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Specialization and niche overlap across spatial scales: Revealing ecological factors shaping species richness and coexistence in Australian songbirds

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Abstract

1. Ecological specialization enables the partitioning of resources and thus can facilitate the coexistence of species and promote higher species richness. Specialization and niche partitioning are expected to exert a decisive influence on local spatial scales, while species richness at regional scales should be shaped mostly by historical factors and abiotic conditions. Moreover, specialization is expected to be particularly important in communities that are exceptionally species rich for their environmental conditions. Concurrently, niche overlap in these communities should be minimized to enable species coexistence.
2. We tested these hypotheses by studying specialization–richness relationship and niche overlap in assemblages of 298 species of songbirds (Passeriformes) across Australia. We used local (2–6 ha) to regional (bioregions) spatial scales and detailed data on habitat, diet and foraging behaviour (method, substrate and stratum).
3. We expected the richness–specialization relationship to be particularly strong (a) on local spatial scales and (b) in communities exceptionally species rich for given environmental conditions (approximated by moisture and vegetation complexity). We also expected (c) low niche overlap in assemblages with specialized species.
4. Only the third prediction was partly supported. First, while the specialization and species richness were often positively related, the strength and the direction of the relationship changed between traits and across spatial scales. The strength of the specialization–richness relationship was consistently positive only in foraging stratum, and it increased towards smaller spatial scales only in case of habitat and diet. Simultaneously, species in local communities demonstrated high overlap in habitat and diet. Second, we did not find particularly strong specialization–richness relationships in exceptionally species-rich communities. Third, we found the expected negative relationship between specialization and overlap in foraging stratum and substrate (in local communities), suggesting that species partition ecological space locally in terms of where they find food.
5. Our expectations were only weakly supported. Specialization on foraging stratum was probably important in facilitating species coexistence. Conversely, although species were often specialized on habitat and diet, high overlap in these traits did

not preclude their local coexistence. Overall, specialization and overlap in foraging traits were more important for species coexistence than habitat or diet.

KEYWORDS
Australia, community assembly, niche partitioning, null models, passeriformes, spatial scales

1 | INTRODUCTION

Niche partitioning is presumed to play a prominent role in shaping species richness by facilitating species coexistence. The assumption is that narrow specialization enables finer partitioning of resources and thus enhances local coexistence of species and allows higher species richness (Eeley & Foley, 1999; Hutchinson, 1959; MacArthur, 1972; Mason, Irz, Lanoiselée, Mouillot, & Argillier, 2008; Pigot, Trisos, & Tobias, 2016). Specialists (i.e. species with narrow niches) use only restricted range of available resources, while generalists can utilize many resources available in their environment (Futuyma & Moreno, 1988). Ecological specialization (or niche breadth) received much attention in attempts to explain patterns in species richness, but the evidence for its role in shaping spatial patterns in species richness is mixed (Belmaker, Sekercioglu, & Jetz, 2012; Pigot et al., 2016). The reason might be that many studies focused on only one or a few coarse traits as a measure of ecological specialization (mostly habitat utilization and diet preferences; e.g. Belmaker et al., 2012; Brändle, Prinzing, Pfeifer, & Brandl, 2002; Julliard, Clavel, Devictor, Jiguet, & Couvet, 2006; Reif, Hořák, Krištín, Kopsová, & Devictor, 2015), yet niche partitioning might take place on finer ecological scales, such as foraging behaviour (substrate or methods used for obtaining food). A classic example represents mixed flocks of titmice (family Paridae), where individual species differ in their foraging sites with larger-bodied species foraging on the inner parts of trees while smaller species using mostly outer branches (Jablonski & Lee, 1998; Lack, 1971; Suhonen, Alatalo, & Gustafsson, 1994). Therefore, even though they share habitat and diet preferences, the interspecific competition is relaxed via the division of foraging space, which thus facilitates species coexistence. However, we mostly lack information on fine niche partitioning in local assemblages (Belmaker & Jetz, 2011; Julliard et al., 2006) and its relationship to species richness studied on a large sample of species.

While niche partitioning is assumed to be most important on fine spatial scales shaping local coexistence of species, the role of abiotic conditions and historical effects should be more prominent on coarser regional scales and thus shaping spatial variation in species richness (Belmaker & Jetz, 2011; Devictor et al., 2010; Ferger, Schleuning, Hemp, Howell, & Böhning-Gaese, 2014; Fergnani & Ruggiero, 2017; Hawkins et al., 2003; Ricklefs, 2006; Royan et al., 2016; Whittaker, Willis, & Field, 2001). However, most studies fail to work across several spatial scales and thus fail to identify relative roles of niche partitioning, abiotic conditions and historical effects on different scales (Belmaker et al., 2012; Ricklefs, 2004). Yet, working across spatial scales is critical, because specialization can operate together with environmental productivity in shaping patterns in species richness at different spatial scales (Belmaker et al., 2012; Pellissier, Barnagaud, Kissling, Sekercioglu, & Svenning, 2018). Thus, specialization should be studied together with, and in relation to, resource availability at several spatial scales simultaneously (Belmaker et al., 2012; Futuyma & Moreno, 1988).

