



Imprints of historical and ecological factors in the phylogenetic structure of Australian Meliphagidae assemblages

Vicente García-Navas^{1,2} | Carlos Martínez-Núñez^{1,3} | Les Christidis⁴

¹Department of Integrative Ecology,
 Estación Biológica de Doñana EBD (CSIC),
 Seville, Spain

²Department of Evolutionary Biology
 and Environmental Studies, University of
 Zurich, Zurich, Switzerland

³Agricultural Landscape and Biodiversity'
 Research Group, Agroscope, Zurich,
 Switzerland

⁴Southern Cross University, Coffs
 Harbour, New South Wales, Australia

Correspondence

Vicente García-Navas, Department of
 Integrative Ecology, Estación Biológica de
 Doñana EBD (CSIC), Seville, Spain.
 Email: vicente.garcianavas@gmail.com

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Abstract

Aims: Understanding how historical and ecological (species interactions) factors affect species and shape community structure is a fundamental goal in ecology. However, these two components are difficult to disentangle and are often confounded. We address the influence of these factors in governing the structure of bird assemblages.

Location: Southeastern Australia.

Taxon: The Meliphagoidea superfamily.

Methods: By adopting a semi-experimental approach (i.e. high vs low interference competition), we examine the influence of a genus (*Manorina*) of honeyeater species that is well known for its hyper-aggressiveness and strong competitive capacity on the phylogenetic and functional structure of local assemblages across three different habitats (eucalypt woodlands, mallee and cleared habitat). We applied a model that explicitly incorporates the effects of neutral colonization and local extinction in shaping community structure and estimated the contributions of niche-based and neutral processes to community assembly using the STEPCAM technique.

Results: Communities with the presence of *Manorina* species were characterized by faster rates of colonization and local extinction and exhibited a higher degree of phylogenetic clustering than communities without these despotic species, which suggests that this model not only mirrors habitat preferences, but also unintendedly accounts for the effect of biotic interactions. Stochastic processes had a lower contribution in the presence of *Manorina* species, whereas the role of filtering tended to be higher. We observed habitat differences in terms of functional (but not phylogenetic) structure, with more functionally clustered assemblages in the cleared habitat.

Main Conclusions: Although recent studies have suggested that neutral-species processes are sufficient to explain local assemblage phylogenetic structure, our capacity to isolate them from contemporary ecological processes is still limited. This study also reinforces the idea that biotic interactions can also lead to patterns of underdispersion and thus, assumptions behind null model approaches for community assembly should be carefully considered in each case.



KEY WORDS

Australia, bird communities, competition, functional structure, interference competition, *Manorina* honeyeaters, neutral processes, phylogenetic clustering

1 | INTRODUCTION

Quantifying spatial variation in community structure has been a long-standing area of research (Keddy & Laughlin, 2021). Theory assumes that ecological communities are assembled according to processes operating over a vast range of spatiotemporal scales, from niche-based interactions (e.g. interspecific competition), which are commonly assumed to take place at a local scale, to broad-scale historical factors such as dispersal events and allopatric speciation (Hubbell, 2001; Vellend, 2010). The relative contribution of local-scale deterministic processes in relation to that of more stochastic biogeographical factors in shaping species assemblages is typically ascertained by comparing the observed patterns to those expected under a null model in which assembly occurs at random in respect to species identity or ecological traits (Gotelli, 2000). Hence, during the last 15 years, null models have been applied in a phylogenetic context to infer, for instance, the phylogenetic dimension of competition (Cardillo et al., 2008; Cavender-Bares, Keen, & Miles, 2006; Cavender-Bares, Kozak, et al., 2006; Cooper et al., 2008). In this vein, it is commonly assumed that a community of distantly related species (i.e. phylogenetic overdispersion) implies competitive exclusion, while the converse (phylogenetic clustering) reflects environmental filtering on the basis of phylogenetically conserved traits (Cavender-Bares et al., 2009). However, although this approach has been widely accepted and has given rise to a large body of literature, it is increasingly acknowledged that phylogenetic structure does not always match trait variation, even when assumptions of niche conservatism hold (Cadotte et al., 2017; HilleRisLambers et al., 2012; Mayfield & Levine, 2010). Consequently, communities can show incongruent phylogenetic and functional dispersion patterns under certain circumstances (e.g. low number of traits; Cadotte et al., 2019). In addition, most null models are based on algorithms that randomize species assemblages (Miller, Farine, & Trisos, 2017), but that do not consider fundamental processes such as colonization and local extinction and thus, neglect the historical component when modeling the way in which communities are assembled (Hubbell, 2001). As indicated above, by historical processes we refer to processes occurring at broader spatial and temporal scales than are typically considered in traditional community ecology (namely, speciation and long-range dispersal) (Vellend, 2010). New dynamic modelling approaches like DAMOCLES (Pigot & Etienne, 2015) account for the historical processes of speciation, colonization and local extinction through which assemblages are built over time. For instance, using DAMOCLES Pigot and Etienne (2015) showed that the overdispersion pattern reported in some studies on communities of birds and primates from the Manu Biosphere Reserve (Peru) and previously interpreted as evidence of competition, did not differ from that expected under a null model of allopatric speciation, colonization

