



RESEARCH ARTICLE

Habitat associations of dryland avian communities during an extended dry period

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Abstract

The influence of resource availability on ecosystem function varies spatially and temporally, among and within ecosystems. Dramatic shifts in moisture-driven resources can drive bottom-up effects on animal behaviours and distributions. Further, complexity arises when landscapes are influenced by large mammalian grazers and predator-induced trophic cascades, such as those mediated by the dingo (*Canis familiaris* (Dingo)) in the eastern arid Strzelecki Desert in Australia. During the driest two-year period on record for this region, we investigated the persistence of avian communities associated with structurally distinct dunes and swale habitats, and across two different land management regimes (pastoral land with livestock and dingoes, and Sturt National Park managed for conservation without these animals). We grouped all birds into dietary functional groups to infer patterns of habitat use associated with available resources. We also compared incidental observations of the 'winter' bird community in part of the study region between the extended dry period of 2018/2019 and wet period of 2020/2021. Despite habitat partitioning, the avian community did not differ between land management regimes except in species richness during the dry period, likely driven by the low numbers of birds present during the surveys. Incidental observations indicated that insectivorous and omnivorous species dominated the bird community in the dry period, with granivorous species forming a greater proportion of the bird community during wet times. Birds with completely or partially insectivorous diets dominated avian species composition on surveys in the dry period, but there were distinct structural vegetation associations among functional groups, indicating that heterogeneity in vegetation structure was likely important for the conservation of refuges, which enable the persistence of avifauna during extended dry periods. Distinct habitat type, structure and available resources shaped avian communities in this landscape, during the extremely resource-limited extended dry period, with implications for conservation and management, particularly given the increasing drying effects of climate change.

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KEYWORDS

arid, bird, diet, drought, functional group, primary productivity, resource limitation, trophic cascade

INTRODUCTION

Resources drive species, population and community dynamics, fundamentally shaping ecosystem form and function. When fluctuations in the availability of resources lead to changes up the trophic ladder, bottom-up (resource-driven) ecosystem regulation occurs (Elton, 1927; Lynam et al., 2017). In the face of ongoing biodiversity losses (Butchart et al., 2010), ecosystem management requires a comprehensive understanding of how component species and communities shift in space and time in response to resource availability. This is particularly important in highly dynamic landscapes such as drylands (Maestre et al., 2012; Reynolds et al., 2007).

Dryland ecosystems are characterised by limited and highly variable inter-annual water availability (Maestre et al., 2012; Reynolds et al., 2007). Rainfall and flooding drive many primary and secondary productivity processes, with short wet periods punctuating long dry spells (Greenville et al., 2014; Morton et al., 2011). In the arid western USA, extended dry periods drive the replacement of native trees and grasses with woody shrub and invasive-dominated communities (Munson et al., 2011; Winkler et al., 2019). In arid Australia, dry periods are increasing in frequency, duration and severity, and wet periods are becoming shorter in duration but more intense, under climate change (BOM & CSIRO, 2020; Harris et al., 2018; Ma et al., 2015), affecting vegetation communities (e.g. Munson et al., 2011). Such changes in primary productivity affect high-level consumers through bottom-up regulation (Báez et al., 2006; Ritchie et al., 2008). Dryland bird communities are indicators of resource-induced change, as widespread consumers of resources (Garnett et al., 2015), and prey for both avian (Aumann, 2001) and nonavian predators (Doherty et al., 2015; Pianka, 1994).

How birds respond to resource-induced changes depends on avian life histories and habitat associations. In Australian drylands, irruptive species respond to spatially patchy refuges of key available resources, such as flowering mistletoes and *Eremophila* spp. (Tischler et al., 2013) or high densities of prey (Pavey & Nano, 2013). Birds also move large distances to find resources (Pedler et al., 2014; Runge et al., 2015). But a species-level approach only provides a limited understanding of community structure and functional responses to limited resources (Pacifci et al., 2014). Grouping species by the resources they require, such as diet (e.g. granivory and insectivory), can help identify how resource limitation affects broad groups of species (Pacifci et al., 2014; Tischler et al., 2013); essential for ecosystem management (Mac Nally et al., 2008). For example, insectivorous and generalist species tend to dominate dryland avian communities during dry times when primary productivity is low (Tischler et al., 2013). However, it is unclear which structural habitat features are used by different functional groups during these resource-limited periods, leaving theoretical and practical gaps in our knowledge of niche and refuge use by foraging birds.

Land management can also add complexity in understanding Australian dryland avian community dynamics. The artificial provision of water for livestock, and the grazing pressure from these animals can cause widespread shifts in dryland bird communities, due to habitat degradation, trampling and removal of vegetation, as well as indirect facilitation of water-limited mammalian predators and grazers (Davies et al., 2010). Long-term exclusion of mammalian predators such as the dingo (*Canis familiaris* (Dingo))

by shooting, baiting and fencing has also been associated with shifts in bird communities compared with regions where dingoes are present. For example, where kangaroo (*Osphranter* and *Macropus* spp.) grazing is not limited by dingo predation due to dingo exclusion, grass seed availability can decrease leading to declines in grass seed feeding bird abundances (Rees et al., 2017; Rees, Kingsford, et al., 2019). Suppression of introduced mesopredators by dingoes can also reduce predation by these mesopredators on ground-nesting and ground-feeding species (Gordon et al., 2017; Moseby et al., 2011; Rees, Kingsford, et al., 2019) and reduce predation pressure on small mammals, promoting an increase in small mammal and their avian predators' abundances (e.g. eastern barn owls (*Tyto javanica*); Rees, Rees, et al., 2019). The potential influence of these many and complex processes associated with land management must be investigated during resource-poor, extended dry periods, as well as resource-abundant wet periods to gain a more complete understanding of how these communities and ecosystems more broadly function.

We aimed to determine how dryland bird communities respond to extended dry conditions, from a community and functional perspective. To do this, we investigated demographic and habitat use patterns of dryland bird communities in the eastern Strzelecki Desert, during an extended dry period (Figure 1; Pedler et al., 2021). We used in situ land management differences between pastoral properties in South Australia (with livestock, dingoes and kangaroos—moderated by dingoes) and Sturt National Park (without dingoes or livestock and with abundant kangaroo populations—noting a mass kangaroo mortality event at the time of the study, due to extended dry conditions and resource depletion; Pedler et al., 2021), separated by the dingo-barrier

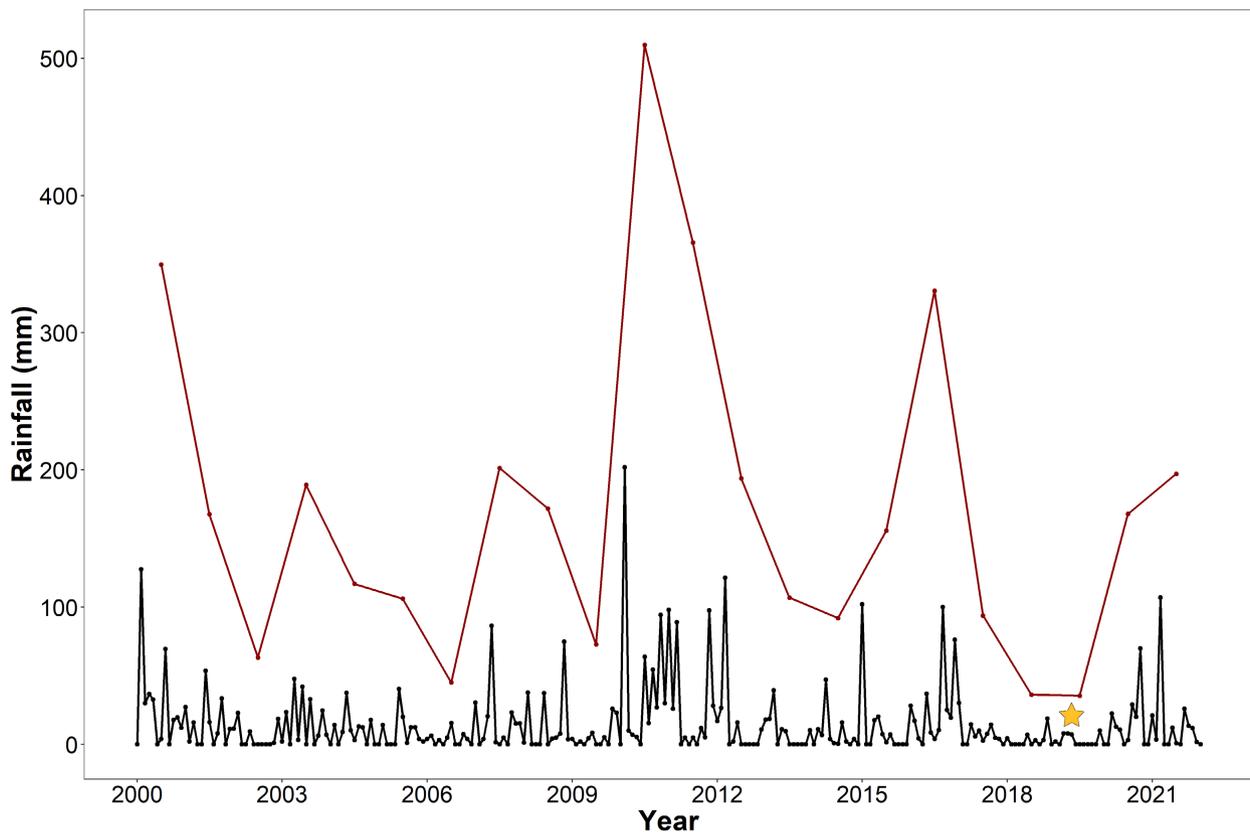


FIGURE 1 Monthly (black line) and annual rainfall (red line; points centred on July of each year) from January 2000–2020 from Lindon Station Homestead (~8 km from the study site, including missing months from Fort Grey; BOM, 2019a). Our sampling period in May 2019 is marked with a yellow star.