Although there is considerable evidence for positive relationships of species richness to various environmental factors (e.g. vegetation heterogeneity) and productivity (Ferger et al., 2014; Hurlbert, 2004; Pellissier et al., 2018), environmental factors themselves do not explain how the assemblages originate and species coexist. Two scenarios were put forward for highly productive environments (defined e.g. by high vegetation heterogeneity or high net primary productivity) harbouring exceptionally species-rich assemblages. First, one can expect a strong richness–specialization relationship due to the partitioning of niche and the division of ecological space in these highly productive assemblages (Evans, Jackson, Greenwood, & Gaston, 2006; Mason et al., 2008; Pellissier et al., 2018). Second, alternatively, high amount of resources could release species from interspecific competition and thus enable low specialization and/or high niche overlap (Evans et al., 2006; MacArthur, 1965; Pigot et al., 2016). A way to reconcile these two expectations is to study specialization in relation to species richness while taking into account environmental productivity (Belmaker et al., 2012). Under this approach, high specialization is to be expected in assemblages that are particularly species rich for the productivity of environments in which they live, while low specialization can be permissible in assemblages particularly species poor for the productivity of the environment they inhabit.

In this study, we use comprehensive data on five sets of ecological traits in 298 species of Australian songbirds (Passeriformes) to test the specialization–richness and niche–richness relationships in assemblages across three spatial scales. Unlike the previous studies, in addition to regional scales, we incorporate the local spatial scale of assemblages inhabiting small (2–6 ha) areas with species abundance data obtained by repeated censuses in homogeneous habitats. Furthermore, we not only employ commonly used habitat and diet categories to calculate specialization, but also use detailed data on foraging (stratum, substrate and method used by birds when foraging), which might play a prominent role in fine-scale niche partitioning. We test the following three predictions. First, if niche partitioning is decisive for species coexistence, we expect to find an increasing strength of richness–specialization relationship from regional to local spatial scales (Figure 1a). Second, richness–specialization relationship should remain positive even when controlled for

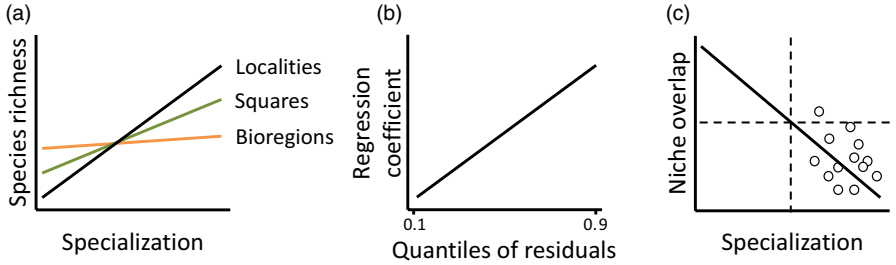

FIGURE 1 Graphical presentation of the tested hypotheses. (a) We expect an increasing strength of species richness–specialization relationship towards small spatial scales, provided niche partitioning drives species coexistence. (b) We expect a particularly strong species richness–specialization relationship (i.e. high regression coefficient) in assemblages exceptionally rich for given environmental conditions (i.e. those in high quantiles of residuals from a richness–environment regression), while weak richness–specialization relationship is possible in assemblages exceptionally depauperate in species for the given environment (i.e. those in low quantiles of residuals from a richness–environment regression). (C) To partition resources and avoid competition, specialization and niche overlap should be negatively correlated and assemblages should be concentrated in the lower right quadrant (highly specialized species which do not overlap in their resource use)

environmental conditions, but species in assemblages that are exceptionally rich relative to the available resources should have higher specialization to be able to coexist locally. Thus, the strength of richness–specialization relationship should be stronger in relatively species-rich assemblages (Figure 1b). Third, specialization and niche overlap should be negatively correlated, because if the species in an assemblage narrowly specialize on a few resources, they should avoid competition by minimizing resource use overlap (Figure 1c).

2 | MATERIALS AND METHODS

2.1 | Assemblage data

We considered three spatial scales of assemblages: *localities* of 2–6 ha area, 1 × 1 degree *grid cells* (longitude × latitude) and *bioregions* in Australia including the island of Tasmania. We obtained data for localities from Australian Bird Count (ABC; Clarke, 1999), which originally consisted of 1962 localities and 77,383 censuses. We used several criteria to ensure standardization and comprehensive sampling of species on localities. In terms of standardization, we included only censuses with the duration between 20 and 30 min and localities with the area between 2 and 6 ha and at least 20 censuses. We excluded strongly human-modified, urban and rural habitats. Next, in terms of sampling, we applied rarefaction based on sample coverage (Chao & Jost, 2012) using iNEXT (Hsieh, Ma, & Chao, 2016) and included only localities with at least 90% coverage. We also performed a final check on the quality of ABC data by removing observations of species on an ABC locality if they were found more than 100 km away from a border of their range (obtained from BirdLife International, & NatureServe, 2014), ending up with 470 localities with 37,250 censuses (median number of censuses per locality was 56). For grid cells, we first created a grid with 1 × 1 degree resolution (longitude x latitude) across Australia and Tasmania in R software (R Core Development Team, 2018) and left only grid cells in which at least one locality was present (n = 87 grid cells). We used IBRA bioregions from the Department of the Environment (2012) and kept only bioregions in which at least one locality was present (n = 49 bioregions). For grid cells and bioregions, we generated lists of species by overlapping each grid cell and bioregion with breeding ranges of bird species obtained from BirdLife International and NatureServe (2014).

