



RESEARCH ARTICLE

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A Stroll Along Australian Ecosystems: Using Bioclimatic Transects to Examine Environmental Drivers of Community Assembly in Birds

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ABSTRACT

Aim: Variation in community composition along environmental gradients provides crucial information for identifying zones where species turnover is rapid and to ascertain whether compositional changes occur gradually or rather abruptly. We examined changes in bird community composition along three bioclimatic transects in Australia to test whether drivers of species turnover are consistent, rather than spatially contingent, across biologically contrasting ecosystems. We also detected potential transition zones associated with environmental thresholds and determined whether certain abiotic conditions promote a higher rate of community compositional turnover.

Location: Mainland Australia.

Taxon: Terrestrial birds.

Methods: We applied multivariate community analysis, generalised dissimilarity modelling (GDM) and threshold indicator taxa analysis (TITAN).

Results: We observed that environmental variables are better predictors of community composition than spatial distance, which indicates that species sorting, rather than dispersal, plays a key role in structuring Australian avian communities. Annual precipitation constitutes a key driver of species turnover regardless of the analysed transect. The most humid landscapes and those with a higher tree canopy show lower spatial heterogeneity in community composition compared to those with less benign environmental conditions (e.g., dryer environments). TITAN detected significant transition points and supported the results obtained using GDM, which suggests that bird composition change along the gradients is not monotonic.

Main Conclusions: Our results suggest that avian beta diversity increases with increasing environmental harshness, presumably through changes in the relative importance of stochastic versus deterministic processes. The obtained findings show that open forests and woodlands are extremely important ecosystems on this continent and deserve special attention in terms of conservation due to their vulnerability to global change. Lastly, this study exemplifies the value of combining community- and taxon-based analyses to identify and interpret community thresholds, which can serve to pinpoint targets for preserving biodiversity.

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1 | Introduction

Beta diversity defined as the change in species identities across space constitutes a measure of biodiversity whose popularity and application in ecological conservation has increased significantly in recent years (Chase et al. 2020; Rolls et al. 2023). Spatial dissimilarity among biological communities in terms of species composition can be explained as a result of species responding to environmental gradients (Tuomisto, Ruokolainen, and Yli-Halla 2003; García-Navas et al. 2022) and dispersal constraints coupled with demographic stochasticity within the framework of neutral ecological theory (Rosindell, Hubbell, and Etienne 2011). Regarding the latter, dispersal limitation is one process that can increase stochasticity and blur relationships between environmental factors and community composition (Vellend 2017). With regard to the first explanation, environmental gradients, defined as gradual changes in abiotic or biotic environmental factors, are key determinants of how diversity is distributed throughout space. Species respond to variations in climate, productivity and habitat heterogeneity (among other factors), and consequently, the composition of biological communities can reflect sharp or smooth transitions as a result of variations in species' physiological responses and abrupt changes in the environment. In this sense, according to some authors, species turnover is largely discontinuous along environmental gradients, with clear boundaries and discontinuities between communities (e.g., Vázquez and Givnish 1998); while several others have suggested the existence of gradual changes in community structure (e.g., Hemp 2006).

Transects that traverse substantial environmental gradients (bioclimatic transects) are important tools for studying ecological change and have a long tradition within the field of community ecology (Caddy-Retalic et al. 2017). Whittaker's (1956) classic study of vegetation change in the Smoky Mountains constitutes a clear example of the utility of this approach to assess community composition and adaptive changes along environmental gradients. Since then, numerous subcontinental-scale transects have been established and nowadays, under a global change scenario, large-scale transects are considered powerful research platforms as they allow to examine the biotic response to environmental change and identify those processes that facilitate species persistence and ecosystem resilience (Guerin, Biffin, and Lowe 2013). Specifically, bioclimatic transects are particularly valuable for identifying points where environmental change drives more rapid community-level responses, making these areas highly sensitive to global warming (Neilson 1993). These boundaries or transition zones are particularly responsive to abiotic perturbations because species are living near the edge of their physiological tolerances (Yarrow and Marin 2007; Kark 2013). Consequently, by means of this approach, it is feasible to address, for instance, what climatic thresholds limit the distribution of species and communities, and to identify areas that should be given priority for conservation since they sustain rich and (sometimes) unique biodiversity (Shmida and Wilson 1985; Kark et al. 2007).

The literature on bioclimatic transects is mainly dominated by plant studies and, to a lesser extent, studies carried out with insects (Andersen, Del Toro, and Parr 2015; Gibson et al. 2017; Guerin et al. 2019; Lira, Salomão, and Alburquerque 2019). Organisms with a high dispersal capacity like birds or mammals

have received less attention regarding this topic. Bird communities may exhibit a different pattern in comparison with communities of less mobile taxa when modelling compositional dissimilarity among them as a function of environmental distance (Legendre et al. 2005; Anderson, Ellingsen, and McArdle 2006; Jost 2007). Consequently, one would expect a less important role of geographic distance (distance–decay relationship) and a greater influence of environmental distances between sites on the beta diversity in birds (Graco-Roza et al. 2022). Distance-based approaches allow regression that includes (and disassociates) both environmental and geographic distances between communities. Although the relationship between composition dissimilarity and environmental distance may be nonlinear, a problem can be circumvented through the employment of generalised dissimilarity models (GDMs) (Mokany, Ware, et al. 2022; Mokany, McCarthy, et al. 2022). This method allows to identify potential drivers of spatial beta diversity and, in turn, makes it possible to infer those areas where species turnover is rapid (steeper curves). Regarding this latter, threshold indicator taxa analysis (TITAN) (Baker and King 2010) provides a complementary approach to detect change points in the community delineated through the synchronous response of multiple species, which are similarly influenced by the environmental gradient. In this context, a synchronous response does not mean that all taxa exhibit exactly the same pattern, but that their greatest declines (change in abundance and frequency) all occur within a narrow range of the gradient. Both community- (GDM) and taxon-based (TITAN) analyses can provide insight into how certain environmental variables shape the composition of biological communities and the existence or not of smooth transitions in species composition (discontinuous turnover) along spatial gradients. However, to our knowledge, no study to date has used these tools together for this purpose.