fence between New South Wales (NSW) and South Australia (SA). Firstly, we compared avian species richness and composition during an extended dry and subsequent wet period to provide context for the extended dry period in which the remaining objectives were investigated, anticipating lower species richness and a generalist and insectivorous species-dominated community in the dry, compared with the wet period (as in Tischler et al., 2013). During the dry period, we then: (1) investigated differences in bird communities at a functional- and species-level between two distinct habitat types (dunes and swales) and land management regimes (pastoral properties and Sturt National Park), expecting these treatments to influence community abundance and composition as has been demonstrated previously (Read et al., 2000; Rees, Kingsford, et al., 2019; Tischler et al., 2013); (2) explored possible structural drivers associated with resources for birds by analysing structural habitat features associated with avian functional group presence, expecting habitat associations would vary among functional groups and between habitat types due to differences in resource use and availability, respectively; and (3) examined microhabitat associations and activity patterns of four common insectivorous and omnivorous species: black-faced woodswallow (*Artamus cinereus*), purple-backed fairywren (*Malurus assimilis*), red-capped robin (*Petroica goodenovii*) and white-winged fairywren (*Malurus leucopterus*); to inform fine-scale habitat use and behavioural patterns, for which we had no *a priori* expectations. Together, these objectives enabled us to investigate habitat and resource factors, which may influence the dynamics of dryland avian communities and their persistence during extended dry periods.

MATERIALS AND METHODS

Study area

We surveyed avian communities in the eastern Strzelecki Desert in arid Australia (Figure 2), a region of highly variable and predominantly summer rainfall (Morton et al., 2011; Pook et al., 2014) with an annual average of 173.8 ± 13.02 SE mm (1901–2018) ranging from 29.0–542.2 mm at Fort Grey (Figure 2; BOM, 2019a). Fieldwork occurred from May–June 2019, after a 2-year period (July 2017–June 2019) of the ‘lowest on record’ rainfall for the study area (monthly mean: 3.93 mm, total: 94.4 mm; BOM, 2019a, 2019b). Average annual rainfall for 2017 and 2018 was lower than every year since 2000 with dry conditions continuing during the study (Figure 1; Pedler et al., 2021).

Vegetated red sand dunes primarily orient north-east to south-west across the study area, interspersed by swales (interdunal plains, claypans and ephemeral swamps; NPWS, 2017; Pedler et al., 2018). Mulga (*Acacia aneura*), sandhill wattle (*Acacia ligulata*), western rosewood (*Alectryon oleifolius*), whitewood (*Atalaya hemiglauca*), hopbush (*Dodonaea viscosa*) and wormwood sennas (*Senna artemisioides*) dominate the dunes (Keith, 2004), while ephemeral herbs (e.g. *Sclerolaena* spp. and *Disocarpus* sp.) and grasses (e.g. *Enneapogon* spp., *Eragrostis* spp., *Aristida* sp., *Astrelba* sp.) occupy the swales. After intense rainfall, water can accumulate in swales, supporting lignum (*Duma florulenta*), swamp canegrass (*Eragrostis australasica*) and golden goosefoot (*Chenopodium auricomum*; Keith, 2004). These habitat features are contiguous across the entire study area, separated by the dingo-barrier fence, across which habitat structure differs (Fisher et al., 2021).

We surveyed either side of the dingo-barrier fence, separating Sturt National Park from pastoral properties in SA (Figure 2). Outside the fence, the land is managed as pastoral (cattle) properties (typically 5000–8000 km²

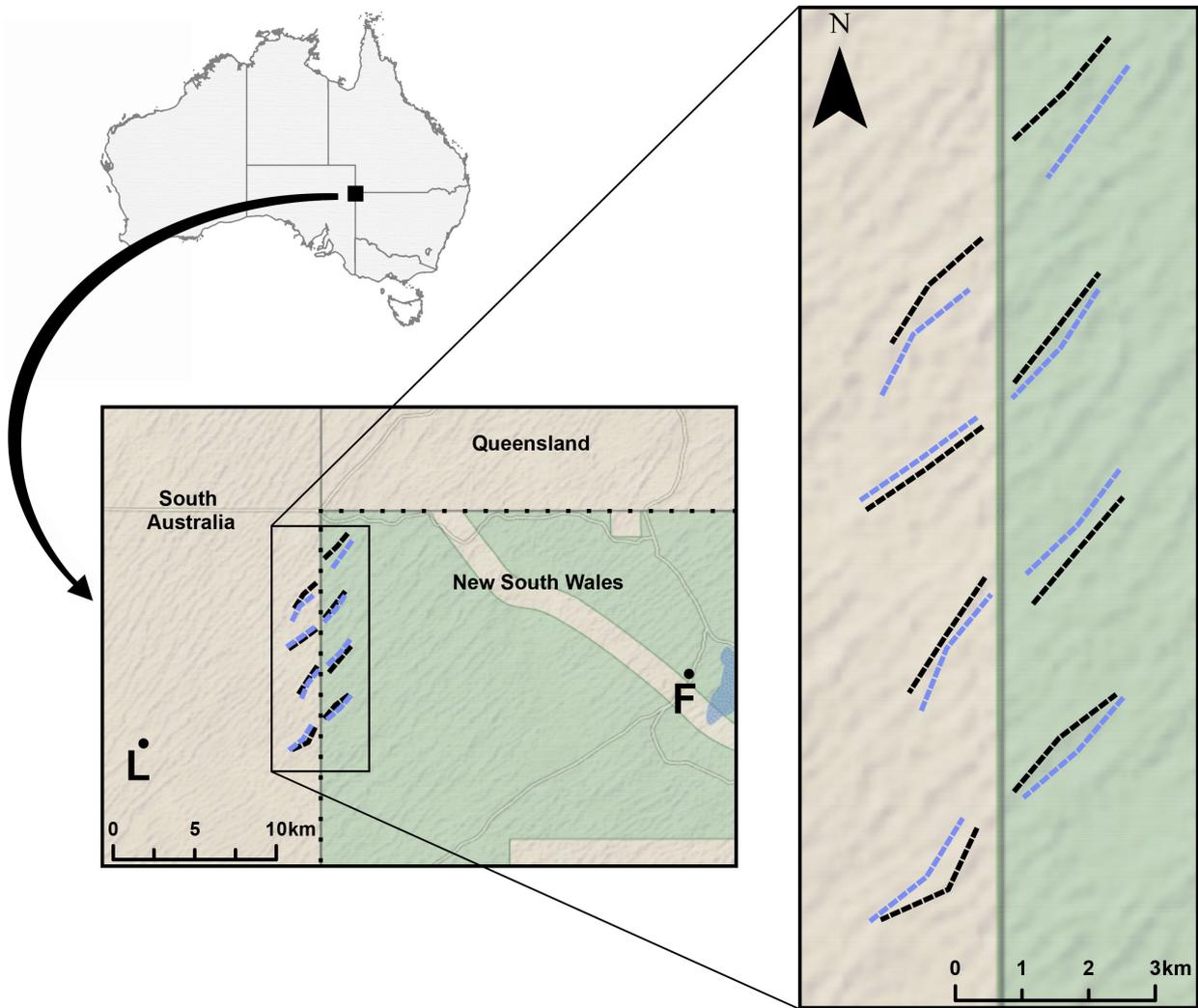


FIGURE 2 Survey area for dryland birds, within two different land management areas: Sturt National Park in NSW without livestock and dingoes (dingo fence exclusion from South Australia and Queensland) and South Australia with these animals. There were four transect pairs on Bollards Lagoon and Lindon Stations in South Australia and in Sturt National Park, including paired 2 km dune (black line) and 2 km swale (blue line) sections, with rainfall data from Fort Grey Homestead (F) and Lindon Station Homestead (L).

per property) where dingo populations mediate kangaroo populations and are managed only by baiting and shooting (Letnic et al., 2012). Lindon and Bollards Lagoon stations were sampled for this treatment, both of which host several artificial water points to support cattle. We compared these areas to Sturt National Park, inside the dingo-barrier fence, where dingoes are physically excluded, baited, shot and functionally extinct (Figure 2).