2.2 | Specialization data

We obtained data on specialization of Australian songbirds from the Handbook of Australian, New Zealand and Antarctic Birds (HANZAB; Higgins & Peter, 2002; Higgins, Peter, & Cowling, 2006; Higgins, Peter, & Steele, 2001). We used five ecological traits to compute the specialization indices, separately for each trait. Each trait was divided into several categories and each category of each trait received a value corresponding to proportional use (percentage) of that category by a given species based on information in HANZAB. The sum of all categories of a given trait for a given species was always 100. The traits and their categories were as follows: habitat (ten categories: rainforest, forest, woodland, shrub, grassland, heats, marshes, marine mangrove, bare ground and human settlements), diet (eight categories: leaves, fruit, nectar and pollen, seeds, insects, other invertebrates, vertebrates and carrion), foraging method (nine categories: gleaning, hang-gleaning, snatching, hover-snatching, probing, manipulating, pouncing, flycatching and flush chasing; see Supplement S1 for details on the definition of these categories), foraging stratum (four categories: ground, shrub, sub-canopy and canopy) and foraging substrate (eight categories: ground, bark, leaves, buds, fruit, flowers, air and other). Due to distinct foraging strategies of swallows (family Hirundinidae) and woodswallows (genus *Artamus*), we removed these species from our analyses, leaving the final number of 298 species.

There were a few cases of missing data in our dataset (stratum: one species, substrate: two species, method: 25 species; no missing data in habitat and diet). To avoid losing species with missing values, we imputed the missing data following Penone et al. (2014) and using the missForest method (Stekhoven & Bühlmann, 2012), which was proved to be a well-performing method for data imputation (Penone et al., 2014; Shah, Bartlett, Carpenter, Nicholas, &

Hemingway, 2014). First, we created a phylogenetic distance matrix for all species using the Bayesian maximum clade credibility tree based on 1,000 phylogenies obtained from birdtree.org (Hackett constraint; Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) and using TreeAnnotator software (BEAST2; Bouckaert et al., 2014). Then, we performed a principal coordinate analysis (PCoA) on the distance matrix, extracted first ten eigenvectors, added them to the dataset as information on the phylogenetic relationships between species and computed missing data using the "MISSFOREST" package (Stekhoven & Bühlmann, 2012) in R (10 iterations with 100 decision trees). As the imputed data were not integer numbers, we corrected the imputed values by rounding them to the nearest integer and ensuring that their sum was equal to 100.

We calculated specialization as an inversed standardized Levins' index (modification by Belmaker et al., 2012) for each of five ecological traits for every species (j) as:

$$\text{Levins}_j = 1 - \frac{\frac{1}{\sum p_i^2} - 1}{n - 1}$$

where p_i is the proportional use of trait category i and n is the total number of trait categories (e.g. 10 for habitat). Assemblage values of specialization for localities, grid cells and bioregions were then calculated as arithmetic means of species' specialization across species present in a given assemblage and, in case of localities, weighted by the species' abundances. The Levins' index calculated in this way ranges from 0 (generalists) to 1 (specialists).

Levins' index does not include information on niche partitioning: assemblages where all the species are specialized on the same trait category and assemblages where species are specialized on several different trait categories both show high specialization, that is high assemblage-level values of Levins' index (Figure S1). However, these two types of assemblages might be expected to experience completely different levels of species competitive interactions. Thus, we also calculated niche overlap index (Pianka, 1973), which measures overlap in trait category use between a pair of species, as:

$$\text{Pianka}_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where p_{ij} and p_{ik} are proportional uses of trait category i by species j and k, respectively, and n is the total number of trait categories. We then calculated assemblage means (only for localities) as a mean of all pairs of species present in a given assemblage weighted by their abundances. Pianka's index values range between 0 (no overlap in trait category use) and 1 (complete overlap). Thus, this index estimates the potential for local competitive interactions between species in the assemblage. R code for calculation of Levins' and Pianka's indices is available in Supplement S2.

We did not compute a single specialization or niche overlap index to study the overall specialization/overlap based on all traits and their categories considered together. The ecological and behavioural traits we used are not mutually exclusive and might show dependencies, so that species specialized on some categories in one trait can probably be constrained to certain categories in other traits (e.g. species eating nectar cannot forage by snatching or flush chasing). A potential solution would probably be to score species into all combinations of the categories of all 5 traits and use this scoring to calculate overall specialization/overlap indices. However, this is not possible with our data due to trait dependencies (see above) and the lack of field data on such fine division of the niche for most of the species (see Supplement S3 for more details). We must thus trade-off the scale of this study with the ecological detail. Consequently, we had to keep our analysis based separately on the five traits, as is always the case in studies based on data from the literature. Moreover, analysing specialization and overlap trait-by-trait can bring interesting insights not obtainable by the analysis of one multidimensional object. For example, we can quantify relative importance of different traits at different spatial scales. Moreover, to account for a possible scenario where species are generalists in one trait, but partition the niche by specializing in another trait, we fit multi-predictor models controlling for all traits at once (see below).

