

ARTICLE

Turnover of bird species along the Nullarbor Plain: Insights from taxonomic, phylogenetic, and functional beta diversity

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Abstract

The Nullarbor Plain constitutes one of the main biogeographic barriers of Australia, and it has been suggested to have played a key role in the disjunct distribution of numerous southern Australian species. Although previous research has shown that the origin of this barrier coincides with the timing of the speciation events in some plant lineages, it is not clear whether the uplift of this barrier promoted divergence events in vertebrates. We addressed the role of the Nullarbor barrier and its fringing semiarid habitats as drivers of beta diversity in bird assemblages. Specifically, we determined the effect of distance from the Nullarbor barrier, environmental conditions, and isolation by distance on the composition of local communities on both sides of the plain. We measured beta diversity using taxonomic, phylogenetic, and functional metrics of composition. The influence of precipitation, geographic distance, and distance to the Nullarbor barrier on these metrics was addressed using generalized dissimilarity models and a moving-window approach. We also tested for differences in local extinction, dispersal and speciation rates, and lineage diversity between two regions, southeastern (SE) and southwestern (SW) Australia. Geological and orogenetic dynamics linked to the appearance of the Nullarbor Plain may have spurred speciation events in SE. However, evidence suggests that subsequent periods in which this region was wetter and forested favored dispersal, mainly from SE to SW. Accordingly, observed dissimilarity in species composition was lower than expected at random, suggesting the existence of considerable turnover between regions. Our results suggest that precipitation deficit (and the xeric vegetation that it promotes) was the most important predictor of beta diversity, whereas the distance to the barrier explained some variation in terms of phylogenetic composition. This study shows that the uplift of the Nullarbor barrier played a minor role in shaping present-day bird diversity in southern Australia. Recent speciation events coupled with historical connectivity can explain the observed patterns.

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Australia, avifauna, biogeographic barrier, bird assemblages, community, diversification, environmental filtering, precipitation

INTRODUCTION

How and why species composition varies among sites constitute two of the most basal research questions in ecology and biogeography (Ricklefs & Jenkins, 2011). At broad scales, the distribution of organisms in space results from synergistic effects of diversification due to dispersal limitation and species adaptations to environmental conditions (González-Trujillo et al., 2021; Tuomisto et al., 2003; Warren et al., 2014). Dispersal limitation and allopatric speciation can give rise to differences in composition across biogeographical barriers (e.g., mountain ranges, large rivers, and floodplains). These barriers can sort species depending on their adaptation and they can structure the distribution of biota on a regional scale (Silva et al., 2019). At finer geographical scales, habitat filtering is expected to limit community members to habitats that resemble the ancestral niches where their lineages originated (Ricklefs, 2006). Abiotic conditions may act as filters selecting only the lineages adapted to the local environment, and, in turn, these impose certain ecological adaptations and shape the expression of traits that maximize the survival and reproduction of individuals locally (Mittelbach & Schemske, 2015). Consequently, species responses to local conditions can lead to patchy species distributions (Gaston et al., 2007; Pyron & Burbrink, 2010). On the other hand, theory predicts that geographically close communities will be more similar than those that are further apart, regardless of the environmental gradient (Dias et al., 2021; Soininen et al., 2007). This generates a pattern—the distance decay of community similarity—that is widely observed in terrestrial environments nowadays (e.g., Martínez-Santalla et al., 2022) and that was first noted by R. H. Whittaker in his seminal study in which he coined the term beta diversity (Whittaker, 1960). Lastly, neutral theory assumes species are “neutral” in their ecological niches, and considers biological communities as dynamic assemblages of species whose composition is the result of stochastic dispersal and drift (Hubbell, 2001, 2005).

Beta (β) diversity quantifies the change in species composition across geographic space (i.e., inter-site differences between species assemblages) and provides insight into the mechanisms underpinning the species replacement (i.e., local gains and losses of species) at ecological and evolutionary timeframes (Anderson et al., 2011). Beta diversity is thus a measure of species

turnover, which can result from different mechanisms (for instance, the loss of species due to environmental filtering) (García-Navas et al., 2022; López-Delgado et al., 2020). In order to disentangle the relative importance of these different mechanisms, beta diversity is often decomposed into two components: turnover *sensu stricto* and nestedness (Baselga et al., 2012). Whereas nestedness is expected along environmental gradients if taxa susceptible to physiological conditions or habitats are selectively removed from homogeneous habitats (Leprieur et al., 2011), turnover—the dominant process of beta diversity—is primarily driven by dispersal ability (or limitation), often due to geographical or other abiotic and biotic limitations (Baselga, 2010; Si et al., 2015). Here, we do not differentiate between these two components, and we refer to species turnover *sensu lato* as an analogous term to beta diversity.

Over and above compositional dissimilarities among communities, two other factors that are highly relevant are the amount of evolutionary history (lineages) shared among the communities and how disparate are the traits of species inhabiting those communities. Consequently, the joint consideration of the multiple facets of beta diversity (taxonomic, phylogenetic, and functional) offers information needed to improve our understanding of the processes underlying biodiversity patterns (Cardoso et al., 2014; Graham & Fine, 2008). For example, phylogenetic beta diversity may help elucidate which lineages are driving turnover patterns between regions or ascertain the relative importance of *in situ* diversification versus extinction in shaping present-day species distributions at a local scale (Davies & Buckley, 2011; Leprieur et al., 2012; Peixoto et al., 2017). Furthermore, the spatial heterogeneity in species functional traits, that is, functional beta diversity, may provide information on changes in species attributes and strategies, which is crucial to unraveling community assembly processes (Villéger et al., 2013). Hence, the replacement of traits may occur along an environmental gradient due to niche filtering, whereas a high level of functional convergence among communities, despite the existence of taxonomic divergence, would indicate the replacement of species performing similar functions across sites (Carvalho et al., 2020).

Several authors have employed this multifaceted approach to study the distribution of beta diversity along elevational gradients and to assess the relative influence of niche-based (environmental filtering) and neutral

processes in driving the observed patterns (e.g., Bishop et al., 2015; Fluck et al., 2020; Machac et al., 2011; Weinstein et al., 2014). Mountain ranges promote rapid species turnover across relatively short geographical distances due to abrupt temperature changes and, thus, constitute excellent scenarios to address these questions (Janzen, 1967; Kennedy et al., 2022). Ecologists are increasingly interested in ascertaining the relative importance of historical processes, such as diversification or vicariance events, and contemporary ones, such as habitat filtering or interference competition, in shaping the composition of local communities (Benicio et al., 2021; Calpa-Anaguano et al., 2021; Cavender-Bares et al., 2018; Hoorn et al., 2010; Linan et al., 2021). In this context, not only mountains but also other landforms that act as biogeographical barriers (e.g., sea straits, former marine basins) can be employed as natural laboratories to examine community assembly across eco-evolutionary scales (i.e., considering the evolutionary processes that have shaped the species pools). For instance, regarding historical processes, spatial compositional dissimilarity has been associated with geographical features such as large rivers in the Amazon (e.g., Silva et al., 2019). Similarly, in relation to contemporary processes, it has been shown that strong environmental gradients, like sandy habitats adjacent to other more nutrient-rich soil habitats, are thought to promote high levels of both phylogenetic and functional beta diversity across habitats reflecting the high turnover of lineages and traits, respectively (e.g., Guevara et al., 2016).

