Interacting disturbances reshape bird assemblages via divergent community trajectories across southeastern Australia

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Abstract

Species counts can remain stable even as ecological communities collapse. This paradox exposes a critical blind spot in biodiversity monitoring: richness metrics miss the compositional upheaval that defines modern ecological change. As human pressures intensify, specialists decline and generalists proliferate, creating numerically similar but functionally different communities. Using three decades of citizen-science data on 272 bird species across southeastern Australia's fragmented eucalypt woodlands, we analysed how woodland conversion, livestock grazing, and dominance by the native noisy miner (*Manorina melanocephala*) reshape species richness and β-diversity. By partitioning β-diversity into turnover and nestedness, we distinguished distinct community change processes. Land conversion and noisy miner presence reduced species turnover whilst increasing nestedness, indicating directional filtering and systematic loss. Lightly grazed woodlands showed the opposite, with higher turnover and lower nestedness, indicating resilience through species replacement. When disturbances co-occurred, communities followed novel trajectories as tolerant and introduced species assembled into unique configurations, boosting turnover at broader scales. Species-level analyses revealed that widespread generalists drove homogenisation while rare, range-restricted species generated local distinctiveness. Critically, high β-diversity was not always ecologically valuable, as some unique sites harboured disturbance-adapted taxa. Consequently, community responses to disturbance followed no single rule. Depending on the combination of stressors, communities underwent filtering, replacement, or novel divergence. Conservation strategies must therefore go beyond simple species counts and aggregate indices. Understanding whether ecosystems are degrading, restorable, or shifting toward alternative stable states requires metrics that capture these underlying processes. In an era of inevitable ecological transformation, the challenge is not only to halt biodiversity loss but to manage the nature of ecological change.

Introduction

Human activity is reshaping Earth's disturbance regimes (Newbold et al. 2015, Turner and Seidl 2023). Events once rare or cyclical now occur more frequently, with greater severity, and at scales unmatched in evolutionary history (e.g., Schwalm et al. 2017, Cunningham et al. 2024). Land clearing, infrastructure development, and biotic invasions further introduce novel pressures, often with no ecological precedent (Turner 2010, Johnstone et al. 2016). Today, over 70% of the land surface is modified by humans, with remaining wilderness bearing signs of extensive environmental degradation (Kerr et al. 2025). As these disturbances increasingly co-occur, the threats to biodiversity amplify. Consequently, red lists grow longer each year as more taxa edge toward extinction. This is now widely known as the biodiversity crisis (Butchart et al. 2010, Johnson et al. 2017).

This crisis manifests inconsistently at local scales (McGill et al. 2015). Many long-term studies report stable or increasing species richness at local sites when facing the same threats (Vellend et al. 2013, Dornelas et al. 2014). This paradox reveals a conceptual blind spot: species numbers may stay constant even as identities shift (Hillebrand et al. 2018). In disturbed landscapes, invaders and disturbance-tolerant taxa often replace specialists, generating communities that are compositionally novel, though not numerically depauperate (Hillebrand et al. 2018, McGeoch et al. 2024). This limitation of alpha diversity points to the power of beta diversity (β-diversity).

β-diversity measures compositional variation among communities (Tuomisto and Ruokolainen 2006, Legendre and De Cáceres 2013). Partitioning β-diversity into nestedness and species replacement (turnover) components distinguishes between disassembly and reassembly: whether sites lose species hierarchically or replace them altogether (Baselga 2010, 2012). Different disturbances produce distinct signatures that reflect underlying mechanisms. For instance, deforestation can cause increases in turnover, accounting for 70–90% of total β-diversity, as environmental filtering drives reassembly (Arroyo-Rodríguez et al. 2013). Hypercompetitive invasive species create the opposite pattern, generating nested subsets via the systematic exclusion of specialist species. Argentine ants, for example, triggered rapid disassembly in California within one year (Sanders et al. 2003). Applying this framework can disentangle whether pressures operate through species sorting or exclusion (Si et al. 2015, Morante-Filho et al. 2016)—critical insights for landscapes facing multiple, interacting threats.

Woodland birds in southeastern Australia serve as indicator taxa for how multiple threats reshape communities. Four decades of monitoring have documented severe declines in woodland bird populations, particularly among woodland and forest specialists (Prowse et. al. 2021). These changes are mainly driven by habitat loss and fragmentation. Once-contiguous pristine habitat has been reduced to remnants from over a century of agricultural expansion, grazing, and infrastructure development. The fragmented remnants, often bordered by cleared farmland, face further cascading disturbance interactions. Grazing and clearing reduce understorey complexity, creating simplified habitats (Val et al. 2018). Such landscapes can turn native species into ecological antagonists: the noisy miner (*Manorina melanocephala*), for instance, thrives in open, disturbed woodlands, aggressively excluding smaller birds (Westgate et al. 2021). Above critical densities of 0.6 individuals per hectare (a threshold typically exceeded in fragmented landscapes), they function as reverse keystone species, excluding smaller insectivores through sustained territorial aggression (Maron et al. 2013, Crates et al. 2023). The result is a feedback loop: habitat degrades, aggressive species expand, and losses intensify.

Land conversion, grazing, and noisy miner dominance co-occur across these landscapes, yet their combined influence on community reassembly remains unclear. While local population trends are well documented, we still lack a regional view of how woodland bird assemblages are being reorganised by multiple, interacting disturbances across southeastern Australia. Communities may be shifting through nested species loss, as woodland specialists disappear systematically, or through compositional turnover, as open-country generalists colonise simplified habitats. Previous landscape analyses using β-diversity have described spatial patterns across woodland mosaics (Neilan et al. 2019), but few have partitioned β-diversity into turnover and nestedness, or linked these components to interacting disturbances. Disentangling these patterns would reveal whether communities are collapsing through loss, restructuring under pressure, or diverging along novel, disturbance-driven trajectories.

Here, we model how woodland conversion, grazing, and noisy miner density shape species richness and β-diversity across southeastern Australia's temperate woodlands. We draw on large-scale citizen-science data collected across three decades, covering 272 terrestrial bird species, yielding a dataset of unprecedented scope and resolution. We quantify local diversity patterns and partition regional β-diversity into turnover and nestedness components. By linking these metrics back to individual sites through local contributions to β-diversity (LCBD), we identify where compositional change is most pronounced and which landscapes

are driving regional reorganisation. We also calculate species contributions to β-diversity (SCBD) to uncover the taxa that are structuring community distinctiveness. This approach reveals where communities are collapsing through systematic loss, where they are converging under generalist dominance, and where novel assemblages are emerging from interacting disturbances. Beyond distinguishing ecosystems that warrant protection from those locked into ecological decline, our findings show how β-diversity partitioning can guide conservation by exposing the mechanisms of community reassembly under multiple pressures. These insights are critical for adaptive management in landscapes where species counts alone fail to capture the scale and complexity of biodiversity change.

Methods

Study region and species selection

We analysed land-bird assemblages across southeastern Australia (Figure 1), from Queensland to Tasmania, an ecologically diverse region once dominated by temperate eucalypt woodlands, now heavily fragmented by agriculture and plantation forestry (Yates and Hobbs 1997). We included 272 native, non-migratory land-bird species regularly recorded in both intact and modified habitats (see full species list in Table S1), encompassing both woodland specialists and habitat generalists.

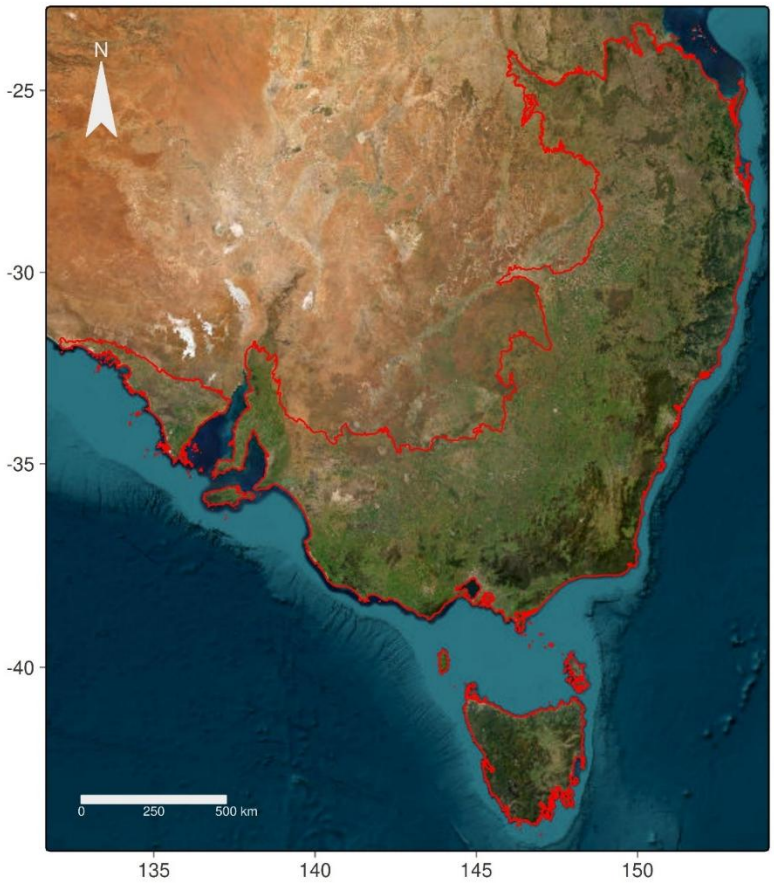


Figure 1. Map showing the study region across southeastern Australia. The red boundary delineates the boundary covering temperate eucalypt woodlands from Queensland to Tasmania. Hexagons (not shown) were distributed across this extent to analyse bird community responses to landscape modification.

We deliberately retained generalist species rather than restricting analyses to woodland specialists alone. This inclusive approach was essential for three reasons. First, environmental filtering operates through both species loss and gain; excluding generalists would obscure how open-country species colonise simplified habitats (Lindenmayer 2022). Second, generalists often drive β-diversity patterns in disturbed systems, becoming locally important even when rare in intact woodlands. Third, excluding them would underestimate the scale of compositional reorganisation as traditional woodland communities shift toward assemblages dominated by disturbance-tolerant taxa (Filgueiras et al. 2021).

Data collection and spatial framework

Occurrence data were sourced from the Atlas of Living Australia using the `galah` package in R (Westgate et al. 2025). We retained records from 1990–2024 with valid dates and accepted species names. Only in situ detections (visual, audio, or camera-trap) were included; museum

specimens and other vouchered records were excluded. Spatial outliers and likely misidentifications were removed through automated and manual screening, yielding over 38 million curated records. Raw occurrences were gridded into 1 km cells to reduce geolocation error.

To assess diversity at the landscape scale, we generated hexagonal grids with 2.5 km cell diameters across the study extent using the `sf` package in R (Pebesma 2018). We chose hexagons as they minimise edge effects and provide equidistant centroid spacing. Each record was assigned to the nearest hexagon centroid by Euclidean distance. The 2.5 km grain size balances the need to capture landscape-scale fragmentation patterns while avoiding aggregation that would obscure patch configuration (Wang et al. 2014). Studies in comparable systems have identified 2.5 km as the optimal scale for detecting biodiversity responses to fragmentation (Steffan-Dewenter et al. 2002): smaller grains miss landscape processes, while larger ones homogenise critical spatial variation (Wang et al. 2014). Although multi-scale analyses would be ideal, the spatial and temporal patchiness of citizen-science data precluded consistent nested sampling. Standardising on a single, ecologically meaningful grain size ensured sampling completeness while maintaining spatial independence among analysis units.

Reducing noise from incomplete samples

Unstructured citizen-science data often include incomplete samples, leading to biases that distort β-diversity patterns (Callaghan et al. 2018). To reduce this bias, we used the Chao2 estimator to approximate asymptotic species richness in each hexagon. Chao2 infers undetected species based on the frequency of rare observations, making it suitable for datasets with uneven sampling effort (Chao et al. 2009). While bootstrap intervals can be estimated using the `iNext` package (Hsieh et al. 2016), we used point estimates without resampling to preserve computational efficiency at scale.

Species detection frequency was defined as the number of unique month–year combinations in that a species was recorded. Let S_h denote the observed richness in hexagon h and let Q_1 and Q_2 represent the number of species observed in exactly one or two sampling unit(s), respectively. Chao 2 asymptotic richness $\hat{S}_h$ was computed as:

177 $$\hat{S}_h = \begin{cases} S_h + \frac{Q_1^2}{2Q_2}, & if\ Q_2 > 0 \\ S_h + \frac{Q_1(Q_1 - 1)}{2(Q_2 + 1)}, & if\ Q_2 = 0 \end{cases}$$

178 Sample completeness was then calculated as the proportion of observed to estimated richness:

179 $$C_h = \frac{S_h}{\hat{S}_h}.$$

180 We retained hexagons that met all of the following criteria: ≥80% completeness, ≥6 months
181 of sampling, and ≥10 recorded species. The 80% completeness threshold preserves spatial
182 coverage while limiting noise from under-sampled sites, thereby improving the reliability of
183 β-diversity estimates (Prenda et al. 2024). The 6-month minimum captures sufficient
184 temporal coverage to account for seasonal variation in bird activity and detectability across
185 Australia's distinct wet and dry seasons. This threshold avoids biases from short-term
186 sampling that miss key phenological events (Callaghan et al. 2019). The 10-species minimum
187 excludes sites with poor sampling or extremely low richness, which contribute little to β-
188 diversity analyses and inflate variance in richness estimates (Duflot and Vähätalo 2024).