Incidental avifaunal responses to rainfall

To provide context on the variability of avian community structure in the study area in response to rainfall and moisture-limitation over a longer period than the dry period data were collected for, we empirically compared 'winter' (May-July) avian species richness and composition during the extended dry period in 2018/2019 to a subsequent wet period in 2020/2021 (Figure 1). This was done using incidental monthly lists of species presence in the Wild Deserts Project Area, which encompassed the transect surveys described below within Sturt National Park (see Figure 1 from Pedler et al., 2018), and was collected by Wild Deserts staff, students and

visitors. Due to unequal recording effort over months and years, total species lists were summed and compared between the dry and wet periods. Species were assigned to dietary functional groups as described below for the transect survey analysis (see [Statistical analyses](#): Community patterns in avifauna). The groupings for this section differed slightly from functional groupings for surveys, in that frugivorous, herbivorous and/or nectivorous diets were included where they likely represented a substantial part of the species' diet at the site during the wet period. Waterbirds were excluded from comparisons. Bird taxonomy aligns with the HBW and BirdLife Taxonomic Checklist v6b (HBW & BirdLife International, [2022](#)).

Community patterns in avifauna

We conducted standardised transect surveys to investigate how habitat type and land management may influence avian community abundance and composition. We used eight transects selected from Google Earth satellite imagery (>200m from the dingo-barrier fence to reduce edge effects, [Figure 2](#)). These were dune-swale transects (2 km of dune and an adjacent north or south swale depending on suitability), paired either side of the dingo-barrier fence ([Figure 2](#)). Suitable transects required two, connected, 1 km, straight-line sections in dune and swale habitats (transects of this length were used due to low bird abundances in the landscape; [Table 2](#)). Once suitable sections were identified, a subset of transects (four on either side of the dingo-barrier fence) was randomly selected for surveys. Each transect was surveyed four times, between 12–24th May 2019, within four hours of sunrise. Start times for individual transects and treatments were alternated between two observers to reduce observer bias. Time spent surveying each transect was controlled to approximately one hour, although this varied with habitat due to terrain, and the number of birds presents due to marking each bird or flock's location (addressed in *Structural vegetation associations*). All birds heard or seen within 50 m of the transect were counted.

Structural vegetation associations

To explore possible structural habitat drivers associated with resources for the bird community, locations at which every individual bird or flock was first detected during transect surveys were marked by GPS and flagging tape. When marking bird locations, additional species were not added to the transect list until the observer returned to the transect line to reduce detection bias with increased time. Each location was subsequently revisited to measure the composition and structure of woody vegetation, using nested quadrats of 5x5m (25m²) and 20x20m (400m²). The nested design enabled the comparison of bird associations with structural habitat features at two different scales. Structural vegetation associations were measured where birds were found at 133 locations in dunes and 73 in swales.

All woody vegetation (including dead vegetation) >50cm in height was identified where possible, and its height and two perpendicular measures of the width measured (within 10 cm using a 2 m measuring pole). Height was the vertical distance between the tallest point of the tree and the ground. Plants >4 m in height were measured by two observers, one holding a measuring pole up to 4 m. Vegetation species' richness and total abundance (overall count of plants) were recorded. Vegetation variables were separated into 'trees' (>2 m) and 'shrubs' (0.5–2 m), except for *Acacia ligulata*, *Acacia tetragonophylla* and *Senna artemisioides* shrubs >2 m, which were

also labelled 'shrubs', given their consistent shrubby growth form. A 'total' vegetation variable was the average height, overall abundance, richness or cover of all individuals per quadrat (e.g. total height, total abundance). The three measurements for each plant occasionally differed between the two quadrat sizes, due to the partial inclusion of a plant in the 25 m² quadrat (e.g. the total width of a plant was 120 cm, but only 80 cm may have fallen within the 25 m² quadrat and only the section inside the quadrat was scored). The cover was estimated from the two measures of width (area of an oval) and then estimated as a sum of all individual plant cover estimates, per vegetation group ('tree', 'shrub' and 'total') for each quadrat. Groundcover was visually estimated as percentage cover separately for both quadrats.

Microhabitat use

To further investigate how birds were using their habitat during the extended dry period and which aspects of the habitat were being used, we selected four common species recorded during the transect surveys (75 individuals) and conducted activity budgets to record behavioural and habitat use patterns. For these, we recorded mutually exclusive activity patterns of individuals (sometimes including multiple individuals per single-species group encountered—no mixed flocks were encountered) from ~20 m, using continuous focal sampling (Altmann, 1974) for up to five minutes (total of 304 min 5 s of observations) before bird movements were obscured by vegetation or birds flew away. These species included: black-faced woodswallow ($n = 18$; 80 min 20 s), purple-backed fairywren ($n = 21$; 97 min 47 s), red-capped robin ($n = 8$; 31 min) and white-winged fairywren ($n = 28$; 94 min 58 s). We started 30 s after detecting birds to reduce disturbance effects. Behaviours were classified as one of four mutually exclusive categories: foraging (pecking, digging, searching, chasing), resting (stationary behaviour, irregular vigilance with no social engagement or foraging, preening), social (clear engagement with other individuals of same or other species) and travelling (in flight but not engaging in foraging or social behaviour). When perched, vigilant behaviour with no clear interaction with other birds or threats was deemed foraging behaviour (only exhibited by woodswallows) and vigilance in the presence of other individuals, conspecific or not, was categorised as social behaviour. Travelling and resting behaviour was rare, thus excluded from comparisons.

We measured the time birds spent in five mutually exclusive microhabitats: tree (all *Acacia aneura* and *Hakea leucoptera* >2.5 m), large shrub (all other vegetation >1 m and *A. aneura* and *H. leucoptera* 1.5–2.5 m), small shrub (all vegetation <1 m), open (on the ground, away from vegetation) and air (flying birds—though this category was excluded from further comparisons, given we were primarily interested in habitat use). We also determined the time birds spent using three different strata of vegetation (excluding open): canopy (atop or in the crown of vegetation), within (neither canopy nor under) and under (on the ground underneath vegetation). To determine microhabitat associations, we empirically compared the proportion of time spent in each behavioural category, microhabitat and vegetation stratum.

Statistical analyses

All statistical analyses were conducted in R (R Core Team, 2021).

Community patterns in avifauna

We used a multivariate abundance modelling approach at a functional and species-level to compare avian communities between habitat types and land management regimes. This approach was used instead of more typical measures of abundance and diversity and to complement richness, which can often be misleading when comparing different treatments (Read et al., 2015). Functional groups of birds were defined by diet (data from Garnett et al., 2015; Table 2). However, while several species recorded on our surveys were listed as frugivores, herbivores and nectivores (Garnett et al., 2015), these food sources were almost completely absent during the dry conditions, so these functional groups were not included. No species were exclusively frugivorous, herbivorous and/or nectivorous, so species that had diets including these food sources were listed under alternative functional groups (for example, as insectivores). Insectivorous aerial foragers, white-backed swallow (*Cheramoeca leucosterna*) and tree martin (*Petrochelidon nigricans*) were listed as aerial insectivores, separating them from terrestrial foraging insectivores. Carnivores were species that fed on either or both 'terrestrial invertebrates' and 'terrestrial vertebrates', or 'scavenged' (Garnett et al., 2015). Species that were granivorous, herbivorous and/or nectivorous, and fed on invertebrates, vertebrates and/or scavenged were listed as omnivores (noting frugivores, herbivores and nectivores were excluded from the analysis of survey data but retained for incidental community comparisons between the dry and wet period). To avoid grouping little crow (*Corvus bennettii*) with small omnivorous species with vastly different ecosystem functions, this species was listed as a carnivore. This resulted in five mutually exclusive functional groupings: aerial insectivores, carnivores, granivores, insectivores and omnivores.

To determine overall differences in avian communities between habitat types and land management regimes, we used the package 'mvabund' (Wang et al., 2012). As replicates were nested within transects (four replicates per habitat type, per transect), we summed counts of species per survey ($n = 64$) to counts per dune or swale survey of each transect ($n = 16$). Species recorded on <3 of these summed surveys were excluded from species-level analyses. We fitted separate generalised linear models (GLM; using the *manyglm* function in 'mvabund' and adjusting p -values for multiple hypothesis testing) for count data of each functional group and species (Appendix S1: Table A1-2; Wang et al., 2012), with a negative binomial distribution (normality of residuals was tested for each model; Brooks et al., 2017; Warton et al., 2016). We compared functional and species-level models using the *anova* function from 'mvabund' with bootstrapping analysis, using land management regime and habitat type as predictors (Appendix S1: Table A1-2).