and extinction. Despite its potential, the number of studies that have used this methodology is practically anecdotal (but see Marx et al., 2017; Pinto-Ledezma et al., 2019; Puga-Caballero et al., 2022) and it is not clear what the capacity of this model is to distinguish between trait-based mechanisms arising from species interactions (competition) and purely historical factors like allopatric speciation.

It must also be noted that, under certain circumstances, community phylogenetic patterns are not conclusive and/or they are not easily detected, mostly when lineages of very different ages whose evolution might have been governed by very different processes (evolutionary lability vs. niche conservatism) are analysed jointly (Elliott et al., 2016; Ndiribe et al., 2013). To tackle this problem, Parra et al. (2010) examined the contribution of different clades to an overall metric of phylogenetic structure in Ecuadorian hummingbird communities using node-based analysis. They found that multiple patterns of phylogenetic structure often occur within a local assemblage and identified clades that exhibit non-random patterns of representation (Parra et al., 2010). This type of analysis was refined by Borregaard et al. (2014) adopting a clade-based approach, which compares the species richness of sister clades, rather than comparing each node to that expected by randomly drawing species from the phylogeny. By means of this method, it is possible to quantify the distributional divergence between the two daughter lineages descending from a given node and identify those nodes responsible for observed patterns of phylogenetic structure and species co-occurrence (Borregaard et al., 2014).

As mentioned above, the analysis of trait diversity patterns of co-occurring species constitutes another commonly used approach to discriminate between alternative community assembly processes (convergence vs. overdispersion). However, the understanding that one can gain from this type of analysis is limited. When filtering and limiting similarity processes operate in concert, at similar spatial scales, it may be very hard to statistically detect both processes using null models. Recent methodological advances like STEPCAM (stepwise species deletion with stepwise community assembly models; van der Plas et al., 2015) constitute a qualitative leap in our capacity to unravel the underlying assembly processes behind observed community patterns since this approach allows us to estimate the relative importance of dispersal, filtering processes and intraspecific competition (Janzen et al., 2017).

In this study, we take advantage of these new tools to investigate the structure of Meliphagidae assemblages (one of the most speciose songbird basal lineages) in Australia under a historical framework in which we explicitly consider the different processes through which assemblages are built over time. Vicariance events within Australia are likely to have been important in the diversification of the Meliphagidae. For instance, the malurid genera *Amytornis* (grasswrens) and *Malurus* exhibit an allopatric



distribution (Black et al., 2020; Christidis et al., 2010; Christidis et al., 2013; Gotelli et al., 1997). Within the Acanthizidae, *Gerygone* clades also are largely allopatric, either in different habitats or geographically (Keast & Recher, 1997). Although founder-event speciation is likely to have an important role in the diversification of honeyeaters due to their broader geographical range, some honeyeater clades (*Melithreptus*, *Ptilotula*, and *Gavicalis* among others) seem to have also evolved in allopatry (Joseph et al., 2014; Nyári & Joseph, 2012).