189

190 **Landscape Predictor**

191 We derived spatial predictors from national vegetation and land-use datasets. Vegetation data
192 were obtained from the National Vegetation Information System (NVIS v7.0 [2024], 30 m;
193 www.dcceew.gov.au), and land-use data from Catchment Scale Land Use Mapping (CLUM
194 v2 [2024], 50 m; www.agriculture.gov.au). Both rasters were aggregated to a 250 m
195 resolution using the modal value within each block and aligned spatially by snapping to the
196 study extent.

197 To avoid overfitting due to overly granular classification, we reclassified vegetation into three
198 structural categories based on NVIS Major Vegetation Groups: (1) closed woodland
199 (including eucalypt tall open forests, open forests, low open forests, and eucalypt woodlands
200 with crown cover 30–80%); (2) open woodland (eucalypt woodlands with crown cover 10–
201 30%); and (3) non-habitat (grasslands, shrublands, and non-eucalypt vegetation). This
202 classification captures a key structural gradient from dense to sparse woody vegetation that
203 influences woodland bird assemblages. Using the `landscapemetrics` package in R
204 (Hesselbarth et al. 2019), we calculated five structural metrics for both closed and open

woodland: percent cover, patch number, mean patch area, aggregation index, and edge density. These represent total habitat amount, degree of fragmentation, fragment size, spatial clustering, and habitat–matrix interface complexity. All metrics were derived from the reclassified NVIS vegetation data at 250 m resolution.

Landscape metrics showed substantial collinearity, with several pairwise correlations exceeding 0.7 (Figure S1, S2). To reduce redundancy, we applied principal components analysis (PCA) to standardised woodland metrics. The first two axes explained 83.4% of variance (Table S2). Open woodland metrics were excluded due to missing values after completeness filtering. Land use was classified as converted (intensive agriculture or plantation forestry, excluding urban infrastructure), grazed native vegetation, or minimal use. We computed the percentage of each land-use type per hexagon using `landscapemetrics`.

Noisy miner (*Manorina melanocephala*) activity was estimated from ALA records accessed via `galah` (Westgate et al. 2025). A visit was defined as a unique combination of hexagon, date, and sampling protocol. Visitation rate was calculated as the proportion of visits with noisy miner detections, restricted to hexagons with at least one detection and five or more visits. Hexagons with no detections were coded as missing to avoid treating unsurveyed or unsuitable areas as true absences. This metric was then standardised prior to modelling. All retained predictors had Pearson correlations < 0.7 and acceptable variance inflation factors (VIF < 5) (Table S3).

Local contributions to β-diversity and its components

We constructed presence–absence matrices for each hexagon and calculated pairwise Jaccard dissimilarity to quantify compositional differences between sites (Legendre and De Cáceres 2013). For any pair of hexagons h_i and h_j, where a is the number of shared species, b is the number of species unique to h_i, and c is the number of species unique to h_j, total β-diversity (β_{tot}) was computed as:

$$\beta_{tot} = \frac{b+c}{a+b+c}$$

To distinguish between different mechanisms of community change, we partitioned total β-diversity into two components following the Podani framework:

$$\beta_{repl} = \frac{2\min(b,c)}{a+b+c} \qquad \beta_{rich} = \frac{|b-c|}{a+b+c}$$

Here, β_{repl} captures species replacement (turnover) and β_{rich} reflects difference in species richness (nestedness).

We computed LCBD from each distance matrix (β_{tot}, β_{repl}, β_{rich}) following Legendre and De Cáceres (2013). With squared dissimilarity matrix D^2, the centred matrix G was:

$$G = -\frac{1}{2} H D^2 H,$$

where $\mathrm{H} = \mathrm{I} - \frac{1}{n}11^T$ is the centring matrix, and G_{ii} denotes the sum of squares associated with site i. LCBD for hexagon i was then:

$$\mathrm{LCBD}_i = \frac{G_{ii}}{\sum_{k=1}^{n} G_{kk}}$$

Statistical Analysis

We modelled α- and β-diversity responses using generalised additive models (GAMs) via the `mgcv` package in R (Wood and Wood 2015). All predictors were included as fixed effects to estimate and interpret their partial contributions. To account for spatial structure and variation in sampling effort, two smooth terms were added: (1) a Gaussian-process spline over hexagon centroids (longitude, latitude) to control for spatial autocorrelation, and (2) a smooth spline over sampling units to account for heterogeneity in sampling effort across space. These terms improve model reliability by absorbing background spatial and sampling-related variation. Because smooth terms are held constant when estimating fixed-effect coefficients, predictor effects are interpreted independently of spatial and sampling noise. We excluded noisy miner from α- and β-diversity calculations to avoid circularity, as its visitation rate was included as a predictor.

Species richness was modelled using a negative binomial distribution to account for overdispersion. LCBD for total, turnover, and nestedness components were modelled using beta regression with logit link functions. LCBD values were transformed using the Smithson and Verkuilen (2006) method to constrain them to the (0,1) interval, satisfying distributional assumptions. Initial exploratory analyses showed no interactions between woodland structure (PC axes) and land-use variables. However, we retained a three-way interaction among

converted land, grazing, and noisy miner visitation to test for compound disturbance effects. Model diagnostics included checks for overdispersion, residual uniformity, and spatial autocorrelation using Moran's I. All final models showed adequately controlled residual spatial structure.

Species contributions to β-diversity

We estimated each species' influence on regional compositional heterogeneity using species contribution to β-diversity (SCBD) (Legendre and De Cáceres 2013). SCBD quantifies the proportion of total β-diversity attributable to each species, based on the variance it creates in community composition. To compute SCBD, we applied a Hellinger transformation (square root of species relative frequencies) to the presence–absence community matrix and used the `beta.div` function from the R package `adespatial` (Dray et al. 2018):

$$\mathrm{SCBD}_j = \frac{\sum_i \left(y_{ij}^{\mathrm{Hel}} - y_j^{-\mathrm{Hel}}\right)^2}{\sum_k \sum_i \left(y_{ik}^{\mathrm{Hel}} - y_k^{-Hel}\right)^2},$$

where y_{ij}^{Hel} is the Hellinger-transformed presence of species *j* in site *i*, and the denominator represents total community variance. Species with high SCBD values contribute strongly to regional β-diversity. Because we used binary (presence–absence) data, SCBD captures compositional leverage rather than abundance.

To further identify the compositional contexts that the species occupied, we calculated ΔLCBD: the mean difference in local contribution to β-diversity (LCBD) between sites where a species was present versus absent. This was done separately for total LCBD, turnover, and nestedness:

$$\Delta_i = \ mean\ LCBD \mid species\ i\ present - mean\ LCBD \mid species\ i\ absent$$

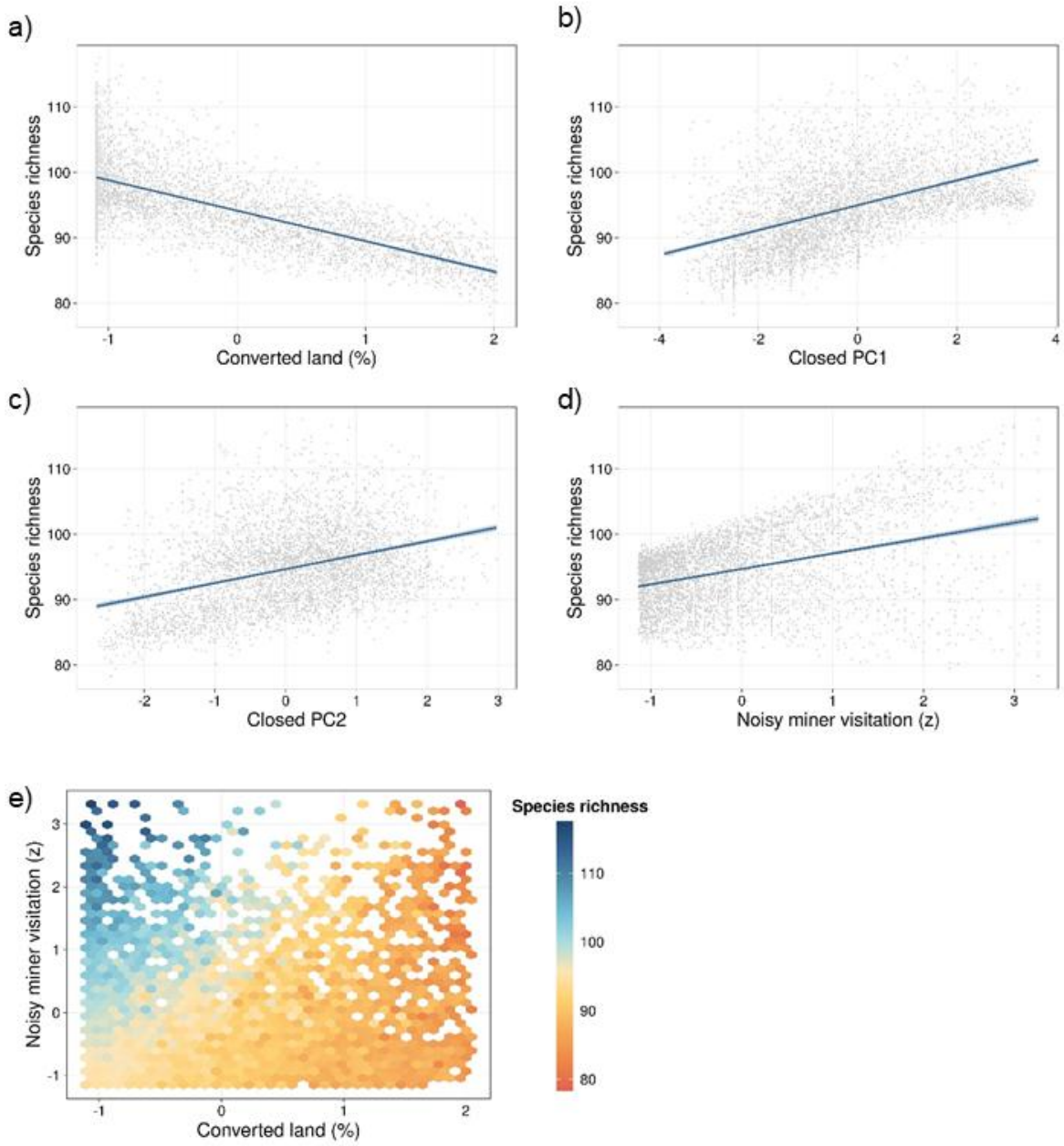
Positive ΔLCBD values indicate that a species increases a site's contribution to β-diversity. For turnover, this reflects species involved in novel assemblages. For nestedness, it indicates presence in compositionally reduced communities. Negative values suggest association with compositionally typical or homogenised sites. Together, SCBD and ΔLCBD identify species that shape regional heterogeneity versus those that track biotic homogenisation.

Results

Response of α-diversity to disturbance

Species richness responded strongly to landscape modification (deviance explained = 72.4%). Richness declined with increasing land conversion (estimate = –0.036, SE = 0.006; Figure 2a), but increased with woodland structure. Both principal component axes were positively associated with richness: PC1, reflecting woodland extent and cohesion (estimate = 0.014, SE = 0.002), and PC2, representing reduced fragmentation (estimate = 0.017, SE = 0.003) (Figure 2b, 2c; Table S4).

Sites with frequent noisy miner activity had higher richness (estimate = 0.030, SE = 0.004), though this effect was context dependent. In heavily converted landscapes, miner presence no longer aligned with increased richness. The negative interaction term (conversion × miner; estimate = –0.016, SE = 0.004) indicated that these gains eroded under intensive modification (Figure 2). Grazing within native vegetation had no detectable effect on species richness (Figure S4).



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306 **Figure 2.** Predicted effects of landscape modification and woodland structure on land bird
307 species richness across southeastern Australia. Plots show partial generalised additive models
308 relationships with 95% confidence bands (grey shading) for: (a) converted land cover, (b)
309 woodland extent and cohesion (PC1), (c) reduced fragmentation (PC2), (d) noisy miner
310 visitation rate, and (e) interaction between conversion and noisy miner visitation rate. Points
311 represent individual hexagon observations; predictions are made with other variables held at
312 their median values. Only significant terms are plotted.

313

Patterns of β-diversity

Highly modified sites increased regional compositional variation (est. = 0.073, SE = 0.014; Figure 3a). Conversely, noisy miner activity reduced local distinctiveness, lowering contributions to β-diversity (est. = –0.062, SE = 0.009; Figure 3). Fragmentation also weakened β-diversity signals, as sites with more fragmented woodlands contributed less to regional variation (est. = –0.057, SE = 0.007; Figure 3c). However, conversion and noisy miner activity interacted positively (estimate = 0.059, SE = 0.009), with co-affected sites more compositionally distinct than expected from either factor alone (Figure 3d). Woodland extent (PC1) and native woodland under grazing showed no effects (Figure S5).