There were four functional groups, but 15 bird species to extract individual effects for using adjusted p -values from the *manyglm* models, which for the species-level model may have resulted in false negatives for weaker significant effects. As such, a second multivariate model—a generalised linear latent variable model (GLLVM; 'gllvm' package, Niku et al., 2019) was applied using the same formula, to investigate species-specific responses to habitat type and land management regime, with a negative binomial distribution to account for zero-inflation (normality of residuals tested). This used a single model to investigate species-level responses, avoiding p -value corrections thus reducing the chance of false negatives. Statistically significant responses were determined by visual assessment of 95% confidence interval estimates with zero. Species richness was analysed using a generalised linear mixed model (GLMM; 'glmmTMB' package, Brooks et al., 2017). Model predictors were habitat types and land management

regimes with species richness as the response, and the model was fit to a Poisson distribution (normality of residuals was tested). As random effects could be incorporated in this modelling approach, richness per dune and swale section was used ($n = 64$) rather than a sum per dune-swale transect as in the multivariate abundance analysis. A random factor was included to account for the pairing of habitat types within transects to enable the use of each dune and swale section as a sampling unit (Appendix S1: Table A3).

Structural vegetation associations

We examined structural vegetation associations with bird species presence by modelling each functional group in relation to vegetation variables ('tree', 'shrub' and 'total' vegetation and groundcover measures per quadrat), using binomial logistic regression. We fitted separate binomial logistic regressions for each habitat type. Due to the sparse distribution of birds on transect surveys, habitat measurements for bird absences could not be randomised during surveys. Instead, we used the lack of presence at a site where a functional group was recorded as an absence for other functional groups. Low sample sizes prevented stratification by land management regimes of relationships between structural vegetation and bird presence.

Variables for each model were first standardised by centring and dividing by two standard deviations (Gelman, 2008). While the same vegetation variables were measured in the field for dunes as in swales, the predictors for the models for each habitat type differed due to higher variable collinearity in the swale model. Substantially lower densities of measured woody vegetation >50 cm tall in swales, than in dunes likely caused this difference. From the full suite of 24 variables, 21 and 11 were included in the respective dune and swale models due to the collinearity of variables, as dunes were generally more vegetated than swales (Appendix S2: Table A1). Reductions were based on reducing variable collinearity, using a cut-off of $\rho \geq 0.8$ (Vatcheva et al., 2016). Collinearity between the same variable at 25 and 400 m² was likely driven by the 400 m² variable, as quadrats were nested. Collinearity between the same shrub and tree variables was likely driven by the shrub variable, as tree and shrub categorisation was not mutually exclusive to account for growth form. Collinearity between total vegetation and shrub variables was likely driven by the shrub variable as most plants were shrubs. Variables that were almost or completely binary, inseparable from the presence-absence of vegetation were removed. Once all correlation coefficients (ρ) were <0.8 in both dune and swale models, each separate model was run using the functional group with the lowest sample size to obtain variance inflation factors (VIFs), from which variables were sequentially excluded until all VIFs < 10 (Prunier et al., 2015). This VIF cut-off was then checked across all functional group models.

For each functional group except carnivores (excluded as model assumptions were not met), we conducted a relative weights analysis, using a binary logistic model, to determine the relative importance of vegetation variables between habitat types with vegetation variables. This analysis identified proportionate contributions of each variable to the global model individually and in relation to other variables, enabling variable ranking by relative importance (Tonidandel & LeBreton, 2011). Resultant orthogonal vegetation variables were then regressed against bird presence using the ('flipRegression' package, Displayr, 2019). Coefficients from relative weights analysis were standardised from 0 to 1 within each model, ranking relative importance among predictors. We applied backwards stepwise Akaike information criterion (AIC) selection to identify the most important variables from the global models (Hegyi & Garamszegi, 2011). This

approach removed variables from the global model, comparing models until the lowest AIC score was attained, with the smallest number of variables. Variables with standardised relative importance scores of >0.5 and those selected by the backwards stepwise AIC selection were included in our final binary logistic models, run per functional group and habitat type (Appendix S2: Figure A1). Model fit was assessed with Tjur's R^2 and was low across all models, varying from 0.04 to 0.16 (Appendix S2: Table A2; Tjur, 2009).

RESULTS

Incidental avifaunal responses to rainfall

From May–July 2018–2021, 72 bird species were recorded, of which 49 (68.1%) species were recorded during the extended dry period (2018/2019) compared with 63 (87.5%) during the subsequent wet period (2020/2021; Table 1; Appendix S3: Table A1). There were nine species present exclusively during the dry period (2018/2019) and 23 species present exclusively during the wet period (2020/2021). The number of species in all functional groups except aerial insectivores and frugivores was fewer during the dry period than the wet period (Table 1). Aerial insectivores, insectivores and omnivores, as well as one frugivore (Mistletoebird *Dicaeum hirundinaceum*) formed a greater percentage of species composition during the dry period compared with the wet period, while the opposite was true for carnivores and granivores (Table 1).

Community patterns in avifauna

A total of 28 bird species from seven functional groups were recorded on transect surveys: 22 in dunes, 20 in swales, 20 in Sturt National Park and 24 in pastoral properties (Figure 1, Table 2). A mean of <9 birds were recorded per survey (Table 2). Birds were most abundant in dunes on the pastoral properties, and least abundant in swales irrespective of land management (Table 2). White-backed swallows were the most numerous species in dunes and swales, and six species were recorded only once across land management regimes (Table 2). Of the species commonly recorded on transects (≥ 3 observations) only masked woodswallows

TABLE 1 The number of species in avian functional groups, recorded incidentally by Wild Deserts staff, students and visitors during the extended dry period (2018/2019) and the subsequent wet period (2020/2021) in the Wild Deserts Project Area (for constituent species, see Appendix S3: Table A1)

Functional group	Species recorded in the dry period	Species recorded in the wet period	Total
Aerial insectivore	4 (8.2%)	2 (3.2%)	4 (5.6%)
Carnivore	9 (18.4%)	15 (23.8%)	16 (22.2%)
Frugivore	1 (2.0%)	0 (0.0%)	1 (1.4%)
Granivore	7 (14.3%)	13 (20.7%)	13 (18.1%)
Insectivore	12 (24.5%)	13 (20.6%)	14 (19.4%)
Omnivore	16 (32.7%)	20 (31.8%)	23 (32.0%)
Total	49 (68.1%)	63 (87.5%)	72

Percentages in italics and parentheses represent the percentage composition of the dry period (% of 49 species) and wet period (% of 63 species) for each functional group, noting the percentage values in the total row and column relate to the total species composition (% of 72 species).

(*Artamus personatus*) were detected exclusively on the pastoral properties in South Australia, and no species were seen exclusively in Sturt National Park (Table 2). Chestnut-crowned babbler (*Pomatostomus ruficeps*) and banded whiteface (*Aphelocephala nigricincta*) were detected only in dunes and swales, respectively (Table 2). Carnivores were not detected in swales, but all functional groups were detected in dunes and across land management regimes (Table 2).

At the functional level, avian communities were statistically different between dunes and swales (Deviance = 19.26, $p = 0.01$), driven by higher insectivore abundance in dunes (Deviance = 8.71, $p = 0.03$; Figure 3a; Appendix S1: Table A1). There were no statistical differences in abundance between habitat types for aerial insectivores, carnivores, granivores or omnivores (all $p > 0.05$; Figure 3a; Appendix S1: Table A1). Avian communities were not statistically different between the two land management regimes (Deviance = 9.47, $p = 0.16$), with no differences in individual functional group abundances between the regimes (all $p > 0.05$; Figure 3b; Appendix S1: Table A1).

Species richness was statistically higher in dunes than in swales ($z = -3.37$, $p = 0.001$; Figure 3c) and was statistically higher in pastoral properties than in Sturt National Park ($z = 2.04$, $p = 0.04$; Figure 3d). Avian communities, at the species level, statistically differed between dunes and swales (Deviance = 35.95, $p = 0.04$; Appendix S1: Table A2). This was driven by statistically higher abundances of chestnut-crowned babbler (also supported by 'mvabund' univariate estimates; Appendix S1: Table A2), masked woodswallow, purple-backed fairywren (*Malurus assimilis*), singing honeyeater (*Gavicalis virescens*) and willie wagtail (*Rhipidura leucophrys*) in dunes, and higher abundances of banded whiteface and orange chat (*Epthianura aurifrons*) in swales (from GLLVM; Figure 3e). Abundances of the remaining nine species analysed showed no statistical differences between habitat types (Figure 3e). Avian communities did not statistically differ between land management regimes at the species-level (Deviance = 24.6, $p = 0.12$; Appendix S1: Table A2); however, abundances of chestnut-crowned babbler, masked woodswallow (also supported by 'mvabund' univariate estimates; Appendix S1: Table A2) and singing honeyeater were statistically higher on pastoral properties in South Australia than the adjacent Sturt National Park, while red-capped robin abundances were statistically higher in Sturt National Park than in the adjacent pastoral properties in South Australia (from GLLVM; Figure 3f). Abundances of the remaining 11 species analysed were not statistically different between land management regimes (Figure 3f).