Despite its predominantly low topographic relief, the evolutionary history of Australian biota has been influenced by different biogeographic barriers, which have given rise to genetic divergence and, in some cases, speciation of allopatric populations (Alpers et al., 2016; Bryant & Krosch, 2016; Edwards et al., 2017; Peñalba et al., 2017). Some of these geophysical frontiers like the Nullarbor Plain and its fringing xeric habitats constitute dry habitat breaks of mesic environments which can be reflected in the distribution of multiple species as congruent gaps if these share similar ecological tolerances and dispersal capacities (e.g., Keast, 1981). At the northern edge of this region, many species show continuity in their distribution due to the presence of mallee habitats throughout the Great Victoria Desert (Ford, 1971). Here, we aimed to evaluate the importance of historical and contemporary processes in shaping the current patterns of bird distributions along the Nullarbor Plain, the main biogeographic barrier of southern Australia. This karst landscape spanning ~700 km forms a barrier of unsuitable (treeless) habitat for mesic-adapted species between Australia's temperate mesic zones in the southwest and southeast (Ansari et al., 2019; Crisp &

Cook, 2007; Rix et al., 2015). The uplift of the Nullarbor Plain is assumed to have occurred around 14 million years ago (Mya), which may have generated vicariance events involved in the separation of the eastern and western mesic biotas (Nge et al., 2019; Webb & James, 2006). In this regard, it has been suggested for numerous plant and animal taxa that this geological contingency has been fundamental in generating regional endemism on either side of the Nullarbor divide (Li et al., 2004). For instance, Crisp and Cook (2007) found that plant taxa with sister species distributed in the SW and SE temperate zones were estimated to have been separated by the Nullarbor Plain during the early to mid-Miocene. Similarly, the avifauna of southern Australia is characterized by an east-west division at the Nullarbor (Cracraft, 1986). Numerous avian species like the musk duck (*Biziura lobata*), chestnut teal (*Anas castanea*), hooded plover (*Charadrius cucullatus*), scarlet robin (*Petroica boodang*), blue-breasted fairywren (*Malurus pulcherrimus*), and several *Melithreptus* honeyeaters display morphological and/or genetic divergence on either side of this vast limestone-based plain, suggesting subspecific differentiation (Dhami et al., 2013; Dolman & Joseph, 2012; Guay et al., 2010; Toon et al., 2007, 2010; Weston et al., 2020). Many of them have ranges that stop well to the east and west of the Nullarbor Plain because of the fringing xeric habitats that enhance the barrier effect. Hence, in comparison with neighboring areas, the Nullarbor region exhibits remarkably low avian diversity (in terms of species richness, phylogenetic structure, and functional diversity) (Brooker et al., 1979; Burbidge et al., 1987; Reilly et al., 1975; Remes & Harmackova, 2018; Schodde & Mason, 1999; Storr, 1986, 1987).

In this study, we combined evolutionary (i.e., phylogenetic comparative methods) and quantitative ecological approaches, which are often applied in isolation, to infer the influence of broadscale biogeographic (neutral) and present-day (deterministic) processes in generating and maintaining the spatial patterns of avian biodiversity in southern Australia. By examining species assembly from a dynamic perspective (in opposition to the classic "snapshot" approach that prevails in community ecology studies), we tested the following hypotheses: (1) the Nullarbor Plain and its fringing semiarid habitats constitute an important biogeographic barrier (historical factor) that caused prevalent differences in local extinction, dispersal, and speciation rates, as well as lineage diversity between the two regions that it separates; (2) the Nullarbor Plain promotes differences in composition, lineages, and traits between bird communities on each side of the barrier; (3) the relative contribution of historical factors (distance to the Nullarbor barrier) to beta diversity are as important as abiotic (precipitation) or geographic factors; and

(4) the influence of the barrier will cause that communities from sites with comparable environmental conditions exhibit a different taxonomic composition if they are on different sides of the barrier and similar taxonomic composition if they are on the same side of the barrier.

MATERIALS AND METHODS

Species abundance data

Bird abundance data were retrieved from the BirdLife Australia Atlas (<https://birddata.birdlife.org.au/>). BirdLife Australia's Atlas data are collected by skilled bird-watchers at plots they choose, with exact coordinates recorded for each survey. Bird surveys are carried out during the austral breeding season using the "2-ha, 20-min" method (Loyn, 1986). This census method involves searching for land birds in a 2 ha plot for 20 min. During this period, the volunteer records the geographical reference at the center of their plot and all birds seen or heard

in their survey area, including those flying overhead. Our original dataset included 1312 sampling sites (comprising 141 species) distributed on both sides of the Nullarbor Plain including the coastal part, the Roe Plain, which constitutes a subset of the Nullarbor region (Appendix S1: Figure S1). This whole dataset was employed to conduct the diversification analyses and obtain estimates as accurately as possible. Raptors and waterbirds were not considered in this study as the employed census method is not appropriate for these species.

For the beta diversity analyses, we only considered a small subset ($n = 199$ assemblages comprising 98 species) that included only those sampling sites close to the coastline (see Figure 1) and consisting of one of the two major habitats in both regions (southeast and southwest), mallee with shrubby or grass understory and cleared habitat. This subset also included saltbush–bluebush shrublands (sometimes with a scattered overstory of mulga) and open eucalypt woodlands, the two main habitats in the Nullarbor Plain and its fringing coastal region (Roe Plain) (Bastin & the ACRIS Management Committee, 2008;

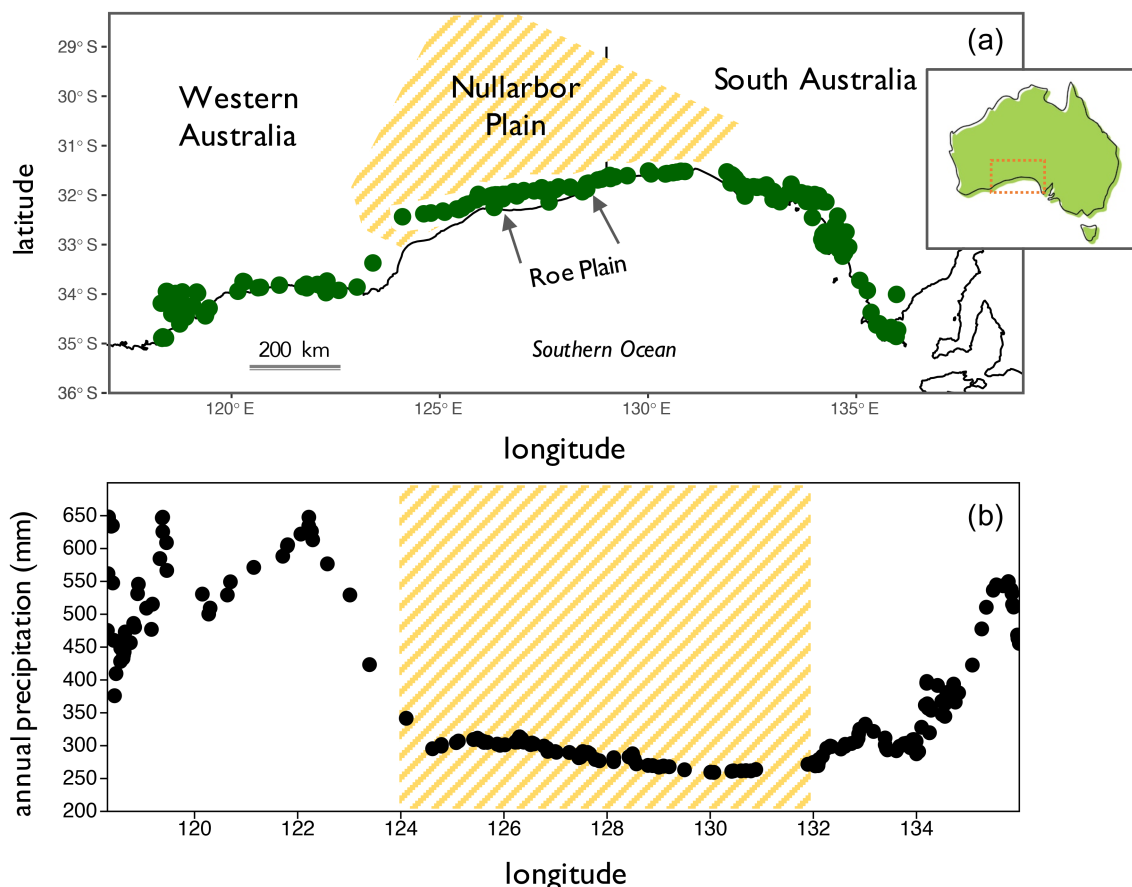


FIGURE 1 (a) Map of the study region in southern Australia with the location of the 199 2-ha sampling sites included in the beta diversity analyses. (b) Variation in annual precipitation (three-point average) along the study region. The blurred area indicates the extent of the Nullarbor Plain whose vegetation is largely treeless chenopod shrubland, grading coastward into sparse, low open woodlands. The epicenter of the barrier was estimated to be around coordinates -31.9172 (lat), 127.4852 (long).