In turn, contemporary ecological processes can play a key role in shaping present-day composition of assemblages. For instance, diversity of honeyeaters is probably maintained by an interaction of two types of competition, exploitation and interference. The larger species use the richest sources of nectar and aggressively exclude the smaller species, whereas the smaller species can use poorer sources of nectar because their energy requirements are lower (Ford, 1979). As an extreme case, honeyeaters of the genus *Manorina* (miners) have disproportionate influence on woodland bird assemblages in eastern Australia (Maron et al., 2011). Miners constitute despotic species that exert a powerful negative effect on small passerines species (regardless of if they are nectarivorous or not), by virtue of their intra-colonial cooperation and hyper-aggressiveness (Thomson et al., 2015). In fact, in southeastern Australia, the over-abundance of *Manorina melanocephala* is listed as a key threatening process under national environmental legislation due to its negative influence on the richness and abundance of woodland birds (Maron et al., 2011; Piper & Catterall, 2003). Although several authors have documented (both observationally and experimentally), the role of *Manorina* honeyeaters in biotic homogenization of the Australian avifauna (e.g. Crates et al., 2018; Davitt et al., 2018; MacNally et al., 2014; Maron et al., 2013; Robertson et al., 2013), no study has evaluated the consequences of these strong competitors at the community level from a phylogenetic and functional perspective. It is striking since the interaction between miners and other bird species constitutes a text-book example of interference competition which can have a particularly strong influence on species assemblages when anthropogenic biotic or abiotic changes favour aggressive generalist species (Beggs et al., 2020).

Thus, this superfamily provides a superb opportunity to address and weight the importance of historical and ecological (species interactions) factors in governing community structure. In particular, we tested whether (i) rates of colonization and local extinction vary across Meliphagides assemblages; (ii) the phylogenetic and functional structure of co-occurring species is affected by the presence of despots (*Manorina* honeyeaters) and/or whether it differs between habitat types; and (iii) the relative contribution of neutral vs. deterministic processes (e.g. competition) varies depending on these two factors (level of interference competition and habitat type). Specifically, we focus on three different habitats (eucalyptus woodland, mallee and cleared habitat) that predominate in southeastern Australia, the region where Meliphagides diversity is the highest.

2 | MATERIALS AND METHODS

2.1 | Study system

The infraorder Meliphagides constitutes the most speciose of the songbird basal lineages and its origin has been suggested to have taken place in Australia during the early Oligocene (31 Mya) (Marki et al., 2017). This radiation comprises five families: Meliphagidae (honeyeaters), Maluridae (fairy-wrens and allies), Acanthizidae (thornbills, scrubwrens and gerygones), Dasyornithidae (bristlebirds) and Pardalotidae (pardalotes). The last two of these families are endemic to Australia, whereas the remaining three (the most speciose) are centred or confined to the continental landmasses of Australia and New Guinea (Hay et al., 2022; Marki et al., 2017).

