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Leveraging historical field notebooks to uncover continental-scale patterns in the diversity of Australian grasshoppers

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Abstract

1. An understanding of how biodiversity is distributed across the broad spatial scales can resolve pure questions about ecological and historical processes and solve applied problems in conservation planning. Invertebrates such as insects make up much of biodiversity yet are rarely a focus in studies of regional-scale diversity patterns, partly due to data deficiency.
2. We took advantage of historical field notebooks to investigate the richness and compositional pattern of grasshoppers across a vast area of Australia (Western Australia, 2.6 million km^2). We extracted grasshopper occurrence records from historical surveys of 1328 locations spanning 1947 to 1985. We developed generalised dissimilarity models to identify species compositional turnover across families and modelled species richness with regression analyses.
3. Species composition was most distinct in mesic south-west, north and north-west regions and was most uniform through the arid interior region with the exception of the topographically complex Pilbara region. Species richness was highest in the arid interior and north and lowest in the cool and wet south-west.
4. The patterns of grasshopper species diversity and endemism were like patterns previously reported for lizards and this may reflect their common independence from water and their phylogenetic bias towards warm environments.
5. Although high species richness was predicted in the Pilbara region, the area remains underrepresented in the national reserve system, with <10% of its area protected. High levels of short-range endemism were found in general, with only ~1/4 of short-range endemics being located in the national reserve system.
6. Our analyses demonstrate that field notebooks can be a valuable resource for biogeographic analyses and for planning invertebrate conservation.

KEYWORDS
biogeography, conservation, endemism, field notebook, generalised dissimilarity modelling, invertebrates, species richness, species turnover

INTRODUCTION

Understanding the rate and magnitude of change in species composition across large spatial gradients can provide insights into the mechanisms of community assembly (Anderson et al., 2016; Pianka, 1973; Powney et al., 2010), coexistence (Pianka, 1973, 1986; Pianka & Schall, 1981), and historical biogeographic forces (Byrne et al., 2008; James & Shine, 2000; Thomassen et al., 2011; Willig et al., 2003). An understanding of these fundamental biogeographic and ecological patterns in species turnover is critical for applied problems in conservation planning (Ferrier et al., 2007).

The Australian continent has a complex palaeo-environmental history involving increasingly strong cycles of aridification on a background transition from cool and wet to warm and dry as it has drifted from Antarctica towards the equator. Species diversity analyses have revealed striking similarities and divergences among vertebrate taxa in patterns of species diversity, with amphibians, mammals and birds sharing a pattern of low diversity in the arid zone and lizards showing the reverse pattern (Pepper et al., 2013; Pepper & Keogh, 2014; Powney et al., 2010; Schall & Pianka, 1978). This raises intriguing questions about the relative roles of ecology, geography, and history in shaping species diversity.

Generalised dissimilarity modelling (GDM) is emerging as an important tool to analyse species turnover at the landscape scale (Bell et al., 2013; Chesters et al., 2019; Deacon et al., 2020; Nipperess et al., 2012; Pennifold et al., 2017). Such studies require systematic survey data using standard methods for a group of interest over a broad region. Such data are common for vertebrates, for example, bird sightings of William McLennan from 1906 to 1923 are available from the Biodiversity Heritage Library: https://www.biodiversitylibrary.org/creator/289083#/titles. Invertebrate biogeography and conservation are frequently limited by a lack of data, especially across large spatial extents (Ballesteros-Mejia et al., 2017; Braby et al., 2021; Sánchez-Bayo & Wyckhuys, 2019, 2021). However, for some taxa, extensive information on species occurrences and habitat associations exists in the form of field notebooks, including butterflies (Sanderson et al., 2021), land snails (developed a citizen science-based Slatyer, Ponder, et al., 2007) and Odonates (Waller et al., 2019). For grasshoppers, Dr Ken H.L. Key and his colleagues conducted 223 field surveys in Australia along the road networks for over 54 years (mostly a single visit to each site), from 1936 to 1989 (Hossain et al., 2023; Kearney et al., 2021). Specimens collected from these field notebooks are preserved in the Australian National Insect Collection. A digitised version of these field notebooks is available from the Biodiversity Heritage Library (https://www.biodiversitylibrary.org/bibliography/176096). These field notebooks give us a unique opportunity to analyse grasshopper species turnover and richness over a large landscape and, therefore, to improve the information base for conservation and management.

Here, we develop GDMs and richness models from grasshopper occurrence records extracted from Key's field notebooks to characterise patterns of species turnover and richness at a broad spatial scale. We focus on the Australian state of Western Australia, where our initial transcription and geocoding efforts have been targeted (Hossain et al., 2023). This large region (2.6 million km^2) encompasses a wide range of climates from cool, humid, and winter-dominant rainfall in the south-west, sparse, aseasonal rainfall in the arid interior, and summer rainfall in the tropical north. The south-west, desert interior, Pilbara and Kimberley, have high diversity and endemism for plants and animals (Beard et al., 2000; Cracraft, 1991; Crisp et al., 2001; Pepper et al., 2013; Pepper & Keogh, 2014; Rix et al., 2015). In this state, a range of land use activities have threatened biodiversity (Abbott, 1997; Armstrong, 2011; Duncan & Dorrough, 2009; Gonzalez, 2000), including a long history of land clearing especially for wheat cultivation in the southwest (Burvill, 1956), mining activity (more recent, especially in the Pilbara) (EPA, 2014), and current plans for expanding agriculture in the Kimberley region (Kimberley Development Commission, 2015).

Approximately 1000 species of grasshoppers occur in Australia within four families (i.e., Acrididae, Morabidae, Pyrgomorphidae, and Tetrigidae) (Key, 1959; Rentz et al., 2003). In this study, we consider 478 species from the Acrididae, Morabidae and Pyrgomorphidae and use our analyses to ask: (i) how the compositional pattern (i.e., beta diversity) of grasshoppers varies spatially between families across WA; (ii) how the species richness (i.e., alpha diversity) varies spatially; (iii) how these patterns compare with other taxonomic groups and what this might mean, and (iv) how well the existing protected area (PA) network encompasses grasshopper diversity and endemism.

