interchange of lineages (i.e. Single/Double connection; Figure 2a and b) increases the skewness of range size distribution. We found that after a breakup event, phylogenetic trees acquire a more balanced shape but this is a transient pattern as the imbalance will gain a similar level before landmass breakup (Figure 2c). Importantly, clades in the never-connected scenario have more balanced trees than clades in the Double Connection scenario, which points to the contribution of lineage interchange to phylogenetic patterns.

Additionally to the never-connected scenario, we simulated a landmass that breaks up into two landmasses that are separated and independent for the rest of the simulation (Figure 1). In Breakup20, the initial landmass remained as a single unit for 20 time units before drifting apart, whereas Breakup40 did for 40 time units. Note that Figure 2b and d show the evolution of the never-connected scenario where two areas of the same size are considered as a single unit but the dynamics of the system under Breakup20 and Breakup40 are shown as they were independent landmasses. This allows showing whether there is an effect of the duration of connection on biodiversity patterns. We found that neither regional richness nor range

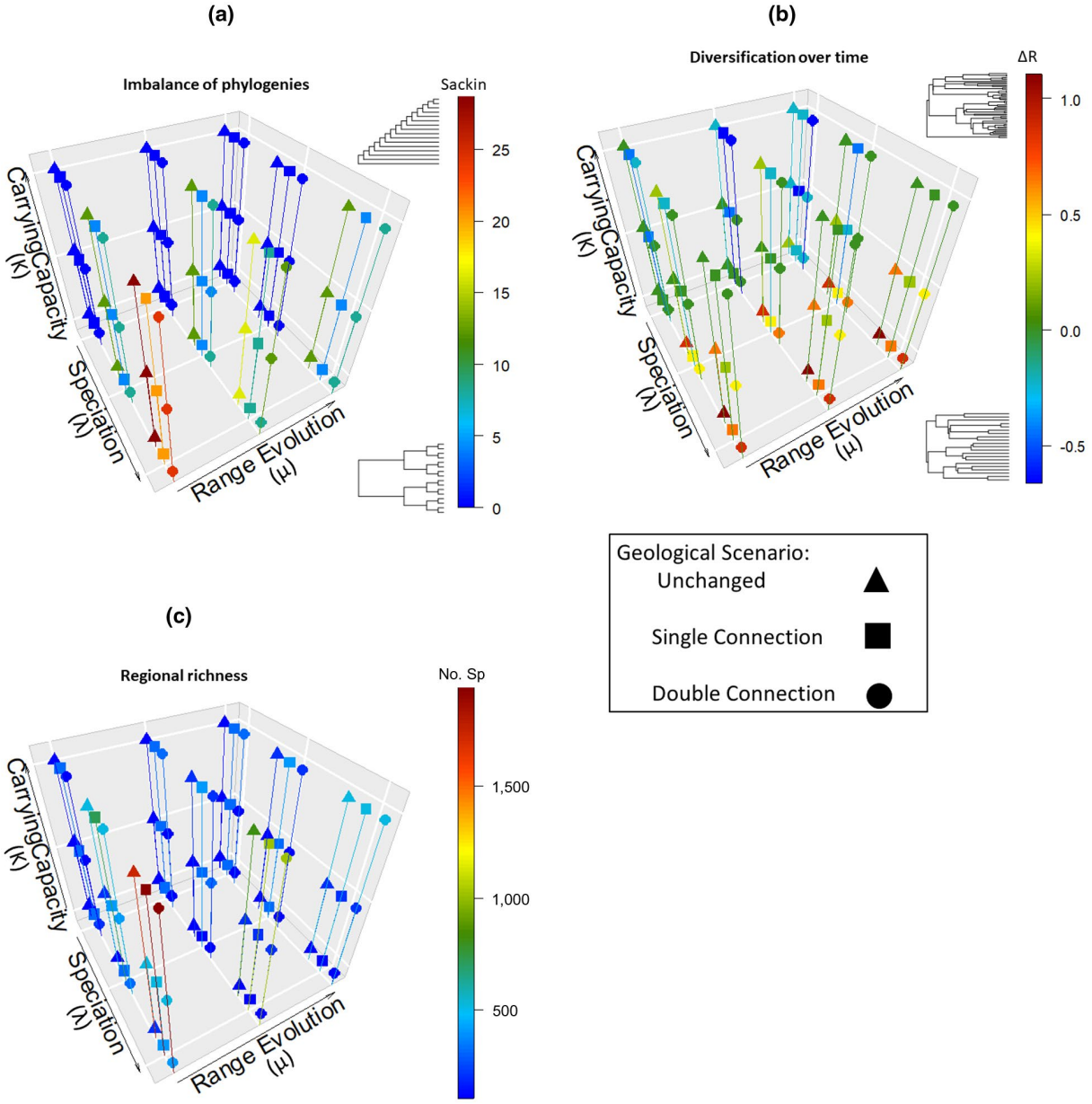

FIGURE 4 The distribution of lineages within a phylogenetic tree (a), changes in diversification rates (b), and number of species in the entire region (c) depend on geological histories and on the combination of ecological and evolutionary processes. The Sackin index is calculated from trees that are reconstructed from clade simulations. ΔR compares the rate of diversification between the first and the second halves of a tree, with negative values suggesting a slowdown. Figure should be read in a similar manner to Figure 3

size distribution show differences between the Breakup20 and Breakup40 simulations across the parameter space (Supporting Information Figure S3).

Values of ΔR, which measures the change in net diversification rates (i.e. the balances between species births and deaths) over time (Pigot et al., 2010), suggest that the diversification rate decreased over time for most parameter combinations (negative values represent a decrease in diversification; Figure 4b) as the landscape became saturated, a common result in spatially explicit diversification models (Price et al., 2014) and a pattern observed in empirical data (Rabosky & Hurlbert, 2015). Lower ΔR values in the Single Connection scenarios suggest that phylogenetic trees show a more pronounced slowdown in diversification than in the Unchanged and Double Connection scenarios, primarily when per-population rates of speciation and local carrying capacity *K* are high (Figure 4b). When λ and *K* were low, however, all three scenarios produced similar values of ΔR (Figure 4b). Although local carrying capacity for some taxa could be far higher than the highest *K* we used (which leads to overall large regional biotas), the impact of geological histories on evolutionary patterns is expected to be the same.