2.2 | Species assemblage data

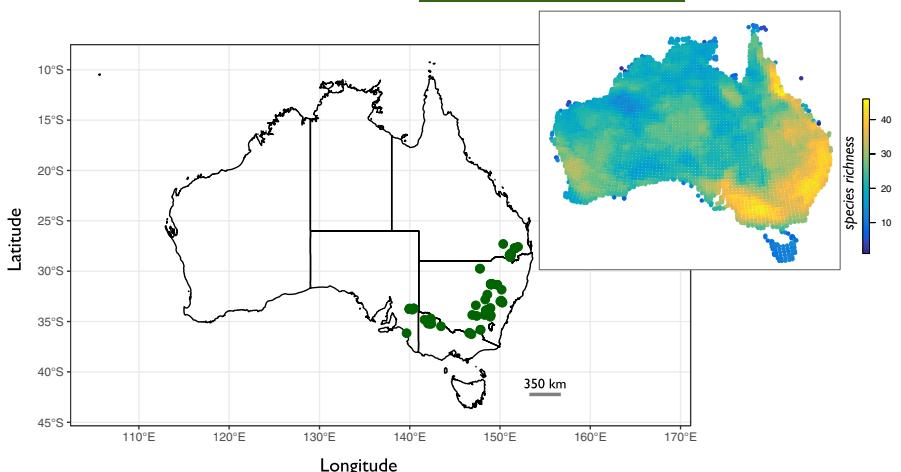
We compiled local assemblages of Meliphagides from the Australian Atlas coordinated by BirdLife Australia (<https://birdatlas.birdlife.org.au/>). BirdLife Australia's Atlas data are collected by skilled birdwatchers at sites they choose, with exact coordinates recorded for each survey. Surveys (1–2 visits per sampling plot) were carried out during the austral breeding season (December–February) using the '2-ha, 20 min' method. This census method involves searching for birds in a 2-ha area for 20 min. During this period, the volunteer records the geographical reference at the centre of their site and all birds seen or heard in their survey area, including those flying overhead. The data are then validated by experts, ensuring that the geographical references are sensible and that the species are within their known range. Our dataset consisted of abundance data for 82 assemblages located in the Murray Darling Depression, Brigalow Belt South and South Western Slopes Bioregions (Figure 1).

By restricting these analyses to a certain geographical region (instead of working on a continental scale), we increase the probability to detect the signature of competition. The relative contribution of biotic interactions including competition is expected to increase as the spatial extent (and thus, the pool size and the steepness of the environmental gradient) decreases (Graham et al., 2018; Münkemüller et al., 2014). We focused on these geographical regions since these sustain the highest diversity of Meliphagides (Figure 1). Sampling plots were classified into three different habitat categories that predominate in these regions (cleared and cultivated areas [$n = 34$], mallee shrublands [$n = 29$] and eucalypt woodlands [$n = 19$]) (Keith, 2017) according to the National Vegetation Information System of the Australian Government (www.awe.gov.au).

We also discerned between plots with and without the presence of miners ($n = 24$ and 58 , respectively). We did not distinguish between the three *Manorina* species (*M. melanocephala*, *M. flavigula* and *M. melanotis*). These 'reverse keystone' species exhibit a despotic, territorial and hyper-aggressive behaviour, by which they actively exclude other species (even non-avian taxa) as has been widely



FIGURE 1 Map of Australia with the location of the 2-ha sampling plots (green dots) employed in this study. Diversity of species of the Meliphagidae superfamily obtained from digitalized range maps is plotted on the map shown in the inset. Observed species diversity in the studied plots (local assemblages) ranged from 6 to 16 species.



documented in previous studies (e.g. Kutt et al., 2012; MacNally et al., 2012, 2014; Maron et al., 2013).

2.3 | Phylogenetic data

We used the recently published supermatrix phylogeny of the Meliphagidae by Marki et al. (2017). This phylogeny was calibrated using a combination of fossils and secondary calibration points and includes 99% (286/289) of the currently recognized taxa. The Maximum Clade Credibility tree provided by Marki et al. (2017) was pruned to incorporate only those species inhabiting our study region (55 species).

2.4 | Trait data

For each species, we collated mean trait values for the following morphological variables: body mass (log-transformed), beak size and wing aspect ratio (quantified using the Hand Wing index, HWI; Sheard et al., 2020). Since beak size and body mass (length) are highly correlated, we performed a phylogenetic size-correction (Revell, 2009) and the residuals (size-corrected beak size) were used as input in the analyses. We also collected information on diet preferences (%) of invertebrates, fruits, seeds, plants and nectar in diet) and foraging strategies (% of time spent foraging on the ground, understorey, mid-high, canopy and in the air). Both subsets (diet preferences and foraging strategies) were reduced to two principal components each by means of a principal component analysis (PCA). The first two axes summarizing diet preferences (PCd_1 and PCd_2) and foraging strategies (PCf_1 and PCf_2) accounted for 60% and 69%, respectively, of the total variance. Thus, our final trait matrix comprised seven variables (log-body mass, size-corrected beak size, HWI, PCd_1 , PCd_2 , PCf_1 and PCf_2) that are relevant in terms of resource competition (Eltonian aspect of the niche) and dispersal capacity. Trait values were compiled from the literature and published datasets (Garnett et al., 2015; Sheard et al., 2020; Tobias, 2021; Tobias et al., 2022).