MATERIALS AND METHODS

Data preparation

The historic field notebooks of Key and associates and their transcription were detailed in (Hossain et al., 2023). Briefly, each notebook contains systematic details of the route of travel, distance recorded by vehicle odometer, and collection stops (identified from suitable geographic references, e.g., towns, creeks, road-junction). In addition, for each collection stop they recorded a general description of the site, common plants in the area, soil type, topography, grasshoppers observed which are often associated with life stages and their relationship with plants. For each site, they spent approximately 30 min of collecting grasshoppers by sweep net and bush shaking/beating and through visual inspection of the vegetation and ground layer (Day & Rentz, 2004; Hossain et al., 2023). We obtained geographical coordinates from Google Earth by following the route directions recorded in the field notebooks with the aid of historic topographic maps. Altogether, 42 field surveys were conducted in WA between 1947 and 1985, encompassing 316 days of collecting grasshoppers from 1328 sites. This resulted in occurrence records for 471 species in WA with an average of eight species recorded per site (range of 1–25 species per site) (Table S1, and S2).

To avoid bias due to potential under sampling, we used a grid with large 0.5° (approximately 50 × 50 km) cells. We used these grid centroids as the location for any survey that fell within the respective grids. For each grid cell, we extracted values for bioclimatic variables (bio1 to bio19), derived from historic temperature and precipitation data between 1942 and 1985 from the Australian Water Availability Project (Raupach et al., 2009). Being herbivores, grasshoppers are closely tied to vegetation and its moisture content, and soil moisture is also important for their oviposition sites and hatching success (Uvarov, 1977). Therefore, we included the following soil predictors: plant available water capacity (%), soil bulk density (g/cm^3), clay content (%), total nitrogen (%), total phosphorus (%), soil pH (pH of 1:5 soil/0.01 M calcium chloride extract) downloaded from the Soil and Landscape Grid of Australia (Grundy et al., 2015). We also extracted values from a hydrologically enforced digital elevation model (demH, Wilson et al., 2011) and topographic wetness index (twi; Gallant & Austin, 2012). The predictors demH and twi capture information about which locations are likely to have greater soil/ground moisture for a standard amount of rainfall, based on their elevation and topographic position which is important for grasshoppers' survival. Finally, to estimate vegetation greenness, we included the seasonal Normalised Difference Vegetation Index (NDVI; available as monthly rasters from https://data.gov.au/). NDVI rasters were averaged for 20 years (1992–2011) as mean, summer, autumn, winter, and spring NDVI.

The resolution of the original data sets was as follows: 5 km for bioclimatic rasters, 1 km for NDVI, 83 m for soil, 27 m for demH and twi rasters. Therefore, to match with our larger grid sizes (up to 50 km), we averaged (mean function) these finer resolution rasters to the coarser scale of ~50 km (0.5°) of the grid cells. However, to capture the variation in terrain elevation and ruggedness (demH and twi rasters), for these variables we calculated the standard deviation for demH and twi rasters. We conducted analyses and predicted species composition and richness using the ~50 × 50 km (0.5° × 0.5°) gridded dataset.

Predicting the pattern of species composition

Grasshopper species compositional turnover was analysed following the GDM approach implemented with the R package 'gdm' (Ferrier et al., 2007; Fitzpatrick et al., 2021; Mokany et al., 2022). GDM is a powerful tool for identifying patterns of species composition (Arponen et al., 2008; Ferrier et al., 2007; Mokany et al., 2014; Overton et al., 2009; Thomassen et al., 2011), and it is best applied with occurrence data resulting from biological surveys (Gibson et al., 2015). The GDM approach models spatial turnover of species composition (compositional dissimilarity) as a function of geographic distance and environmental difference (Ferrier et al., 2007). Compositional dissimilarity between a pair of sites is measured as proportion of species occurring between sites—ranging from '1' if two sites do not have any common species to '0' if they have exactly the same species composition. Currently, GDM uses Bray–Curtis dissimilarity (Bray & Curtis, 1957), with a generalised linear modelling (GLM) framework to model species turnover relative to geographic and environmental variables. A fitted GDM resulting from sampled biological data can be used to predict compositional dissimilarity in unsampled locations over a region of interest.

The model fitting procedures of GDM involved the calculation of Bray-Curtis distances between site pairs to produce a site-by-site distance matrix as the response variable. The site-pair distance matrix was created based on grid centroids of the ~50 × 50 km (0.5°) grid cells. We used the *gdm.varImp* function of the *gdm* package to perform a permutation test on the influence of our predictor variables on the GDM (Mokany et al., 2022). We randomly permuted the predictor variables across the sites 1000 times and used a backwards selection approach to sequentially remove predictors using a 5% threshold. We further eliminated one of each pair of highly correlated (>70%) predictors from the subset, selected from the above step. Our final predictors for the GDM analysis included: annual mean temperature (bio1), annual precipitation (bio12), soil bulk density, and winter NDVI. A final GDM was fitted using the distance matrix as a response variable and the selected environmental variables as predictors (Ferrier et al., 2007). Finally, the fitted GDM was used to predict the uniqueness of grasshoppers of each location by calculating the predicted mean similarity between that location and all other grid cells in the region (Western Australia). To capture the possible variation of compositional turnover between families, the whole process was repeated for three grasshopper families separately: Acrididae, Morabidae, and Pyrgomorphidae. We did not include the family Tetrigidae due to the very low number of occurrences.

Predicting species richness

For predicting species richness, we calculated mean species count for surveys in each grid of Western Australia (0.5°, ~50 × 50 km). We modelled species richness by fitting generalised linear models using the lognormal distribution of the Gaussian family because it can account for variable survey effort per grid cell. As a preliminary step, we considered linear and quadratic terms separately for each predictor ($n = 32$) and eliminated five predictors from the set, which we considered uninformative ($p < 0.1$). For the remaining predictors, we calculated pairwise correlations. From each pair of highly correlated (>0.70) variables, we selected one variable resulting in a final subset of 11 predictors. Afterwards, we fitted the model the same way using linear and quadratic terms of the selected subset of predictors. Then predictors were removed by stepwise backward elimination based on the lowest t-value until a subset of significant predictors was left in the model ($p < 0.05$). Our final subset of predictors was: mean temperature diurnal range (bio2), isothermality (bio3), mean temperature of wettest quarter (bio8), precipitation of coldest quarter (bio19), and twi. We then fitted a model using the linear and quadratic terms of the selected predictors and the final model was selected based on the lowest AIC. The final model (see equation) contained only linear terms for all variables except bio3.

$$\mathrm{glm}\left(\log\left(\mathrm{richnessPerEffort}\right) \sim \mathrm{bio2} + \mathrm{bio3} + \mathrm{bio3}^2 + \mathrm{bio8} + \mathrm{bio19} + \mathrm{twi}, \mathrm{family} = \mathrm{gaussian}\right)$$

To test the performance of our lognormal model we applied a 100-fold cross-validation in which 1% of spatially distant sites were held for model testing (using R package 'blockCV', Valavi et al., 2019) and the remainder of sites were used for model training. Finally, we calculated the coefficient of variation based on spatial predictions resulting from 100 iterations.