Parsons, 1970). In this way, we reduced the noise associated with variation in species composition merely attributed to habitat differences. The study sites are distributed along a U-shaped precipitation gradient, which ranges from 250 mm in the middle zone (Nullarbor Plain) to 550–650 mm (on the east and west sides, respectively) (Figure 1). For each plot, we obtained the mean annual precipitation (in millimeters) and mean vegetation height (in decimeters) from the WorldClim dataset (Fick & Hijmans, 2017) and Scarth (2013), respectively.

Phylogenetic inference

We computed a Maximum Clade Credibility (MCC) tree from a sample of 1000 trees retrieved from BirdTree (www.birdtree.org). The MCC tree was obtained with the *maxCladeCred* function of the R package “phangorn” (Schliep, 2011) and pruned to incorporate only those species included in our analyses. From this consensus tree, we computed a matrix of phylogenetic (patristic) pairwise distances using the *cophenetic* function of the “ape” package (Paradis & Schliep, 2019).

Species traits

Species traits were compiled from the literature and published datasets (Bird et al., 2020; Garnett et al., 2015; Tobias, 2021; Tobias et al., 2022). For each species (each of the 98 species that make up the selected 199 assemblages), we collated mean trait values for the following morphological variables: body mass, beak size, and wing aspect ratio (quantified using the Hand Wing Index, HWI). We also collected information on generation length (based on modeled values of age at first breeding, maximum longevity, and annual adult survival), diet preference (percentage of insects, fruits, seeds, plants, and nectar in diet), and foraging strategy (percentage of time spent foraging on the ground, understory, mid-high, canopy, and in the air). Both subsets (diet preferences and foraging strategies) were reduced to three principal components by means of a principal components analysis (PCA). The first three axes summarizing diet preferences (PCd1-3) accounted for 60% of the total variance. The first three axes summarizing foraging strategies (PCs1-3) accounted for 64% of the total variation. Thus, our final trait matrix comprised 11 variables (body mass, beak size, generation length, HWI, PCd1, PCd2, PCd3, PCf1, PCf2, and PCf3). From this matrix, we computed pairwise functional dissimilarities using Euclidean distance. This distance matrix was used as input to perform a hierarchical clustering analysis using the “hclust” function of the

“stats” package (v. 4.0.3) and obtain a functional dendrogram (Borcard et al., 2011).

Diversification and dispersal between regions

We tested for differences in speciation (λ), extinction (μ), and dispersal (d) rates between the east and west sides of the Nullarbor divide using Geographic State Speciation and Extinction (GeoSSE; Goldberg et al., 2011) implemented in the R package “diversitree” (FitzJohn, 2012). This approach uses phylogenetic stochastic processes to infer how species evolve among discrete regions through dispersal, regional extinction, and cladogenesis events. We built nine models with varying speciation, extinction, and migration rates between both regions, southwest and southeast (see Table 1). Then, we fitted the models to the data and ranked them according to the corrected Akaike information criterion (AIC_c). To account for parameter uncertainty, we sampled the posterior probability distribution of those parameters using Markov chain Monte Carlo (MCMC) after running 1000 iterations. We classified the species into three categories according to our bird records and species distribution maps from the Handbook of Birds of the World Alive (www.hbw.com): A, restricted to SE; B, restricted to SW; and AB, ranges that span SW and SE. We then tested for differences in speciation or local extinction rates between both regions.

The formation and uplift of the Nullarbor Plain has been completed by approximately 14–15 Mya, during the mid-Miocene, coinciding with vicariance events of multiple plant lineages (Crisp & Cook, 2007). Consequently, based on this scenario, we examined whether periods of increased species diversity in this region corresponded to this period by means of lineage through-time (LTT) plots computed using the *mltt.plot* function of the “ape” package (Paradis & Schliep, 2019).

Taxonomic, phylogenetic, and functional dissimilarities

The different patterns of beta diversities (in its multiple dimensions; taxonomic, phylogenetic, and functional) provide insight into the relative importance of historical processes, such as in situ speciation, and contemporary ones on spatial variation among assemblages (Calpa-Anaguano et al., 2021). Hence, speciation and dispersal can lead to different scenarios. For instance, the existence of high taxonomic beta diversity ($T\beta$) and low phylogenetic beta diversity ($P\beta$) would imply that assemblages may have different species compositions but harbor closely related

TABLE 1 Comparison of alternative GeoSSE models of geographically dependent diversification run in the “diversitree” package.

Model	logLik	ΔAIC_c	df	Weight	λ_A	λ_B	λ_{AB}	μ_A	μ_B	d_{AB}	d_{BA}
model 1 ($\lambda_{AB} \sim 0$)	−736.2	0.0	6	0.29	0.04	0.00	0.00	0.02	0.03	0.25	0.06
model 3 ($\mu_A \sim \mu_B$)	−736.5	0.6	6	0.22	0.04	0.00	0.00	0.02	0.02	0.22	0.10
model 5 ($d_A \sim d_B$, $\mu_A \sim \mu_B$)	−737.6	0.7	5	0.20	0.04	0.00	0.00	0.04	0.04	0.24	0.24
model full (parameters free to vary)	−735.7	1.1	7	0.17	0.04	0.00	0.00	0.01	0.03	0.26	0.03
model 4 ($d_A \sim d_B$)	−737.2	2.0	6	0.11	0.05	0.00	0.00	0.04	0.03	0.27	0.27
model 8 ($d_A \sim d_B$, $\mu_A \sim \mu_B$, $\lambda_A \sim \lambda_B$) sB	−744.0	11.6	4	<0.001	0.02	0.02	0.00	0.04	0.04	0.29	0.29
model 7 ($\mu_A \sim \mu_B$, $\lambda_A \sim \lambda_B$)	−743.8	13.2	5	<0.001	0.02	0.02	0.00	0.04	0.04	0.27	0.33
model 6 ($d_A \sim d_B$, $\lambda_A \sim \lambda_B$)	−743.9	13.4	5	<0.001	0.02	0.02	0.00	0.04	0.05	0.29	0.29
model 2 ($\lambda_A \sim \lambda_B$)	−743.6	14.8	6	<0.001	0.02	0.02	0.00	0.06	0.03	0.42	0.21

Note: logLik, logarithm of likelihood; ΔAIC_c , difference between the interest model and the model with the lowest AIC_c value; weight expresses the weight of evidence favoring the model as the best among all the models compared. λ_A , speciation within SE; λ_B , speciation within SW; λ_{AB} , speciation between SE and SW regions; μ_A , extinction from SE; μ_B , extinction from SW; d_{AB} , dispersal from SE to SW; d_{BA} , dispersal from SW to SE. Models with good support based on $\Delta AIC_c < 2.0$ and weight $> 10\%$ appear in boldface.