We estimated the phylogenetic signal of each selected morphological trait using Pagel's λ , which measures the statistical

dependence of trait values among species given their phylogenetic relationship (Revell et al., 2008). Values of λ range from 0 (labile or convergent traits) to 1 (conserved traits). Phylogenetic signal analyses were calculated using the 'phylosig' function in *phytools* (Revell, 2012) for R.

2.5 | Clade-level analysis

To evaluate whether our assemblages are overrepresented by descendant species of particular sister clades within the Meliphagidae, we calculated the specific overrepresentation scores for all nodes in the phylogenetic tree as a measure of clade overrepresentation. We used the *node_analysis* function of the 'nodiv' package, with 999 randomizations (Borregaard et al., 2014). This function goes through each node in the phylogeny, compares the distributions of the two descendant nodes and compares the result to a null model (e.g. 'quasiswap' algorithm). This highlights nodes where major distributional divergence have occurred (high geographical node divergence GND scores). GND scores quantify the distributional divergence between the two daughter lineages descending from a given node, which oscillates between 0 and 1 (Borregaard et al., 2014). This analysis was run separately for each of the sampling areas (Murray Darling Depression, Brigalow Belt South and South Western Slopes) and including all areas together. Since we obtained identical results (the same nodes were consistently identified as the top-ranked ones regardless of the data subset), we only report the results obtained jointly.

2.6 | Phylogenetic and functional structure of local assemblages

To explicitly model stochastic assembly processes, we generated an expectation of community structure under a species-neutral model of colonization and local extinction (DAMOCLES model) that accounts for inferred phylogenetic history of past speciation events (assumed to be allopatric) (Pigot & Etienne, 2015). Because allopatric speciation reduces the probability that a descendant lineage will be present



within any given local community, older species with more opportunity for colonization or those descended from more slowly diversifying branches are more likely to be locally present. This non-random variation in the probability of community membership translates into non-random phylogenetic structure, with co-occurring species less closely related than expected if species were randomly sampled from across the tips of the tree (Pigot & Etienne, 2015). In the DAMOCLES model, local assemblages evolve over time by speciation (λ), colonization (γ) and local extinction (μ), where species at any time can exist in one of two geographical states (i.e. locally absent = 0 or locally present = 1). A transition from 1 to 0 implies that a species became locally extinct (range contraction), and a transition from state 0 to state 1 implies that a species is added to a local community via colonization (range expansion) (Pigot & Etienne, 2015). The phylogenetic structure of assemblages was quantified using the mean phylogenetic distance (MPD) and mean nearest taxon distance (MNTD) metrics (Mazel et al., 2016). We summarized the results using standardized effect sizes (ses), which compare the value of an assemblage to mean expected values obtained from simulating 100 null communities under an equal-rates null model (Pigot & Etienne, 2015).

Since the prevalence of *Manorina* honeyeaters differed among habitats, which might lead to indirect (i.e. mediated by the presence/absence of this strong interactors) habitat differences, we also tested for differences in phylogenetic structure between habitat types for plots without colonies of *Manorina*.

Similarly, we computed the functional analogues of the above-mentioned phylogenetic metrics, MFD (that averages functional distances between all pairs of co-occurring taxa) and MNFD (which averages distances in functional characters for pairs of taxa). Both metrics of functional structure were obtained using a Euclidean distances matrix (computed from the seven traits) as implemented in the R package *picante* (Kembel et al., 2010). Since DAMOCLES yields negative MPD and MNTD structure measurements, we multiplied results by -1, which allowed us to compare these with values obtained from *picante* using the 'sample.pool' null model. The values of MPD/MFD and MNTD/MNFD indicate the three possible patterns: MPD (or MFD) and MNTD (or MNFD) values <-1.96 indicate clustering; $x > 1.96$ indicate overdispersion, and values between -1.96 and 1.96 indicate a random pattern.