Centres of endemism

At the continental scale, most grasshopper species (>90%) are endemic to Australia. However, within Australia, large regions are also recognised as centres of endemism (Crisp et al., 2001; Slatyer, Rosauer, & Lemckert, 2007). While a few species of grasshoppers are widely distributed and cause periodic outbreaks, many species were very rarely recorded (Hossain et al., 2023) and can likely be regarded as short-range endemics within Australia. Because the measure of endemism is dependent on scale, we used *weighted endemism* (WE) following Crisp et al. (2001), Slatyer, Ponder, et al. (2007) and others. WE is now favoured over previous approaches of defining endemism that uses an arbitrary range threshold (i.e., 1–4 cell distribution). To calculate WE, we made grids of ~50 × 50 km (0.5° × 0.5°). For each cell, higher scores (weights; w_i) were assigned to species with smaller ranges ($w_i = 1/n_i$; where n_i is the number of grid cells that species i occurred in). The final endemism score of a cell was calculated as the total score contributed by all species occurring in that cell (WE $= \Sigma w_i$, presented in Appendix 1). We also calculated the endemism score for species occurring in between one to four cells, following the same approach as WE, to illustrate the distribution of these small-range endemics. In our analyses, WE was highly correlated ($r^2 = 0.84$) with species richness (measured as the total number of unique species in each cell), as every species contributed to the score. To overcome the high correlation between WE and species richness we measured the *Corrected Weighted Endemism* which is calculated by dividing the WE score in each cell by the richness score of that cell, following Crisp et al. (2001). Similarly, to capture the variation of endemism among families, we repeated the process for Acrididae, Morabidae, and Pyrgomorphidae grasshoppers. In addition, we used GDM predictions to assess how well—PAs in Western Australia represent grasshopper diversity. This was done by calculating the *natural uniqueness* of each location to locations that are within the PA network (Mokany et al., 2022; Williams et al., 2016). The natural uniqueness of each location was calculated using the mean similarity between that location and all other grid cells in the study region based on the fitted GDM (see predicting species turnover, above). All analyses were conducted in R version 4.2.3 (R Core Team, 2023) and ArcGIS (ESRI, 2023).

RESULTS

Patterns of grasshopper communities

The GDM (Figure 1) was fitted using the four environmental predictors (out of 32) selected for the ~50 × 50 km (0.5°) gridded dataset for three families of grasshoppers (i.e., Acrididae, Morabidae, and Pyrgomorphidae). The amount of deviance explained by the models varied across families being 22.2% for Acrididae (51,360 site-pairs), 24.9% for Morabidae (12,090 site-pairs), 43.3% for Pyrgomorphidae (2850 site-pairs), and 23.38% for all species (52,650 site-pairs). Geographic distance between site-pairs was found to be the most important predictor of compositional turnover in pyrgomorphid grasshoppers, whereas annual mean temperature was most important for the Morabidae; for Acrididae, all variables contributed similarly to compositional turnover (Figures 2 and 3a). Soil bulk density had no contribution to compositional turnover for Pyrgomorphidae (Figures 2 and 3c). Substantial variation was found across families for the remainder of the environmental predictors included in the final model (Figures 2 and 3). For example, different response curves for geographic distance and annual precipitation were observed for pyrgomophids, and morabids, respectively (Figure 3). Across three families of grasshoppers, the predicted biological uniqueness (mean similarity of a location compared to the whole region) indicates low compositional uniqueness of the arid central region of WA in comparison to the higher levels of compositional uniqueness of the south-west and the Kimberley regions (Figure 4). However, there were high levels of predicted uniqueness in the Pilbara for acridid and morabid grasshoppers (not pyrgomorphids), and acridids on the Nullarbor plain had low compositional uniqueness (Figure 4). Acridids, being the most abundant family of grasshoppers, had similar responses when all species were included in the model (Figures 1, 3 and 4).

Species richness

The selected lognormal model (Figures S1–S3) of grasshopper species richness explained 28.5% of the total deviance. The predicted species richness varied from 1.9 to 10.3 species per survey per cell (Figure 5a). Spatial interpolation of the species richness model showed that sites in the south-west were depauperate. Species richness increased towards the equator, peaking in the Pilbara in the north-west and the Kimberley in the north (Figure 5a). The coefficient of variation based on 100 iterations ranged from 0.5% to 4.6%, with the highest variation observed in remote areas around the Pilbara, Kimberley, and north of the Nullarbor (i.e., Great Victorian Desert) (Figure 5b). Due to the smaller sample size and the absence of significant predictors in our family-level models for Morabidae and Pyrgomorphidae, we did not predict species richness for these families.