In the present study, we examined changes in bird community composition along three bioclimatic transects in mainland Australia using a comprehensive approach in which we combined different analytical tools. First, we used multivariate community analysis to link species composition to environmental variables. Second, using generalised dissimilarity modelling, we tested whether drivers of avian community compositional turnover are consistent, rather than spatially contingent, across biologically contrasting ecosystems. Lastly, we employed TITAN to detect potential transition zones associated with environmental thresholds and determine whether certain abiotic conditions promote a higher rate of species turnover.

2 | Materials and Methods

2.1 | Transects

Bird census plots distributed along three bioclimatic transects were employed to characterise changes in bird communities in relation to environmental variation at a regional scale on mainland Australia (Figure 1a). The three transects span a range of eco-climate types across the continent. The first one (QUEENS) runs along the Queensland coastline covering the Wet Tropics and Brigalow Belt regions, whose climate is tropical and subtropical. The second transect (SOUTH) is located in Southern Australia and comprises five biogeographic regions (Eyre York Block, Gawler, Great Victoria Desert, Stony Plains and Finke) dominated by

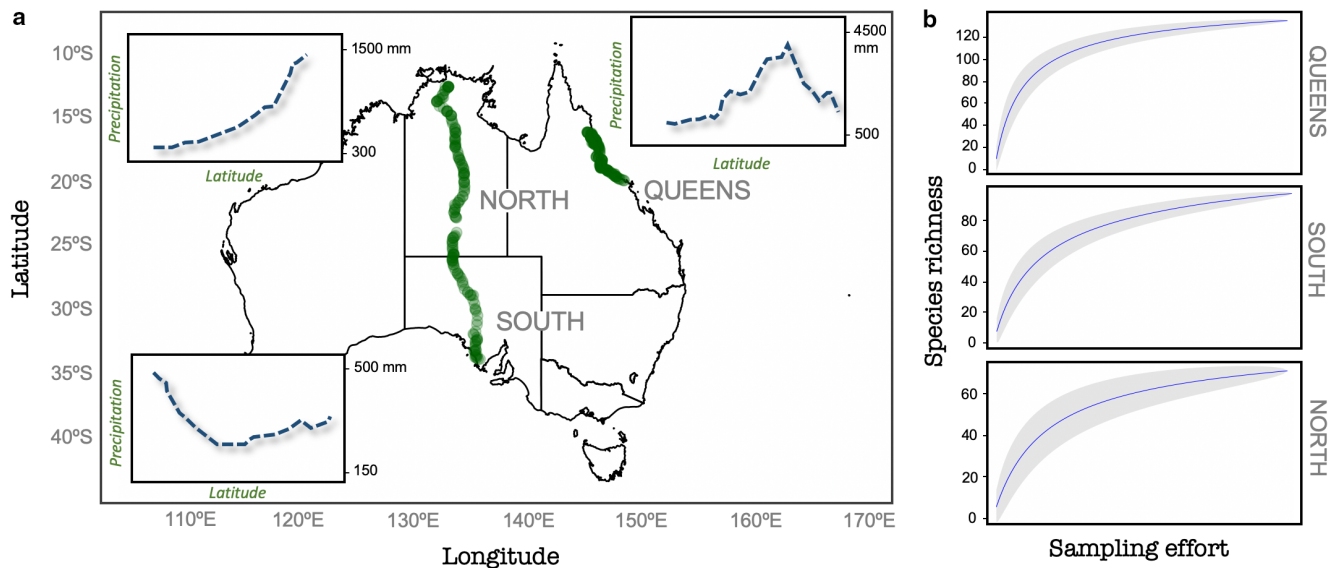


FIGURE 1 | (a) Location of the three Australian bioclimatic transects examined in the present study. The transects sample a wide range of ecosystems (semiarid, Mediterranean, cool-wet, warm-wet and seasonal tropics). Insets show latitudinal variation in annual precipitation (mm) along the three transects (note that scale of the y axis varies across transects). (b) Cumulative species-richness curves for the three transects.

TABLE 1 | Main characteristics of the three studied bioclimatic transects (NORTH, QUEENS and SOUTH; see main text for details) in mainland Australia.

	Northern (NORTH)	Southern (SOUTH)	Queensland coast (QUEENS)
Length of the transect (km)	1150	976	543
Number of plots	98	71	162
Average distance between plots (km)	14.3	23.9	0.06
Mean annual temperature (°C)	25.9 [21.4; 28.0] (0.35)***	19.4 [16.3; 21.5] (0.24)***	23.3 [19.6; 25.6] (0.48)***
Annual precipitation (mm)	723.9 [310; 1469] (0.48)***	257.2 [154; 458] (0.20)***	1904.7 [910; 3817] (0.19)***
Elevation (m)	273.2 [7; 663] (0.39)***	281.8 [16; 579] (0.06)	248.9 [3; 1276] (0.48)***
Habitat heterogeneity	7186.8 [3706; 8743] (0.13)***	5976.7 [514; 9132] (0.08)*	8358.6 [2734; 9347] (0.11)**
Vegetation height (dm)	22.8 [1; 110] (0.18)***	19.8 [1; 102] (0.08)*	120.1 [1; 367] (0.42)***
Species richness	7.27 ± 4.39 [1–23]	5.66 ± 4.06 [1–20]	9.38 ± 5.60 [1–36]

Note: Means and ranges (in square brackets) are provided. In addition, individual environmental variable correlations (R^2) with NMDS ordinations for each transect based on bird community composition are shown. Relative importance was determined by summing the coefficients of the I -splines from GDM. Permuted variable importance was quantified as the per cent change in deviance explained between a model fit with and without that predictor permuted. Model significance is also given.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

semiarid and desert environments. The third transect (NORTH) crosses the Northern Territory from Darwin Coastal to Burt Plain where savanna and semiarid climate predominates (see Table 1 for details). The northern and southern transects are virtually aligned longitudinally so that they could be seen as a single large transect across the Australian continent, from north to south. However, since central Australia was not conveniently sampled (there is a sampling gap corresponding to the desert region of Alice Springs), two independent transects were considered (NORTH and SOUTH).