Lastly, we computed the community-weighted mean (CWM) of (log-transformed) body mass, relative beak size and HWI (i.e. dispersal capacity) using the R package 'BAT' (Cardoso et al., 2015). CWM represents the sum of each species trait value weighted by its relative abundance in the community (de Bello et al., 2007). Thus, by averaging trait values over a community, we quantitatively describe variations in morphological trait composition.

We evaluated the influence of habitat type and the presence of *Manorina* species on community structure measures using ANOVAs and Kruskal-Wallis tests. There was no significant interaction between both factors for any of the analysed variables (i.e. the sign and magnitude of the effect of the presence of despots was consistent across habitat types). Therefore, to keep the analyses as simple as possible, we pooled together communities belonging to different

habitats. Similarly, since the effect of the presence of *Manorina* species did not depend on the geographical region (interaction effects were not statistically significant) and the response variables did not differ among regions, all communities were analysed jointly.

2.7 | Trait-based community assembly

We used the STEPCAM approach devised by van der Plas et al. (2015) to determine the relative contribution of stochasticity, limiting similarity and habitat filtering to community assembly in our study area ($n = 82$ local assemblages). The STEPCAM model is a STEPwise Community Assembly Model that applies three types of processes to select species from the species pool into the local community. Starting with all observed species in the dataset, these are removed in a step-wise fashion until reaching the number of species observed in the local community. Removal of species occurs (i) because their traits are too similar to those of the remaining species ('limiting similarity'), (ii) because their traits are too dissimilar from the observed mean trait distribution in the community, which is assumed to be the trait optimum for that habitat ('habitat filtering') or (iii) due to a stochastic event, which results in a random removal step, where the probability of removal is inversely proportional to the number of local communities in the dataset where the species is observed, which is used as a proxy for the species pool ("dispersal assembly", DA) (Janzen et al., 2017). The STEPCAM model was fitted using approximate Bayesian computation, in which, using the STEPCAM model, data are simulated and compared with the observed data. In each model, first dispersal assembly steps are run, then habitat filtering steps and finally limiting similarity steps. The implemented order assumes a sequence of community assembly following Cornwell and Ackerly (2009). STEPCAM models were run with the STEPCAM package (Janzen & van der Plas, 2016) with a final acceptance rate of 1 in 10,000 simulated communities following Hauffe et al. (2016).

3 | RESULTS

3.1 | Patterns of overrepresentation in Meliphagidae assemblages

Most nodes showed a low to moderate degree of node allopatry (GND score: 0.25–0.50) (Figure 2). Only a single node (node 57) presented a score higher than 0.55 (GND = 0.59), which represents the basal split between acanthiszids (thornbills and gerygone warblers) and honeyeaters (Figure 2). Two nodes in the phylogenetic tree presented medium (>0.4) GND scores (Figure 2). The second-ranked node (node 58; GND = 0.51) represents the separation of the major clades within the Meliphagidae, with *Lichenostomus*, *Manorina* (miners), *Anthochaera* (wattlebirds) and *Ptilotula* (among others) on one side and *Melithreptus*, *Philemon* and *Myzomela* (among others) on the other. The third-ranked node in terms of distributional change