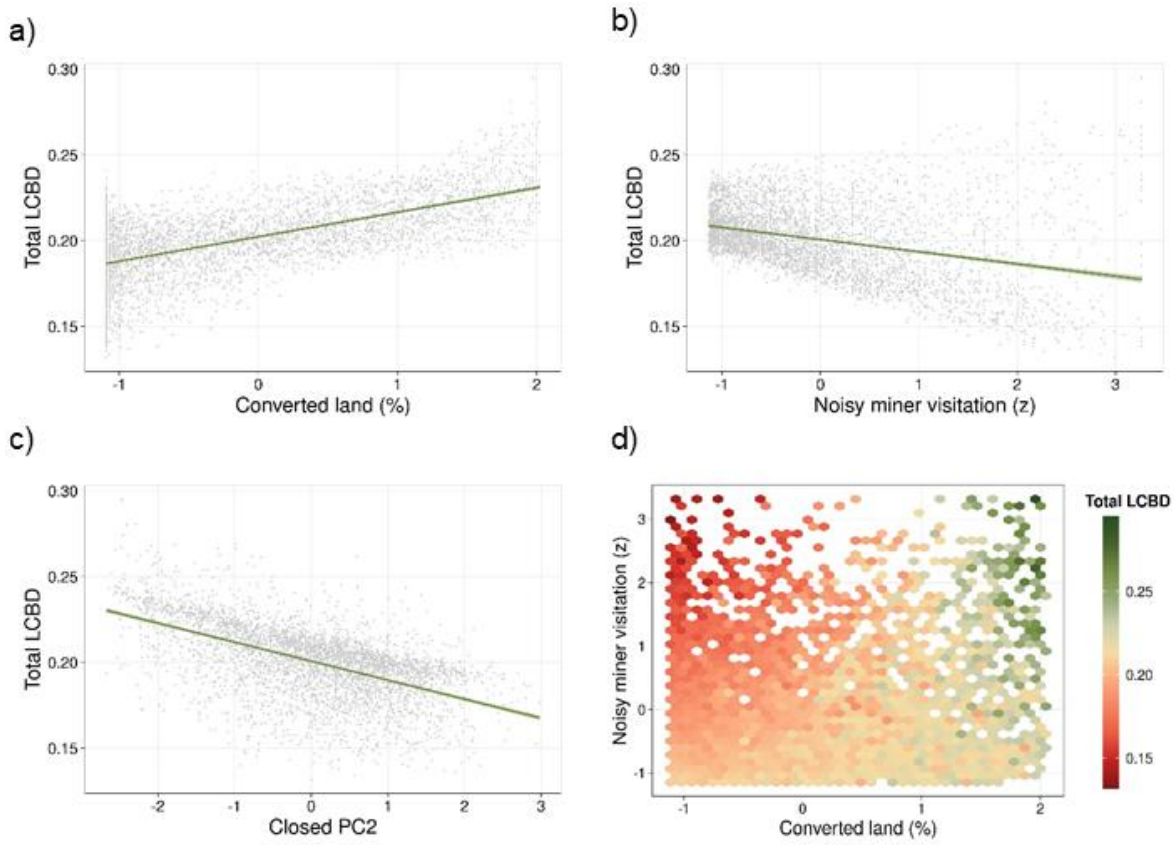
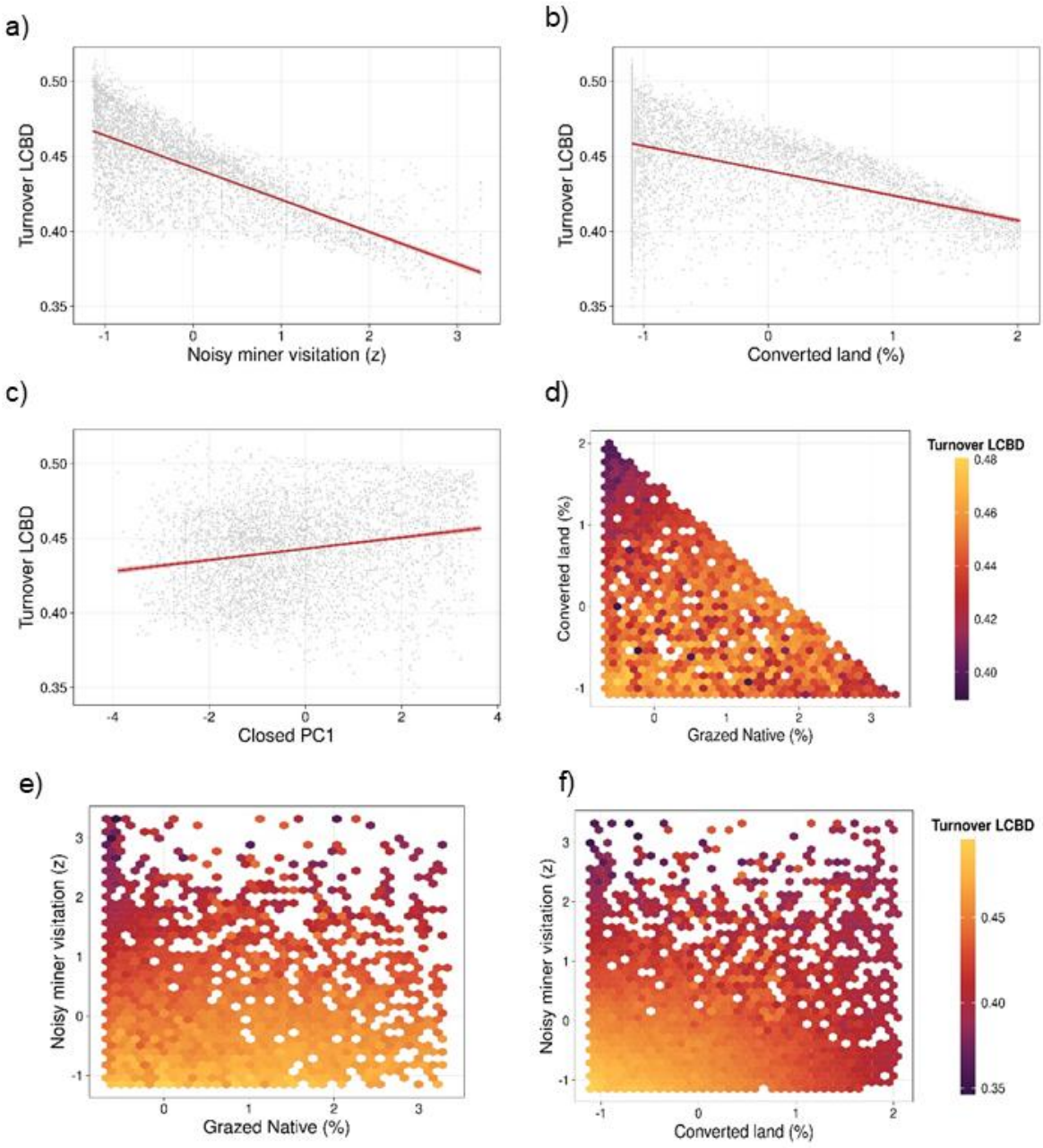


Figure 3. Predicted effects of landscape modification on total local contributions to β-diversity (LCBD) across southeastern Australia. Plots show partial relationships from generalised additive models with 95% confidence bands (grey shading). Effects are shown for: (a) converted land cover, (b) noisy miner visitation rate, (c) reduced fragmentation (PC2), and (d) heatmap showing interaction effects between converted land cover and noisy miner visitation. Points represent individual hexagon observations; predictions are made with other variables held at their mean values. Only significant terms are plotted.

Interactions between land conversion and noisy miner activity reduced site-level contributions to turnover-based β-diversity (conversion: estimate = –0.062, SE = 0.013; miners: estimate = –0.083, SE = 0.009; Figure 4f), indicating homogenisation. Native woodland under grazing amplified turnover when combined with either land conversion (estimate = 0.045, SE = 0.014; Figure 4d) or miner activity (estimate = 0.027, SE = 0.010; Figure 4e). The interaction between conversion and miner activity was also positive (estimate = 0.050, SE = 0.009; Figure 4f). Woodland extent (PC1) had a weak negative association with turnover (estimate = –0.013, SE = 0.005; Figure 4), while fragmentation (PC2) had no detectable influence on turnover (Figure S6).



341

342 **Figure 4.** Predicted effects of landscape modification on turnover local contributions to β-
343 diversity (LCBD) across southeastern Australia. Plots show partial relationships from
344 generalised additive models with 95% confidence bands (grey shading). Effects are shown
345 for: (a) noisy miner visitation rate, (b) converted land cover, (c) reduced fragmentation (PC2),
346 and heatmaps showing interaction effects between (d) converted land cover and grazed native
347 woodland cover, (e) noisy miner visitation rate and grazed native woodland cover, and (f)
348 noisy miner visitation rate and converted land cover. Points represent individual hexagon
349 observations; predictions are made with other variables held at their mean values. Only
350 significant terms are plotted.

Nestedness increased with land conversion (estimate = 0.148, SE = 0.022; Figure 5a) and noisy miner activity (estimate = 0.075, SE = 0.014; Figure 5b), indicating systematic species loss. Conversion within grazed native vegetation lowered nestedness contributions (estimate = –0.056, SE = 0.024), as did miner activity within the same context (estimate = –0.047, SE = 0.018; Figure 5c, 5d). The interaction between conversion and miner activity was negative (estimate = –0.035, SE = 0.015). We found no effects for grazing or woodland PC1 on nestedness (Figure S7).

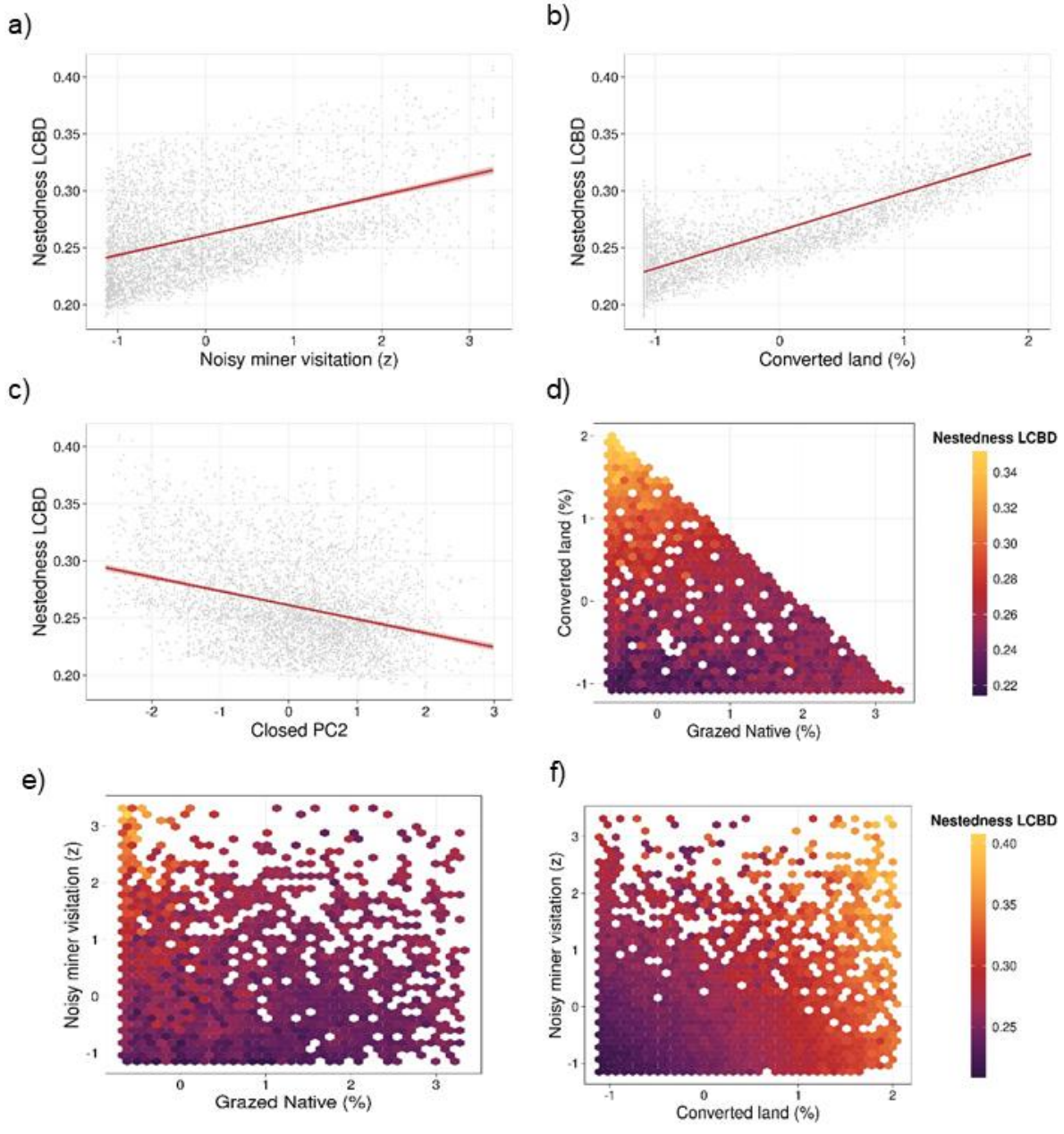


Figure 5. Predicted effects of landscape modification on nestedness local contributions to β-diversity (LCBD) across southeastern Australia. Plots show partial relationships from generalised additive models with 95% confidence bands (grey shading). Effects are shown for: (a) noisy miner visitation rate, (b) converted land cover, (c) reduced fragmentation (PC2), and heatmaps showing interaction effects between (d) converted land cover and grazed native woodland cover, (e) noisy miner visitation rate and grazed native woodland cover, and (f) noisy miner visitation rate and converted land cover. Points represent individual hexagon observations; predictions are made with other variables held at their mean values. Only significant terms are plotted.

Species-level Responses

Open-country generalists such as *Platycercus elegans*, *Anthochaera carunculata*, and *Acanthiza lineata* exhibited strongly negative ΔLCBD values (Figure 6a). Tasmanian endemics, including *Pardalotus quadragintus*, *Acanthornis magna*, and *Melithreptus validirostris* produced positive ΔLCBD values (Figure 6b). Woodland specialists with broader, but still constrained, distributions (e.g. *Glossopsitta concinna*) showed more moderate ΔLCBD values.