Structural vegetation associations

Avian functional groups were associated with distinct structural habitat variables (Table 3). Groups mostly differed in their associations with vegetation structure, particularly in relation to groundcover, and vegetation abundance, cover, height and richness variables in dunes, and vegetation height and cover variables in swales (Table 3). There was some statistical support for a positive association between aerial insectivore presence and *total mean height of vegetation* at 400 m² in dunes ($z = 1.95$, $p = 0.051$), but no statistical support for associations in swales (all $p > 0.1$; Table 3). Granivore presence was significantly positively associated with the *total richness* of vegetation at 400 m² ($z = 2.32$, $p = 0.02$), with some statistical support for a negative association with *mean shrub height* at 25 m² in dunes ($z = -1.69$, $p = 0.091$; Table 3). In swales, there was some statistical support for associations between granivore presence and *mean shrub*

TABLE 2 Number of recorded presences of 28 bird species, within four functional groups and their mean abundance ± standard error per replicate survey (italics within parentheses) recorded between land management regimes (pastoral properties and Sturt National Park) and habitat types (dune and swale)

Functional group	Species	Scientific name	Sturt National Park		Pastoral Properties		Total
			Dune	Swale	Dune	Swale	
Aerial insectivore	White-backed swallow	<i>Cheramoeca leucosterna</i>	12 (1.50 ± 0.16)	4 (0.38 ± 0.09)	18 (1.75 ± 0.20)	13 (1.63 ± 0.21)	47 (1.31 ± 0.18)
Omnivore	White-winged fairywren	<i>Malurus leucoptera</i>	4 (0.69 ± 0.20)	6 (0.88 ± 0.22)	18 (2.69 ± 0.43)	3 (0.31 ± 0.09)	29 (1.14 ± 0.28)
Insectivore	Purple-backed fairywren	<i>Malurus assimilis</i>	4 (0.69 ± 0.20)	2 (0.25 ± 0.10)	11 (1.31 ± 0.23)	0 (0 ± 0)	17 (0.56 ± 0.17)
Insectivore	Black-faced woodswallow	<i>Artamus cinereus</i>	5 (0.63 ± 0.20)	3 (0.19 ± 0.07)	4 (0.63 ± 0.19)	4 (0.38 ± 0.14)	16 (0.45 ± 0.15)
Granivore	Crested pigeon	<i>Ocyphaps lophotes</i>	4 (0.63 ± 0.16)	5 (0.50 ± 0.16)	5 (0.81 ± 0.28)	2 (0.38 ± 0.14)	16 (0.58 ± 0.19)
Insectivore	Singing honeyeater	<i>Gavicalis virescens</i>	3 (0.19 ± 0.05)	0 (0 ± 0)	6 (0.44 ± 0.09)	3 (0.19 ± 0.07)	12 (0.20 ± 0.06)
Insectivore	Masked woodswallow	<i>Artamus personatus</i>	0 (0 ± 0)	0 (0 ± 0)	5 (6.38 ± 2.04)	3 (0.75 ± 0.26)	8 (1.78 ± 1.06)
Insectivore	Willie wagtail	<i>Rhipidura leucophrys</i>	2 (0.25 ± 0.10)	0 (0 ± 0)	3 (0.19 ± 0.05)	3 (0.19 ± 0.07)	8 (0.15 ± 0.06)
Insectivore	Red-capped robin	<i>Petroica goodenovii</i>	5 (0.38 ± 0.09)	1 (0.06 ± 0.03)	0 (0 ± 0)	1 (0.06 ± 0.03)	7 (0.13 ± 0.05)
Omnivore	Chestnut-crowned babbler	<i>Pomatostomus ruficeps</i>	2 (0.63 ± 0.20)	0 (0 ± 0)	4 (1.69 ± 0.50)	0 (0 ± 0)	6 (0.58 ± 0.27)
Omnivore	Southern whiteface	<i>Aphelocephala leucopsis</i>	2 (0.25 ± 0.09)	0 (0 ± 0)	2 (0.56 ± 0.19)	2 (0.25 ± 0.09)	6 (0.27 ± 0.11)
Omnivore	Banded whiteface	<i>Aphelocephala nigriflata</i>	0 (0 ± 0)	3 (0.50 ± 0.14)	0 (0 ± 0)	1 (0.12 ± 0.06)	4 (0.16 ± 0.08)
Omnivore	Crimson chat	<i>Epthianura tricolor</i>	1 (0.75 ± 0.38)	0 (0 ± 0)	0 (0 ± 0)	3 (0.50 ± 0.22)	4 (0.31 ± 0.22)
Omnivore	Brown falcon	<i>Falco berigora</i>	1 (0.06 ± 0.03)	0 (0 ± 0)	2 (0.12 ± 0.06)	0 (0 ± 0)	3 (0.05 ± 0.03)
Omnivore	Chirruping wedgebill	<i>Psophodes cristatus</i>	0 (0 ± 0)	1 (0.06 ± 0.03)	2 (0.13 ± 0.04)	0 (0 ± 0)	3 (0.05 ± 0.03)
Insectivore	Orange chat	<i>Epthianura aurifrons</i>	0 (0 ± 0)	1 (0.31 ± 0.16)	1 (0.25 ± 0.13)	1 (0.06 ± 0.03)	3 (0.16 ± 0.10)

(Continues)

TABLE 2 (Continued)

Functional group	Species	Scientific name	Sturt National Park		Pastoral Properties		Total
			Dune	Swale	Dune	Swale	
Carnivore	Wedge-tailed eagle	<i>Aquila audax</i>	3 (0.19 ± 0.07)	0 (0 ± 0)	0 (0 ± 0)	0 (0 ± 0)	3 (0.05 ± 0.03)
Granivore	Bourke's parrot	<i>Neopsephotus bourkii</i>	0 (0 ± 0)	2 (0.38 ± 0.18)	0 (0 ± 0)	0 (0 ± 0)	2 (0.09 ± 0.09)
Granivore	Eastern bluebonnet	<i>Northiella haemogaster</i>	0 (0 ± 0)	0 (0 ± 0)	1 (0.73 ± 0.06)	1 (0.73 ± 0.06)	2 (0.06 ± 0.04)
Carnivore	Nankeen kestrel	<i>Falco cenchroides</i>	1 (0.06 ± 0.03)	0 (0 ± 0)	1 (0.06 ± 0.03)	0 (0 ± 0)	2 (0.03 ± 0.02)
Insectivore	Spiny-cheeked honeyeater	<i>Acanthagenys rufogularis</i>	0 (0 ± 0)	0 (0 ± 0)	2 (0.73 ± 0.04)	0 (0 ± 0)	2 (0.031 ± 0.02)
Granivore	Zebra finch	<i>Taeniopygia guttata</i>	0 (0 ± 0)	0 (0 ± 0)	0 (0 ± 0)	2 (1.38 ± 0.48)	2 (0.34 ± 0.25)
Insectivore	Black-eared cuckoo	<i>Chalcites osculans</i>	0 (0 ± 0)	1 (0.06 ± 0.03)	0 (0 ± 0)	0 (0 ± 0)	1 (0.02 ± 0.02)
Omnivore	Cinnamon quail-thrush	<i>Cinclosoma cinnamomeum</i>	0 (0 ± 0)	0 (0 ± 0)	0 (0 ± 0)	1 (0.73 ± 0.06)	1 (0.03 ± 0.03)
Carnivore	Little crow	<i>Corvus bennetti</i>	0 (0 ± 0)	0 (0 ± 0)	1 (0.06 ± 0.03)	0 (0 ± 0)	1 (0.02 ± 0.02)
Insectivore	Pallid cuckoo	<i>Heteroscenes pallidus</i>	0 (0 ± 0)	0 (0 ± 0)	1 (0.06 ± 0.03)	0 (0 ± 0)	1 (0.02 ± 0.02)
Aerial insectivore	Tree martin	<i>Petrochelidon nigricans</i>	0 (0 ± 0)	1 (0.063 ± 0.03)	0 (0 ± 0)	0 (0 ± 0)	1 (0.02 ± 0.02)
Omnivore	White-winged triller	<i>Lalage tricolor</i>	0 (0 ± 0)	0 (0 ± 0)	1 (0.06 ± 0.03)	0 (0 ± 0)	1 (0.02 ± 0.02)
Total			49 (6.88 ± 1.80)	30 (3.63 ± 1.01)	88 (17.44 ± 4.92)	43 (6.44 ± 1.77)	208 (8.59 ± 1.52)