2.3 | Environmental predictors

We used moisture and vegetation structure to account for species richness–environment relationships while studying species richness–specialization/niche overlap relationships. Moisture index was expressed as the annual mean of the monthly ratio of precipitation to potential evaporation in 0.2 × 0.2 degree resolution (The Atlas of Living Australia, 2018). We obtained values for localities as a value of the 0.2 × 0.2 degree cell in which a particular locality was present, and for grid cells and bioregions as means from all 0.2 × 0.2 degree cells present in each grid cell or bioregion. Data on vegetation cover and height were already included in the ABC dataset for localities (29 classes based on a combination of the vegetation cover and height), from which we excluded three rural and urban categories (see above). For grid cells and bioregions, we used vegetation height and structure with 17 classes (TERN, 2018). For consistency, we merged classes in both datasets according to the vegetation height and cover into the 11 following classes of vegetation complexity: no trees, shrubs and low open woodland, tall open woodland, shrubs and low woodland, tall woodland, very tall woodland, low open forest, tall open forest, very tall open forest, closed forest and tall closed forest (see Table S1 for full details on category conversion). In the following analyses, we used vegetation complexity as a continuous variable (values ranging from one to 11 according to the classes). Vegetation data were originally in 30 × 30 m resolution, so we projected them into 0.1 × 0.1 degree resolution (longitude × latitude) and then obtained values for grid cells and bioregions as a class with the highest occurrence in a given grid cell or bioregion. Maps of the spatial distribution of moisture and vegetation complexity for each spatial scale are available in Figure S2.

2.4 | Null models

To distinguish whether observed patterns could have originated by random sampling of species or were a result of non-random ecological processes during the assembly of bird communities, we constructed null models in which we randomized the species list in each assemblage. Species in localities, grid cells and bioregions were randomly drawn from pools consisting of all species present in localities (n = 238), grid cells (n = 281) and bioregions (n = 286), respectively, weighted by the number of assemblages they were present in (i.e. a species found in most assemblages on a respective spatial scale had a higher chance to be picked than a species occurring in just a few assemblages). We thus explicitly omitted any dispersal constraints on species assembly, but we weighted the membership in species pool by overall species occurrence across all sampling units. This model preserves local species richness and, in case of localities, also species abundances in each assemblage (abundances were assigned randomly to species drawn from the localities pool). The explicit aim of this null model was to model species assembly from our species pool while ignoring species traits. By this process, we obtained communities with realistic species richness, abundance and occurrence, while randomizing ecological specialization across sampling units. We created 1,000 random communities for localities, grid cells and bioregions. Subsequently, we computed standardized effect sizes (SES) of Levins' and Pianka's indices from these replications of each assemblage as the difference between the observed value and the mean of the expected values divided by the standard deviation (*SD*) of the expected values. SES values higher than zero represent assemblages that are more specialized/have higher overlap than expected by chance and vice versa for SES values lower than zero. Subsequently, we used SES values of the indices in our statistical analyses. In this way, our analyses were already adjusted for expected relationships based on randomly drawn communities.

2.5 | Statistical analyses

We conducted three sets of analyses to investigate relationships between species richness, specialization, niche overlap, and environmental conditions. First, we fit bivariate spatial generalized least squares (GLS) regressions of species richness (response variable) versus SES of the specialization or niche overlap (explanatory variable) for each spatial scale to explore bivariate correlations between richness and specialization/overlap on different spatial scales. On the scale of localities, we used SES of the specialization and niche overlap calculated both without and with species' abundances to preserve consistency across all spatial scales (no abundance data were available for grid cells and bioregions) but also to keep the indices with more detailed information (i.e. species abundance) on assemblage composition on the local level.

Second, we tested how specialization/overlap explains richness while accounting for environmental conditions. We fit multi-predictor spatial GLS models with species richness as a dependent variable and SES of the specialization/overlap for all five traits (stratum, substrate, method, habitat and diet), together with two environmental variables (moisture and vegetation complexity), as predictors. In case of localities and bioregions, we also fit the area (ha in localities, km^2 in bioregions) as an additional predictor. We did not include range size or body size as additional predictors. We accounted for range size in the null models where wide-ranging species had a higher probability to be picked than locally occurring ones. Body mass was suggested to be related to specialization (Pineda-Munoz, Evans, & Alroy, 2016), but evidence is missing (Reif et al., 2015). We fit these regressions for all three spatial scales, resulting in six models: specialization and niche overlap (both with and without species' abundances) in localities, and specialization in grid cells and bioregions. We used combinations of all specialization/overlap traits and did not perform any model selection. Thus, we checked for collinearity among our predictors by computing variance inflation factors (VIF) which showed that there was very low collinearity present (min. = 1.04, max. = 2.11, median = 1.23).

We use spatial GLS regression model that take spatial autocorrelation into account because assemblages are not distributed randomly in space and nearby assemblages are usually more similar than the distant ones. We accounted for spatial autocorrelation by fitting a model with a spatial structure of the residuals. We used exponential, Gaussian, linear, rational quadratic, and spherical correlation structures and then selected the model with the structure that showed the lowest AIC value. Latitudinal and longitudinal values necessary to fit the spatial structure were obtained as geographical coordinates of the localities, as centres of the cells for the grid cells and as centroids of the bioregions. Residuals of GLS models were tested for remaining spatial autocorrelation by Moran's I. Pseudo-R^2 for GLS analyses were computed as Cox and Snell pseudo-R^2 using the function "nagelkerke" from the "rcompanion" R package (Mangiafico, 2016).