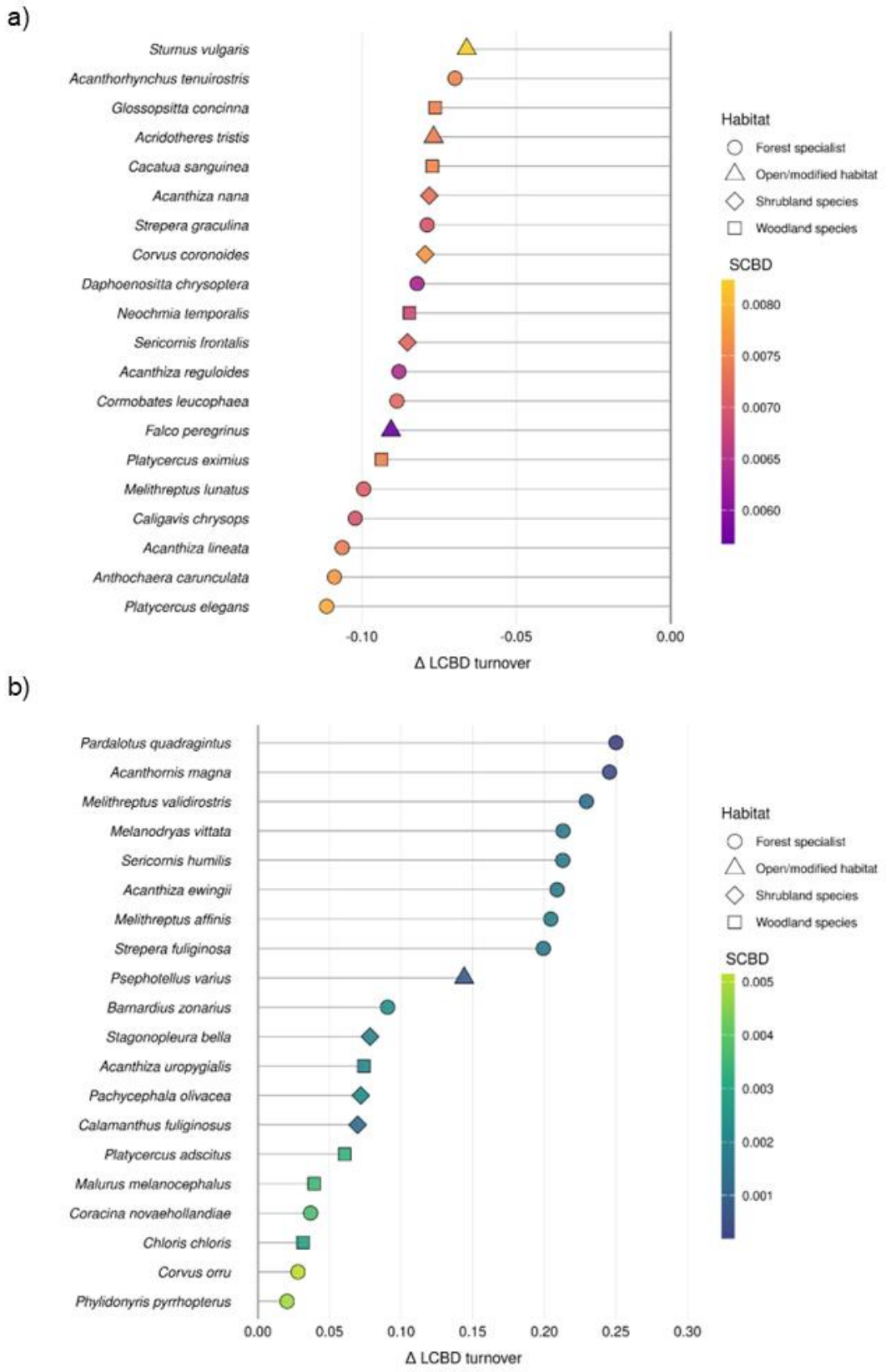


Figure 6. Species-level contributions to turnover-based β-diversity. Panel (a) shows species most associated with homogenised assemblages (negative ΔLCBD), while panel (b) shows species associated with high compositional distinctiveness (positive ΔLCBD). Points show

the mean difference in local contribution to β-diversity (ΔLCBD) between sites where a species was present versus absent. Colours indicate species contributions to total β-diversity (SCBD); shapes denote primary habitat affinity. Together, SCBD and ΔLCBD identify taxa that contribute to regional distinctiveness versus those linked to simplified communities. Only species with the top 20 positive and negative ΔLCBD values are shown.

Discussion

Biodiversity loss is often framed as a decline in species richness. Our findings reveal a more complex picture. While richness declined under land conversion, bird communities also reorganised along divergent trajectories, exposed by partitioning β-diversity. Across southeastern Australia's temperate woodlands, some sites lost species through nested filtering, while others shifted toward novel assemblages. Where disturbances overlapped, communities responded in ways distinct from the effects of single pressures. These patterns show that ecological change is not just erosion: it is reassembly, shaped by the type and combination of stressors. Similar shifts have been reported globally, from generalist filtering in European farmland (Santana et al. 2017) to rising nestedness in fragmented tropical forests (Morante-Filho et al. 2016). Disturbance does not simply reduce diversity, it reshapes it (Mori et al. 2018).

Both land conversion and noisy miner dominance reduced turnover and increased nestedness, indicating a shift from dynamic species replacement to ordered species filtering through systematic species loss. As human pressures intensify, β-diversity transitions from variation driven by environmental sorting to nested disassembly driven through exclusion (Legendre and De Cáceres 2013, Si et al. 2015). This shift appears linked to the selective loss of woodland specialists; species that are more sensitive to structural simplification and miner aggression (Maron et al. 2013). These communities are not enriched by new arrivals but hollowed by repeated loss: a structural convergence that mimics stability but eroding distinctiveness. The noisy miner paradox exemplifies this. Though these birds appeared to raise diversity, they homogenised communities by excluding smaller species and promoting generalist-dominated assemblages. Their role as reverse keystone species demonstrates how native taxa can become ecological antagonists in simplified landscapes (Howes et al. 2014).

While livestock grazing reduced understorey cover, grazed woodlands retained enough canopy structure to enable persistence of edge-tolerant woodland birds, altering the dominant pattern of systematic species loss. As a result, nestedness declined and turnover increased, suggesting that species were replaced, not simply lost. This supports earlier findings that low-intensity grazing can sustain avifauna if adequate woodland cover is retained and commercial-scale grazing is excluded (Martin and McIntyre 2007, Dorrough et al. 2012). Unlike intermediate disturbance effects, this outcome reflects minimal structural retention that enables partial persistence, rather than peak diversity.

Where disturbances co-occurred, communities followed unexpected trajectories. Sites with both conversion and miners contributed more to β-diversity than expected, but not through nestedness. Instead, they hosted unique combinations of tolerant and introduced species. Grazing intensified this effect. When combined with conversion or miners, turnover increased further. Even modest retained structure in grazed woodlands appeared sufficient for varied generalists to establish, even as original assemblages disappeared. These findings echo broader evidence that interacting disturbances can trigger unexpected ecological shifts (Buma 2015, Côté et al. 2016), proving that community responses to multiple stressors cannot be predicted from single disturbance effects alone.

Open-country raptors, generalists and introduced species drove community homogenisation across the disturbance gradient. European starling (*Sturnus vulgaris*) and red wattlebird (*Anthochaera carunculata*) were frequent in low-turnover, low-distinctiveness sites. Their broad environmental tolerances enabled establishment under varied disturbance regimes. Though high in SCBD, their presence marked convergence toward simplified, disturbance-adapted assemblages with low LCBD. These findings reinforce how individual disturbances impose directional environmental filtering. These species emerge as ‘winners’ in degraded landscapes, shaping homogenised communities under both land conversion and miner dominance (Devictor et al. 2008).

In contrast, range-restricted species and island endemics were linked to high-turnover sites with narrow distributions. Tasmanian endemics, including the forty-spotted pardalote (*Pardalotus quadragintus*) and scrubtit (*Acanthornis magna*), contributed little to SCBD but drove extreme local distinctiveness (high LCBD) where they persisted. These species delineate ecological boundaries between functional woodland assemblages and simplified

systems, their occurrence signalling habitat patches where conditions remain viable for range-restricted taxa (Sverdrup-Thygeson et al. 2017).

These findings reshape how β-diversity metrics should inform conservation. High LCBD does not always equate to ecological value, as many such sites were dominated by tolerant generalists and behavioural dominants like noisy miners. Though compositionally distinct, these assemblages often reflected degradation. Conversely, sites with modest β-diversity might support rare specialists. Without species-level context, β-diversity can mislead conservation priorities (Landeiro et al. 2018, Rocha et al. 2023). Turnover and nestedness, therefore, do not map cleanly onto value. Turnover may reflect resilience, endemism, or disturbance-driven reassembly. Nestedness can signal loss, but also survival in harsh or species-poor sites. These results challenge simple dichotomies of 'intact' versus 'degraded' by revealing continuous gradients of community structure. Effective conservation must identify where specialists persist, and where systems have crossed ecological thresholds. This needs matching strategy to condition. Such landscapes require adaptive management (Landeiro et al. 2018).

Limitations and methodological considerations

We cannot infer direct mechanisms linking disturbance to community change, as our models are correlational rather than causal. While citizen science data provided broad spatial coverage, they introduced biases toward accessible areas and more visible species. We mitigated this using completeness thresholds (Callaghan et al. 2022) and spatial smoothing, but under-detection of cryptic ground birds likely inflates nestedness in under-sampled interiors. Our Gaussian-process spline absorbed spatial autocorrelation but cannot compensate for unobserved data (Barve et al. 2011): Inference is likely stronger in well-sampled areas. Furthermore, our analysis summarises dynamic processes in a static view. Communities currently showing high turnover may transition toward nestedness as landscapes continue to degrade. Incorporating temporal data would provide a fuller picture of how communities reorganise over space and time (Legendre 2019).

Implications for biodiversity science

Across southeastern Australia, bird communities are not merely declining but restructuring along complex trajectories that become apparent when β-diversity is partitioned into its constituent components. Some undergo systematic filtering; others reassemble around tolerant taxa; a few persist through retained complexity. These patterns demand conservation

strategies that interpret spatial structure cautiously and recognise the ecological context behind it. Though region-specific, our approach may apply across fragmented temperate woodlands globally. As pressures intensify, distinguishing disassembly from functional reassembly becomes vital. Some sites retain restoration potential; others have shifted beyond conventional targets. Recognising these differences is critical for efficient resource allocation. Future research should focus on predicting how landscape features influence β-diversity trajectories and detect tipping points in community structure. Conservation planning must combine compositional metrics with species-level insight to protect not only diversity counts but also the ecological relationships that sustain them. As environmental change accelerates, the challenge is no longer to halt every loss but to steer systems away from tipping points. The real threshold is no longer between pristine and degraded, but between dynamic community reassembly and irreversible functional collapse.

References

Arroyo-Rodríguez, V., M. Rös, F. Escobar, F. P. Melo, B. A. Santos, M. Tabarelli, and R. Chazdon. 2013. Plant β-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. Journal of Ecology **101**:1449-1458.

Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S. P. Maher, A. T. Peterson, J. Soberón, and F. Villalobos. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecological Modelling **222**:1810-1819.

Buma, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere **6**:1-15.

Butchart, S. H., M. Walpole, B. Collen, A. Van Strien, J. P. Scharlemann, R. E. Almond, J. E. Baillie, B. Bomhard, C. Brown, and J. Bruno. 2010. Global biodiversity: indicators of recent declines. Science **328**:1164-1168.

Callaghan, C. T., D. E. Bowler, S. A. Blowes, J. M. Chase, M. B. Lyons, and H. M. Pereira. 2022. Quantifying effort needed to estimate species diversity from citizen science data. Ecosphere **13**:e3966.

Callaghan, C. T., J. M. Martin, R. E. Major, and R. T. Kingsford. 2018. Avian monitoring–comparing structured and unstructured citizen science. Wildlife Research **45**:176-184.

Callaghan, C. T., A. G. Poore, R. E. Major, J. J. Rowley, and W. K. Cornwell. 2019. Optimizing future biodiversity sampling by citizen scientists. Proceedings of the Royal Society B **286**:20191487.

Chao, A., R. K. Colwell, C.-W. Lin, and N. J. Gotelli. 2009. Sufficient sampling for asymptotic minimum species richness estimators. Ecology **90**:1125-1133.

Côté, I. M., E. S. Darling, and C. J. Brown. 2016. Interactions among ecosystem stressors and their importance in conservation. Proceedings of the Royal Society B: Biological Sciences **283**:20152592.

Crates, R., P. G. McDonald, C. B. Melton, M. Maron, D. Ingwersen, E. Mowat, M. Breckenridge, L. Murphy, and R. Heinsohn. 2023. Towards effective management of an overabundant native bird: The noisy miner. Conservation Science and Practice **5**:16.

Cunningham, C. X., G. J. Williamson, and D. M. Bowman. 2024. Increasing frequency and intensity of the most extreme wildfires on Earth. Nature Ecology & Evolution **8**:1420-1425.

Devictor, V., R. Julliard, and F. Jiguet. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos **117**:507-514.

Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. Assemblage time series reveal biodiversity change but not systematic loss. Science **344**:296-299.

Dorrough, J., S. McIntyre, G. Brown, J. Stol, G. Barrett, and A. Brown. 2012. Differential responses of plants, reptiles and birds to grazing management, fertilizer and tree clearing. Austral Ecology **37**:569-582.

Dray, S., G. Blanchet, D. Borcard, G. Guenard, T. Jombart, G. Larocque, P. Legendre, N. Madi, H. H. Wagner, and M. S. Dray. 2018. Package 'adespatial'. R package **2018**:3-8.