height, which was positive at 400 m² ($z = 1.93, p = 0.054$) and negative at 25 m² ($z = -1.74, p = 0.081$; Table 3). Insectivore presence in dunes was significantly negatively associated with the *total richness* of vegetation at 25 m² ($z = -2.07, p = 0.039$). There was some statistical support for a positive association with *shrub abundance* at the same scale ($z = 1.76, p = 0.078$; Table 3). In swales, there was some statistical support for a negative association between insectivore presence and *total cover* of vegetation at 400 m² ($z = -1.83, p = 0.067$; Table 3). Omnivore presence in dunes was significantly positively associated with *groundcover* at 25 m² ($z = 2.93, p = 0.003$; Table 3). In swales, omnivore presence was significantly positively associated with *shrub cover* at 25 m² ($z = 2.39, p = 0.017$) and *total cover* of vegetation at the 400 m² scale ($z = 2.56, p = 0.01$), and was significantly negatively associated with mean shrub height at the 400 m² scale ($z = 2.21, p = 0.027$; Table 3).

Most avifauna were associated with structural vegetation at a smaller scale (25 m²) rather than the 400 m² scale on dunes, suggesting selection for relatively localised habitat features in the landscape; however, this was not as clear in swales (Table 3). Insectivores and omnivores were associated only with variables at the 25 m² scale in dunes, while all other functional groups' presence was associated with structural vegetation at both scales in dunes and swales, when recorded (Table 3). In dunes, avian functional groups showed no associations with structural vegetation features (Table 3). However, in swales, granivores and omnivores were, respectively, positively and negatively associated with *mean shrub height* at 400 m², and omnivores and insectivores were, respectively, negatively and positively associated with *total cover* of vegetation at 400 m² (Table 3). Granivores were the only functional group associated with the same variable at the same scale between dunes and swales, with some statistical support for a negative association with mean shrub height at 25 m² across both habitat types (Table 3).

Microhabitat use

The four common dryland birds (black-faced woodswallow, purple-backed fairywren, red-capped robin and white-winged fairywren) spent most of their time foraging (72.3% total time) and exhibiting social behaviours (24.6%), rarely travelling (1.8%) or resting (1.3%) (Figure 4; note travelling and resting behaviours were subsequently excluded from further comparisons due to their rare occurrence). They mostly foraged in large shrubs (48.7%), spending relatively less time in trees (1.3× less; 38.8%), in the open (5.6× less; 8.6%) and in small shrubs (12.8× less; 3.8%; Figure 4). Generally, when foraging behaviour was associated with vegetation, birds spent most time within the vegetation (50.2%), spending less time in the canopy (2.1× less; 23.4%) and underneath (2.9× less; 17.1%; Figure 4). They also spent most of their time exhibiting social behaviours in large shrubs (52.7%) than: in trees (1.7× less; 30.8%); in the open (4.3× less; 12.3%); or in small shrubs (12.9× less; 4.1%; Figure 4). When social behaviour was associated with vegetation, birds also spent most time within the vegetation (56.7%) than: in the canopy (1.7× less; 32.8%) and underneath (10.1× less; 5.6%; Figure 4). Three species (purple-backed fairywren, red-capped robin and white-winged fairywren) spent most of their time within vegetation, compared with either the canopy or underneath, while black-faced woodswallows spent more time in the canopy, rather than within the vegetation (Figure 4).

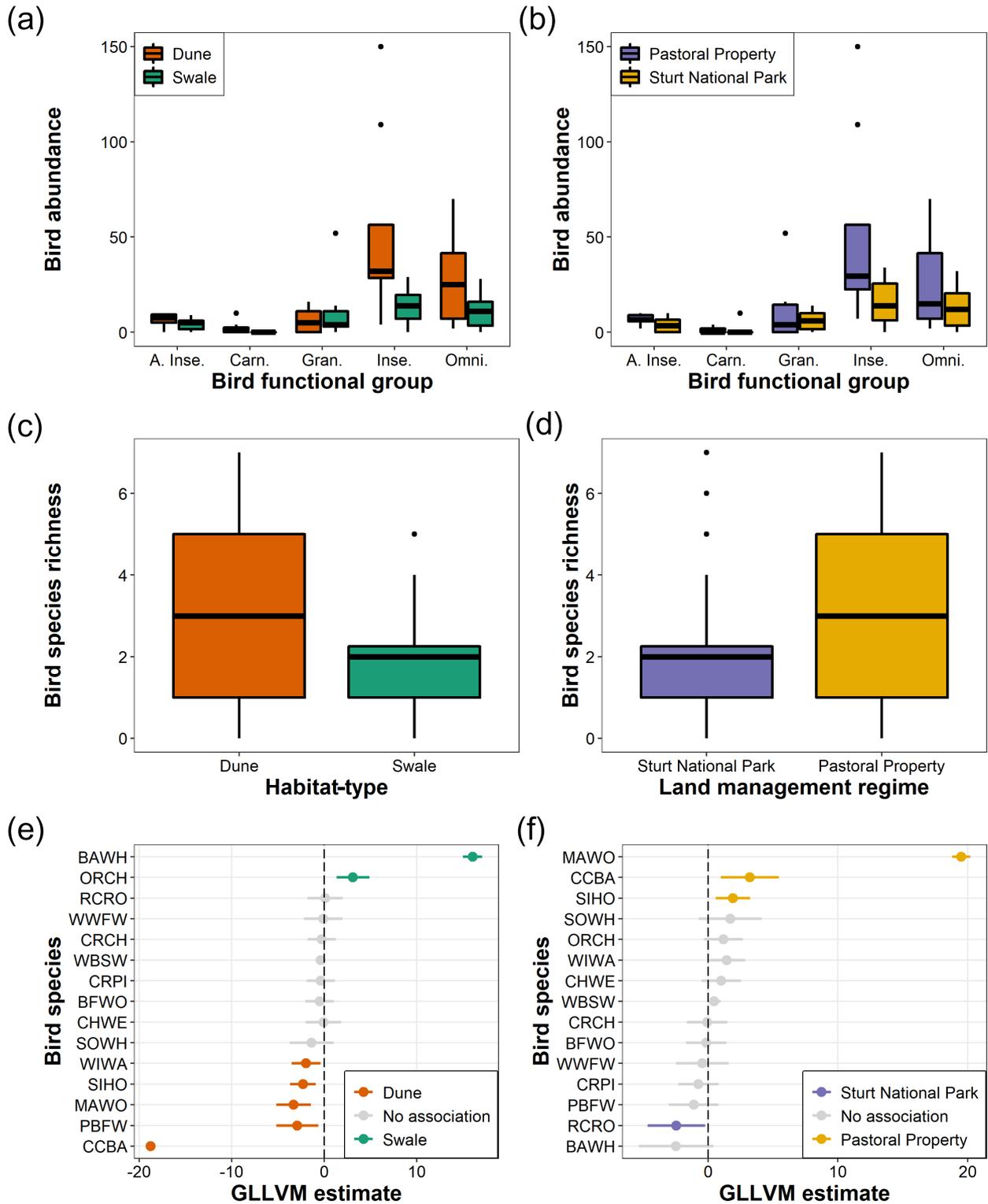


FIGURE 3 Comparisons of summed abundances of four avian functional groups: aerial insectivore (A. Inse.), carnivore (Carn.), granivore (Gran.), insectivore (Inse.) and omnivore (Omni.) between (a) habitat types (dunes and swales) and (b) land management regimes (Sturt National Park in NSW without livestock and dingoes and South Australia with these animals present). Species richness was compared between (c) habitat types and (d) land management regimes. Boxplots were used for these comparisons, which show the median (midline through box), interquartile ranges (extent of box; IQR), minimums and maximums ($Q3 \pm 1.5 \times IQR$; the 'whiskers') and outliers (dots). Data were summed per dune/swale transect ($n = 16$). Comparisons of coefficients ($\pm 95\%$ confidence intervals) for 15 bird species (see Appendix S2: Table A3 for acronyms) from generalised linear latent variable modelling (GLLVM) showing differences (e) between dune (orange) and swale (green) habitat types and (f) land management regimes in Sturt National Park (purple) and pastoral properties in South Australia (yellow), with nonsignificant associations shown in grey.