Abbreviations: AIC_c , corrected Akaike information criterion; GeoSSE, Geographic State Speciation and Extinction; SE, southeastern; SW, southwestern.

species due to recent allopatric speciation, whereas high $T\beta$ and $P\beta$ would indicate that assemblages harbor completely different lineages due to in situ radiation and long-term geographic barriers limiting connectivity (Weinstein et al., 2014). Pairwise taxonomic beta diversity was computed using the *beta.pair.abund* function (Bray–Curtis option) of the R package “betapart” (Baselga & Orme, 2012). The Bray–Curtis and Sørensen indices are very similar. Both indices take values from zero to one. While the Bray–Curtis index is based on abundance data, the Sørensen index is based on presence/absence data. Pairwise phylogenetic and functional beta diversity ($F\beta$) were estimated using the Phylosor index and its functional analogous, which were computed in the R package “picante” (Swenson, 2011). This index represents the proportion of branch lengths (from either the phylogenetic tree or the functional dendrogram) shared by two assemblages and ranges from 0 (no species shared) to 1 (all species shared). Conceptually, the Phylosor index is similar to the Sørensen/Bray–Curtis taxonomic similarity reference (Bryant et al., 2008; Leprieur et al., 2012). Thereby, we minimized the potential lack of correlation between taxonomic, phylogenetic, and functional beta diversity due to differences in index properties. We computed $T\beta$, $P\beta$, and $F\beta$ considering all sites together and separately for each side, SW and SE.

Drivers of beta diversity

We used a nonlinear regression-based method of generalized dissimilarity model (GDM) to model the taxonomic, phylogenetic, and functional beta diversity (Mokany et al., 2022). Pairwise dissimilarities were modeled as a function of geographic (mean Euclidean) distance

between sites, geographic distance of each plot with respect to the Nullarbor barrier, and environmental dissimilarity in terms of both mean annual precipitation (in millimeters) and mean vegetation height (in decimeters). GDM is an extension of matrix regression where different covariates are fitted using splines (Ferrier et al., 2007). GDM is designed specifically to accommodate two types of nonlinearity commonly encountered in large-scale ecological datasets: (1) the curvilinear relationship between increasing environmental distance and observed compositional dissimilarity between sites (Graco-Roza et al., 2022); and (2) the variation in the rate of compositional turnover at different positions along environmental gradients. This approach enables plotting predicted community turnover rates as a function of each variable (Ferrier et al., 2007). GDM uses monotonic I splines that constrain the coefficients of the regressions to be positive for a nondecreasing fit and nonpositive for a nonincreasing fit. The I splines allow the examination of predictor effects on the dissimilarity matrices through the height and slope. The maximum height represents the total deviance explained by the predictor while keeping all the other predictors constant, while the slope displays the rate of compositional change across the predictor’s range (Wayman et al., 2021). The variance explained by each predictor variable was computed using the *gdm.varImp* function in “gdm” package (Fitzpatrick et al., 2022).

Beta diversity along environmental gradients

Complementarily, we adopted the approach depicted by Dala-Corte et al. (2019) to calculate beta diversity along environmental gradients (directional turnover sensu

Anderson et al., 2011). Beta diversity values for each site comprised the dissimilarity values of the focal site in relation to its four neighboring plots (window size of nine) along (1) a gradient of precipitation, (2) a gradient of vegetation height, and (3) a gradient of distance from the Nullarbor barrier. Values were calculated separately for each of the three gradients. For this, we arranged sites from the lowest to the highest values of each gradient (mixing up sites from both regions, SE and SW) and calculated the beta diversity of a focal site in relation to its neighboring sites in the gradient (i.e., by comparing taxonomic composition in the focal site with its four neighboring sites included in a moving window of the gradient under study). This moving-window approach consists of the following steps: (1) sort sites in the sites-by-species matrix according to a predefined gradient, (2) select neighboring sites according to a window size of nine, and (3) calculate beta diversity metrics for each site window (Dala-Corte et al., 2019). Thus, unlike the previous method, this approach only calculates beta diversity (total multiple-site dissimilarity; computed using the Bray–Curtis Index) between neighboring plots (not across the whole matrix). The analysis was implemented using the “CommEcol” package (Melo, 2021). We then built models for each gradient using beta diversity as a continuous variable to test against predictors. In each model, the explanatory variables included were precipitation, vegetation height, or distance from the Nullarbor barrier plus average geographic distance among sites. Geographic distance was included to account for the known relationship between spatial distance and decay in similarity (e.g., Morlon et al., 2008). Sites near each other in space are expected to have similar faunas (low beta diversity), so including geographical distance in the models was necessary to control for any spatial structure. Because the effect of the explanatory factor (precipitation, distance to the barrier, and vegetation structure) on diversity can be nonlinear, we also included a quadratic term. We assessed the goodness of fit of all models for each gradient using the AIC_c. We also compared the observed values with those generated at random using the *taxo.null* function of the R package “NST” (Ning et al., 2019) to examine whether these patterns differ from that expected by chance. This analysis was only performed for the taxonomic dimension (i.e., compositional dissimilarities).

RESULTS

Diversification of bird lineages in southern Australia

We explored whether signatures of the temporal increase in the number of species (i.e., change in the slope of the

line describing lineage diversity) corresponded to the estimated uplift of the Nullarbor Plain around the mid-Miocene (14–16 Mya). The LTT plot for the southeastern (SE) region showed a subtle change in the slope of lineage diversity about 14–15 Mya, after a brief period of stasis (Figure 2; Appendix S1: Figure S2). It suggests that the emergence of this former shallow seabed promoted speciation events on this side of the barrier. This change in the accumulation of lineages over time was not evident for the southwestern (SW) region, which showed a more gradual and relatively constant pattern over time (Figure 2; Appendix S1: Figure S2).

Our GeoSSE analysis comparing diversification patterns between the SE and SW regions revealed that at least four models had good support (Table 1). The model in which speciation between both regions is constrained to 0 provided the best fit with a weight of 29% (Table 1). The model with equal extinction rates for SW and SE ($\mu_A \sim \mu_B$) was the second-ranked model, while the model with equal dispersal and extinction rates between regions ($d_A \sim d_B$, $\mu_A \sim \mu_B$) had the next best fit (Table 1). Nevertheless, none of these three equal-rate models significantly improved the full model in which all parameters were free to vary (Table 1). Median speciation rate estimates across the 1000 trees were 0.039 in SE and 0.002 in SW clades (units of lineages per time unit) (Figure 2b). Median extinction rate estimates were 0.011 and 0.032 in SE and SW clades, respectively. The model estimated a higher dispersal rate from SE to SW region ($d_{AB} = 0.259$) than the contrary ($d_{BA} = 0.032$).

Taxonomic, phylogenetic, and functional dissimilarities

The average (pairwise) taxonomic beta diversity ($T\beta$) was two times higher than the average phylogenetic beta diversity ($P\beta$) (Table 2), whereas the functional beta diversity ($F\beta$) showed intermediate values (Table 2). Results were similar regardless of the analyzed dataset (side), SW or SE (Table 2).

Drivers of beta diversity

Our GDM model including geographic distance between sites, precipitation, vegetation height, and distance to the barrier explained 8% of the variance for the taxonomic dimension of beta diversity; the proportion of variance explained was much lower (0.1%–0.2%) for the phylogenetic and functional components (Table 3). The results of spatial GDM showed that precipitation constitutes an important predictor in terms of $T\beta$, $P\beta$, and $F\beta$ (Table 3; Figure 3).