Duflot, R., and A. V. Vähätalo. 2024. Identifying sites with high biodiversity value using filtered species records from a biodiversity information facility. Diversity and Distributions **30**:e13864.

Filgueiras, B. K., C. A. Peres, F. P. Melo, I. R. Leal, and M. Tabarelli. 2021. Winner–loser species replacements in human-modified landscapes. Trends in Ecology & Evolution **36**:545-555.

Hesselbarth, M. H., M. Sciaini, K. A. With, K. Wiegand, and J. Nowosad. 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography **42**:1648-1657.

Hillebrand, H., B. Blasius, E. T. Borer, J. M. Chase, J. A. Downing, B. K. Eriksson, C. T. Filstrup, W. S. Harpole, D. Hodapp, and S. Larsen. 2018. Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. Journal of Applied Ecology **55**:169-184.

Howes, A., R. Mac Nally, R. Loyn, J. Kath, M. Bowen, C. McAlpine, and M. Maron. 2014. Foraging guild perturbations and ecological homogenization driven by a despotic native bird species. Ibis **156**:341-354.

Hsieh, T., K. Ma, and A. Chao. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (H ill numbers). Methods in ecology and evolution **7**:1451-1456.

Johnson, C. N., A. Balmford, B. W. Brook, J. C. Buettel, M. Galetti, L. Guangchun, and J. M. Wilmshurst. 2017. Biodiversity losses and conservation responses in the Anthropocene. Science **356**:270-275.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, and G. L. Perry. 2016. Changing disturbance

regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment **14**:369-378.

Kerr, M. R., A. Ordonez, F. Riede, J. Atkinson, E. A. Pearce, M. Sykut, J. Trepel, and J.-C. Svenning. 2025. Widespread ecological novelty across the terrestrial biosphere. Nature Ecology & Evolution:1-10.

Landeiro, V. L., B. Franz, J. Heino, T. Siqueira, and L. M. Bini. 2018. Species-poor and low-lying sites are more ecologically unique in a hyperdiverse Amazon region: Evidence from multiple taxonomic groups. Diversity and Distributions **24**:966-977.

Legendre, P. 2019. A temporal beta-diversity index to identify sites that have changed in exceptional ways in space–time surveys. Ecology and evolution **9**:3500-3514.

Legendre, P., and M. De Cáceres. 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecology letters **16**:951-963.

Lindenmayer, D. 2022. Birds on farms: a review of factors influencing bird occurrence in the temperate woodlands of south-eastern Australia. Emu-Austral Ornithology **122**:238-254.

Lindenmayer, D. B., and R. B. Cunningham. 2011. Longitudinal patterns in bird reporting rates in a threatened ecosystem: Is change regionally consistent? Biological Conservation **144**:430-440.

Maron, M., M. J. Grey, C. P. Catterall, R. E. Major, D. L. Oliver, M. F. Clarke, R. H. Loyn, R. Mac Nally, I. Davidson, and J. R. Thomson. 2013. Avifaunal disarray due to a single despotic species. Diversity and Distributions **19**:1468-1479.

Martin, T. G., and S. McIntyre. 2007. Impacts of livestock grazing and tree clearing on birds of woodland and riparian habitats. Conservation Biology **21**:504-514.

McGeoch, M. A., D. A. Clarke, N. A. Mungi, and A. Ordonez. 2024. A nature-positive future with biological invasions: theory, decision support and research needs. Philosophical Transactions of the Royal Society B **379**:20230014.

McGill, B. J., M. Dornelas, N. J. Gotelli, and A. E. Magurran. 2015. Fifteen forms of biodiversity trend in the Anthropocene. Trends in Ecology & Evolution **30**:104-113.

Morante-Filho, J. C., V. Arroyo-Rodríguez, and D. Faria. 2016. Patterns and predictors of β-diversity in the fragmented Brazilian Atlantic forest: a multiscale analysis of forest specialist and generalist birds. Journal of Animal Ecology **85**:240-250.

Mori, A. S., F. Isbell, and R. Seidl. 2018. β-diversity, community assembly, and ecosystem functioning. Trends in Ecology & Evolution **33**:549-564.

588 Neilan, W. L., P. S. Barton, C. A. McAlpine, J. T. Wood, and D. B. Lindenmayer. 2019.
589 Contrasting effects of mosaic structure on alpha and beta diversity of bird
590 assemblages in a human-modified landscape. Ecography **42**:173-186.
591 Newbold, T., L. N. Hudson, S. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Börger, D. J.
592 Bennett, A. Choimes, and B. Collen. 2015. Global effects of land use on local
593 terrestrial biodiversity. Nature **520**:45-50.
594 Pebesma, E. 2018. Simple features for R: standardized support for spatial vector data.
595 Prenda, J., J. L. Domínguez-Olmedo, E. López-Lozano, R. Fernández de Villarán, and J. J.
596 Negro. 2024. Assessing citizen science data quality for bird monitoring in the Iberian
597 Peninsula. Scientific Reports **14**:20307.
598 Rocha, M. P., T. J. Morris, K. Cottenie, and A. N. Schwalb. 2023. Limitations of beta
599 diversity in conservation site selection. Ecological Indicators **154**:110732.
600 Sanders, N. J., N. J. Gotelli, N. E. Heller, and D. M. Gordon. 2003. Community disassembly
601 by an invasive species. Proceedings of the National Academy of Sciences **100**:2474-
602 2477.
603 Santana, J., M. Porto, L. Reino, F. Moreira, P. F. Ribeiro, J. L. Santos, J. T. Rotenberry, and P.
604 Beja. 2017. Using beta diversity to inform agricultural policies and conservation
605 actions on Mediterranean farmland. Journal of Applied Ecology **54**:1825-1835.
606 Schwalm, C. R., W. R. Anderegg, A. M. Michalak, J. B. Fisher, F. Biondi, G. Koch, M.
607 Litvak, K. Ogle, J. D. Shaw, and A. Wolf. 2017. Global patterns of drought recovery.
608 Nature **548**:202-205.
609 Si, X., A. Baselga, and P. Ding. 2015. Revealing beta-diversity patterns of breeding bird and
610 lizard communities on inundated land-bridge islands by separating the turnover and
611 nestedness components. PLoS ONE **10**:e0127692.
612 Smithson, M., and J. Verkuilen. 2006. A better lemon squeezer? Maximum-likelihood
613 regression with beta-distributed dependent variables. Psychological methods **11**:54.
614 Steffan-Dewenter, I., U. Münzenberg, C. Bürger, C. Thies, and T. Tscharntke. 2002. Scale-
615 dependent effects of landscape context on three pollinator guilds. Ecology **83**:1421-
616 1432.
617 Sverdrup-Thygeson, A., O. Skarpaas, S. Blumentrath, T. Birkemoe, and M. Evju. 2017.
618 Habitat connectivity affects specialist species richness more than generalists in
619 veteran trees. Forest Ecology and Management **403**:96-102.
620 Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology
621 **91**:2833-2849.

622 Turner, M. G., and R. Seidl. 2023. Novel disturbance regimes and ecological responses.
623 Annual Review of Ecology, Evolution, and Systematics **54**:63-83.
624 Val, J., D. J. Eldridge, S. K. Travers, and I. Oliver. 2018. Livestock grazing reinforces the
625 competitive exclusion of small-bodied birds by large aggressive birds. Journal of
626 Applied Ecology **55**:1919-1929.
627 Vellend, M., L. Baeten, I. H. Myers-Smith, S. C. Elmendorf, R. Beauséjour, C. D. Brown, P.
628 De Frenne, K. Verheyen, and S. Wipf. 2013. Global meta-analysis reveals no net
629 change in local-scale plant biodiversity over time. Proceedings of the National
630 Academy of Sciences **110**:19456-19459.
631 Walsh, J. C., M. R. Gibson, J. S. Simmonds, H. J. Mayfield, C. Bracey, C. B. Melton, A. E.
632 Reside, and M. Maron. 2023. Effectiveness of conservation interventions for
633 Australian woodland birds: A systematic review. Biological Conservation **282**.
634 Wang, X., F. G. Blanchet, and N. Koper. 2014. Measuring habitat fragmentation: An
635 evaluation of landscape pattern metrics. Methods in Ecology and Evolution **5**:634-
636 646.
637 Westgate, M. J., M. Crane, D. Florance, and D. B. Lindenmayer. 2021. Synergistic impacts of
638 aggressive species on small birds in a fragmented landscape. Journal of Applied
639 Ecology **58**:825-835.
640 Wood, S., and M. S. Wood. 2015. Package 'mgcv'. R package version **1**:729.
641 Yates, C. J., and R. J. Hobbs. 1997. Temperate eucalypt woodlands: a review of their status,
642 processes threatening their persistence and techniques for restoration. Australian
643 Journal of Botany **45**:949-973.
644 Westgate M, Kellie D, Stevenson M, Newman P (2025). galah: Biodiversity Data from the
645 GBIF Node Network. R package version 2.1.2.

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Supplementary

Table S1. List of the included land bird species across southeast Australia

Family	Genus	Species Name	Vernacular Name
Meliphagidae	Acanthorhynchus	*Acanthorhynchus tenuirostris*	Eastern Spinebill
Meliphagidae	Anthochaera	*Anthochaera phrygia*	Regent Honeyeater
Meliphagidae	Antochaera	*Anthochaera carunculata*	Red Wattlebird
Meliphagidae	Antochaera	*Anthochaera paradoxa*	Yellow Wattlebird
Meliphagidae	Antochaera	*Anthochaera chrysoptera*	Little Wattlebird
Meliphagidae	Caligavis	*Caligavis chrysops*	Yellow-faced Honeyeater
Meliphagidae	Entomyzon	*Entomyzon cyanotis*	Blue-faced Honeyeater
Meliphagidae	Epithianura	*Epthianura albifrons*	White-fronted Chat
Meliphagidae	Gavicalis	*Gavicalis fasciogularis*	Mangrove Honeyeater
Meliphagidae	Gliciphila	*Gliciphila melanops*	Tawny-crowned Honeyeater
Meliphagidae	Grantiella	*Grantiella picta*	Painted Honeyeater
Meliphagidae	Lichenostomus	*Lichenostomus melanops*	Yellow-tufted Honeyeater
Meliphagidae	Lichmera	*Lichmera indistincta*	Brown Honeyeater
Meliphagidae	Manorina	*Manorina melanophrys*	Bell Miner
Meliphagidae	Manorina	*Manorina melanocephala*	Noisy Miner
Meliphagidae	Meliphaga	*Meliphaga lewinii*	Lewin's Honeyeater
Meliphagidae	Melithreptus	*Melithreptus gularis*	Black-chinned Honeyeater
Meliphagidae	Melithreptus	*Melithreptus validirostris*	Strong-billed Honeyeater
Meliphagidae	Melithreptus	*Melithreptus brevirostris*	Brown-headed Honeyeater
Meliphagidae	Melithreptus	*Melithreptus albogularis*	White-throated Honeyeater
Meliphagidae	Melithreptus	*Melithreptus lunatus*	White-naped Honeyeater
Meliphagidae	Melithreptus	*Melithreptus affinis*	Black-headed Honeyeater
Meliphagidae	Myzomela	*Myzomela sanguinolenta*	Scarlet Honeyeater
Meliphagidae	Nesoptilotis	*Nesoptilotis leucotis*	White-eared Honeyeater
Meliphagidae	Nesoptilotis	*Nesoptilotis flavicollis*	Yellow-throated Honeyeater
Meliphagidae	Philemon	*Philemon corniculatus*	Noisy Friarbird
Meliphagidae	Philemon	*Philemon citreogularis*	Little Friarbird
Meliphagidae	Phylidonyris	*Phylidonyris pyrrhopterus*	Crescent Honeyeater
Meliphagidae	Phylidonyris	*Phylidonyris novaehollandiae*	New-Holland Honeyeater
Meliphagidae	Phylidonyris	*Phylidonyris niger*	White-cheeked Honeyeater
Meliphagidae	Plectorhyncha	*Plectorhyncha lanceolata*	Striped Honeyeater
Meliphagidae	Ptilotula	*Ptilotula fusca*	Fuscous Honeyeater
Meliphagidae	Ptilotula	*Ptilotula penicillata*	White-plumed Honeyeater
Pardalotidae	Pardalotus	*Pardalotus punctatus*	Spotted Pardalote
Pardalotidae	Pardalotus	*Pardalotus quadragintus*	Forty-spotted Pardalote
Pardalotidae	Pardalotus	*Pardalotus striatus*	Striated Pardalote
Pardalotidae	Dasyornis	*Dasyornis brachypterus*	Eastern Bristlebird