In addition to these multi-predictor regression models, we also tested the assumption that richness–specialization relationship should be stronger in assemblages, which are exceptionally species rich relative to prevailing environmental conditions using quantile regression. To do this, we calculated residuals from spatial GLS regressions relating species richness to environmental variables (moisture, vegetation complexity and, in case of localities and bioregions, also area). We then fitted a quantile regression relating these residuals to SES of the specialization/overlap (R package "quantreg"; Koenker, 2018) for each trait at all spatial scales (in case of localities we included species' abundances). This method cuts the richness–environment residuals into 0.1 quantiles and runs the regression analysis on each of them. The low and high quantiles represent assemblages that are species depauperate or rich for the given environmental conditions, respectively.

Third, we used bivariate spatial GLS analyses to study the relationships between specialization (explanatory variable) and niche overlap (response variable; both as empirical values and not SES) and therefore the partitioning of the niche within assemblages on the local scale. We expected to find negative relationships between specialization and niche overlap (Figure 1). Moreover, to assess

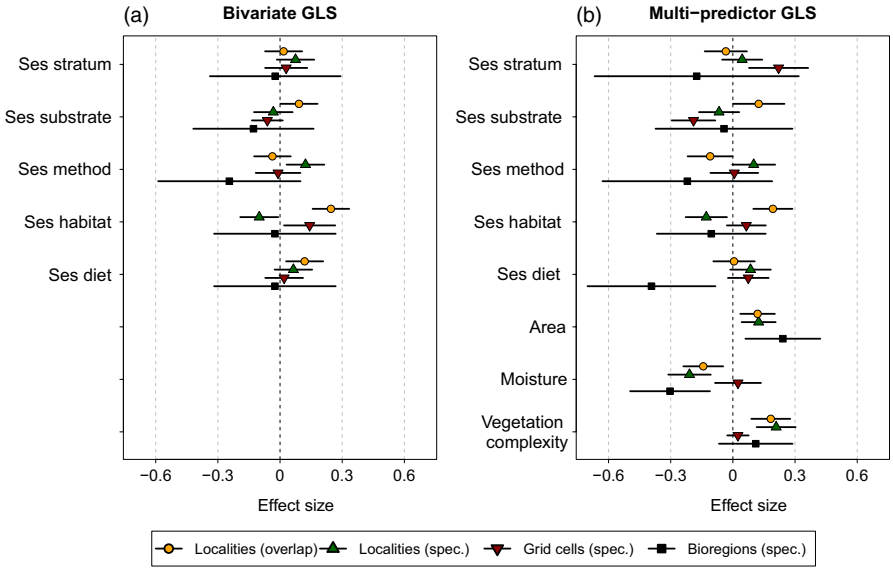

FIGURE 2 Forest plots of effect sizes with 95% confidence intervals from the relationships between species richness (our response variable) and the predictor variables listed on the left side of both panels. (a) Bivariate spatial generalized least squares (GLS) analyses between species richness and each predictor fit separately. (b) Multi-predictor GLS analyses between species richness and all predictors fit simultaneously. Results of the local scale are based on indices computed with species' abundances. Colour coding symbolizes different spatial scales. For full results of these analyses, see Tables S2 and S3

independent effects of both specialization and niche overlap on species richness, we also fitted multi-predictor spatial GLS models with species richness as a dependent variable and SES of the both specialization and niche overlap as predictors on the scale of localities. All analyses on the local scale were performed with indices computed using species' abundances to embody more precise information on niche division.

All variables were tested for the normal distribution, transformed if necessary (detailed transformations are in results tables), and all were scaled so that their mean was zero and the standard deviation was one prior to each analysis. All analyses were performed in R version 3.5.1 (R Core Development Team, 2018).

3 | RESULTS

The SES values of assemblage specialization did not show any latitudinal gradient (Figure S3), even though variability across assemblages was not very distinct, with most of them being relatively specialized in all ecological traits except for stratum (Figure S4). In grid cells and bioregions, assemblages in the northern and south-eastern Australia and in Tasmania were noticeably more generalist in most of the traits then the rest of the assemblages. Highest specialization in stratum, substrate, method and diet appeared to be mostly located in the south-western Australia and on the eastern coast.

In bivariate analyses, there was a clear positive relationship between species richness and the standardized effect sizes (SES) of the specialization in at least one ecological trait at all spatial scales except for bioregions (Figure 2, Table S2). Richness increased with increasing specialization for habitat in localities and grid cells, while foraging method was negatively and diet positively related to richness at the scale of localities. However, these relationships at local scales changed when we accounted for species' abundances. While the effect of diet was much smaller and ceased to be statistically significant, the relationships were even opposite in case of method and habitat (Table S2). Overall, the expectation that the strength of the richness–specialization relationship should increase with decreasing spatial scale was supported only in habitat and diet (Figure 2, Table S2). Niche overlap at the finest spatial scale of localities was positively correlated with richness for the SES of substrate and diet and negatively for method (Figure 2, Table S2). Both diet and substrate remained significant even after including species' abundances, but method ceased to be significant and overlap in habitat became positively related to richness.

The richness–specialization and overlap–specialization relationships retained similar strength in multi-predictor models which accounted for the SES of the specialization/overlap in the other ecological traits and for environmental variables. Environmental variables had significant positive (vegetation complexity) or negative (moisture index) effects on species richness, mostly on the finest spatial scale of localities (Figure 2, Table S3). The expectation that the intensity of the richness–specialization relationship should increase with decreasing spatial scale was again supported only in habitat and diet in these multi-predictor spatial GLS analyses (Figure 2, Table S3).