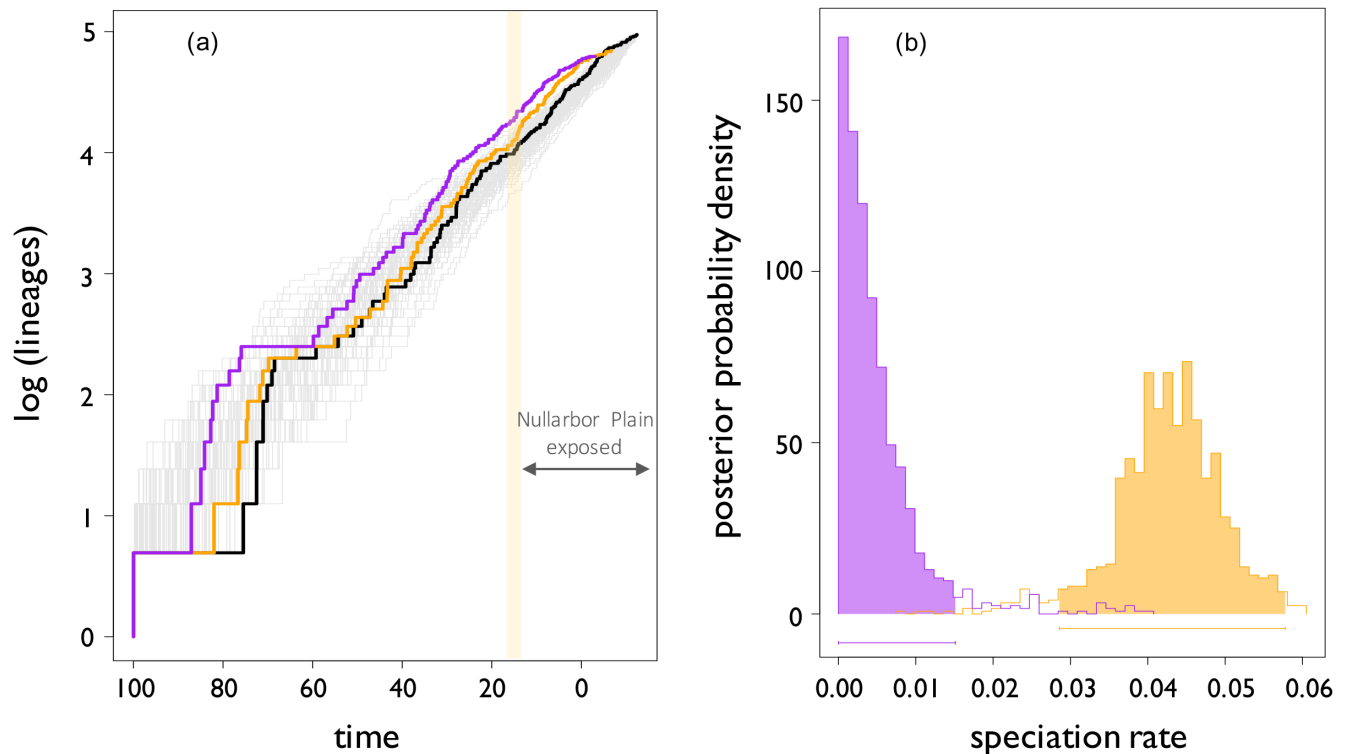


FIGURE 2 (a) Lineage-through-time plot of bird lineages sampled at both sides of the Nullarbor Plain. Purple line indicates species occurring in southwestern (SW) Australia, orange line indicates species occurring in southeastern (SE) Australia, black line indicates all species, and gray lines indicate simulations based on pure birth model (100 trees). The yellow area indicates the period (13–15 Mya) in which it has been estimated that crustal movements lifted the Nullarbor Plain. (b) Posterior probability distributions for the speciation rates within SW (λ_A ; purple color) and SE (λ_B ; orange color) Australia for 1000 phylogenies from the Bayesian posterior distribution, from a GeoSSE analysis in which all parameters were free to vary (full model). Horizontal bars represent 95% CIs estimated using Markov chain Monte Carlo method. Rates are in events per million year.

TABLE 2 Taxonomic, phylogenetic, and functional pairwise beta diversity (means with ranges in parentheses) computed considering the whole study region and separately for each side (southeastern [SE] and southwestern [SW]).

Dataset	Taxonomic β	Phylogenetic β	Functional β
All sites ($n = 199$ sites)	0.848 (0.111–1)	0.434 (0.083–0.976)	0.690 (0.405–0.995)
SW ($n = 94$ sites)	0.837 (0.111–1)	0.413 (0.057–0.987)	0.689 (0.405–0.995)
SE ($n = 105$ sites)	0.828 (0.143–1)	0.443 (0.156–0.940)	0.699 (0.458–0.994)

While precipitation was the sole driver for $F\beta$, a substantial part of variation in the taxonomic component is explained by other variables: geographic distance and vegetation height (Table 3; Figure 3). Distance to the Nullarbor barrier was the most important variable regarding $P\beta$ (Table 3; Figure 3).

The slopes of the GDM splines indicate the relative importance of a predictive variable across the study region. For example, the slope of the precipitation spline for both functional and phylogenetic diversity is steep at the beginning and then it reaches a plateau (Figure 3), indicating that the trait and lineage composition of communities is most explained by arid and semiarid conditions (precipitation <350 mm). Beyond a certain threshold

(500 km), the distance to the Nullarbor barrier explains little of the variation observed in lineage composition (Figure 3). However, it is from this threshold onward that the distance to the barrier explains the greatest taxonomic dissimilarity for bird communities (Figure 3).

Beta diversity along environmental gradients

Taxonomic beta diversity was best fitted by a model including the quadratic term of distance to the Nullarbor barrier and geographical distance (Table 4). The second top-ranked model was the one including distance to the

TABLE 3 Deviance of taxonomic, phylogenetic, and functional beta diversity explained by models including geographical distance between sites, precipitation, vegetation height, and distance to the barrier, as well as the relative importance of each variable.

Facet	Null deviance	GDM deviance	Deviance explained (%)	Importance of geographical distance	Importance of precipitation	Importance of vegetation height	Importance of distance from the Nullarbor barrier
Taxonomic β	4303.2	3975.6	7.61	CS 1: 0.19	CS 1: 0.01	CS 1: 0.09	CS 1: 0
				CS 2: 0.17	CS 2: 0.40	CS 2: 0.39	CS 2: 0.04
				CS 3: 0.16	CS 3: 0.11	CS 3: 0	CS 3: 0.06
				[13.14]	[14.10]	[8.55]	[0.29]
Phylogenetic β	1320.5	1317.4	0.24	CS 1: 0	CS 1: 0.02	CS 1: 0	CS 1: 0.03
				CS 2: 0	CS 2: 0	CS 2: 0	CS 2: 0
				CS 3: 0	CS 3: 0	CS 3: 0	CS 3: 0
				[<0.01]	[18.84]	[<0.01]	[52.21]
Functional β	1917.7	1916.0	0.09	CS 1: 0	CS 1: 0.06	CS 1: 0	CS 1: 0
				CS 2: 0	CS 2: 0	CS 2: 0	CS 2: 0
				CS 3: 0	CS 3: 0	CS 3: 0	CS 3: 0
				[<0.01]	... ^a	[<0.01]	[<0.01]

Note: Coefficient splines (CS n) and predictor importance (in square brackets) for each diversity facet are given. Estimated variable coefficients in models explaining phylogenetic and functional dissimilarity were 0 for some variables.

Abbreviation: GDM, generalized dissimilarity model.

^aWe were unable to estimate the importance of this predictor as it requires at least two predictor variables (see Mokany et al., 2022).

Nullarbor barrier together with geographical distance (Table 4). The model that incorporated vegetation height as the sole explanatory factor also received substantial support (Table 4).