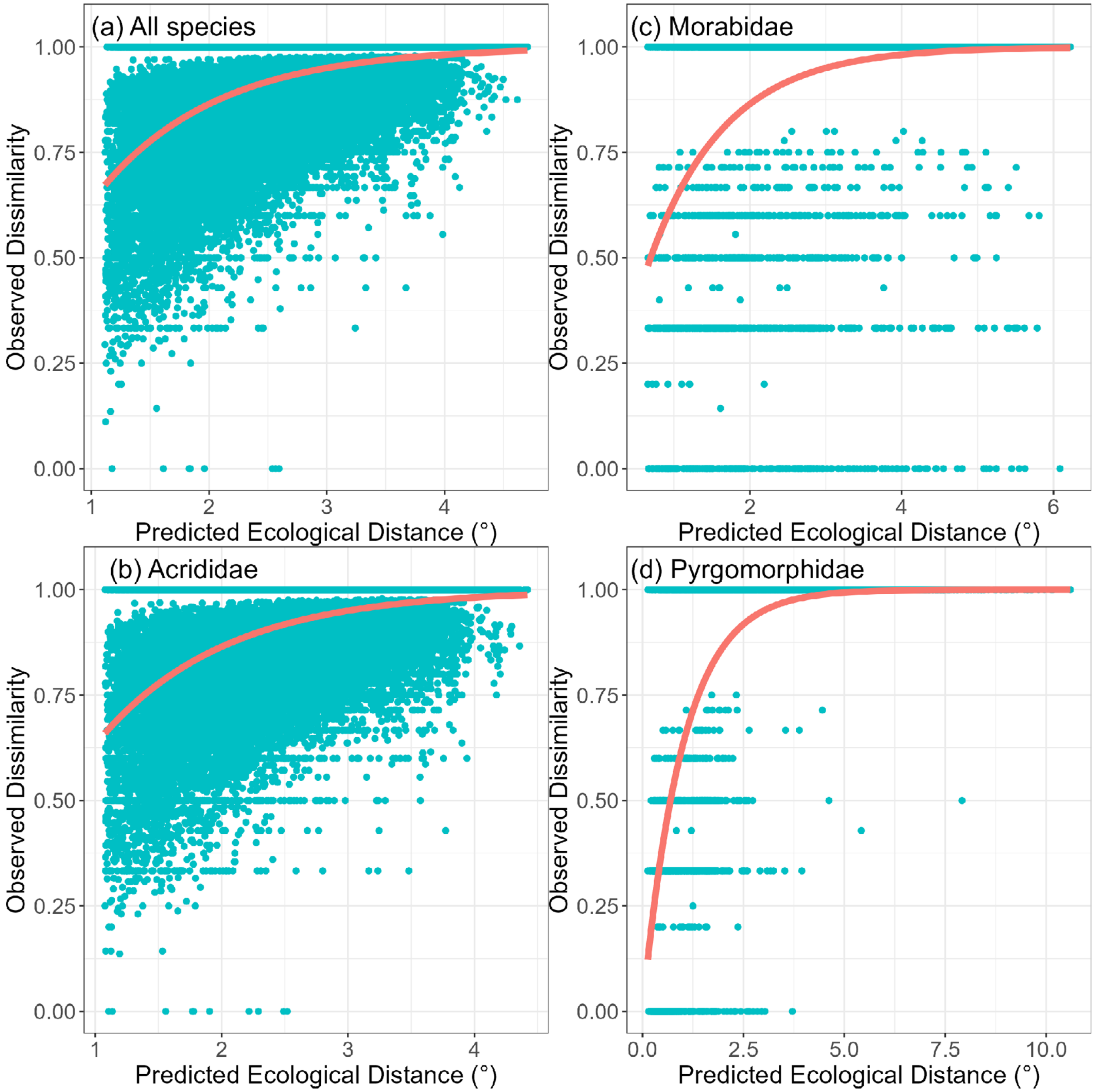

FIGURE 1 The fitted generalised dissimilarity model for grasshoppers of the Acrididae, Morabidae, and Pyrgomorphidae in Western Australia. (a–d) Orange line indicates predicted ecological distance (*x*-axes) versus predicted dissimilarity (*y*-axes). 1° is approximately 100 km.

Patterns of endemism and representativeness to protected areas

Out of 1328 locations surveyed, 162 sites fell within the PA network. Many species were rarely encountered, with 59.8% of species (237 out of 396 species having a confirmed/putative taxonomic name) having a 1–4 cell distribution in the survey data (Figure 6). Of these rarer 237 species, only 61 species (26%) were recorded within the PA network (Figure 6). However, the distribution of these rare species of grasshoppers was not concentrated in a specific region; rare species were found throughout. This was again highlighted with the distribution of corrected WE (Figure S4). The predicted representativeness of grasshopper community diversity within PA ranged from 12% to 36% with assemblages in the arid centre having the highest protection and assemblages in the south-west having the least (Figure 7). Overall, PAs in WA represent an estimated 20% of grasshopper community diversity.

DISCUSSION

General patterns of alpha and beta diversity

The last time the biogeographic patterns of Australia grasshoppers were considered was Key (1959) who, following Spencer (1896), divided Australia up into four broad regions: (1) an interior hot and

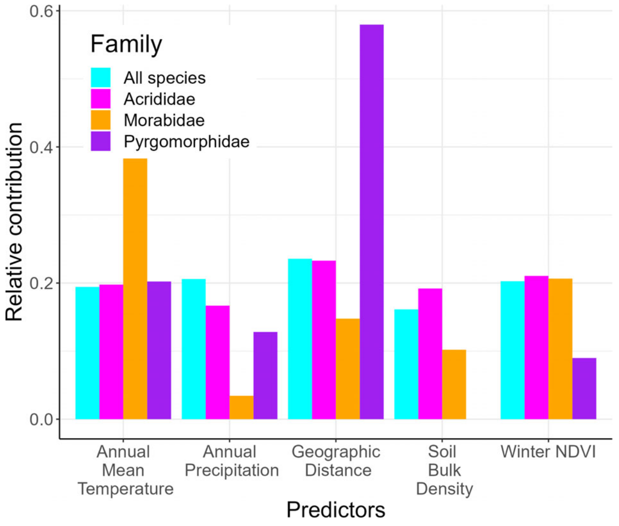

FIGURE 2 Relative contribution of each predictor in explaining grasshopper species' compositional turnover pattern. Within each family, the coefficient of each predictor was divided by the sum of coefficient values of all predictors in the model fitting to calculate the relative contribution of each predictor. NDVI, Normalised Difference Vegetation Index.

arid region with aseasonal limited rainfall; (2) a hot semi-arid to subhumid region in the north and east with summer rainfall; (3) a corresponding cooler region in the south and east with winter rainfall; and (4) a humid belt along the east coast and south-west of Western Australia. He further divided zone four into: (a) a northern section with preponderance of summer rainfall with higher temperature, and (b) southern cooler section with winter rainfall. The patterns revealed in our analyses correspond broadly to Key's zoogeographic zones. Species turnover, and hence uniqueness, was high in the southwest (Key's zone 4b), in the Pilbara region of the north-western part of the arid zone (Key's zone 1), and in the Kimberley region of the north (Key's zone 2) (Figure 4). Species turnover was lowest in the arid zone, and yet this region had relatively high richness compared to the southwest (Figure 5). The Pilbara and Kimberley regions were the most diverse overall, with high richness and turnover (Figures 4 and 5), as well as high endemism (Figure 6).

Patterns in grasshopper turnover were most strongly related to geographic distance for Acrididae and Pyrgomorphidae, and geographic distance was also an important predictor for the Morabidae (Figure 2). In the Acrididae and Morabidae, there was rapid turnover over ~7° (~700 km) after which turnover rate plateaued whereas in