The expectation that the richness–specialization relationship should be steeper in assemblages that are exceptionally species rich for given environmental conditions was not supported by the analyses run separately within quantile cut-offs of the residuals from the regression of species richness on the environmental conditions (Figure 3, Figure S5). The positive and negative relationships between the SES of the specialization and species richness were equally common across our ecological and behavioural traits. Moreover, when positive relationships seemed to prevail (at the scale of localities), they seemed to be concentrated in lower quantile values, that is in communities depauperate in species for given environmental conditions (Figure 3b).

The prediction that specialization and niche overlap should be negatively correlated was supported only in foraging stratum and

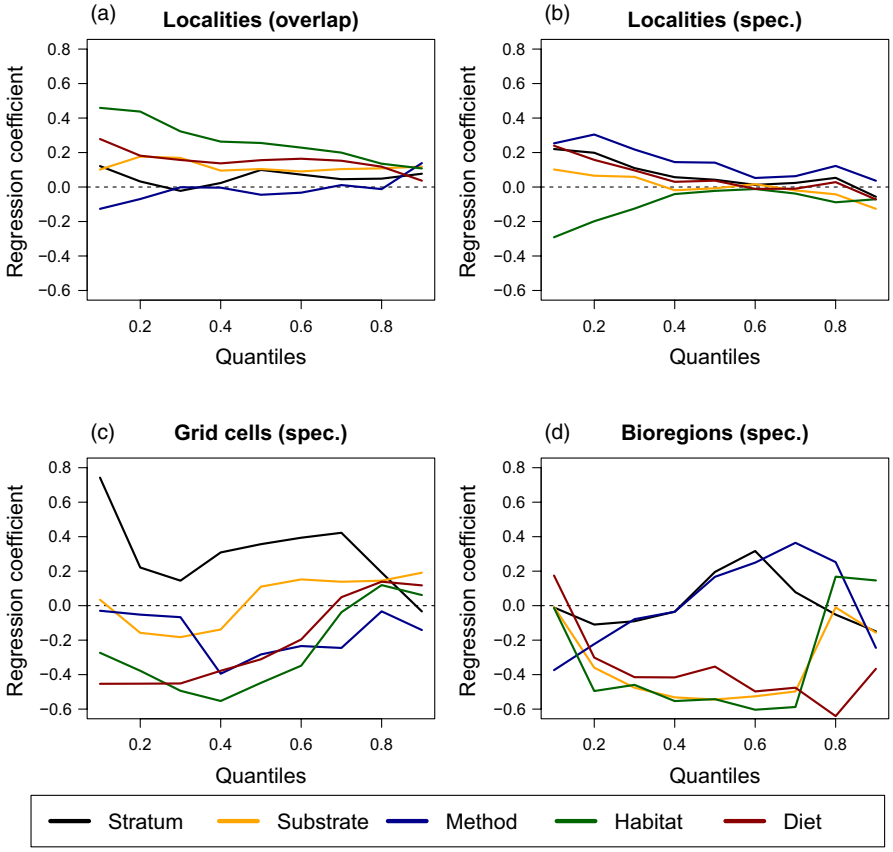

FIGURE 3 Quantile-specific analyses of the relationships between species richness and specialization or niche overlap. Quantiles (the *x*-axis) are divided into quantile cut-offs according to species richness–environment residuals. The highest quantiles contain assemblages that are most species rich given their environmental conditions, while the lowest quantile contains assemblages with the least species given the environment. Regression coefficients (the y-axis) then show the estimates from the model relating residual species richness in these quantiles to the SES of the specialization or niche overlap. Estimates for localities (niche overlap, a, and specialization, b, computed with species' abundances), grid cells (c) and bioregions (d) are shown separately

substrate, which showed the expected strongly negative relationships (Table S4). On the other hand, foraging method, habitat and diet showed significant positive relationships between specialization and niche overlap, although effect sizes were comparatively smaller than in the negative relationships (Table S4). All traits except for stratum displayed on average high specialization, while niche overlap was more variable (Figure S4). We also expected most assemblages to fall into the lower right quadrant, with high values of specialization and low niche overlap due to niche partitioning. However, this expectation was supported only for foraging substrate (Figure 4). Assemblages showed both high specialization and high niche overlap in the other three traits (method, habitat and diet), while stratum demonstrated intermediate values of both specialization and overlap with a negative relationship between these two. For consistency, we repeated the analyses with the SES of the specialization and niche overlap instead of empirical values of the indices but the directions of relationships and their significance were the same (Table S5, Figure S6).

In multi-predictor models with both SES of the specialization and SES of the niche overlap as explanatory variables, specialization was significantly positively related to species richness in stratum and method and negatively in habitat, while niche overlap was positively related to richness in case of stratum, habitat and diet (Table S6). These results mirror the bivariate analyses presented above but differ in the effect of substrate overlap that ceased to be significant, and in the effect of stratum on richness, which became significant (both specialization and overlap) when controlled for each other. The relationship of species richness to both SES of the niche overlap and specialization remained similar after accounting for each other in one model, showing that their relationships with species richness were largely independent of each other.