Pardalotidae	Dasyornis	*Dasyornis broadbenti*	Rufous Bristlebird
Pardalotidae	Pycnoptilus	*Pycnoptilus floccosus*	Pilotbird
Pardalotidae	Origma	*Origma solitaria*	Rockwarbler
Pardalotidae	Neosericornis	*Neosericornis citreogularis*	Yellow-throated Scrubwren
Pardalotidae	Sericornis	*Sericornis frontalis*	White-browed Scrubwren
Pardalotidae	Sericornis	*Sericornis humilis*	Tasmanian Scrubwren
Pardalotidae	Sericornis	*Sericornis magnirostra*	Large-billed Scrubwren
Pardalotidae	Acanthornis	*Acanthornis magna*	Scrubtit
Pardalotidae	Hylacola	*Hylacola pyrrhopygia*	Chestnut-rumped Heathwren
Pardalotidae	Hylacola	*Hylacola cauta*	Shy Heathwren
Pardalotidae	Calamanthus	*Calamanthus fuliginosus*	Striated Fieldwren
Pardalotidae	Calamanthus	*Calamanthus campestris*	Rufous Fieldwren
Pardalotidae	Pyrrholaemus	*Pyrrholaemus brunneus*	Redthroat
Pardalotidae	Pyrrholaemus	*Pyrrholaemus sagittatus*	Speckled Warbler
Pardalotidae	Smicrornis	*Smicrornis brevirostris*	Weebill
Pardalotidae	Gerygone	*Gerygone mouki*	Brown Gerygone
Pardalotidae	Gerygone	*Gerygone levigaster*	Mangrove Gerygone
Pardalotidae	Gerygone	*Gerygone fusca*	Western Gerygone
Pardalotidae	Gerygone	*Gerygone palpebrosa*	Fairy Gerygone
Pardalotidae	Gerygone	*Gerygone olivacea*	White-throated Gerygone
Pardalotidae	Acanthiza	*Acanthiza pusilla*	Brown Thornbill
Pardalotidae	Acanthiza	*Acanthiza apicalis*	Inland Thornbill
Pardalotidae	Acanthiza	*Acanthiza ewingii*	Tasmanian Thornbill
Pardalotidae	Acanthiza	*Acanthiza uropygialis*	Chestnut-rumped Thornbill
Pardalotidae	Acanthiza	*Acanthiza reguloides*	Buff-rumped Thornbill
Pardalotidae	Acanthiza	*Acanthiza iredalei*	Slender-billed Thornbill
Pardalotidae	Acanthiza	*Acanthiza chrysorrhoa*	Yellow-rumped Thornbill
Pardalotidae	Acanthiza	*Acanthiza nana*	Yellow Thornbill
Pardalotidae	Acanthiza	*Acanthiza lineata*	Striated Thornbill
Pardalotidae	Aphelocephala	*Aphelocephala leucopsis*	Southern Whiteface
Petroicidae	Microeca	*Microeca fascinans*	Jacky Winter
Petroicidae	Petroica	*Petroica boodang*	Scarlet Robin
Petroicidae	Petroica	*Petroica goodenovii*	Red-capped Robin
Petroicidae	Petroica	*Petroica phoenicea*	Flame Robin
Petroicidae	Petroica	*Petroica rosea*	Rose Robin
Petroicidae	Petroica	*Petroica rodinogaster*	Pink Robin
Petroicidae	Melanodryas	*Melanodryas cucullata*	Hooded Robin
Petroicidae	Melanodryas	*Melanodryas vittata*	Dusky Robin
Petroicidae	Tregellasia	*Tregellasia capito*	Pale-yellow Robin
Petroicidae	Eopsaltria	*Eopsaltria australis*	Eastern Yellow Robin
Petroicidae	Eopsaltria	*Eopsaltria griseogularis*	Western Yellow Robin
Petroicidae	Drymodes	*Drymodes brunneopygia*	Southern Scrub-robin
Orthonchidae	Orthonyx	*Orthonyx temminckii*	Australian Logrunner
Pomatostomidae	Pomatostomus	*Pomatostomus temporalis*	Grey-crowned Babbler
Pomatostomidae	Pomatostomus	*Pomatostomus superciliosus*	White-browed Babbler
Cinclosomatidae	Psophodes	*Psophodes olivaceus*	Eastern Whipbird

Cinclosomatidae	Psophodes	*Psophodes nigrogularis*	Western Whipbird
Cinclosomatidae	Cinclosoma	*Cinclosoma punctatum*	Spotted Quail-thrush
Cinclosomatidae	Cinclosoma	*Cinclosoma castanotum*	Chestnut Quail-thrush
Neosittidae	Daphoenositta	*Daphoenositta chrysoptera*	Varied Sittella
Pachycephalidae	Falcunculus	*Falcunculus frontatus*	Crested Shrike-tit
Pachycephalidae	Oreoica	*Oreoica gutturalis*	Crested Bellbird
Pachycephalidae	Pachycephala	*Pachycephala olivacea*	Olive Whistler
Pachycephalidae	Pachycephala	*Pachycephala rufogularis*	Red-lored Whistler
Pachycephalidae	Pachycephala	*Pachycephala inornata*	Gilbert's Whistler
Pachycephalidae	Pachycephala	*Pachycephala pectoralis*	Golden Whistler
Pachycephalidae	Pachycephala	*Pachycephala rufiventris*	Rufous Whistler
Pachycephalidae	Colluricincla	*Colluricincla megarhyncha*	Little Shrike-thrush
Pachycephalidae	Colluricincla	*Colluricincla harmonica*	Grey Shrike-thrush
Cacatuidae	Calyptorhynchus	*Calyptorhynchus banksii*	Red-tailed Black-cockatoo
Cacatuidae	Calyptorhynchus	*Calyptorhynchus lathami*	Glossy Black-cockatoo
Cacatuidae	Zanda	*Zanda funerea*	Yellow-tailed Black-cockatoo
Cacatuidae	Callocephalon	*Callocephalon fimbriatum*	Gang-gang Cockatoo
Cacatuidae	Eolophus	*Eolophus roseicapilla*	Galah
Cacatuidae	Cacatua	*Cacatua tenuirostris*	Long-billed Corella
Cacatuidae	Cacatua	*Cacatua sanguinea*	Little-corella
Cacatuidae	Cacatua	*Cacatua galerita*	Sulphur-crested Cockatoo
Cacatuidae	Nymphicus	*Nymphicus hollandicus*	Cockatiel
Psittacidae	Trichoglossus	*Trichoglossus haematodus*	Rainbow Lorikeet
Psittacidae	Trichoglossus	*Trichoglossus chlorolepidotus*	Scaly-brested Lorikeet
Psittacidae	Glossopsitta	*Glossopsitta concinna*	Musk Lorikeet
Psittacidae	Parvipsitta	*Parvipsitta pusilla*	Little Lorikeet
Psittacidae	Parvipsitta	*Parvipsitta porphyrocephala*	Purple-crowned Lorikeet
Psittacidae	Alisterus	*Alisterus scapularis*	Australian King-parrot
Psittacidae	Aprosmictus	*Aprosmictus erythropterus*	Red-winged Parrot
Psittacidae	Polytelis	*Polytelis swainsonii*	Superb Parrot
Psittacidae	Polytelis	*Polytelis anthopeplus*	Regent Parrot
Psittacidae	Platycercus	*Platycercus caledonicus*	Green Rosella
Psittacidae	Platycercus	*Platycercus elegans*	Crimson Rosella
Psittacidae	Platycercus	*Platycercus eximius*	Eastern Rosella
Psittacidae	Platycercus	*Platycercus adscitus*	Pale-headed Rosella
Psittacidae	Barnardius	*Barnardius zonarius*	Australian Ringneck
Psittacidae	Northiella	*Northiella haematogaster*	Bluebonnet
Psittacidae	Lathamus	*Lathamus discolor*	Swift Parrot
Psittacidae	Psephotus	*Psephotus haematonotus*	Red-rumped Parrot
Psittacidae	Psephotus	*Psephotellus varius*	Mulga Parrot
Psittacidae	Melopsittacus	*Melopsittacus undulatus*	Budgerugar
Psittacidae	Neophema	*Neophema chrysostoma*	Blue-winged Parrot
Psittacidae	Neophema	*Neophema elegans*	Elegant Parrot
Psittacidae	Neophema	*Neophema chrysogaster*	Orange-bellied Parrot
Psittacidae	Neophema	*Neophema pulchella*	Turquoise Parrot
Psittacidae	Pezoporus	*Pezoporus wallicus*	Ground Parrot

Cuculidae	Cuculus	*Cuculus optatus*	Oriental Cuckoo
Cuculidae	Heteroscenes	*Heteroscenes pallidus*	Pallid Cuckoo
Cuculidae	Cacomantis	*Cacomantis variolosus*	Brush Cuckoo
Cuculidae	Cacomantis	*Cacomantis flabelliformis*	Fan-tailed Cuckoo
Cuculidae	Chalcites	*Chalcites osculans*	Black-eared Cuckoo
Cuculidae	Chalcites	*Chalcites basalis*	Horsfield's Bronze-cuckoo
Cuculidae	Chalcites	*Chalcites lucidus*	Shining Bronze-cuckoo
Cuculidae	Chalcites	*Chalcites minutillus*	Little Bronze-cuckoo
Cuculidae	Eudynamys	*Eudynamys orientalis*	Asian Koel
Cuculidae	Scythrops	*Scythrops novaehollandiae*	Channel-billed Cuckoo
Cuculidae	Centropus	*Centropus phasianinus*	Pheasant Coucal
Alcedinidae	Ceyx	*Ceyx azureus*	Azure Kingfisher
Halcyonidae	Dacelo	*Dacelo novaeguineae*	Laughing Kookaburra
Halcyonidae	Dacelo	*Dacelo leachii*	Blue-winged Kookaburra
Halcyonidae	Todiramphus	*Todiramphus macleayii*	Forest Kingfisher
Halcyonidae	Todiramphus	*Todiramphus pyrrhopygius*	Red-backed Kingfisher
Halcyonidae	Todiramphus	*Todiramphus sanctus*	Sacred Kingfisher
Meropidae	Merops	*Merops ornatus*	Rainbow Bee-eater
Coraciidae	Eurystomus	*Eurystomus orientalis*	Dollarbird
Meliphagidae	Acanthagenys	*Acanthagenys rufogularis*	Spiny-cheeked Honeyeater
Meliphagidae	Manorina	*Manorina flavigula*	Yellow-throated Miner
Meliphagidae	Manorina	*Manorina melanotis*	Black-eared Miner
Meliphagidae	Gavicalis	*Gavicalis virescens*	Singing Honeyeater
Meliphagidae	Lichenostomus	*Lichenostomus cratitius*	Purple-gaped Honeyeater
Meliphagidae	Ptilotula	*Ptilotula ornata*	Yellow-plumed Honeyeater
Meliphagidae	Ptilotula	*Ptilotula plumula*	Grey-fronted Honeyeater
Meliphagidae	Purnella	*Purnella albifrons*	White-fronted Honeyeater
Meliphagidae	Sugomel	*Sugomel niger*	Black Honeyeater
Meliphagidae	Certhionyx	*Certhionyx variegatus*	Pied Honeyeater
Meliphagidae	Myzomela	*Myzomela obscura*	Dusky Honeyeater
Meliphagidae	Epthianura	*Epthianura tricolor*	Crimson Chat
Meliphagidae	Epthianura	*Epthianura aurifrons*	Orange Chat
Pittidae	Pitta	*Pitta versicolor*	Noisy Pitta
Menuridae	Menura	*Menura alberti*	Albert's Lyrebird
Menuridae	Menura	*Menura novaehollandiae*	Superb Lyrebird
Atrichornithidae	Atrichornis	*Atrichornis rufescens*	Rufous Scrub-bird
Climacteridae	Cormobates	*Cormobates leucophaea*	White-throated Treecreeper
Climacteridae	Climacteris	*Climacteris affinis*	White-browed Treecreeper
Climacteridae	Climacteris	*Climacteris erythrops*	Red-browed Treecreeper
Climacteridae	Climacteris	*Climacteris picumnus*	Brown Treecreeper
Maluridae	Malurus	*Malurus cyaneus*	Superb Fairy-wren
Maluridae	Malurus	*Malurus splendens*	Splendid Fairy-wren
Maluridae	Malurus	*Malurus lamberti*	Variegated Fairy-wren

Maluridae	Malurus	*Malurus pulcherrimus*	Blue-breasted Fairy-wren
Maluridae	Malurus	*Malurus melanocephalus*	Red-backed Fairy-wren
Maluridae	Stipiturus	*Stipiturus malachurus*	Southern Emu-wren
Accipitridae	Aviceda	*Aviceda subcristata*	Pacific Baza
Accipitridae	Elanus	*Elanus axillaris*	Black-shouldered Kite
Accipitridae	Milvus	*Milvus migrans*	Black Kite
Accipitridae	Haliastur	*Haliastur indus*	Brahminy Kite
Accipitridae	Haliastur	*Haliastur sphenurus*	Whistling Kite
Accipitridae	Haliaeetus	*Haliaeetus leucogaster*	White-bellied Sea-eagle
Accipitridae	Circus	*Circus assimilis*	Spotted Harrier
Accipitridae	Circus	*Circus approximans*	Swamp Harrier
Accipitridae	Accipiter	*Accipiter novaehollandiae*	Grey Goshawk
Accipitridae	Accipiter	*Accipiter fasciatus*	Brown Goshawk
Accipitridae	Accipiter	*Accipiter cirrocephalus*	Collared Sparrowhawk
Accipitridae	Aquila	*Aquila audax*	Wedge-tailed Eagle
Accipitridae	Hieraaetus	*Hieraaetus morphnoides*	Little Eagle
Accipitridae	Lophoictinia	*Lophoictinia isura*	Square-tailed Kite
Accipitridae	Erythrotriorchis	*Erythrotriorchis radiatus*	Red Goshawk
Falconidae	Falco	*Falco berigora*	Brown Falcon
Falconidae	Falco	*Falco cenchroides*	Nankeen Kestrel
Falconidae	Falco	*Falco longipennis*	Australian Hobby
Falconidae	Falco	*Falco subniger*	Black Falcon
Falconidae	Falco	*Falco peregrinus*	Peregrine Falcon
Megapodiidae	Alectura	*Alectura lathami*	Australian Brush-turkey
Monarchidae	Monarcha	*Monarcha melanopsis*	Black-faced Monarch
Monarchidae	Symposiachrus	*Symposiachrus trivirgatus*	Spectacled Monarch
Monarchidae	Carterornis	*Carterornis leucotis*	White-eared Monarch
Monarchidae	Myiagra	*Myiagra rubecula*	Leaden Flycatcher
Monarchidae	Myiagra	*Myiagra cyanoleuca*	Satin Flycatcher
Monarchidae	Myiagra	*Myiagra alecto*	Shining Flycatcher
Monarchidae	Myiagra	*Myiagra inquieta*	Restless Flycatcher
Monarchidae	Grallina	*Grallina cyanoleuca*	Magpie-lark
Rhipiduridae	Rhipidura	*Rhipidura rufifrons*	Rufous Fantail
Rhipiduridae	Rhipidura	*Rhipidura albiscapa*	Grey Fantail
Rhipiduridae	Rhipidura	*Rhipidura leucophrys*	Willie Wagtail
Dicruridae	Dicrurus	*Dicrurus bracteatus*	Spangled Drongo
Campephagidae	Coracina	*Coracina novaehollandiae*	Black-faced Cuckoo-shrike
Campephagidae	Coracina	*Coracina lineata*	Barred Cuckoo-shrike
Campephagidae	Coracina	*Coracina papuensis*	White-bellied Cuckoo-shrike
Campephagidae	Edolisoma	*Edolisoma tenuirostre*	Cicadabird
Campephagidae	Coracina	*Coracina maxima*	Ground Cuckoo-shrike
Campephagidae	Lalage	*Lalage leucomela*	Varied Triller
Oriolidae	Oriolus	*Oriolus sagittatus*	Olive-backed Oriole
Oriolidae	Sphecotheres	*Sphecotheres vieilloti*	Australasian Figbird
Artamidae	Artamus	*Artamus leucorynchus*	White-breasted Woodswallow
Artamidae	Artamus	*Artamus personatus*	Masked Woodswallow