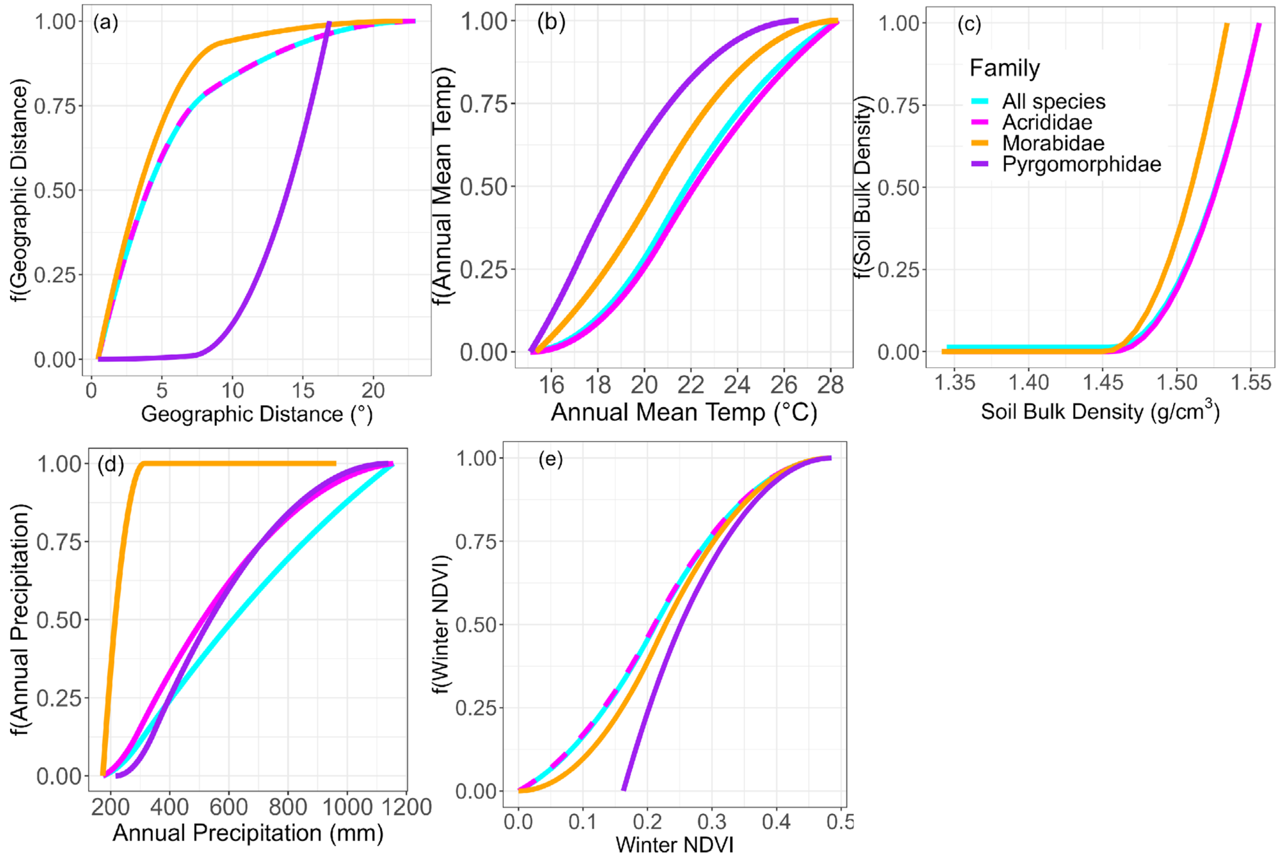

FIGURE 3 Relative importance of the predictors in determining species turnover using the dataset aggregated for ~50 × 50 km (0.5°) according to the fitted generalised dissimilarity model. The *x*-axes represent the native unit of each explanatory variable. The *y*-axes represent the standardised transformed explanatory variable, and the non-linearity of the response indicates which section of the environmental gradient would have steeper compositional turnover. NDVI, Normalised Difference Vegetation Index.

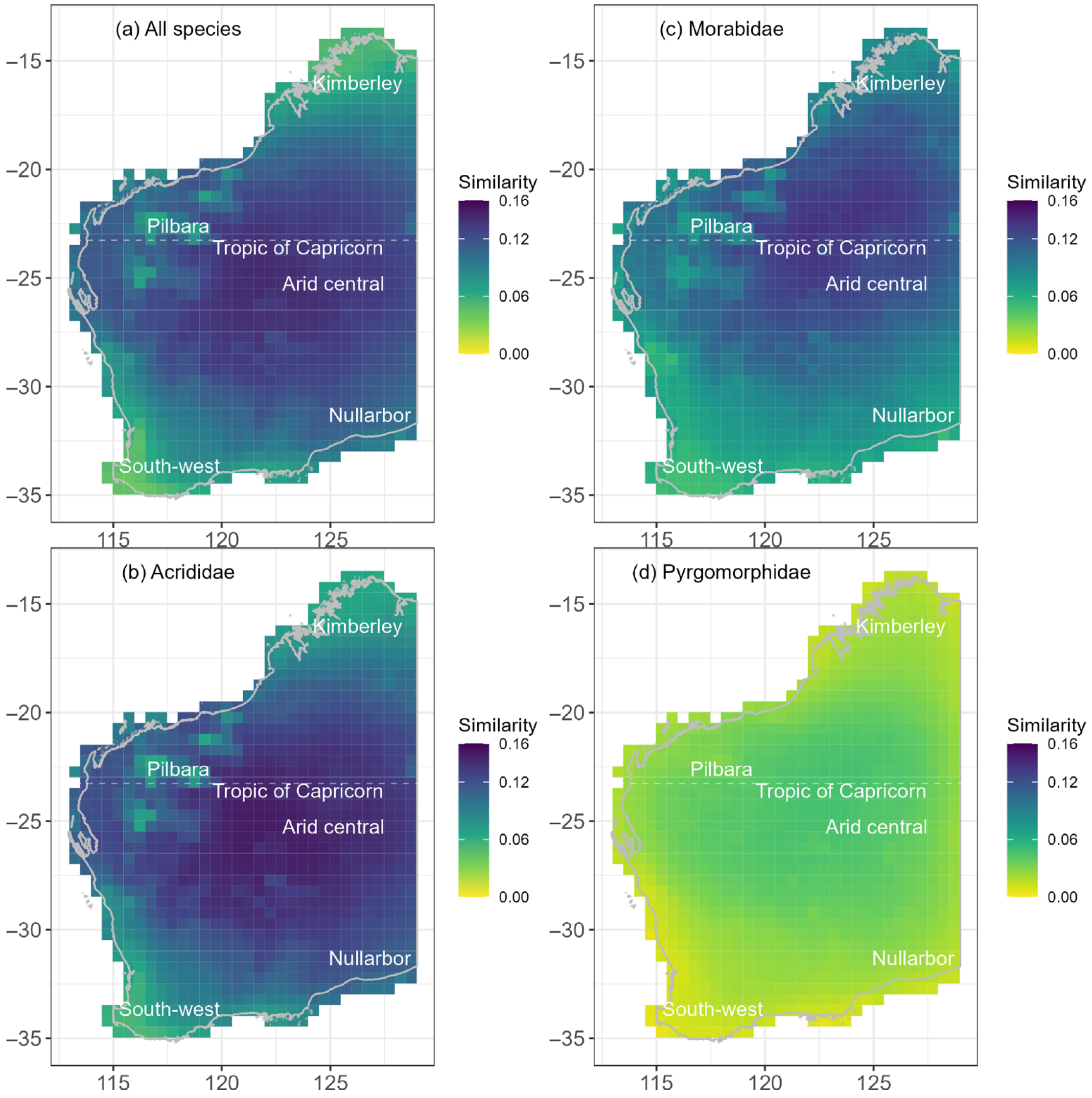

FIGURE 4 Predicted biological uniqueness (average similarity of each location compared to the whole region) of grasshopper species in Western Australia. Grid size is ~50 × 50 km (0.5°).