4 | DISCUSSION

Theory predicts that species in species-rich assemblages should be specialized so that long-term coexistence is facilitated (Eeley & Foley, 1999; Hutchinson, 1959; MacArthur, 1972; Mason et al., 2008; Pigot et al., 2016). Here, we tested three predictions stemming from this theory. First, we showed that species richness and specialization in Australian songbirds were often positively related, but the relationship changed between individual ecological and behavioural traits and across spatial scales (from local to regional). This was true for both bivariate and multi-predictor models and also when we controlled the analyses for area, available moisture and vegetation complexity. We expected to find stronger richness–specialization correlations at local spatial scales due to localized species competitive interactions potentially leading to niche partitioning. Surprisingly, our results did not agree with this expectation: richness–specialization relationships varied largely inconsistently in both steepness (in terms of positive standardized effects, Figure 2 and Table S3) and strength (in terms of model R^2, Table S3) across spatial scales. We found the expected increase in effect size with

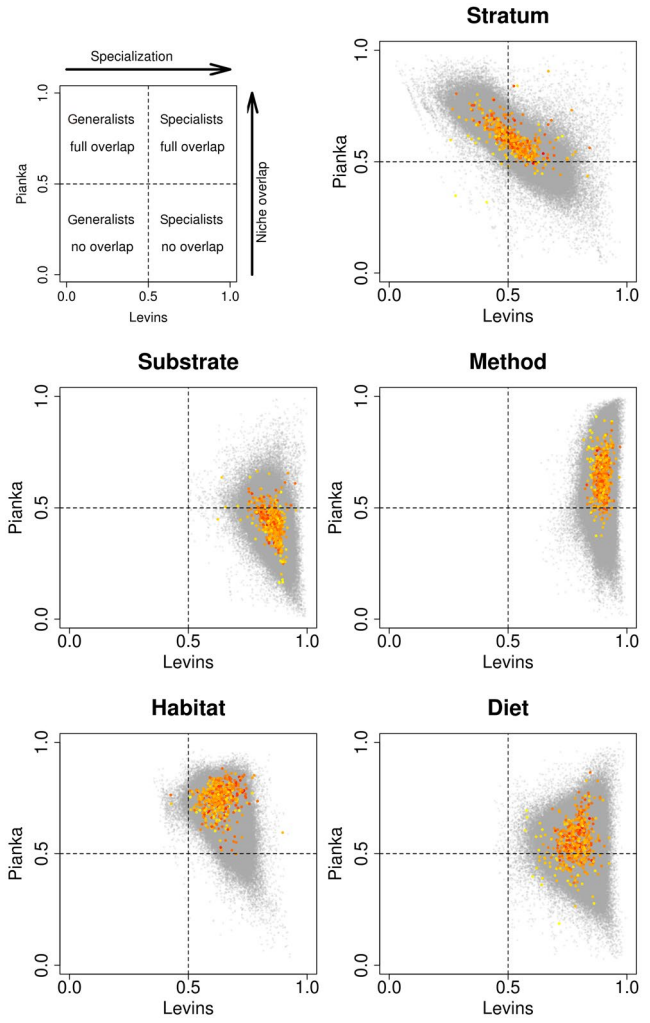

FIGURE 4 Correlations between Levins' specialization index and Pianka's niche overlap index in local communities (i.e. the scale of localities). The conceptual panel (upper left) shows that if most assemblages contained specialized species with low resource use overlap, they would be concentrated in the lower right quadrant of each panel. Grey points are derived from null model expectations, while coloured points are empirical values for real communities. Their colour represents species richness, ranging from five (yellow) to 71 (red)

decreasing spatial scale only in habitat and diet (Figure 2, Table S3). Taken together, these findings hardly support the idea that richness at the small spatial scales of localities is mainly driven by competition and partitioning of resources (species sorting sensu Leibold & Chase, 2018; Evans et al., 2006; Mason et al., 2008; Pellissier et al., 2018). Therefore, current assemblage structures do not seem to be particularly strongly influenced by current ecological processes. Alternatively, they might be more strongly shaped by historical processes (Hawkins, Diniz-Filho, & Soeller, 2005; Remeš & Harmáčková, 2018) that are thought to be more prominent on large spatial scales (Ricklefs, 2006, 2008), for example faster diversification of clades with specialized species (Belmaker et al., 2012).

Second, we expected the richness–specialization relationship to be particularly steep and strong in assemblages exceptionally rich for the environment that they inhabited. This would show that specialization is particularly important in assemblages with high potential for interspecific competition limiting species coexistence. We accounted for two generally important predictors of species richness and correlates of niche space, namely productivity (via moisture availability) and vegetation complexity (e.g. Evans et al., 2006; Hurlbert, 2004; Remeš & Harmáčková, 2018). Moreover, it is worth stressing that our analyses were weighted by species abundance and thus considered not only species' ecological strategy but also its quantitative importance in structuring the assemblage. However, surprisingly, quantile-based analyses did not support our expectations. In contrast, positive richness–specialization relationships were equally common across different quantile cut-offs, that is in assemblages both exceptionally species rich and exceptionally depauperate in species for given environmental conditions. Moreover, in case of specialization and overlap on the scale of localities, the steepness of the richness–specialization/overlap relationship actually seemed to increase towards lower quantiles, that is in assemblages which are depauperate in species for the given environment. These results again support the suggestion that species richness is probably not strongly limited by competitive species interactions and partitioning of resources, not even at local spatial scales. Interestingly, strong positive richness–specialization relationships were often found in assemblages that were depauperate in species given the present environment (at least in some ecological traits). This might be caused by the fact that regional avian diversity in Australia is particularly low in arid, low-productive environments (Remeš & Harmáčková, 2018), which might drive species to specialize on scarce resources in these harsh conditions (Wiens, Kozak, & Silva, 2013