2.2 | Bird Data

Each transect consisted of a series of 2-hectare (ha) plots (98, 71 and 162 plots for NORTH, SOUTH and QUEENS respectively) aligned along a latitudinal/climatic gradient. The plots were surveyed using the standard 20-min 2-ha method by local birdwatchers during the austral breeding season (December–February). This census technique involves identifying the different bird species detected visually or acoustically within

the entire 2-ha area over a timed 20-min period (Loyn 1986; Barrett et al. 2003). We constructed species accumulation curves using iNEXT (Hsieh, Ma, and Chao 2016) to visually inspect if the observed richness may increase with further sampling effort. In all cases, we found that the curve reached a plateau suggesting that the number of plots sampled was enough to describe the biodiversity of each region (Figure 1b). We used incidence data (presence/absence) instead of abundances in further analyses.

2.3 | Environmental Data

Microclimate and landscape structure are major driving forces that influence avian community composition and abundance. We selected five environmental factors (elevation [m], annual precipitation [mm], mean annual temperature [°C], average vegetation height [dm] and habitat heterogeneity [estimated using the Simpson diversity index; Tuanmu and Jetz 2015]) that characterise the abiotic conditions of each sampling site. These variables were chosen because they are known to significantly influence bird distribution, species richness and community composition (e.g., Currie et al. 2004; McCain 2009). Elevation was retrieved from the Landscape Grid of Australia (raster data at 3 arc-second or approximately 90 m resolution; Grundy et al. 2015), with values associated with the centroids of plots. Climate data were extracted at the coordinates of each plot in ArcGIS Pro from WorldClim 2.0 interpolated climate data (derived from the Australian Bureau of Meteorology records; Fick and Hijmans 2017). The remaining predictor variables (vegetation height and habitat heterogeneity) were compiled from the EarthEnv project (<https://www.earthenv.org/texture>) and the Centre for Water and Landscape Dynamics of the Australian National University (Scarth 2013).

We explored the relationship between these environmental variables and species richness (alpha diversity) by means of linear regressions. Because the effect of the explanatory factor (e.g., precipitation) on diversity can be nonlinear (with saturation points at which biodiversity increases no further and may even decrease), we also considered the possible existence of a curvilinear response (second-order term) (see e.g., Chen and Khanna 2024).

2.4 | Multivariate Community Analysis

First, to quantify bird beta diversity, we computed a dissimilarity matrix between sampling plots in terms of species composition using Jaccard's dissimilarities distances for each transect. Values in the dissimilarity matrix range from 0 to 1, with 0 representing complete similarity and 1 representing no species in common. Next, the incidence-based dissimilarity matrix was used as input to perform a nonmetric multidimensional scaling (NMDS) and visualise similarities in composition between plots. We assessed which environmental variable showed the strongest association with community composition change by correlating all environmental variables against the NMDS ordination using the *envfit* function of the R package 'vegan' (Oksanen et al. 2017). Complementarily, we ran principal correspondence analyses (PCoA) (also known as metric multidimensional scaling, MDS) using the 'bray' method on

environmental variables for each transect. We obtained similar results using this ordination technique (Figure S1).

Beta diversity was subsequently decomposed into two components, spatial turnover (which is independent of species richness) and nestedness (type of richness difference, whereby species of low-diversity sites are a subset of species belonging to high-diversity sites; i.e., ordered loss/gain of species), using the approach devised by Baselga (2010) and implemented in 'betapart' (Baselga and Orme 2012). We then calculated for each transect the pairwise dissimilarity between all plots to explore the distance-decay relationships between β diversity (and its two components) and environmental distances between plots in terms of annual precipitation. For comparative purposes, we focused on annual precipitation since this was the only variable that was identified as a significant driver of beta diversity in the three transects (see next section).

2.5 | Generalised Dissimilarity Modelling

We employed generalised dissimilarity modelling (GDM) to examine compositional turnover with respect to environmental gradients and spatial structure. GDM is a nonlinear matrix regression technique for analysing spatial patterns in the compositional dissimilarity between pairs of sites as a function of environmental dissimilarity and geographical distance (Ferrier et al. 2007; Fitzpatrick et al. 2022). Unlike classical linear matrix regression, GDM accommodates (a) variation in the rate of compositional turnover (nonstationarity) at different positions along a given gradient, and (b) the curvilinear relationship between compositional dissimilarity and increasing environmental/geographical distance between sampling sites. We employed the default of three *I*-spline basis functions per predictor. The maximum height of each *I*-spline represents the total amount of compositional turnover associated with that predictor, keeping all other variables constant. That is, the *I*-splines are partial regression fits that serve as an indicator of the importance of each variable in determining patterns of beta diversity. The slope of the *I*-spline reflects the rate of species turnover and how this rate varies at any point along the gradient (Ferrier et al. 2007). We summed the coefficients of the *I*-splines to assess the relative importance of each variable in describing patterns of beta diversity. To account for the influence of species richness, we removed all plots in which the number of recorded species was < 4 as it improved the performance of the GDMs.

2.6 | Threshold Indicator Taxa Analysis

Lastly, we assessed community change using 'TITAN2' (Baker, King, and Kahle 2023), the R implementation of TITAN (de Cáceres et al. 2010; Baker and King 2013; King and Baker 2014). TITAN uses a combination of change-point analysis (King and Richardson 2003) and indicator species analysis (Dufrene and Legendre 1997; de Cáceres and Legendre 2009) to identify sharp, nonlinear changes in relative abundance and frequency of occurrence of species across an environmental gradient. By means of binary partitioning, TITAN distinguishes taxa that negatively (z^-) or positively (z^+) respond to the gradient (Baker and King 2010). We excluded species found at less than three plots

and used 500 bootstrap replicates for each transect. Two diagnostic indices of indicator response quality are obtained from bootstrap resampling: indicator *purity* and *reliability*. *Purity* is the per cent of bootstrap replicates with the same change-point response directions (negative or positive) as the observed response. *Reliability* is the per cent of bootstrapped change-point indicator value scores that consistently have significant p -values ($p < 0.05$). We considered taxa as indicators if their purity and reliability indices were $\geq 95\%$, and only included responses of indicator species in our analyses (i.e., filtered scores). For each transect, we performed indicator species analyses for those environmental variables that were identified as the best predictors of community composition in previous analyses.