the Pyrgomorphidae there was little turnover until ~7° (~700 km), with rapid turnover thereafter (Figure 3). For Morabidae, annual mean temperature was found to be the most important in predicting species turnover (Figure 2). Overall, the GDM had the greatest explanatory power for the Pyrgomorphidae (~40% vs. ~20%–25%). The reasons for these family-level differences are not obvious. The turnover rates could conceivably be related to vagility in which case the Morabidae, which are all entirely wingless, would be expected to stand out from the other two families. However, winglessness or brachyptery has evolved multiple times within Acrididae and Pyrgomorphidae. The Pyrgomorphidae tend to be the most specialised feeders and most of the Western Australian species (six of eight) are brachypterous, which may explain why they have the highest turnover rates. However, this is the least diverse of the families and they had the fewest site pairs. The strong effect of temperature for the Morabidae may reflect relatively strong phylogenetic conservatism in their thermal preferences. Their diversity declined rapidly away from the equator with only one genus making it to the south coast whereas there are relatively more species of Acrididae and Pyrgomorphidae in the south.

Comparisons with other taxa

Schall and Pianka (1978) compared lizard and bird diversity patterns in Australia and found birds to have the highest diversity along the mesic east coast, whereas the lizard diversity was highest in the arid centre. They excluded scincid lizards from their comparison, other than the hyper-diverse genus *Ctenotus*, because scincid lizards tend to follow the bird pattern. Powney et al. (2010) expanded Schall and Pianka's comparison to include amphibians and mammals and found that the latter two groups followed the mesic richness bird pattern whereas the lizard pattern of arid richness held. Our study shows that within

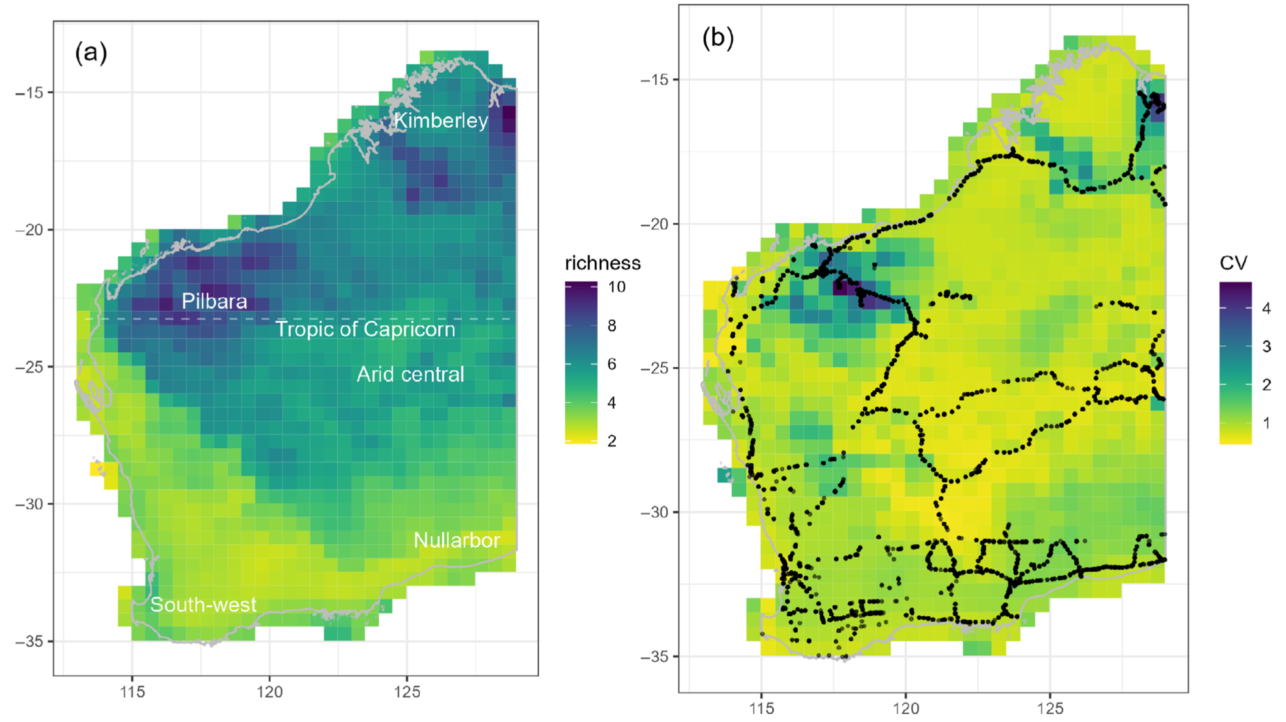

FIGURE 5 (a) Predicted grasshopper species richness in Western Australia based on species occurrences from historic grasshopper surveys. (b) Coefficient of variation (CV) of species richness based on 100-fold cross-validation. Dots indicate the locations of surveys. Grid size is ∼50 × 50 km (0.5°). The estimated value is for a sample site within a grid cell (not the total number of species within that cell).

Western Australia the richness pattern of the grasshoppers follows a lizard-like pattern of relatively high arid zone richness.

What processes might be driving the arid richness pattern in grasshoppers? For lizards, Pianka and colleagues focused on the role of niche partitioning in permitting coexistence, while Morton and James (1988) emphasised the importance of termites as food sources. James and Shine (2000) proposed an alternative hypothesis—that high local species diversity is the outcome of a large number of species with large geographic ranges occupying a climatically homogeneous region. That is, the high alpha diversity is due to a high gamma diversity of the arid zone biome, but the turnover (beta diversity) is low. James and Shine's hypothesis seems most consistent with the pattern we found for grasshoppers in the arid zone, where species richness was high, but the GDM predicted very low turnover. Why should grasshoppers be more similar in their patterns to lizards than to birds, mammals, and amphibians? It seems most likely that this is because grasshoppers and lizards are less constrained by food and especially water availability, and also have a phylogenetic bias to prefer open, high-temperature environments (Key, 1959; Sergeev, 2021; Uvarov, 1977).