Observed beta diversity was lower than expected at random, especially for the precipitation and distance to Nullarbor gradients (Figure 4) suggesting the existence of significant replacement between the SW and SE. Beta diversity tended to be lower at both extremes of the precipitation gradient (<320 and >550 mm), as the window was composed of sites belonging to a single region. Regarding the vegetation height gradient, beta diversity decreased once the vegetation reached a 10-m height (Figure 4).

DISCUSSION

The Australian terrestrial avifauna differs from that of Europe and North America in its higher diversity and uniqueness: the result of a deep evolutionary history that spans roughly 60 million years (Christidis & Norman, 2010). Despite their high dispersal capacity, it has been shown that geographic and climatic barriers have also played a key role in the diversification of several groups of Australian birds (e.g., Dolman & Joseph, 2015, 2016). Up to 22 major zones of coincident turnover or common disjunction in species' distributions have been identified

as putative barriers to dispersal and gene flow, the Nullarbor divide (as well as all of its fringing xeric habitats) being the largest and most significant climatic and edaphic biogeographic barrier of southern Australia together with the Eyrean barrier (Bryant & Krosch, 2016; Schodde & Mason, 1999). Here, we found support for two of the four hypotheses formulated (Hypotheses 3 and 4; see *Introduction*). We showed that although many species of birds confined to southern Australia show distinct allopatric SE and SW populations with no dispersal evident across the Nullarbor Plain, it does not constitute an important driver of community composition. Overall, we found that the Nullarbor Plain and its fringing xeric habitats had a weak barrier effect for bird assemblages; assemblages from localities with analogous environmental conditions were similar despite being located on opposite sides of the barrier. These results contrast with those reported in studies testing the role in species sorting of less extensive geographical barriers such as Amazonian rivers (e.g., Pomara et al., 2014; Vieira et al., 2022).

Diversification and dispersal between regions

Despite being relatively similar bioclimatically, the two temperate zones of southern Australia have been disconnected for ages and harbor different biota. About a

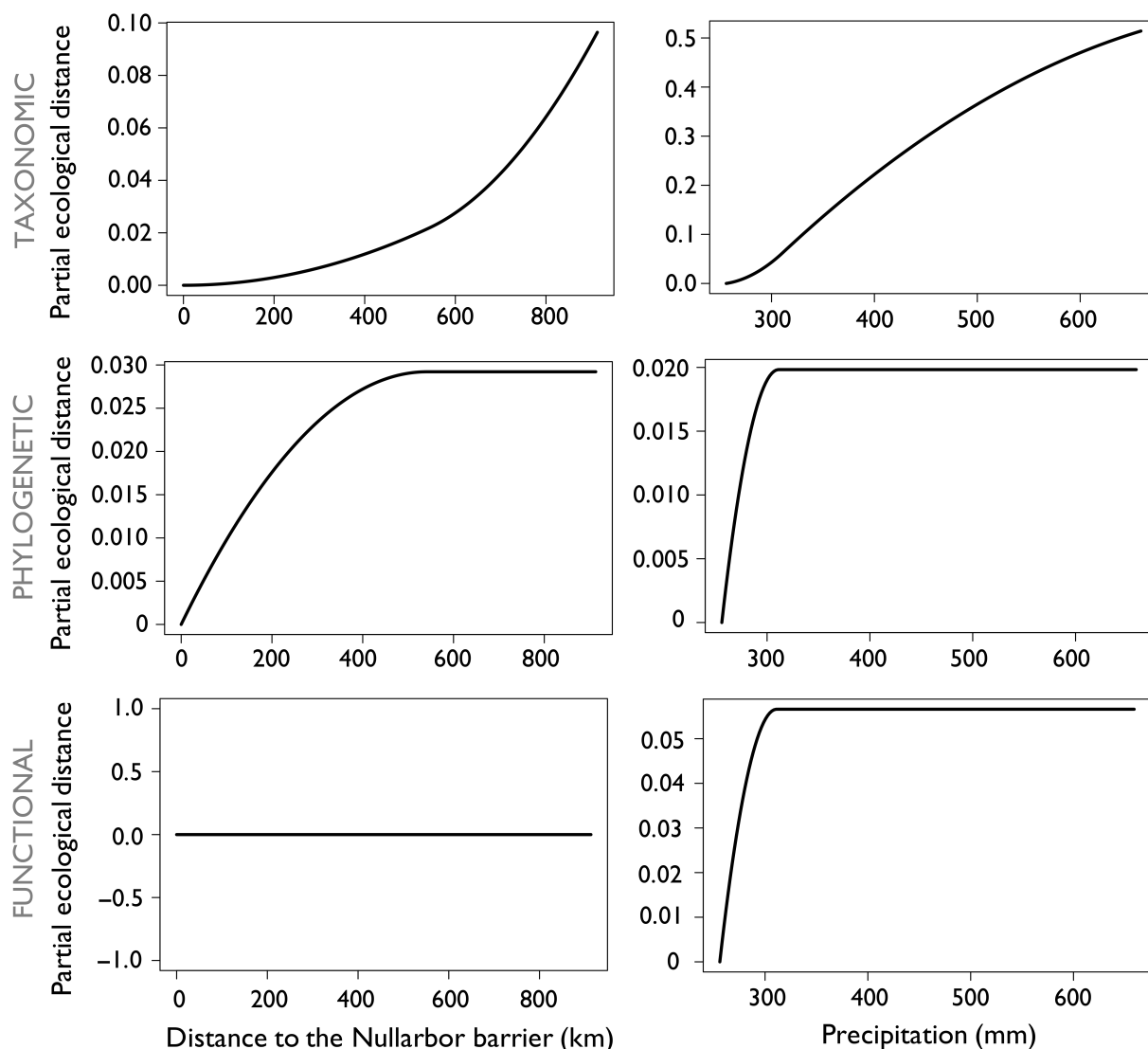


FIGURE 3 Plotted *I* splines of the two most important factors (determined from the variable importance score) from generalized dissimilarity models analyzing the relationship between abiotic (precipitation) and historic (distance to the Nullarbor barrier) gradients, and spatial community composition in terms of taxonomic, phylogenetic, and functional dissimilarity.

quarter of the bird species recorded in each of the two regions are missing or replaced by sister taxa on the other side of the Nullarbor barrier (e.g., Billerman et al., 2022). Here, we observed that, although both regions harbor a similar number of species, bird lineages restricted to the SW were older (~3 Mya on average) than those only circumscribed to the SE region whose appearance in most cases was after the uplift of the Nullarbor barrier. Accordingly, the LTT revealed that a slight change in the slope of lineage diversity for the SE region overlaps with the final phase of the uplift, suggesting that geological and orogenetic dynamics linked to the appearance of this barrier may have spurred speciation events in this region. In line with this, we found that all the GeoSSE models with good support suggested the existence of differences

in speciation rates between the SE and SW regions. From this period (mid-Miocene) and coinciding with the elevation of the Nullarbor barrier, differences in lineage diversity between both zones tended to decrease. It is likely that mesic pulses that occurred later during the late Pliocene led to an increase in the turnover rate between assemblages from the SW and SE. After these mesic pulses, a wet environment was established, which could have caused a homogenization of the biota. This may also explain the minor role of this vast plain as an effective barrier. In this vein, it has been estimated that between about three and five million years ago, the Nullarbor Plain was two to four times wetter than nowadays, populated with forests of eucalypts and banksias (Sniderman et al., 2016; Woodhead et al., 2019). Thus, during this

TABLE 4 Taxonomic beta diversity based on abundance data of bird communities in response to annual precipitation (“precip”; gradient 1), distance to the meridian of the Nullarbor region (i.e., the epicenter of the barrier: “dist”; gradient 2), vegetation height (“height”; gradient 3) plus geographical distance among sites (“geo”; gradients 1, 2 and 3).