3 | Results

We analysed three independent bioclimatic transects on mainland Australia spanning $\sim 10^\circ$ of latitude for the Northern and Southern transects, and 4° for the Queensland coast transect. Latitudinal variation of environmental variables differed among transects (Figure 1).

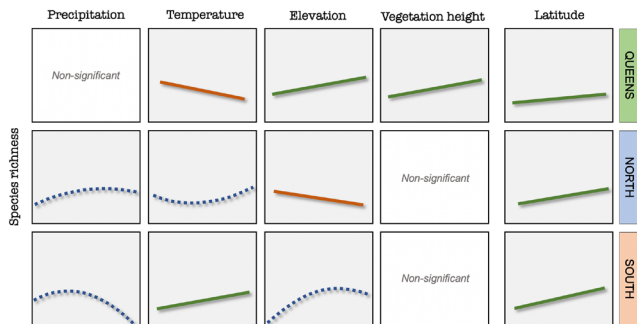


FIGURE 2 | Graph summarising the relationship between alpha diversity (species richness) and different environmental variables considered in the present study for each of the three transects. The association between species richness and habitat heterogeneity is not presented as it was nonsignificant ($p > 0.05$) in all cases. Latitudinal variation in species richness is also shown.

Average bird species richness per plot oscillated between 5.7 for the Southern transect (SOUTH) and 9.4 for the Queensland coast transect (QUEENS) (Table 1). Species richness was linearly correlated with latitude in the three transects (Figure 2). Species richness increased with elevation and vegetation height and decreased with temperature in QUEENS (Figure 2). For the SOUTH transect, species richness increased with elevation and temperature and decreased with precipitation above a certain threshold (Figure 2), whereas in NORTH, it showed the opposite pattern: a negative association with elevation and a positive association with precipitation only for the first third of the gradient (Figure 2). All relationships shown in Figure 2 were significant ($p < 0.05$) unless otherwise stated.

The most common species in NORTH were *Grallina cyanoleuca* (found in 32% of the plots), *Artamus cinereus* (29%) and *Geopelia striata* (29%). *Trichoglossus haematodus* (34%), *Sphecotheres vieilloti* (34%) and *Rhipidura leucophrys* (24%) were the species with presence in a higher number of plots for QUEENS, whereas *Taeniopygia guttata* (31%), *Gavicalis virescens* (26%) and *Acanthagenys rufogularis* (25%) were the most common species in SOUTH.

3.1 | Changes in Community Composition Along the Gradient

We used NMDS ordinations to examine the even spread of plots in environmental space and determine the dominant environmental factors across space. We found no obvious evidence of community disjunctions on the gradients. We observed a relatively smooth transition between precipitation isohyets, especially for the NORTH and SOUTH plots (Figure 3). NMDS ordination of the NORTH and QUEENS transects showed a temperature-elevation gradient (Figure 3), whereas for the SOUTH transect, the first axis (NMDS1) revealed a temperature-precipitation gradient (Figure 3). Mean annual temperature and annual precipitation were the variables best able to represent the gradients based on R^2 scores for NMDS ordinations (Table 1). Both variables were highly correlated with the NMDS ordination in the

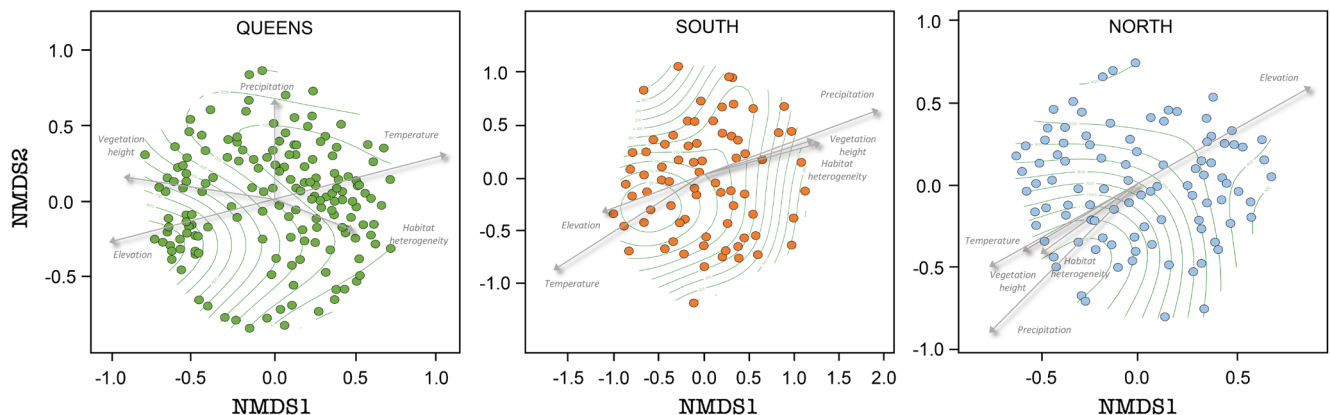


FIGURE 3 | Nonmetric multidimensional scaling (NMDS) ordinations of QUEENS, NORTH and SOUTH sites based on bird species composition, with fitted surfaces of mean annual precipitation (green isohyets). The length of the arrows is proportional to the goodness-of-fit (R^2) with the ordination. Stress ranged between 0.29 and 0.31. These stress values are not too high for ecological data considering that points are close making it difficult to establish large differences in a few dimensions.