Another striking similarity between lizard and grasshopper diversity patterns is the high diversity in the Pilbara and Kimberley regions (compare our Figure 4 to Powney et al.'s (2010) fig. 3). The Pilbara region, traversed by the Fortescue River and deeply incised gorge systems, is a geologically distinct entity from its surrounding regions with the presence of the Indian Ocean to the west, vast sand deserts to the east and north, and highly metamorphosed rocks to the south (Cracraft, 1991). The Kimberley is similarly geologically unique comprising heavily dissected sandstone plateaux. These geological settings have promoted exceptionally high biotic diversity and endemism for many taxa, including insects (Byrne et al., 2008; Cracraft, 1991; McKenzie et al., 2009; Pepper et al., 2013; Pepper & Keogh, 2014).

Endemism and protected areas

Out of 237 species having distribution limited to 1–4 grid-cells, 25.7% (61 species) fell within the current PA network in WA (Figure 5a), with about half of these (31 species) located in Indigenous Pas (Figure 5a). Most of the Pas encompassing the distribution of small-range grasshoppers, such as those in the Pilbara, were proposed/declared in or after the year 2000 (CAPAD, 2018), which is long after the field surveys were conducted (1947–1985). Therefore, it is not known whether there has been any loss of range-restricted grasshoppers residing in those areas in the intervening time. Furthermore, it is uncertain whether Pas provides any specific protection to grasshoppers persisting in those areas. Some species might have specific requirements such as the presence of native remnant vegetation, specific fire regimes, and habitat connectivity for their persistence. The incorporation of insects into the PA management would require specific actions that benefit insect life-histories (Kawahara et al., 2021; Sands, 2018). This might include, for example, the reduction of pesticide usage in the region around the Pas (Samways et al., 2020). In addition to small-range endemics, a substantial number of species also

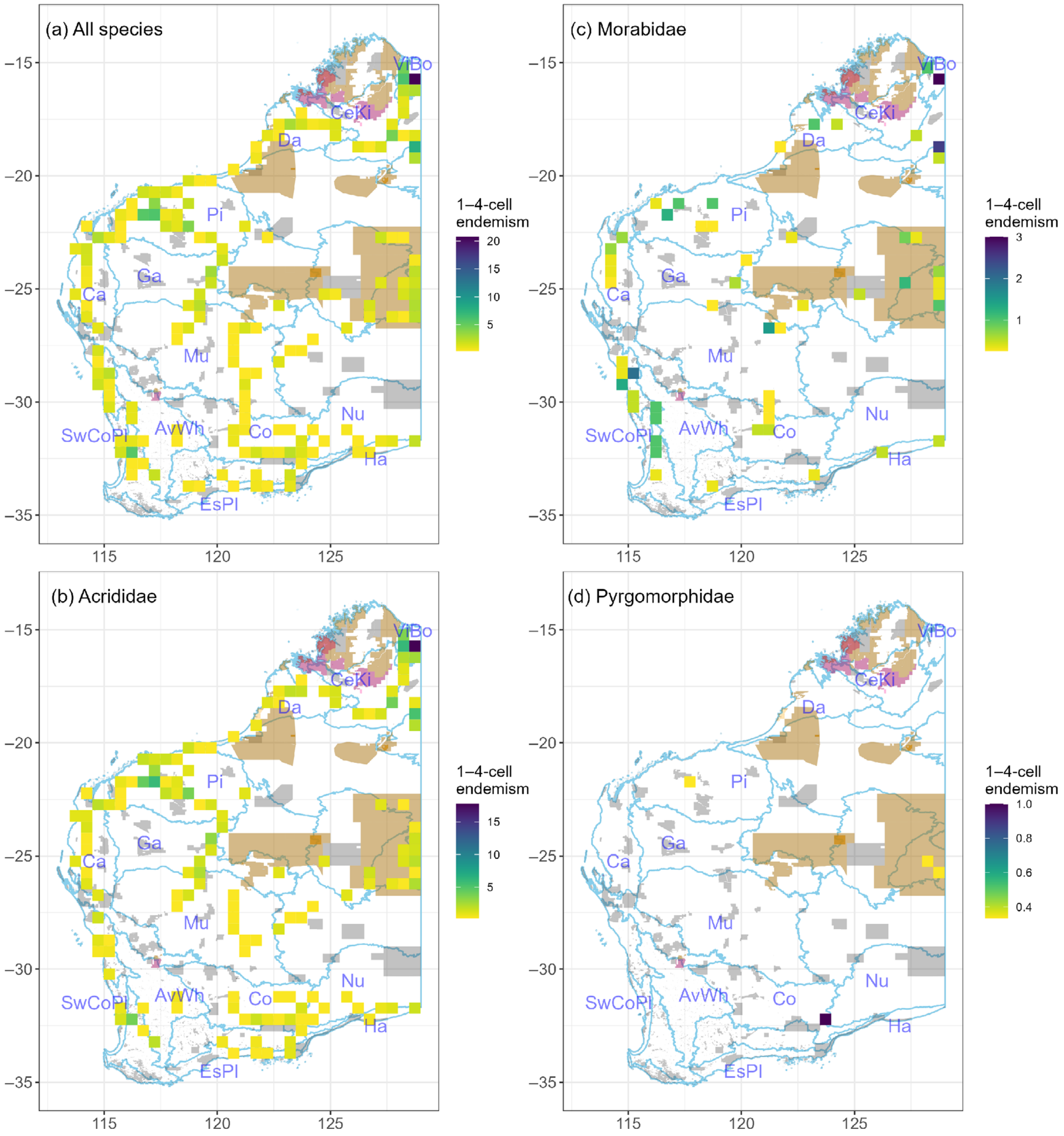

FIGURE 6 Endemism of 237 grasshopper species that were only recorded in 1–4 grid cells. Higher values indicate higher number of short-range species occurring in that cell. White cells are unsurveyed (a). Background shading represents Protected Areas (PA; orange: Indigenous PA, pink: Private Nature Reserves, grey: other PAs). Blue lines represent the boundary of bioregions (AvWh, Avon Wheatland; Ca, Carnarvon; CeKi, Central Kimberley; Co, Coolgardie; Da, Dampierland; EsPl, Esperance Plains; Ga, Gascoyne; Ha, Hampton; Mu, Murchison; Nu, Nullarbor; Pi, Pilbara; SwCoPl, South-west Coastal Plains; ViBo, Victorian Bonaparte).

have very few occurrences, making some areas particularly rich in endemic species (Figure 5b).