Gradient	Model	df	ΔAIC_c	R^2
Gradient 1 (precipitation)	<i>geo</i>	3	0	0.11
	<i>geo + precip</i>	4	0.9	0.11
	<i>precip</i>	3	18.1	0.02
	<i>geo + precip</i> ²	5	2.9	0.11
	<i>precip</i> ²	4	8.7	0.07
	<i>null</i>	2	21.3	0.00
Gradient 2 (distance to the Nullarbor barrier)	<i>geo</i>	3	30.5	0.29
	<i>geo + dist</i>	4	3.84	0.38
	<i>dist</i>	3	25.1	0.31
	<i>geo + dist</i> ²	5	0	0.39
	<i>dist</i> ²	4	18.7	0.33
	<i>null</i>	2	94.1	0.00
Gradient 3 (vegetation height)	<i>geo</i>	3	85.5	0.01
	<i>geo + height</i>	4	29.5	0.27
	<i>height</i>	3	31.6	0.25
	<i>geo + height</i> ²	5	2.0	0.36
	<i>height</i> ²	4	0	0.37
	<i>null</i>	2	86.3	0.00

Note: The null expectation fitted with the intercept only (“null”) is also shown. Italicized entries indicate the best models according to the corrected Akaike information criterion (AIC_c).

period in which the Nullarbor Plain was wet and forested, more favorable environmental conditions could have allowed some species to disperse and recolonize (Prideaux et al., 2007), thus favoring gene flow between regions, mostly from SE to SW, as most GeoSSE models estimated a higher dispersal rate in that direction. For instance, Austin et al. (2013) showed the existence of gene flow across the Nullarbor Plain in the Western grasswren *Amytornis textilis* group. Our results, thus, support the hypothesis that the emergence of the Nullarbor Plain favored divergence events, but only east of the barrier.

Taxonomic, phylogenetic, and functional dissimilarities

Few studies focused on bird communities have simultaneously considered the taxonomic, functional, and phylogenetic facets of beta diversity. This is despite the opportunity that integration of these three dimensions provides a more comprehensive understanding of the role of ecological and evolutionary processes in shaping how diversity is distributed across space (Carvalho et al., 2023; Corbelli et al., 2015; Devictor et al., 2010;

Weinstein et al., 2014). Here, by means of this approach, we found a high level of compositional turnover across the study region that was not accompanied by a similar degree of replacement in terms of evolutionary lineages or traits, the latter suggesting the existence of phylogenetic and functional homogenization. For all biodiversity facets, there was no greater dissimilarity when analyzing all communities together than when restricting the analyses to those located on one of the two sides of the barrier as would be expected if the Nullarbor Plain acted as a significant structuring agent of biotic regionalization. The existence of high taxonomic beta diversity, in conjunction with low phylogenetic beta diversity ($P\beta$), implies that both recent speciation due to geographic isolation and dispersal (historical connectivity) shape diversity patterns in this region. Specifically, taxonomic beta diversity was double that of phylogenetic diversity, which is indicative that bird species are replaced by closely related ones (i.e., phylogenetic redundancy). The observed low values of $P\beta$ suggest that assemblages on both sides of the Nullarbor Plain do not harbor completely different lineages as would be expected if this region acted as a barrier limiting connectivity and/or if in situ radiation played a significant role in biodiversity generation in this region. In terms of

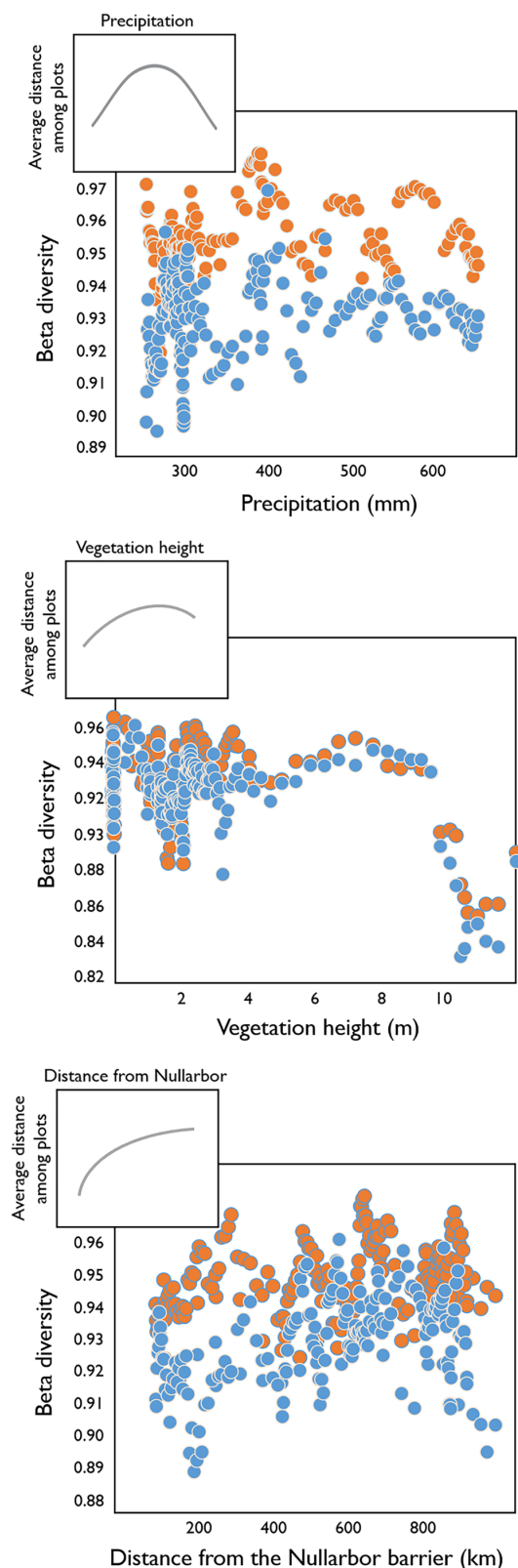


FIGURE 4 Observed (blue dots) and expected (orange dots) beta diversity computed using a moving-window approach (window size of nine) in relation to annual average precipitation, vegetation height, and distance to the Nullarbor barrier. The insets show the relationship between each variable and the average distance among sites for each window (see [Materials and methods](#) for more details).

functional beta diversity, our estimates point to a moderate replacement of traits across the study region. Our results contrast with those previously reported by Weinstein et al. (2014) in hummingbird communities along an elevation gradient in the Andes, which exhibited rapid clade replacement over short distances. The observation of low taxonomic, high phylogenetic, and high functional beta diversity allowed them to conclude that different clades may have evolved specific adaptations for different conditions along the gradient, probably in response to high environmental heterogeneity in comparison with our study system (Weinstein et al., 2014; see also Graham et al., 2009). Our findings thus suggest the existence of less restrictive environmental constraints allowing the colonization and establishment of phylogenetically distant lineages in opposition to the clustering pattern reported in studies from the Neotropics (Maximiano et al., 2020; Pomara et al., 2014). A nonexclusive hypothesis when it comes to explaining the differences found in this study compared with what was observed in Neotropical studies regarding the role of biogeographical barriers on the composition of communities is the different degree of specialization of birds. Australian bird species are more generalist in comparison with bird species from South America, which exhibit the highest level of habitat and diet specialization (Belmaker et al., 2012; Morelli et al., 2021). It could lead to a moderate functional replacement, indicating that communities across the entire Nullarbor region tend to share certain species' traits (e.g., high dispersal capacity to find water bodies). Our results do not corroborate our second hypothesis, as differences in terms of lineages and traits between communities on each side of the barrier were low or moderate, respectively.