TABLE 3 Model estimates for structural vegetation associations for four avian functional groups between dune and swale habitat types, grouped across land management regimes (aerial insectivores, granivores, insectivores and omnivores; dune ($n = 133$) and swale ($n = 73$))

Vegetation variable	Scale (m ²)	Dune				Swale				
		Aerial Insectivore		Granivore		Aerial Insectivore		Granivore		
		Insectivore	Omnivore	Insectivore	Omnivore	Insectivore	Omnivore	Insectivore	Omnivore	
Groundcover	25									
Mean shrub height	25			-0.016	0.034			-0.019		
Mean shrub height	400							0.019		-0.017
Shrub abundance	25				0.303					
Shrub cover	25									0.058
Total cover	400									-0.086
Total mean height	400	0.014								
Total richness	25									
Total richness	400									

Estimates in: blue indicate a positive significant ($p \leq 0.05$) association with functional group presence; red indicates a significant negative association, and faded colours indicate those with weak statistical support ($0.05 < p < 0.1$). The scale column indicates the quadrat size (centred on the point the bird was observed), where the relevant vegetation variable was measured. Carnivores were excluded as they were not observed in swales and models assumptions for dune observations could not be appropriately met. Only vegetation variables with which there was some statistical support for an association with a given functional group in a habitat type were included, while model outputs and all variables used and excluded can be found in Appendix S2.

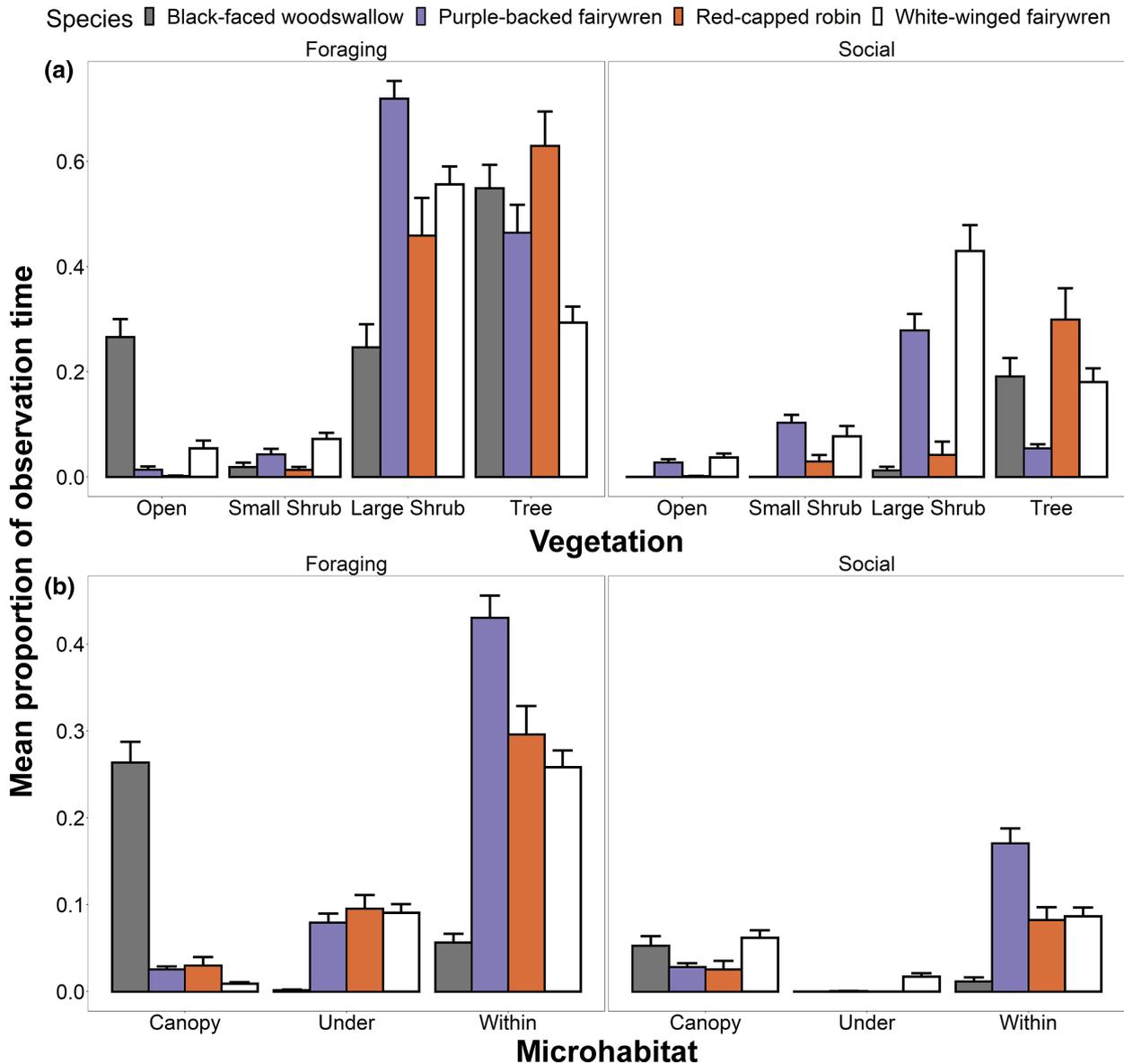


FIGURE 4 Mean (+SE) proportions of time spent foraging and social behaviour by four common dryland bird species: black-faced woodswallow ($n = 18$), purple-backed fairywren ($n = 21$), red-capped robin ($n = 8$), white-winged fairywren ($n = 28$) in different (a) vegetation strata and (b) microhabitats

DISCUSSION

We detected no differences aside from species richness, between avian communities on pastoral properties and the adjacent National Park during the driest period on record in the eastern Strzelecki Desert, contrary to expectations based on prior, broader-scale findings (Gordon et al., 2017; Rees et al., 2017; Rees, Kingsford, et al., 2019; Rees, Rees, et al., 2019). This was likely due to extreme resource limitation and consequent very low bird abundances during this period compared with wetter periods (Rees, Kingsford, et al., 2019). We did, however, find expected community differences between dune and swale habitats. Overall, substantially fewer bird species consisting of a greater proportion of insectivores and omnivores were recorded during this dry period (2018–2019), compared with a subsequent period of high rainfall (2020–2021), as we predicted (Table 1; Tischler et al., 2013). The ability of birds to persist across the landscape during prolonged and extremely dry periods may suggest a degree of resilience

to drying conditions under climate change. In variable, low-productivity landscapes, avian communities vary spatially and temporally, strongly influenced by habitat, even during periods of resource abundance and limitation (Pascoe et al., 2021; Pavey & Nano, 2009; Tischler et al., 2013). We describe avian functional and species-level patterns and possible mechanisms of bottom-up regulation, associated with landscape and habitat use during a period of extreme resource limitation.

During an extended dry period in our study, avian communities did not differ across the two management regimes: Sturt National Park, without dingoes and cattle; and adjacent pastoral properties, managed for cattle grazing with dingoes present. This was despite differences in vegetation structure and ecosystem functioning (Gordon et al., 2015; Letnic et al., 2011; Mills et al., 2021), and previously reported differences in bird communities across the dingo-barrier fence (Gordon et al., 2017; Rees et al., 2017; Rees, Kingsford, et al., 2019; Rees, Rees, et al., 2019). Extreme resource limitation and resultant low overall abundances likely drove this pattern, which may indicate a case of trophic switching from top-down to bottom-up regulation (e.g. Letnic et al., 2011; Wijas & Letnic, 2021), but this idea requires further research. Long-term overgrazing by kangaroos supported by artificial water in the absence of dingoes alongside severe dry conditions (Pedler et al., 2021) considerably reduced conservation benefits in Sturt National Park, creating a relatively homogeneous, resource-scarce landscape, which may have reduced previously detected differences in bird communities. Avian species richness and abundances were substantially lower during our study period, compared with mesic times in which survey transects covered four times the area of ours (Rees, Kingsford, et al., 2019). Suppressed primary productivity probably reduced resource availability (Pascoe et al., 2021; Tischler et al., 2013), contributing to reduced avian richness and abundance. Of the 14 species recorded in our study and by Rees, Kingsford, et al. (2019), only 5 were associated with the same side of the dingo-barrier fence across both studies: chirruping wedgebill (*Psophodes cristatus*), singing honeyeater and willie wagtail was more common outside the dingo-barrier fence, and crested pigeon (*Ocyphaps lophotes*) and purple-backed fairy wren showed no pattern. This may indicate that despite the extended dry conditions, these species were able to exploit the remaining differences in the resource landscape between these management regimes, while the other species no longer responded to the management regime due to resource limitation.