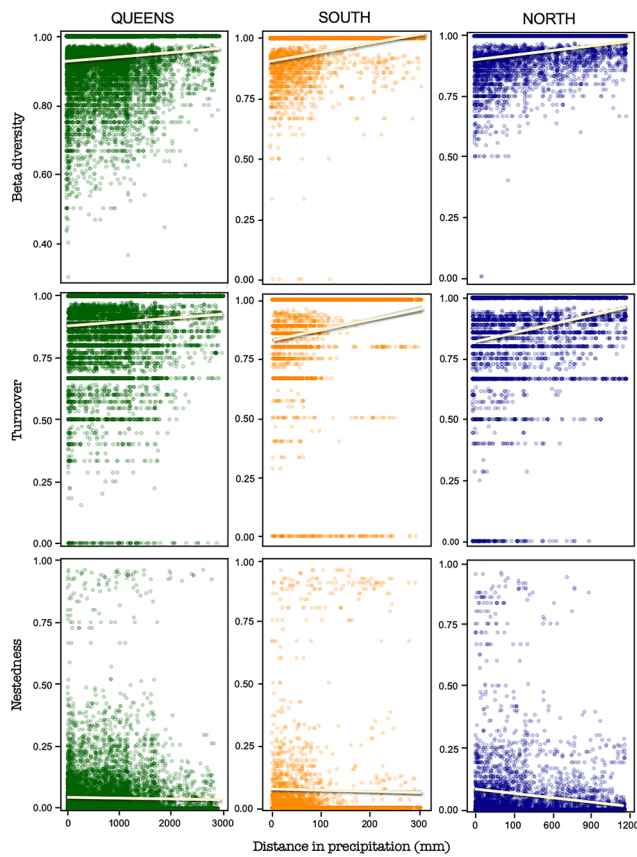


FIGURE 4 | Relationship between total β diversity (and the two components, turnover and nestedness, in which it can be decomposed) and increasing environmental distance between plots in terms of annual precipitation. These relationships indicate whether the increase of compositional dissimilarity is driven by species replacement (turnover) or ordered species loss (nestedness). The dots depict all pairwise comparisons and the lines represent linear models.

three transects. QUEENS showed greater overall R^2 values than NORTH and SOUTH, potentially due to the greater environmental extent of this transect. NMDS ordination for the QUEENS transect showed a higher level of clustering with respect to the other two transects due to slightly greater differentiation of plots receiving over 700 mm of precipitation located at mid-elevation (900 m) (Figure 3).

The overall lack of significant clustering was probably related to the low nestedness (multiple-site dissimilarities; NORTH: 0.006; SOUTH: 0.009; QUEENS: 0.008) and high degree of species replacement (NORTH: 0.984; SOUTH: 0.978; QUEENS: 0.984), indicating that most species were not shared between many plots.

With increasing environmental distance between plots (i.e., contrasting annual precipitation), the overall dissimilarity between communities (pairwise dissimilarities) increased (Figure 4). However, when β diversity was partitioned, the two components exhibited different patterns. The distance–decay of species turnover was positive in the three transects whereas the nestedness component decreased with increasing environmental distance in the NORTH or remained almost constant (in QUEENS and SOUTH; Figure 4).

TABLE 2 | Results of generalised dissimilarity models (GDMs) analysing the beta diversity of Australian breeding birds along three bioclimatic transects (NORTH, QUEENS and SOUTH; see main text for details) as a function of environmental variables and geographical distance.

	NORTH	QUEENS	SOUTH
GDM deviance	509.82	1269.88	346.65
Null deviance	570.39	1560.65	411.16
Variance explained	10.62	18.63	15.69
Intercept	1.98	1.53	2.06
Relative variable importance			
Temperature	0	0.89	0.69
Precipitation	0.80	0.33	1.38
Elevation	0.69	1.01	0.53
Vegetation height	0.09	0.96	0.26
Habitat heterogeneity	0.53	0.26	0.22
Geographic distance	0	0.33	0
Permuted variable importance			
Temperature	0	2.54	11.98*
Precipitation	14.55**	7.04*	28.03**
Elevation	2.23	5.60	0.89
Vegetation height	0.51	19.28**	0.91
Habitat heterogeneity	6.51	0.51	0.34
Geographic distance	0	0	0

* $p < 0.05$.

** $p < 0.01$.

3.2 | Drivers of Beta Diversity

Results from the GDMs showed that the environmental variables, rather than geographical distance, influenced the observed beta diversity patterns in bird communities of the three transects. The most important variables explaining species dissimilarity patterns in the study areas (i.e., community dissimilarity between plots along the transect) were precipitation, for SOUTH and NORTH, and elevation for QUEENS (Table 2). Geographic distance explained variation in beta diversity only in QUEENS. The deviance explained by the fitted GDM was 18.6% for QUEENS, 15.6% for SOUTH and 10.6% for NORTH (Table 2). The relative importance of variables differed among transects as detailed in Table 2. Beta diversity was found to increase asymptotically with both precipitation and vegetation height in QUEENS; changes in bird communities appear to stabilise above a threshold value (1800 mm and 14 m for precipitation and vegetation height respectively) (Figure 5). A similar response was observed for precipitation in NORTH; rate of species turnover was more pronounced at around 400–800 mm and then declined to reach a plateau at 1200 mm (Figure 5). In SOUTH, compositional turnover per mm of rainfall was rapid at the arid extreme of the gradient (< 230 mm), with the rate slowing as precipitation increased (Figure 5). Beta diversity increased asymptotically with temperature before levelling off around 19°C (Figure 5).

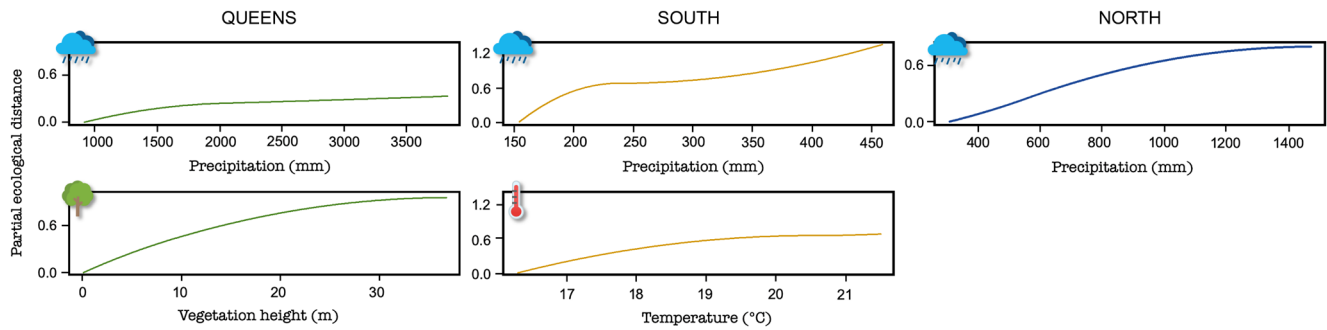


FIGURE 5 | Fitted I-splines of the generalised dissimilarity models (GDMs)—Bird community compositional dissimilarity responses along environmental gradients across the three examined bioclimatic transects in Australia (QUEENS, NORTH and SOUTH). Plots show nonlinear, monotonic functions fitted to variables using GDMs, in which the slope represents the rate of compositional turnover and maximum function height indicates total compositional turnover (i.e., summed spline coefficients). Only those variables for which a significant relationship was found in at least one of the three transects are shown (see Table 2).