When fitting a standard birth–death process to the phylogenetic trees, the estimates of per-lineage extinction (estimated from

reconstructed phylogenetic trees) showed differences across the parameter space but often failed to be informative for the geological events in a region. This suggests that despite the fact that the distribution of branching events over time does change across geological histories (ΔR), the average number of speciation events per-lineage remains the same. In the case of per-lineage speciation rate estimates, however, Double Connection scenarios yielded lower rates when compared to Single Connection and Unchanged scenarios across many parameter combinations (Supporting Information Figure S1). Overall, the per-lineage estimates of speciation and extinction were consistent with per-population rates λ and μ (i.e. the higher λ the higher the estimate for per-lineage speciation) and this relationship held true across geological scenarios.

Although we found significant differences in the response variables across geological histories, population parameters have a larger impact on richness and phylogenetic patterns. Local carrying capacity has higher influence on regional richness than per-population speciation or extirpation rates; however, its contribution to shaping phylogenetic patterns seems rather modest when compared with varying speciation rates. Together, this suggests that for a given combination of speciation and extirpation rates, geological processes are expected to produce phylogenetic trees with the same properties (i.e. imbalance and changes in diversification rates over time) but varying in size according to a gradient of local coexistence.

4 | DISCUSSION

We found that regions of similar size, age and ecology differ in richness and macroevolutionary patterns based solely on the geological history of landmass collision–breakup over a large range of parameter combinations. As the regional area and parameters used were the same for the contrasting geological scenarios during the simulations, similar ecological and evolutionary patterns might have been expected, but this was not the case in our simulations. Therefore, the dissimilarities we report reflect purely the geological legacy of the simulated regions, and phylogenetic reconstructions retain information about this legacy. Clades inhabiting continuous regions that had been separated in the past were richer in species, had phylogenetic trees that were more balanced and also geographic range sizes that were more homogeneous than areas with no past geological activity.