Artamidae	Artamus	*Artamus superciliosus*	White-browed Woodswallow
Artamidae	Artamus	*Artamus cinereus*	Black-faced Woodswallow
Artamidae	Artamus	*Artamus cyanopterus*	Dusky Woodswallow
Artamidae	Artamus	*Artamus minor*	Little Woodswallow
Artamidae	Cracticus	*Cracticus torquatus*	Grey Butcherbird
Artamidae	Cracticus	*Cracticus nigrogularis*	Pied Butcherbird
Artamidae	Strepera	*Strepera graculina*	Pied Currawong
Artamidae	Strepera	*Strepera fuliginosa*	Black Currawong
Artamidae	Strepera	*Strepera versicolor*	Grey Currawong
Artamidae	Gymnorhina	*Gymnorhina tibicen*	Australian Magpie
Paradisaeidae	Ptiloris	*Ptiloris paradiseus*	Paradise Riflebird
Corvidae	Corvus	*Corvus coronoides*	Australian Raven
Corvidae	Corvus	*Corvus tasmanicus*	Forest Raven
Corvidae	Corvus	*Corvus mellori*	Little Raven
Corvidae	Corvus	*Corvus orru*	Torresian Crow
Corvidae	Corvus	*Corvus bennetti*	Little Crow
Corcoracidae	Corcorax	*Corcorax melanorhamphos*	White-winged Chough
Corcoracidae	Struthidea	*Struthidea cinerea*	Apostlebird
Ptilonorhynchidae	Ailuroedus	*Ailuroedus crassirostris*	Green Catbird
Ptilonorhynchidae	Sericulus	*Sericulus chrysocephalus*	Regent Bowerbird
Ptilonorhynchidae	Ptilonorhynchus	*Ptilonorhynchus violaceus*	Satin Bowerbird
Ptilonorhynchidae	Chlamydera	*Chlamydera maculata*	Spotted Bowerbird
Alaudidae	Mirafra	*Mirafra javanica*	Horsfield's Bushlark
Alaudidae	Alauda	*Alauda arvensis*	Eurasian Skylark
Passeridae	Passer	*Passer domesticus*	House Sparrow
Passeridae	Passer	*Passer montanus*	Eurasian Tree Sparrow
Estrildidae	Taeniopygia	*Taeniopygia guttata*	Zebra Finch
Estrildidae	Stizoptera	*Stizoptera bichenovii*	Double-barred Finch
Estrildidae	Aidemosyne	*Aidemosyne modesta*	Plum-headed Finch
Estrildidae	Neochmia	*Neochmia temporalis*	Red-browed Finch
Estrildidae	Stagonopleura	*Stagonopleura guttata*	Diamond Firetail
Estrildidae	Stagonopleura	*Stagonopleura bella*	Beautiful Firetail
Estrildidae	Lonchura	*Lonchura punctulata*	Nutmeg Mannikin
Fringillidae	Chloris	*Chloris chloris*	European Greenfinch
Fringillidae	Carduelis	*Carduelis carduelis*	European Goldfinch
Motacillidae	Anthus	*Anthus novaeseelandiae*	Australasian Pipit
Motacillidae	Motacilla	*Motacilla tschutschensis*	Yellow Wagtail
Dicaeidae	Dicaeum	*Dicaeum hirundinaceum*	Mistletoebird
Hirundinidae	Cheramoeca	*Cheramoeca leucosterna*	White-backed Swallow
Hirundinidae	Hirundo	*Hirundo neoxena*	Welcome Swallow
Hirundinidae	Petrochelidon	*Petrochelidon nigricans*	Tree Martin
Hirundinidae	Petrochelidon	*Petrochelidon ariel*	Fairy Martin
Pycnonotidae	Pycnonotus	*Pycnonotus jocosus*	Red-whiskered Bulbul
Acrocephalidae	Acrocephalus	*Acrocephalus australis*	Australian Reed Warbler
Locustellidae	Cincloramphus	*Cincloramphus timoriensis*	Tawny Grassbird
Locustellidae	Poodytes	*Poodytes gramineus*	Little Grassbird

Locustellidae	Cincloramphus	*Cincloramphus mathewsi*	Rufous Songlark
Locustellidae	Cincloramphus	*Cincloramphus cruralis*	Brown Songlark
Locustellidae	Cisticola	*Cisticola exilis*	Golden-headed Cisticola
Zosteropidae	Zosterops	*Zosterops lateralis*	Silvereye
Turdidae	Zoothera	*Zoothera lunulata*	Bassian Thrush
Turdidae	Zoothera	*Zoothera heinei*	Russet-tailed Thrush
Turdidae	Turdus	*Turdus merula*	Common Blackbird
Sturnidae	Sturnus	*Sturnus vulgaris*	Common Starling
Sturnidae	Acridotheres	*Acridotheres tristis*	Common Myna

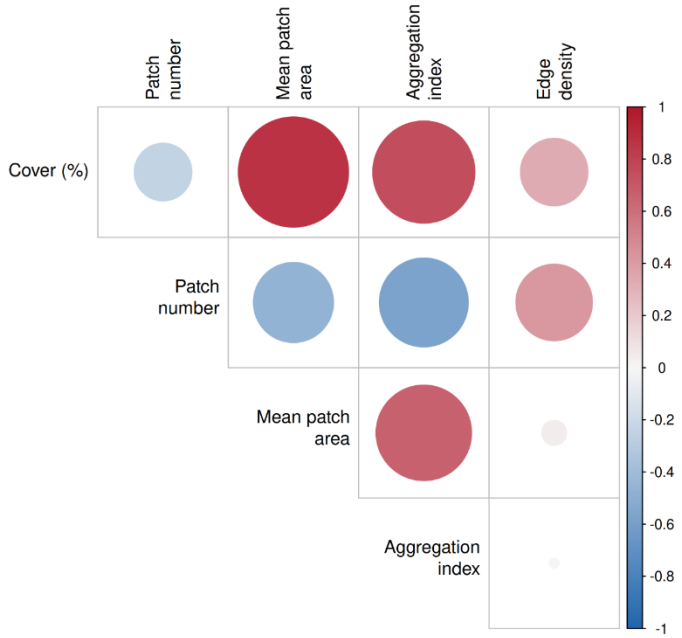

Figure S1. Pairwise Pearson correlation matrix among landscape structure metrics in closed woodland patches. Size and colour of circles indicate strength and direction of correlation. Woodland cover was strongly collinear with mean patch area and aggregation index and was retained for modelling alongside PCA-derived patch structure metrics.

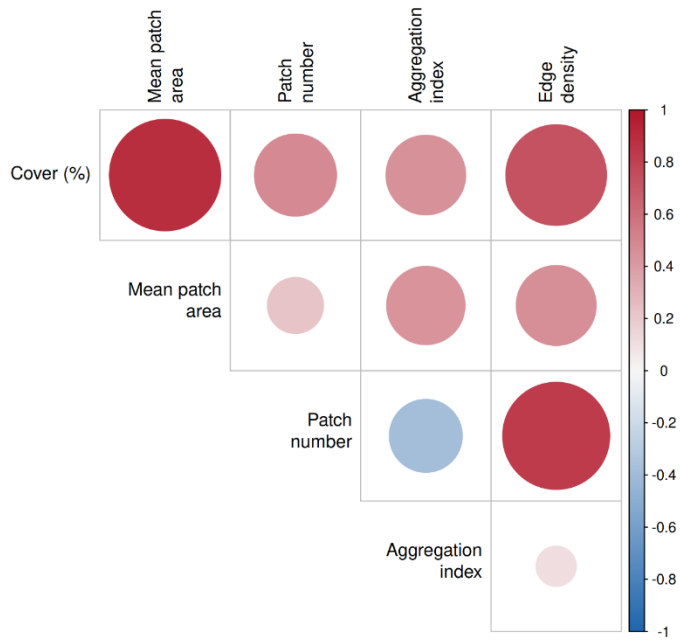

Figure S2. Pairwise Pearson correlation matrix among landscape structure metrics in open woodland patches. Woodland cover showed strong positive correlations with mean patch area, patch number, and aggregation index. Patch metrics were summarised using PCA to reduce dimensionality and collinearity.

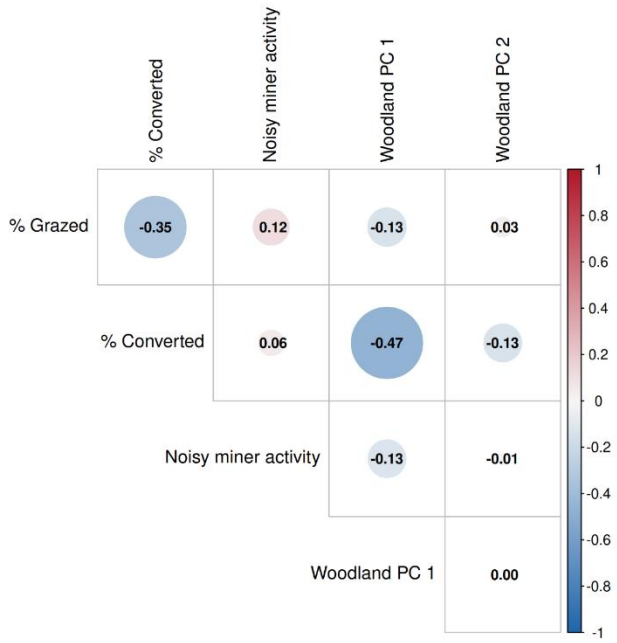

Figure S3. Correlation matrix among predictor variables used in generalised additive models. All predictor pairs show $|r| < 0.5$ except for a moderate negative correlation between grazing and land conversion ($r = -0.35$). Low correlations and variance inflation factors below 2 indicate acceptable multicollinearity among fixed effects.

Table S2. Variance explained by each principal component used to summarise woodland patch structure.

statistic	Standard deviation	Proportion of Variance	Cumulative Proportion
1	1.7374967	0.60378	0.60378
2	1.0739833	0.23069	0.83447
3	0.6456685	0.08338	0.91784
4	0.5909583	0.06985	0.98769
5	0.2480839	0.01231	1.00000

Table S3. Variance inflation factors (VIF) for fixed effects used in generalised additive models. All VIF values were below 2, indicating low collinearity among predictors.

term	VIF
Grazed_native_pland	1.281774
Converted_pland	1.562226
nm_visit_rate_z	1.028308
Closed_PC1	1.377535
Closed_PC2	1.033282

Table S4. Principal component loadings for woodland structure in closed canopy habitats. PC1 captures increasing woodland area, aggregation, and cover; PC2 is strongly associated with edge density. These components were used to summarise patch structure in GAMs.

variable	PC1	PC2
Woodland_pland	0.52073406	0.278478288
Woodland_np	-0.44397097	0.339464668
Woodland_area_mn	0.53306661	-0.007705067
Woodland_ai	0.49491577	0.112080091
Woodland_ed	-0.05122684	0.891399051