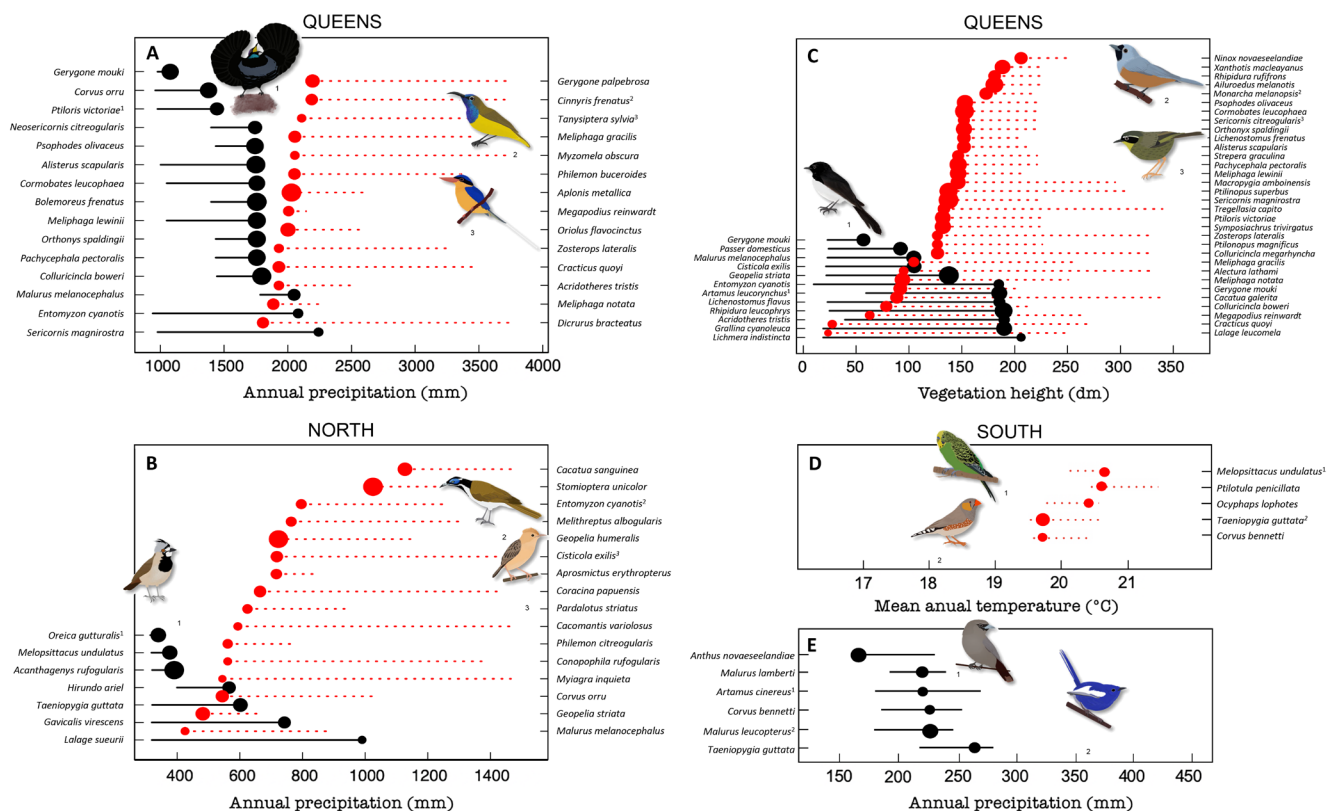


FIGURE 6 | Significant indicator taxa identified by TITAN across the environmental gradient defined by annual precipitation (a–c), mean annual temperature (c) and vegetation height (d), and for different bioclimatic transects (QUEENS, NORTH and SOUTH; see main text) in mainland Australia. Black dots represent negative indicator taxa (z^- ; abundance declines) and red dots correspond to positive taxa (z^+ ; abundance increases). Change point symbols are sized in proportion to response (z scores). Horizontal lines represent 5%–95% bootstrap quantiles (500 bootstrap replicates). Illustrations: Alba Martín del Campo.

3.3 | Threshold Indicator Taxa Analysis

TITAN threshold analysis based on precipitation indicated that the area of highest species turnover occurred between 400 and 700 mm for the NORTH (based on 23 significant species; Figure 6), whilst TITAN suggested the existence of a transition zone around 230 mm for the SOUTH. That is, bird communities

above 250 mm are different from those located in more arid conditions although this result must be interpreted with caution due to the low number of pure and reliable taxa (six species; Figure 5). In QUEENS, TITAN revealed high turnover between 1700 and 2100 mm (29 significant species; Figure 6) and suggested the existence of an ecotone around 14–15 m height when the analysis of indicator species scores was based

on vegetation height (44 significant species; Figure 6). Lastly, five species showed positive responses as mean annual temperature increased above 19°C for the SOUTH. Overall, these results were congruent with those obtained using GDMs (see previous section).

4 | Discussion

Variation in both species richness and composition along environmental gradients provides crucial information for identifying points where rates of compositional change are particularly rapid and deserve high-conservation investment (Ferrier et al. 2007; McKnight et al. 2007; Socolar et al. 2016). In this study, we combined community- and taxon-based analyses to examine changes in bird community composition along three bioclimatic transects in mainland Australia. Overall, our findings show that climatic factors like rainfall are more important in determining species composition than geographical distance, which indicates that species turnover is driven by environmental filtering rather than by dispersal limitation and/or stochastic processes. Drier landscapes, in turn, exhibit a higher rate of species turnover in comparison with wetter environments suggesting that harsher environmental conditions may promote higher spatial heterogeneity of avian communities.