According to our results, areas with a complex geological history are more likely to accumulate higher regional diversity than areas not subject to landmass movement activity at all, when rates of speciation are low. This suggests that regions of differing geological histories can hold different numbers of species even when they have the same characteristics (age, size and local ecological limits) and if they contain populations whose rates of speciation and range evolution are the same. These findings provide an alternative explanation for the existence of some hotspots of diversity in areas of high geological activity, without claiming exceptionally favourable conditions for life (i.e. high productivity areas, low climatic variability; Jetz & Fine, 2012) or increased per lineage rates of speciation (Hughes et al., 2013). In fact, recent evidence suggests that speciation rates are not higher in the most biodiverse regions (Igea & Tanentzap, 2020; Lancaster & Kay, 2013).

We showed that the Single Connection case had similar species richness to a scenario where two landmasses remain separate (i.e. without any exchange species) so that their species are regarded as a single biota. This is equivalent to two small-sized Unchanged scenarios that are considered to be part of one single and larger region. This suggests that the relationship between regional richness and geological activity is strongly influenced by restrictions imposed by the area of individual landmasses early in the simulation/clade history, rather than the total landmass area or the outcome of lineage exchange. In contrast, Holland's (2018) application of the Hubbellian neutral model on geological movements produced diversity dynamics where shifts in habitable area (regardless of when in time they occur) had an important impact on species accumulation. He showed that after increasing (or decreasing) the area of the metacommunity, diversity will grow (or shrink) to eventually equilibrate at values of diversity characteristic of a metacommunity of that size. We argue that this difference between our model, where diversity is constrained by area since its early stages, and Holland's model, where diversity can fluctuate with area availability, is due to the saturation process itself. Once the domain is full of species (local saturation) in our model, species' range sizes will change until an equilibrium between colonization and extirpation is reached. Then, the addition of another landmass at the same equilibrial state will not present a completely new set of vacant niches as it would also be saturated. If, however, the collision takes place before saturation, the outcome should be similar to the one reported by Holland (2018).

Although we did not track local species turnover, species did cross from one landmass to the other during the collision, which leaves a signature on phylogenetic reconstructions in the form of increased tree imbalance (Figure 2d). This is likely to occur because geographic boundaries are more rigid than ecological ones, which are dynamic due to local extinction (as niche space is opened up by local extinction). Indeed, the set of most widespread species contribute to most of the speciation events so that the difference in range size between widespread and restricted species will influence tree imbalance. In the case of two small-sized Unchanged scenarios, the variation in range size across species (and therefore the tree balance) is limited by the area available, but when the regions are allowed to exchange lineages, species can colonize new communities if space is available (i.e. once local extinction has removed populations). This causes further expansion of widespread species increasing their chances of speciation to finally unbalance the phylogenetic tree. Because we only looked at equilibrium in regional richness to determine the time duration of landmasses to stay together, we ignore whether an equilibrium in community turnover also was reached, or the extent of the species interchange during the connection. We expect that a long period of time is necessary for the invading lineages to expand well into the new landmass as niche space must be emptied at rate μ. Communities in the vicinity of the crossing border will exhibit a higher integration of biotas than other zones in the region. A model where global dispersal is enabled (i.e.

populations are not bound to colonize only adjacent cells) should not feature such a high-turnover border; however, both dispersal modes are likely to result in the same evolutionary and richness patterns (Herrera-Alsina et al., 2018).

The extirpation of populations opens up new niche spaces so other species can further colonize and expand their range. When extirpation rate is increased, this process of [local] species turnover is also increased, which results in preventing a single species (or a handful of species) from occupying most of the grid. In turn, this decreases the otherwise elevated rate of speciation of a few species, which yields more homogeneous probabilities of speciation across species and more balanced phylogenetic trees. It is likely that geological histories that feature a drastic reduction of landmass size will have a similar effect than cases with high rate of extirpation by limiting the range expansion of a few species and maintaining low variability in the chances of speciation across lineages. The relationship between extirpation rate and tree imbalance breaks when the total rate of species production is low and, therefore, competition for niche space is less strong. Figure 4a shows that in the presence of low speciation rates, an increase in extirpation rate has no effect on tree balance, even at the lowest carrying capacity ($K = 2$). With an even lower carrying capacity, a link between extirpation and tree balance would exist again (for an example with $K = 1$, see fig. 6 in Herrera-Alsina et al., 2018).