Third, we expected the specialization and niche overlap to be negatively correlated across assemblages, because if the species in an assemblage narrowly specialize on a few resources, minimizing resource use overlap might relax competition (see Figure S1). We found the expected negative relationship only in foraging stratum and substrate, while the rest of the traits showed an unexpected positive relationship (although not so strong; Table S4). The reason for these contrasting results might be that even our detailed trait categories may not still be fine enough to capture actual partitioning of the ecological space. This is apparent especially in habitat and diet, where the categories are quite coarse. For example, several fruit-eating species can coexist in the same place because they differ in the type of fruit they eat, yet in our analyses, they represent competing specialists. Unfortunately, information on such a fine division of diet categories is hard to obtain for most of the species. However, we also used fine categories of foraging behaviour to analyse the division of foraging space, which probably plays a prominent role in niche partitioning (Jablonski & Lee, 1998; Lack, 1971; MacArthur, 1958; Suhonen et al., 1994). In this case, results were closer to what we expected. Our assemblages displayed i) the negative relationship between specialization and overlap in foraging stratum and substrate, and ii) the combination of high specialization with low niche overlap in

foraging substrate (i.e. the assemblages occupied the lower right quadrant, Figure 4). Overall, these results suggest that species partition the ecological space in terms of what part of vegetation substrate they forage on, but not in terms of the foraging method they use for obtaining food.

Relationship between species richness and niche overlap was highly inconsistent across traits. We expected to find a negative correlation between species richness and niche overlap, as species in species-rich assemblages should have divergent niches to facilitate coexistence. However, this was true only for foraging method. This again shows that dividing niche space according to foraging behaviour (see also above) might facilitate species coexistence. On the other hand, we also revealed several positive correlations between species richness and overlap, especially in habitat, diet and foraging substrate. This opposite correlation might be caused by a sampling effect: increasing the number of species in assemblages can lead to higher niche overlap, because there are only a finite number of categories in each ecological trait and thus a limited potential for niche divergence. However, this is probably not the sole explanation, because using the SES values already accounted for the random sampling of species (simulated in our null models). It thus seems that higher than expected overlap in certain ecological traits does not preclude local species coexistence.

On the local scale, results differed for specialization and niche overlap indices computed with or without species' abundances. The most striking difference was in case of the specialization in foraging method, which showed significantly negative correlation with species richness, yet it changed to positive after accounting for the number of individuals. Similarly, in case of habitat, the relationship changed from significantly negative to positive. We included both ways of computing niche overlap indices for the consistency of the analyses carried on various spatial scales as it was not possible to obtain species' abundances for spatial scales of grid cells and bioregions. However, the inclusion of abundances is critical when analysing the composition and evolution of assemblages (Tokeshi & Schmid, 2002). For example, assemblages with the identical number and identity of species might differ in their abundances, which could shift both inter- and intraspecific relationships, the overall biomass of assemblages and their relation to environment. The analyses carried on local scales that took into account abundances should thus better reflect the actual interspecific interactions and niche partitioning that potentially take place in local assemblages.

Finally, we conceived our analyses with species richness as a dependent variable and the specialization and niche overlap as explanatory variables. However, this decision was driven by analytical convenience rather than by our intention to imply one-directional causality. Accordingly, we focused on the pattern and strength in the richness–specialization and richness–overlap relationships. These relationships can be explained by different mechanisms. For example, high specialization of species can lead to tighter packing of species in functional space and thus enable higher richness. However, high specialization of species can also be caused by their need to differentiate niches due to high local/regional species richness that might be, for example, of a historical origin. Similarly, as we point above, specialized clades might generate a large number of species, which might carry over to local assemblages. Thus, more work is needed to get insight into the drivers and causality of the richness–specialization and richness–overlap relationships, including experiments and theoretical modelling.

5 | CONCLUSIONS

Using comprehensive data on habitat, diet and three foraging characteristics of birds, we tested the specialization–richness relationship in Australian songbirds at several spatial scales. We improved on previous studies in four respects, namely by (a) analysing local spatial scales (localities of 2–6 hr area) besides the regional ones, (b) using three characteristics of foraging behaviour besides traditionally studied habitats and diets, (c) adding niche overlap index besides the specialization index to better dissect niche partitioning in local assemblages and iv) using local abundance of species in calculating the specialization and overlap indices. We showed that specialization in Australian songbirds was related to species richness both positively and negatively, depending on the ecological trait under scrutiny, and this was true even after accounting for environmental conditions. The effect of increased niche partitioning towards local spatial scales seemed to be supported at least for habitat and diet. These results do not consistently support the view that interspecific interactions are decisive for species coexistence and richness. On the other hand, species in local communities partitioned ecological space in terms of foraging stratum and substrate, suggesting that coexistence on local scales might actually be facilitated by simultaneous high specialization and low overlap of foraging niches.

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AUTHORS' CONTRIBUTIONS

L.H. and V.R. designed the study; E.R. and L.H. collected the data; L.H. performed data analyses with input from V.R.; and L.H. wrote the manuscript with the contribution of V.R. All authors were acquainted with the final version of the manuscript and gave approval for the publication.

DATA AVAILABILITY STATEMENT

Specialization data used in this study are archived in the Dryad Digital Repository: https://doi.org/10.5061/dryad.79v0d8r (Harmáčková, Remešová, & Remeš, 2019).

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