4.1 | Changes in Species Richness and Community Composition Along the Gradient

Alpha diversity (i.e., species richness) showed different patterns with environmental variables such as elevation, mean annual temperature or annual precipitation depending on the analysed transect. This can partly be explained as a consequence of the different range of values covered by each of them. The existence of opposite diversity–environment trends may also arise due to differences in physiological tolerances and environmental preferences for the bulk of species recorded in each transect. For instance, species that thrive in dry inland zones like *Corvus bennetti* were relatively common in the SOUTH transect.

In terms of compositional differences, our results revealed that bird community composition responds principally to variation in annual precipitation and mean annual temperature. These two variables were consistently found to be significant predictors regardless of the analysed transect, which highlights the pivotal role of rainfall and temperature in determining the makeup of avifaunal assemblages in Australia, a continent with a predominantly hot and arid climate (e.g., Hawkins, Diniz-Filho, and Soeller 2005; McKechnie et al. 2017).

When partitioning multiple-site beta diversity into its two components; turnover (replacement) and nestedness, we observed that the SOUTH transect exhibited the most significant contribution of the nestedness component. This suggests a priori that local extinction–colonisation dynamics may be more important in semiarid ecosystems due to the existence of a filtering effect that progressively extirpates species on the basis of their physiological capabilities. However, we did not find evidence

for this when exploring the relationship between compositional dissimilarities between communities (pairwise beta diversity) and environmental distance in terms of precipitation. The component of beta diversity owing to nestedness declined or remained almost constant with precipitation, indicating that species found in drier landscapes are not a subset of assemblages located in wetter environments which would indicate an environmental filtering effect (e.g., Montañó-Centellas, Loiselle, and Tingley 2021). That is, there is no ordered loss of species between plots with increasing precipitation irrespective of the examined transect. In all cases, changes in community composition along the precipitation gradient are mainly driven by species replacement, which agrees with that observed in previous studies with birds (Soininen, Heino, and Wang 2018). However, we did not find latitudinal breakpoints in beta diversity in contrast to what has been reported by some authors (Figure S2). For instance, Castro-Insua, Gómez-Rodríguez, and Baselga (2016) documented that differences in species composition in America are mainly due to species replacement from the equator to c. 30°, but are dominated by nested species losses from this point to higher latitudes. Our results, thus, indicate that species are not filtered out but replaced with new taxa as precipitation increases. At this point, it must be noted that our set of environmental variables was reduced and we cannot rule out the possibility that other factors not considered (e.g., ecosystem productivity) have a greater influence on the composition of bird communities.

4.2 | GDMs: Drivers of Beta Diversity

We observed that environmental variables are better predictors of community composition than spatial distance, which suggests that niche-based processes have dominated the sorting of bird species along gradients. The absence of significant geographic barriers (large rivers and mountain ranges) coupled with the dispersal capacity of these organisms can explain this finding (see also García-Navas et al. 2024).

When inferring what drives turnover in bird community composition (beta diversity), results of the GDMs showed that precipitation is the most important of the examined predictors. Responses to mean annual precipitation followed a congruent pattern in which compositional turnover per mm of rainfall was rapid at the dryer end of the gradient, with the rate slowing over increasingly wet areas and typically plateauing in higher rainfall zones, especially for NORTH and QUEENS. In these two transects, beta diversity tends to plateau above 1200 mm, which suggests that above this threshold communities tend to be spatially more homogeneous. Although we found that mean annual rainfall transitions (subintervals with the highest compositional turnover rate) were consistently located across the more arid ends of precipitation gradients, we were unable to detect the existence of overlapping across transects as they did not cover similar mean annual precipitation gradients. However, our results show that regardless of eco-climate type, the composition of bird communities inhabiting more xeric environments tends to be more variable across the landscape. Why do less productive environments exhibit a higher rate of species composition change (i.e., higher beta diversity)? Several factors could explain this pattern. First, water and

food resources are often limited and patchily distributed in environments with more xeric conditions (at least in comparison with mesic environments). Birds must travel between patches of suitable habitat to find resources, leading to spatial turnover in species composition. Second, the lower availability of food resources, in turn, could make populations smaller and more vagile increasing the spatial heterogeneity of bird communities (Santini et al. 2023). In addition, several studies have reported a marked decline of species associated with open forests and woodlands in Australia (Ford et al. 2001; Mac Nally et al. 2009; Ford 2011; Bennett and Watson 2011), which can have knock-on effects at the community level. The obtained results are in line with previous Australian studies in which it has been shown that rainfall is a key driver of vegetation composition (Fitzpatrick et al. 2013; Guerin et al. 2019), which can also play an important role in determining the identity and structure of bird communities (e.g., Cody 1994; Johnson, Reich, and MacNally 2007; Jankowski et al. 2013; Zellweger et al. 2017; Dagan and Izhaki 2019; Davison et al. 2023).

In fact, vegetation height outranked mean annual precipitation for the QUEENS transect. GDM analysis revealed a transition zone associated with medium-height (14–15 m) canopies, whereas the compositional turnover rate slowed down over landscapes with increasing vegetation height. This pattern suggests that vegetation structure and forest closeness level out community dissimilarity. Regarding this, populations inhabiting transitional areas or ecotones are predicted to be smaller, be under stronger extinction pressure, and have more erratic demographic trajectories (i.e., less stable population size) than populations located in cores or vast forested areas (e.g., Karanth et al. 2006; Remeš et al. 2022). Semi-open landscapes can harbour forest- and open-habitat specialists, which are not well adapted to this zone but due to its proximity may still be present albeit in a transient state (i.e., propagules from neighbouring communities). This may prompt a higher level of reshuffling of bird species in these environments.

Our finding agrees with that reported by Blondel and Farré (1988) in four habitat gradients in Europe. Blonde and Farré found that forest bird communities in different areas were very similar, whereas those of more open habitats differed significantly. They concluded that there is greater variation in species composition in the earlier seral stages than in the later forested stages (Blondel and Farré 1988). In the same vein, Herrando, Brotons, and Llacuna (2003) reported that Mediterranean bird communities inhabiting open or semi-open burnt zones were more spatially heterogeneous than those inhabiting unburnt forested areas. The existence of a higher compositional turnover in areas with medium-height canopies cannot be explained as a result of increased diversity since average richness species reached its maximum when the vegetation height exceeds 20 m (see also e.g., Baker, French, and Whelan 2002; Remeš et al. 2022).