Drivers of beta diversity

Based on our results, we can conclude that variation in spatial taxonomic beta diversity of avian communities in southern Australia is driven by a combination of factors including abiotic variables (e.g., vegetation height, precipitation) and geographical distance per se. It suggests that taxonomic diversity is affected by the influence of different factors underlining the more integrative character (and its less specific nature) of this dimension with respect to the other two (see also Belcik et al., 2020). While the deviance explained by our GDM models was low in terms of functional and phylogenetic beta diversity, this suggests that other factors not considered in this study shape the observed variation among assemblages. For all facets of beta diversity, precipitation was the most

important factor (or the second most important) in explaining the observed variation across the space. Specifically, phylogenetic and functional beta diversity were found to sharply increase with precipitation before leveling off around 320 mm (Figure 3). That is, arid and semiarid environments (<400 mm) in this region harbor some species capable of coping with these harsher conditions (arid-adapted species like the white-browed treecreeper *Climacteris affinis*, the Nullarbor quail-thrush *Cinclosoma alisteri*, or the slender-billed thornbill *Acanthiza iredalei*) increasing the distinctiveness of these communities in relation to others (Fisher et al., 1972; Toon et al., 2012). Functional beta diversity was only explained by this abiotic factor, suggesting that among the factors tested, only precipitation drives functional dissimilarity among communities. In this vein, it has been shown that functional diversity decreases in areas of lower productivity (low precipitation) because aridity acts as a sieve; only species with certain traits can establish and persist in these environments (e.g., Seymour et al., 2015). Likewise, because species in these regions share traits to endure aridity (trait convergence), functional beta diversity should be lower too.

The distance to the Nullarbor barrier also impacted the spatial variation of communities in phylogenetic (but not functional) terms (Figure 3). After an initial increase in dissimilarity between communities with increasing distance from the barrier, there was a leveling off. In other words, above a certain threshold (500 km), the distance from the Nullarbor barrier ceases to be determinant and beta diversity remains relatively constant. Lastly, we found that the geographical distance between sites did not constitute a predictor of functional or phylogenetic dissimilarity. The results found here align with previous evidence that indicates the limited role of distance as a driver of beta diversity patterns in birds at small and intermediate scales due to their high vagility (Sinha et al., 2022). This is in contrast with that observed for other taxa with a lower dispersal capacity like anurans, insects, or fungi in some previous studies (Amador et al., 2019; Boraks et al., 2021; Chesters et al., 2019). Our results indicate that the examined factors (precipitation, distance to the Nullarbor barrier, and geographic distance per se) have different effect strengths over different beta diversity dimensions. It shows that in addition to differences in terms of taxonomic composition, studies on beta diversity patterns must also take into account functional and phylogenetic aspects to gain a better understanding of factors driving differences among local species assemblages. Overall, these findings support our hypothesis that the Nullarbor barrier constitutes a remarkable structuring agent promoting dissimilarities between bird communities as well as other environmental factors.

Beta diversity along environmental gradients

Taxonomic beta diversity was lower than expected by chance, suggesting that assemblages from both regions (SE and SW) are more similar than would be expected at random due to a high number of taxa shared between both sides of the barrier. The hump-shaped relationship between annual precipitation and taxonomic beta diversity was mainly due to the existence of a greater distance among sites at both extremes of the gradient. That is, when all sites conforming to the nine-plot window belonged to the same region, the level of dissimilarity among sites was lower. Although the average distance among sites tended to increase as the distance from the Nullarbor barrier increased, we did not find greater dissimilarity among sites located far (>500 km) from the Nullarbor barrier. In other words, the level of resemblance of assemblages on both sides of the barrier does not decrease as we move away from the Nullarbor Plain. The decline in beta diversity observed beyond that distance from the barrier (>500 km; see Figure 4) reveals that the xeric habitats surrounding the Nullarbor Plain could have a greater effect than the barrier itself (Dolman & Josep, 2012). In this sense, we found a lower dissimilarity among assemblages in those localities where the vegetation structure (and thus, the proportion of forested area) was higher.

The observed patterns suggest that in terms of avifauna both regions (SW and SE) are not that different, possibly due to the more favorable conditions that birds in this region would have faced during the Pliocene, when environmental conditions were less rigorous and more benign (mild climate, extensive tree cover) (Sniderman et al., 2009). These results thus indicate that the Nullarbor Plain had only a weak effect on the composition of land bird communities. It is likely that we would have detected a more important barrier effect on the communities of estuarine and freshwater species (plovers, sandpipers, and other waders) because the absence of inland surface water and coastal cliffs may limit the opportunities for east–west exchange in this species group (Weston et al., 2020). Consequently, our findings provide partial support to the last hypothesis, because although we found a high level of similarity between communities located on the same side of the barrier, the proximity or remoteness to it was not particularly relevant as shown by the reported hump-shaped pattern.

Conservation implications

Understanding the impact of geological and orogenic dynamics on biodiversity can help in the conservation of

ecosystems, as such dynamics may have spurred speciation events in certain regions promoting a high level of endemism. Yet, our results suggest that current environmental conditions such as precipitation exert a stronger influence than important historical events (i.e., the uplift of the Nullarbor barrier) on the multifaceted diversity of birds in this region. From these results, it is distilled that a climate-change-driven variation in the regime of precipitation might have a significant impact on the composition of these communities. This is an important finding in light of predictions that climate change may exacerbate levels of aridity in southern Australia (Hope et al., 2015). Our study also showcases that the integration of taxonomic, functional, and phylogenetic facets of beta diversity provides a comprehensive understanding of how diversity is distributed across space, which can aid in conservation planning by identifying key areas that are critical for the maintenance of biodiversity (Socolar et al., 2016).

Conclusions

Previous studies have shown that the Nullarbor Plain and its fringing xeric habitats promoted genetic population divergence for a selection of taxonomic groups (see, e.g., Alpers et al., 2016; Weston et al., 2020). However, as far as we know, our study is the first to address its importance as a geographical barrier at the assemblage level. Our results did not identify a significant role of the Nullarbor Plain as a major driver of beta diversity in land birds. A plausible explanation for this result is that throughout its history, the Nullarbor Plain has been subjected to substantial changes in terms of environmental conditions and habitat characteristics including tree cover expansion and a more humid climate, which may have contributed to erasing signatures in species distributions linked to the uplift of this arid barrier. It must also be considered that a considerable proportion of species has evolved within the past 5 million years, during the Pliocene–Pleistocene period, when glacial cycles caused repeated expansion and contraction of the Australian arid zone culminating in the most severe arid phase at the Last Glacial Maximum (Byrne et al., 2008). Consequently, Plio–Pleistocene divergence events (2–4 Mya) may explain a substantial proportion of the present-day composition of bird assemblages in this region. Our results thus support the findings of Dolman and Joseph (2016), who concluded that the Eyrean barrier (which peaked in impact during the last arid period, 18,000–16,000 years ago) has been critical in shaping present-day bird diversity in mainland Australia and that other more ancient barriers such as the Nullarbor Plain and its fringing semiarid habitats have played a lesser role. Overall, this study demonstrates

the strength of combining evolutionary and ecological approaches constitutes a robust procedure to determine the extent to which present-day communities reflect the historical legacy of past climatic and geological events. This is important because it has been shown that the species composition of most local assemblages is more strongly governed by regional and historical factors than by local ecological interactions (Mittelbach & Schemske, 2015; Weeks et al., 2016). Our results advance the understanding of the spatial heterogeneity of Australian communities, providing basic information on the influence of one of the most important geographic barriers of this continent in shaping species composition.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (García-Navas et al., 2024) are available from Figshare: <https://doi.org/10.6084/m9.figshare.25305643>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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