We rarely detected grass seed specialists such as zebra finches (*Taeniopygia guttata*), while budgerigars (*Melopsittacus undulatus*) were not detected on our surveys or incidentally, compared with wet periods when grass seeds were more available and these species were abundant (Rees, Kingsford, et al., 2019; Appendix S3: Table A1). Persistence of larger, non-grass seeds in the soil seed bank during the extended dry period (Moles et al., 2003), likely supported other granivores such as Bourke's parrots (*Neopsephotus bourkii*) and crested pigeons (Gorta et al., 2021; Meissner & Facelli, 1999; Morton & Davies, 1983). Despite the absence of dingo predators, emus were not detected in the National Park during our surveys, possibly due to mortality or emigration from the study site due to low resource availability, which reduced differences between treatments (Wijas & Letnic, 2021). Low resource availability probably also affected ground-nesting species, either observed in low abundances (e.g. cinnamon quail-thrush (*Cinlosoma cinnamomeum*)) or absent (e.g. Australian pipit (*Anthus australis*) and little button-quail (*Turnix velox*)). Species reliant on available drinking water (e.g. pigeons, parrots and some honeyeaters) were either in comparatively low numbers or absent, compared with mesic periods (Rees, Kingsford, et al., 2019; Appendix S3: Table A1). We also

detected no resident avian predators (e.g. brown goshawks (*Accipiter fasciatus*) and collared sparrowhawks (*Accipiter cirrocephalus*)), contrasting with mesic periods (Rees, Kingsford, et al., 2019; Appendix S3: Table A1), probably reflecting low abundance of prey or mortality.

Functional patterns in avian community composition and abundance matched our expectations based on prior findings (e.g. Tischler et al., 2013). Insectivores, aerial insectivores and omnivores, including both sedentary and nomadic species, were the most frequently recorded functional groups during the dry period, while granivores and carnivores were relatively rare (carnivores were exclusively found in dunes, which were elevated, where they perched in trees to detect prey). These three dominant functional groups tend to persist in dry periods, buffered by persistent prey availability and diverse diets, while granivorous species, dependent on available seeds and moisture, immigrate into areas after high rainfall when seed availability is high (e.g. Jordan et al., 2017; Tischler et al., 2013). Abundances of all functional groups and species were also low compared with mesic periods (Rees, Kingsford, et al., 2019; Appendix S3: Table A1), probably reflecting the scarcity of food resources and drinking water (Pascoe et al., 2021; Selwood et al., 2017). There were also habitat differences among functional groups and at the species level.

Consistent with our expectations, structural vegetation associations differed among functional groups, and within functional groups between dunes and swales, reflecting differences in avian resource use and availability in these habitats (Table 3). Insectivores associated with localised areas of low vegetation richness and high shrub abundance on dunes—possibly exploiting largely single-species stands of shrubs (e.g. *Acacia ligulata*), which may represent a refuge for invertebrates during dry periods (e.g. Kwok & Eldridge, 2015, 2016; Segoli et al., 2008)—compared with broad areas of reduced vegetation cover in swales, in which a distinct invertebrate community would have been found (Kwok & Eldridge, 2015). We found no structural vegetation associations with aerial insectivores (almost exclusively white-backed swallows) in swales, likely due to their aerial foraging behaviour (Higgins et al., 2006). However, they often land on elevated perches, which may explain their association with taller vegetation height on dunes. Granivores were associated with increased broadscale vegetation richness in dunes—possibly due to increased available seed diversity (DeFalco et al., 2009; Wright et al., 2021)—and increased broadscale shrub height in swales, which may be linked to increased seed availability and moisture under larger, older shrubs (e.g. *Senna* and *Acacia spp.*; Facelli & Temby, 2002; Pugnaire & Lázaro, 2000; Ward et al., 2018). However, in both habitats, they are associated with localised areas of low shrub height, which may correlate with areas of greater short-lived plant seed availability where competitive exclusion of these plants by larger, well-established shrubs is reduced (Facelli & Temby, 2002; Weedon & Facelli, 2008), and/or where detection of avian predators is not inhibited by taller vegetation. Omnivores associated with four distinct vegetation variables—increased groundcover in dunes, but increased shrub and broadscale vegetation cover, where shrub height was low in swales—probably reflecting their generalised niche and diet. Vegetated areas and increased groundcover probably retained moisture and had higher nutrient availability than non-vegetated areas, providing habitat for invertebrates and increased seed availability on which omnivores could feed (Facelli & Temby, 2002; Pugnaire & Lázaro, 2000; Segoli et al., 2008; Ward et al., 2018).

Microhabitat use by common insectivores and an omnivore further highlighted species-specific variation within functional group habitat use (Figure 4). For example, the three common insectivores: black-faced woodswallow, purple-backed fairywren and red-capped robin; foraged mostly at

large shrubs and trees, consistent with broader insectivore associations with shrubs on dunes (Table 3). However, while the latter two species largely foraged within this vegetation, black-faced woodswallows often perched on the canopy from where they would dive to the ground for prey in more open areas or capture insects in flight. Furthermore, omnivorous white-winged fairywrens foraged predominantly in large shrubs and trees in dunes, likely on invertebrates (Figure 4), which contrasted with overall omnivore association with low shrubs in swales where this group may have fed on seeds, like the granivorous species (Table 3). The substantial use of dunes by white-winged fairywrens also differs from their typical habitat of low shrublands, vegetated swales and claypans (Higgins et al., 2001), which may be explained by the combination of reduced competition and greater resource availability on dunes during extended dry periods. Invertebrates and seeds represent an important food source for avian communities during dry periods. We found substantial variations in these resources are exploited, among species and functional groups and between dunes and swales, providing complex but important insights into the characteristics of dry period refugia for avian communities.

The persistence of these communities despite reduced numbers during the extended dry period may indicate resilience to increased drying conditions under climate change, although large fluctuations in abundance may also increase extinction risk (Runge et al., 2015). Aerial and terrestrial insectivores and omnivores, including white-backed swallows, fairywrens, woodswallows, willie wagtails, red-capped robins and others persisted in low abundances during the driest two-year period on record. Granivores such as crested pigeons and Bourke's parrots also persisted, likely due to the provision of artificial water (Gorta et al., 2021). While land and conservation managers cannot control drying associated with climate change, habitat retention for species and groups of birds, which currently appear to be resilient in extended dry conditions should be a priority. A more detailed understanding of habitat requirements for many of these species and groups is required, with our study identifying potential habitat associations for functional groups, which persisted during the extended dry period. This will be important for conserving dryland avian communities under increased drying scenarios (BOM & CSIRO, 2020; Harris et al., 2018; Ma et al., 2015). There is also a need to identify how spatial and temporal variability in resources (Heath et al., 2014; Vinuela et al., 2014; Wollrab et al., 2012) drive community composition, habitat and resource use.

Extended dry periods reduce landscape-scale resource availability, which can shift ecosystem regulation (Letnic et al., 2011; Wijas & Letnic, 2021). Differences in avian communities between land management regimes were not prominent during the extended dry period while differences were detected between dunes and swales, with functional groups associating with different structural vegetation features between these habitats in the eastern Strzelecki Desert. Long-term monitoring of avifaunal communities, under the Wild Deserts project (Kingsford et al., 2021), will provide further insights into potential links between resources, habitat and land management associations. Studies on avian diets may further highlight the importance of habitats and the availability of essential resources for different species. For example, linking differences in invertebrate abundance associated with habitat types and vegetation features (as in Kwok et al., 2016) with insectivorous bird diets may identify causal relationships and explain differences. Habitat heterogeneity (inferred from varied responses of functional groups and species to structural and microhabitat features, and broader differences between habitats) was also clearly important, providing different refuges and resources for avian communities during a period

of extreme resource limitation. Clearly, some species are more resilient to dry periods than others, with wet conditions enabling recruitment and population recovery of resident species, as well as influxes of more transitory species absent during extended dry periods. As drying becomes more pervasive across drylands under climate change, the ability of species and communities to adapt, exploit limited resources and respond to periods of relative resource abundance will increasingly drive community composition and ecological functioning across these landscapes.

AUTHOR CONTRIBUTIONS

Simon B. Z. Gorta: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (equal); investigation (lead); methodology (lead); project administration (equal); resources (equal); software (equal); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Corey T. Callaghan:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); methodology (supporting); project administration (supporting); software (supporting); supervision (equal); validation (supporting); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Reece D. Pedler:** Conceptualization (supporting); funding acquisition (supporting); investigation (supporting); methodology (supporting); project administration (equal); resources (equal); supervision (supporting); validation (supporting); writing – original draft (supporting); writing – review and editing (supporting). **John L. Read:** Conceptualization (supporting); funding acquisition (supporting); investigation (supporting); methodology (supporting); supervision (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Rebecca S. West:** Conceptualization (supporting); funding acquisition (supporting); investigation (supporting); methodology (supporting); project administration (supporting); resources (supporting); supervision (supporting). **Richard T. Kingsford:** Conceptualization (supporting); formal analysis (supporting); funding acquisition (equal); investigation (supporting); methodology (supporting); project administration (equal); resources (equal); supervision (lead); validation (supporting); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from Wild Deserts.

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