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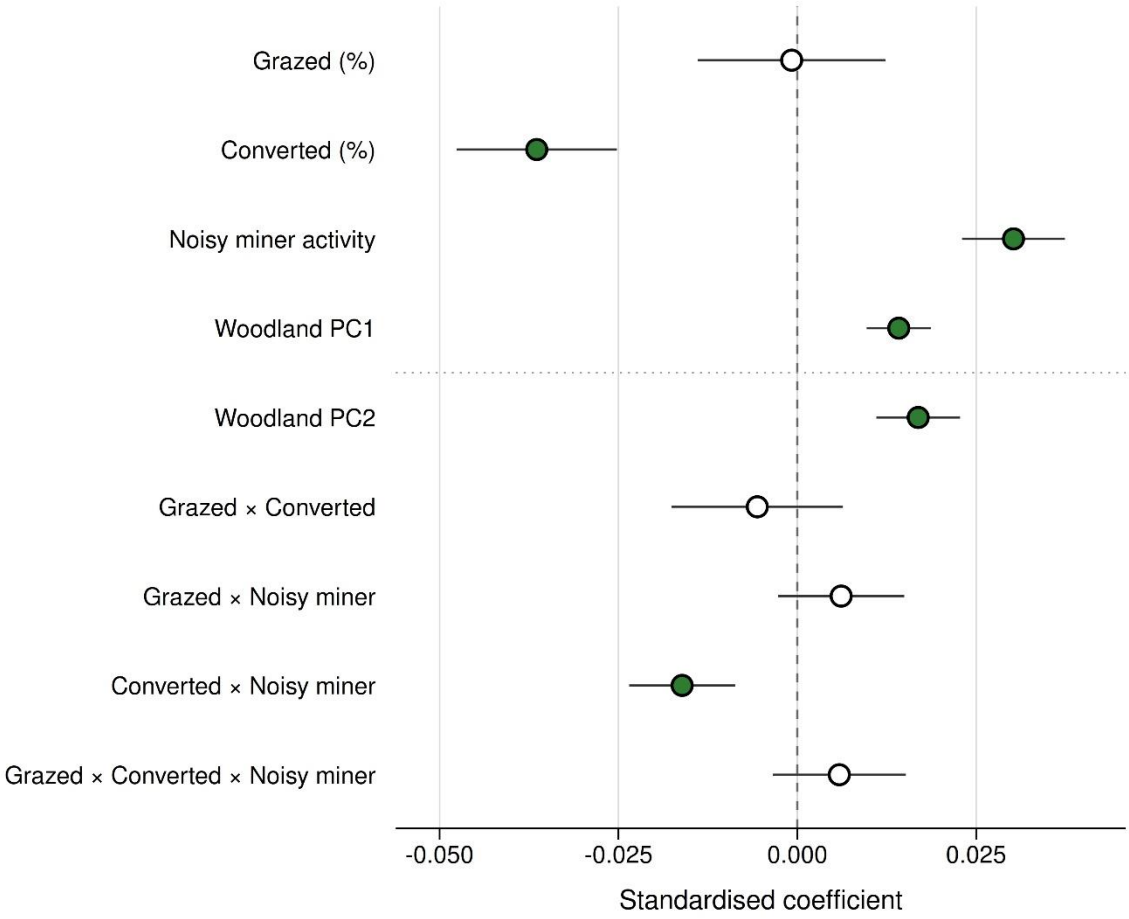

679

680 **Figure S4**. Standardised coefficients from generalised additive models predicting species
681 richness across southeastern Australia. Points show effect sizes with 95% confidence
682 intervals. Filled circles indicate statistically significant effects ($p < 0.05$); open circles

683 indicate non-significant effects. Positive values indicate increased species richness; negative
684 values indicate decreased richness.

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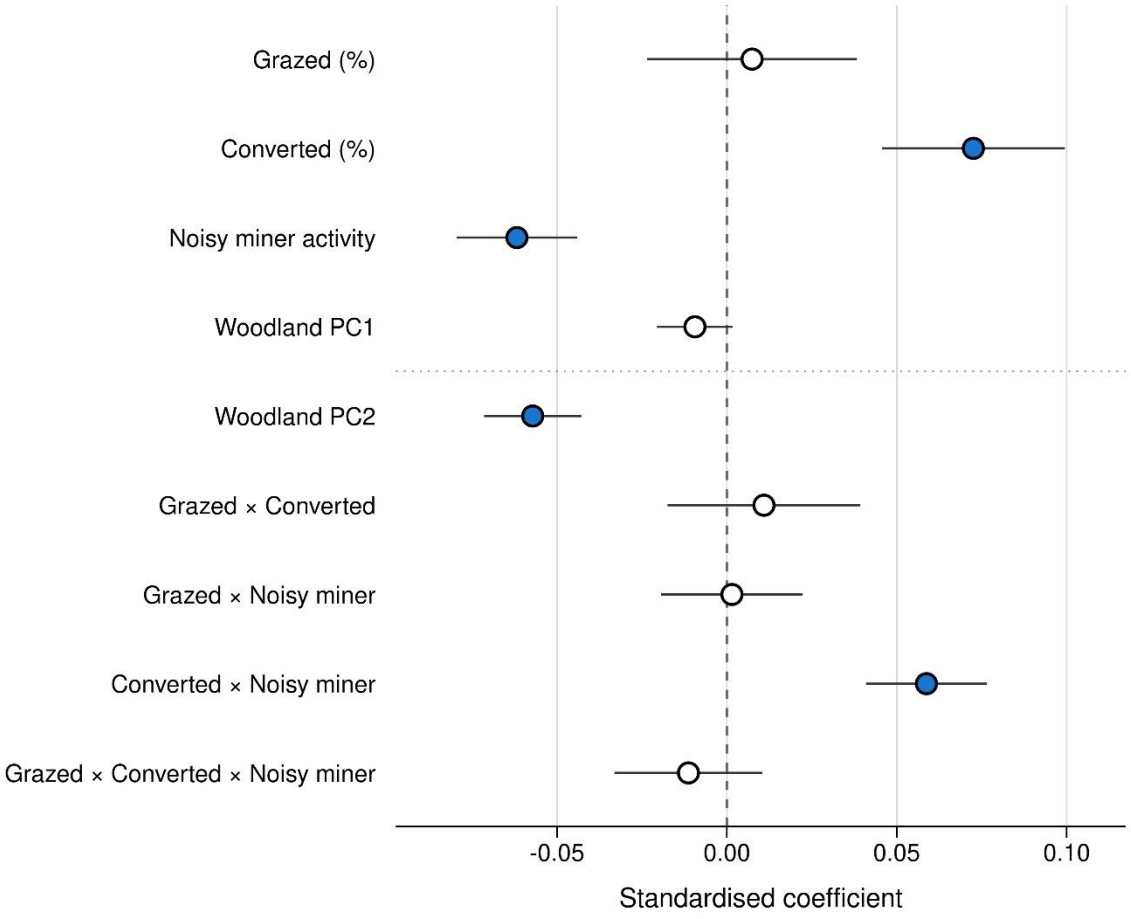
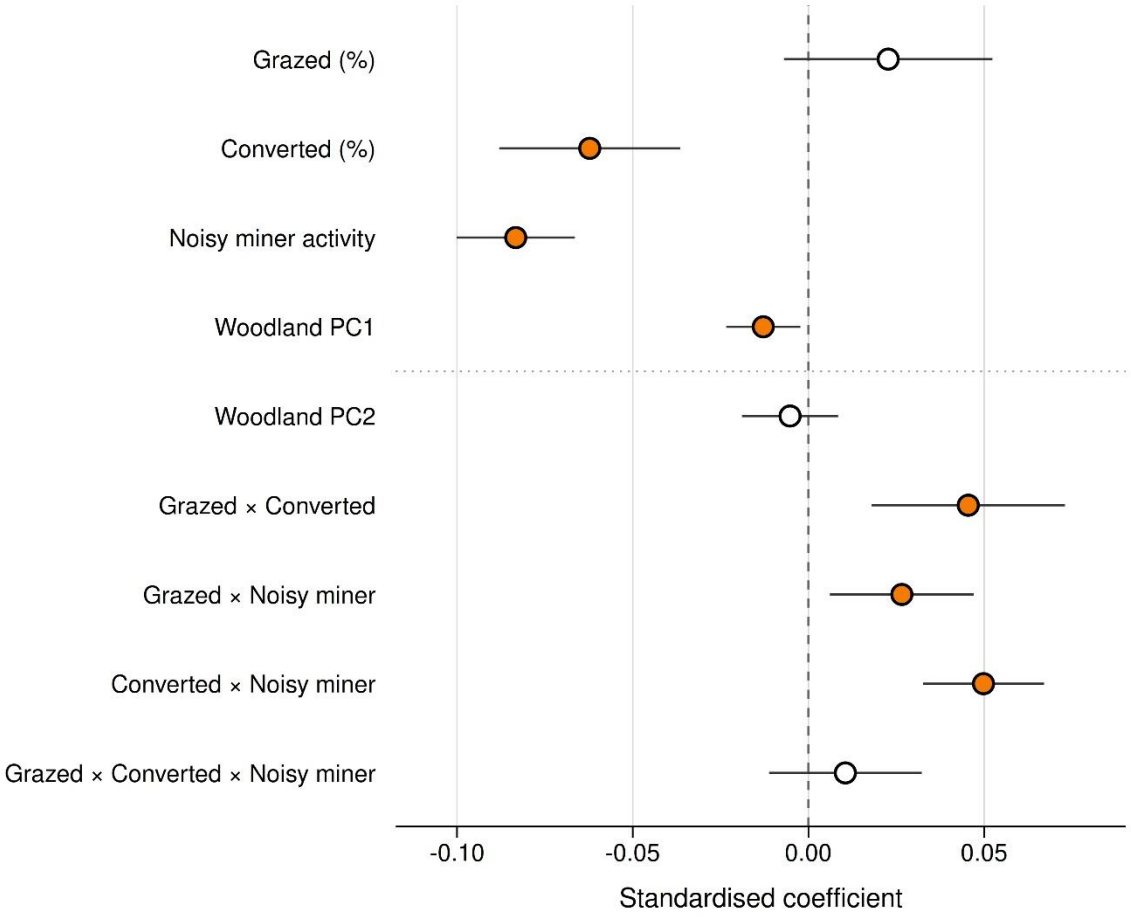


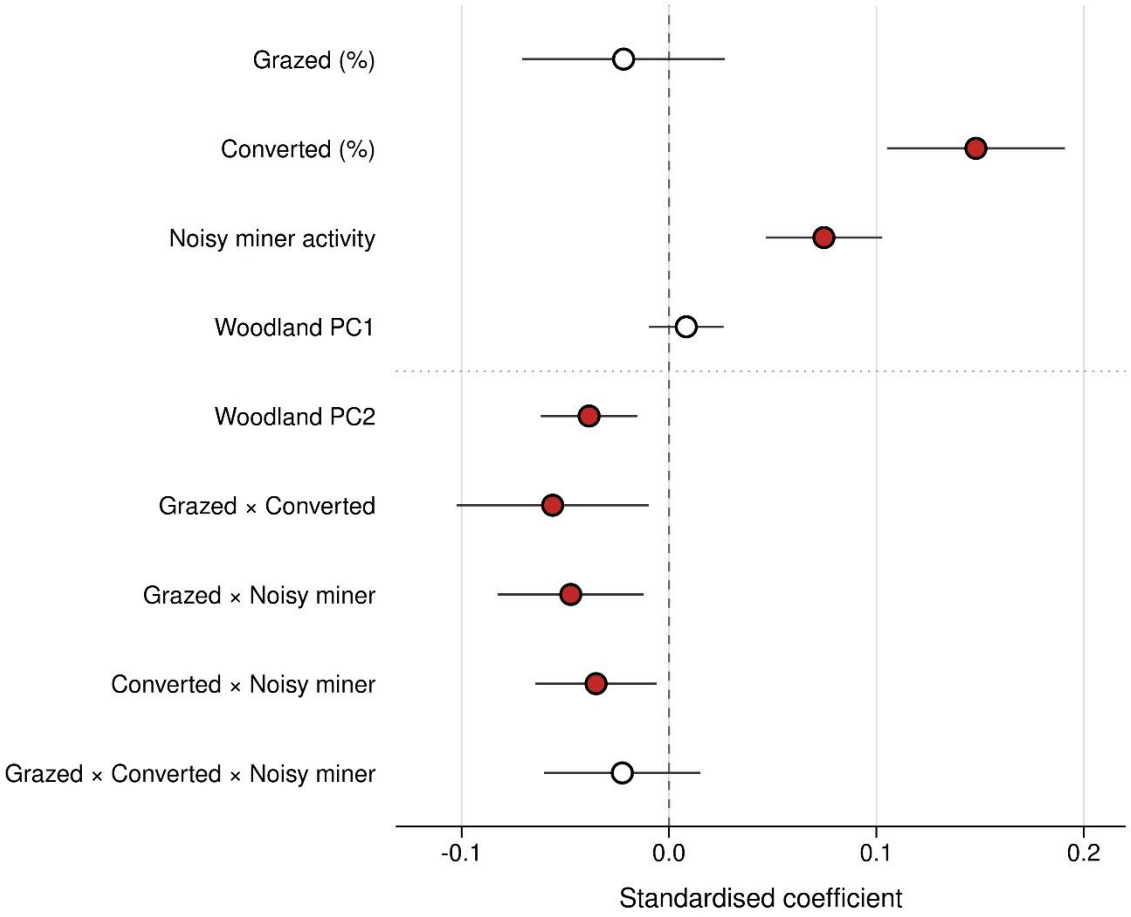
686

687 **Figure S5.** Standardised coefficients from generalised additive models predicting total local
688 contributions to β-diversity (LCBD) across southeastern Australia. Points show effect sizes
689 with 95% confidence intervals. Filled circles indicate statistically significant effects ($p <$
690 0.05); open circles indicate non-significant effects. Positive values indicate increased
691 contribution to regional compositional variation; negative values indicate decreased
692 contribution.



693

694 **Figure S6.** Standardised coefficients from generalised additive models predicting turnover
695 local contributions to β-diversity (LCBD) across southeastern Australia. Points show effect
696 sizes with 95% confidence intervals. Filled circles indicate statistically significant effects ($p <$
697 0.05); open circles indicate non-significant effects. Positive values indicate increased
698 contribution to species replacement patterns; negative values indicate decreased contribution.



699

700 **Figure S7.** Standardised coefficients from generalised additive models predicting nestedness
701 local contributions to β-diversity (LCBD) across southeastern Australia. Points show effect
702 sizes with 95% confidence intervals. Filled circles indicate statistically significant effects ($p <$
703 0.05); open circles indicate non-significant effects. Positive values indicate increased
704 contribution to nested species loss patterns; negative values indicate decreased contribution.

705