Although our model is conceptualized in a geological framework, its predictions can also be applied to a general context of habitat connectivity. When the continuity of a habitat breaks down—and large portions of it stop exchanging species over a long time period—then the dynamics of clades might produce patterns similar to those described here. Such a notion strengthens the importance of Pleistocene refugia, where habitats became disconnected for a long time before being re-connected (Hawlitschek et al., 2012; Hope et al., 2012), in shaping current distributions of species and hotspots. Our model suggests that diversity in a region will increase when two previously disconnected habitats are connected, even if microevolutionary processes (e.g. the cessation of gene flow leading to speciation) are not explicitly considered. Flantua et al. (2019), in their study of Pleistocene dynamics, argue that pulses of diversification are expected due to phases of connection–disconnection. It is likely that we find no evidence of this because in our model, landmasses are fully saturated with species prior to the collision, which prevents the increase in species' geographic extent and, therefore, an increase in diversification rate. This leads to the prediction that those regions exhibiting such pulses, had not reached their ecological limits (previous to connection phase) and the system was far from equilibrium.

Furthermore, the capacity of some taxonomic groups for long-distance dispersal could confound the analysis of the geological effect on biodiversity. When two landmasses are not physically connected and lineage interchange takes place, diversity patterns may be similar to those expected under the Unchanged scenario. For instance, Cody et al. (2010) found that the long-dispersal capabilities of plants facilitate the movement of lineages across the Strait of Panama. The contact between plant lineages was therefore constant over time, which is equivalent (in our model) to a region with no geological activity. Moreover, taxonomic groups within the same region but with lower dispersal potential and therefore lower lineage exchange, might show evolutionary patterns that are more in line with our geologically dynamic cases. A prediction follows that, for the same region, the imbalance in phylogenetic trees should be lower in organisms that experience very limited long-distance dispersal.

The landmasses simulated in our model are equal in size and shape, which is a major simplification of reality; the biodiversity predictions we provide might not be fully applicable when connecting landmasses differing greatly in size. Because area availability is tightly linked to global population size and thus the per-lineage rates of speciation, we expect that landmasses of very different sizes will be merging with very dissimilar richnesses and phylogenetic tree shapes. Another assumption we made in our model is the extent of the junction between landmasses. If in reality the physical contact of newly connected landmasses is minimal, the interchange of lineages should be slower as very few cells/assemblages will serve as a bridge across subregions. However, in the case of high rates of range evolution (i.e. high extirpation rate) even a narrow bridge will be effective at allowing species to cross from one landmass to the other. Future work focussing explicitly on the size and shape of the different landmasses and on the geometry of the junction(s) between them would be valuable and our framework can be adapted to fit more specific regional scenarios, where the geometry of historical connections and splitting is known from geological reconstructions.

This study describes the consequences of collision and breakup of landmasses on large-scale patterns of biodiversity. According to our results, two clades whose populations have the same features will differ in richness, past diversification trajectory, tree shape, and geographic extent when they inhabit regions with different geological histories—even if the regions have identical area and niche availability. These findings provide a new perspective on the processes generating diversity in geologically active regions. We have provided an alternative explanation to adaptive or niche-based processes for variation in evolutionary histories and species richness across regions that focuses on the power of geological dynamics to generate biodiversity patterns even in the absence of changes in ecological opportunity.

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DATA AVAILABILITY STATEMENT

Code to perform simulations and process the output is available at: https://doi.org/10.5061/dryad.zs7h44j8j

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BIOSKETCH

Leonel Herrera-Alsina focuses on how species diversity is spread across space and time. Rates of diversification and species coexistence are regulated by the distribution of standing diversity and by geographic constraints that vary over time. To understand the interactions of these factors, he develops dynamic models of diversification that provide theoretical predictions or are applied to empirical datasets.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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