The majority of short-range endemic species possess ecological and life history characteristics such as poor dispersal ability and confinement to discontinuous habitats (Harvey, 2002). Therefore, it is possible that species having very few occurrences that do not receive any conservation protection might become more restricted, or even extinct over the long term, due to various anthropogenic and natural impacts such as land modification and bushfires (Legge et al., 2022). Out of 1328 sites surveyed in WA, 53 survey sites have since been completely or partially cleared for agriculture or other forms of development, thinned, burnt, modified, or impacted by other forms of disturbances, based on a visual assessment with Street View in Google Earth and the original site description mentioned in the notebook.

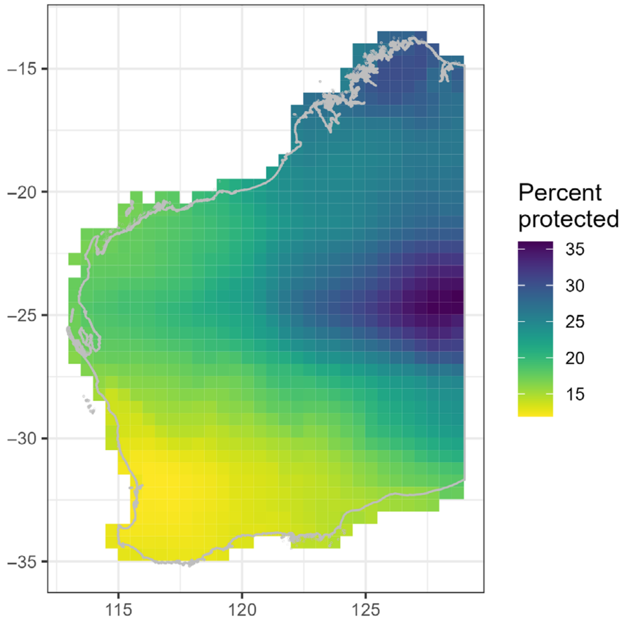

FIGURE 7 Representativeness of grasshopper community diversity in the protected areas in Western Australia. This was calculated by comparing the natural uniqueness of each location to locations (based on the fitted generalised dissimilarity model) that are within the protected area network.

However, the actual extent of impact of site modification could be much more severe if surveyed on the ground, including sites that seem to be unimpacted from Google Earth (see, ABARES, 2022 for land-use change in Australia). In addition, species might be impacted by the use of pesticides in the surrounding agricultural areas (Tooker & Pearsons, 2021), which is not observable from satellite images. Of the pristine sites, we noticed 26 sites were disturbed by clearing or other forms of modification at the time of geolocation using Street View. In addition, one site in the Pilbara has been modified completely for mining activity (trip no: 170; odometer: 46,879.2; coordinates: −21.776727 116.232069). Fifteen species were recorded from this site including one species having a 1–4 cell distribution (i.e., *Capraxa* sp3).

Estimates suggested that 75% of the vegetation in arable areas has been cleared for various purposes since the settlement of Europeans in Australia in 1788 (Braby et al., 2021). The remaining 25% of native vegetation is also significantly impacted by the ever-increasing anthropogenic pressure for mining activity, agriculture, climate change, and invasive species (Taylor et al., 2018). While the last field surveys included in this study were conducted in 1985, the status of the substantial number of small-range grasshoppers remains uncertain unless further field surveys are initiated. Although high species richness was predicted around the Pilbara, the region is poorly represented by the PA network (i.e., <10% of the region is protected) (CAPAD, 2018). Furthermore, evidence suggests that many components of the Australian insect fauna are declining, echoing the global trends of insect decline (Braby et al., 2021; Sánchez-Bayo & Wyckhuys, 2019, 2021). Therefore, it is recommended that targeted surveys and research activities should be undertaken to assess the status of identified small-range endemic species and provide appropriate conservation measures. It is hoped that the new information provided by our study will help to attract more targeted research and conservation efforts for the safeguard of Australia's grasshopper fauna into the future.

AUTHOR CONTRIBUTIONS

Md Anwar Hossain: Conceptualization; investigation; data curation; formal analysis; writing – original draft; methodology; writing – review and editing; funding acquisition; resources. **José J. Lahoz-Monfort:** Methodology; supervision; writing – review and editing. **Karel Mokany:** Supervision; writing – review and editing; methodology. **Michael R. Kearney:** Conceptualization; supervision; writing – review and editing; funding acquisition; resources; validation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The historic occurrence records of Australian grasshoppers from field notebooks were published in Dryad repository (https://doi.org/10.5061/dryad.2fqz612sn) and described in Hossain et al. (2023). All other spatial datasets used in this study were cited within the text.

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SUPPORTING INFORMATION

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

Figure S1. The fitted log-normal model shows the observed versus predicted species count per survey per site.

Figure S2. Relationship of predictors to species count per survey for each site in a ~50 × 50 km (0.5°) gridded dataset. Here, site refers to the grid centroid for all surveys conducted within that cell. Blue line indicates the relationship between *x*-, and *y*-axes.

Figure S3. Regression coefficients for predicting grasshopper richness in Western Australia. The *x*-axis represents standardised regression coefficient (i.e., estimate), and *y*-axis indicates predictors. The dots indicate the coefficient means, and horizontal lines represent the 90% confidence intervals. Predictors were abbreviated as: bio = mean diurnal range, bio3 = isothermality, bio8 = mean temperature of wettest quarter, bio19 = precipitation of coldest quarter, and topoWetness = topographic wetness.

Figure S4. Corrected weighted endemism of grasshoppers in WA as measured by dividing the weighted endemism by the total count of individual species in each grid. White cells are unsurveyed. Background shading represents Protected Areas (PA; orange: Indigenous PA, pink: Private Nature Reserves, grey: other PAs). Blue lines represent the boundary of bioregions (AvWh, Avon Wheatland; Ca, Carnarvon; CeKi, Central Kimberley; Co, Coolgardie; Da, Dampierland; EsPl, Esperance Plains; Ga, Gascoyne; Ha, Hampton; Mu, Murchison; Nu, Nullarbor; Pi, Pilbara; SwCoPl, South-west Coastal Plains; ViBo, Victorian Bonaparte).

Table S1. Summary of species included in the study.

Table S2. List of grasshoppers included in this study and their locality of geographic distribution. Species designations were retained as they were mentioned in the field notebook (Hossain et al., 2023). Family name of each species was identified from Rentz et al., 2003 and Orthoptera Species File (https://orthoptera.speciesfile.org/). Specimens collected from the historic field surveys of Australian grasshoppers was preserved in the Australian National Insect Collection (ANIC). Field Notebooks are available from Biodiversity Heritage Library (https://www.biodiversitylibrary.org/bibliography/176096). The dataset resulting from the historic field surveys of Australian grasshoppers were described in Hossain et al., 2023.

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