The annual mean temperature was also a significant environmental predictor for the SOUTH transect; bird communities located in dryer and cooler landscapes exhibit a higher rate of species turnover in comparison with those settled in a priori more benign environments. Thus, in line with that indicated above for rainfall gradients, one could conclude that harsher environmental conditions may promote higher beta diversity. This

result could potentially be explained by higher relative importance of stochastic processes under low environmental quality and more stressful conditions (Chase 2010; Busse et al. 2018; García-Navas et al. 2021).

4.3 | Ecological Thresholds

Results obtained using TITAN were congruent with those yielded by the GDMs. The main advantage of TITAN lies in the fact that it allows the species responsible for the observed changes to be identified, which facilitates the ecological interpretation of these patterns. TITAN analyses revealed that in the NORTH, dry-environments specialists like *Oreoica gutturalis*, *A. rufogularis* or *T. guttata*, were associated with the more arid end of the gradient, whereas a set of species with higher water requirements (*Geopelia humeralis* and *Stomioptera unicolor* among others) were associated with the wetter extreme. For the transect along the Queensland coastline, an abrupt shift was detected at about 1700–2100 mm, separating species associated with wet landscapes where vegetation is not sparse (e.g., *Tanysiptera sylvia* and *Myzomela obscura*) from those that thrive in drier environments and/or do not show an overwhelming preference for wet forests (*Gerygone mouki* or *Cormobates leucophaea* among others). In Queensland, several taxa ($z = 32$) significantly increased with vegetation height; the density of most of them rose once the tree canopy reached the critical threshold of 14 m. Above this height, species that forage on the leaves and stems of grasses and shrubs (and rarely in the tree canopy) like *Malurus melanoccephalus* or *Cisticola exilis* tend to disappear. TITAN analyses, thus, support the idea that landscapes with sparse and medium-sized trees can harbour more diverse communities since generalists (e.g., *Passer domesticus*), ground-dwelling species (e.g., *G. striata*) and forest specialists (e.g., *Meliphaga* and *Colluricincla* spp.) can coexist there. These landscapes, thus, comprise meeting areas between adjoining communities, and hold biodiversity not present in the surrounding environments and that may be particularly susceptible to the effects of global change (e.g., Gaston et al. 2001; Fraser et al. 2019). Lastly, in the SOUTH, synchronous changes in increasing species occurred at 19°C ($z = 5$ species), whereas six species responded negatively to rainfall when it exceeded 250 mm. The obtained results in conjunction with those derived from the GDMs point towards the existence of a higher rate of species turnover in the cooler and dryer zones of this transect which, of the three analysed, is the one with the most adverse environmental conditions.

4.4 | Conservation Implications

A couple of lessons can be drawn from our results. First, there is evidence that rainfall constitutes a key driver of bird community composition. According to climate projections for the near future (2030), winter and spring rainfall is predicted to decrease in the southern part of mainland Australia (Climate Change in Australia 2024). Thus, communities inhabiting semiarid and Mediterranean or temperate environments are likely to become more heterogeneous across space, especially those largely composed of insectivorous species like *O. gutturalis*, *Artamus* spp., *Climacteris* spp., whose populations are heavily affected by rainfall (Stevens and Watson 2014).

Secondly, our findings show that the rate of species turnover is higher in areas dominated by open forests with a medium-height tree canopy. This highlights the ecological importance of these landscapes, which are particularly threatened due to different reasons including loss and fragmentation of habitat, ecosystem dysfunction and firewood removal among others, as well as the synergistic interaction of these factors (Rayner et al. 2014; Keith 2022; Walsh et al. 2023).

4.5 | Conclusions

Fine-scale beta diversity, with sampling distributed continuously over a gradient, has been examined in a few studies, most of them focused on plants and invertebrates (e.g., Vázquez and Givnish 1998; Enkhtur et al. 2021). Here, we examined changes in bird community composition along three transects in the Australian continent. The present study shows that rainfall constitutes a key driver of bird community composition regardless of the eco-type and the range that this abiotic variable presents in a certain region. Based on our results, we can conclude that the most productive landscapes show lower spatial heterogeneity in terms of community composition in comparison with those where environmental conditions are less benign (e.g., dryer environments). This suggests that beta diversity increases with increasing environmental harshness, presumably through changes in the relative importance of stochastic versus deterministic processes, an idea that, to our knowledge, has hardly been explored in the literature (but see e.g., Marks, Muller-Landau, and Tilman 2016; Garcia-Navas et al. 2021). Regarding this, we consistently found that beta diversity was driven by species replacement rather than species loss in the three analysed transects. It is likely that this result mirrors the importance of organism characteristics (dispersal capacity, physiological traits) over environmental variation when interpreting large-scale patterns of the nestedness and turnover components of beta diversity. Lastly, the fact that environmental distance has greater explanatory power than geographic distance supports the idea that species show a deterministic distribution to the detriment of the neutral theory.

To sum up, the present study shows the convenience of integrating community- and taxon-based analyses to detect critical levels of alteration and interpret/understand mechanisms of biodiversity loss. The establishment and determination of ecological thresholds based on community data can be extremely helpful when implementing conservation actions like ecological restoration underpinned by quantitative measures or when forecasting those regions whose biodiversity will be most threatened as a consequence of global warming.

Author Contributions

Vicente García-Navas: conceptualization, investigation, resources, methodology, software, validation, formal analysis, data curation, writing – original draft, writing – review and editing, and visualization, project administration, and funding acquisition. **Carlos Martínez-Núñez:** formal analysis, writing – review and editing. **Les Christidis:** resources, writing – review and editing. **Arpat Ozgul:** writing – original draft, writing – review and editing, and visualization, project administration, and funding acquisition.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used in this work are publicly available at: <https://doi.org/10.6084/m9.figshare.25139282.v2>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.