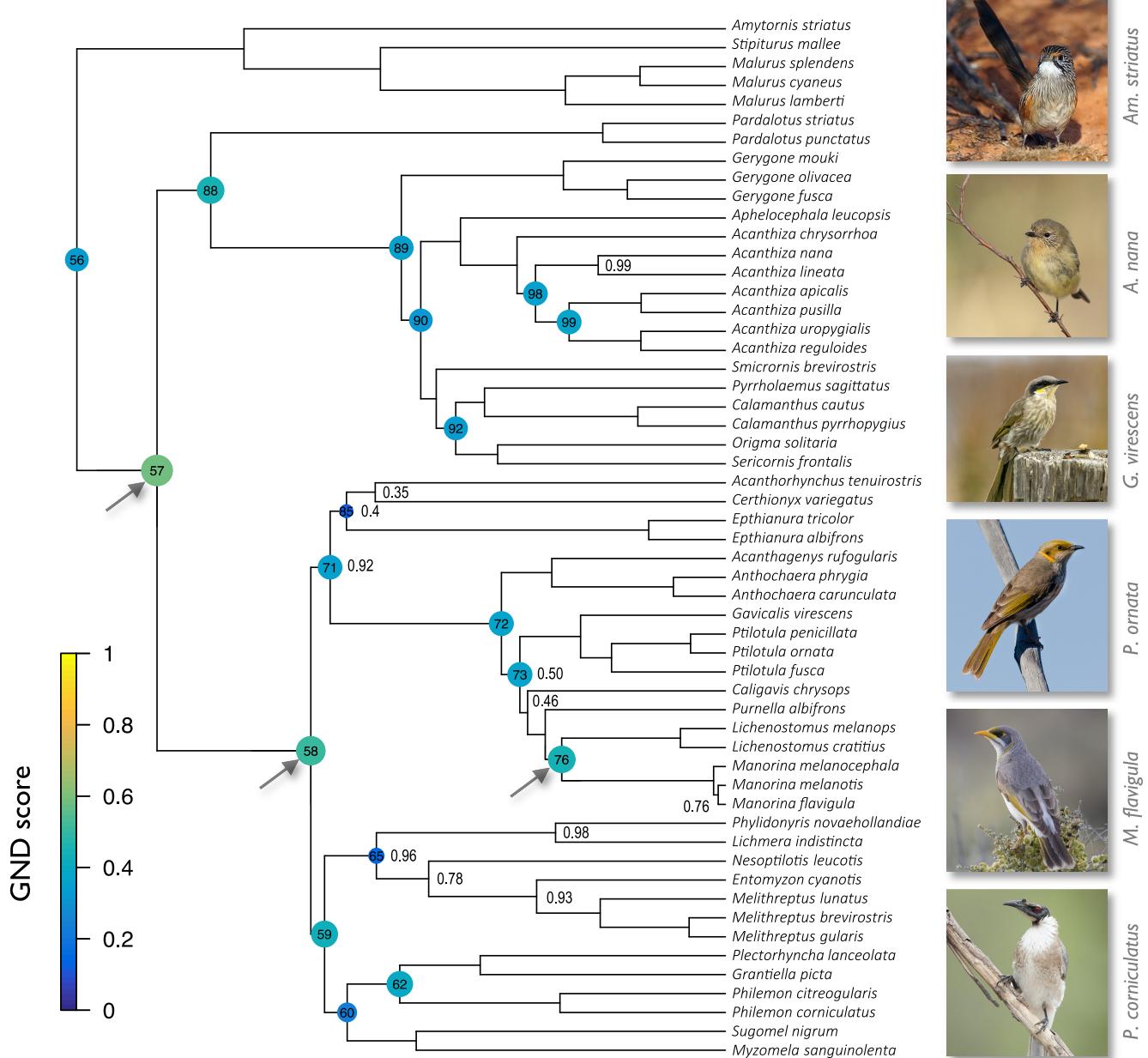


FIGURE 2 Geographical node divergence (GND) scores for Meliphagidae communities from Southeastern Australia obtained using node-based analysis (Borregaard et al., 2014). The colour scale and symbol sizes are proportional to GND for each node. Node numbers indicate node identity. The arrows indicate the three top-ranked nodes (node 57, 58, and 76; see main text). Tree adapted (all tips not present in our study region were pruned) from the time-calibrated phylogeny inferred by Marki et al. (2017). All nodes have a support (Bayesian posterior probability, PP) = 1.0, except where noted.

is a relatively young node (node 76; GND = 0.44), which separates *Lichenostomus* from *Manorina* species.

3.2 | Phylogenetic structure of Meliphagidae assemblages

The number of species that co-occur in local assemblages was quite similar in the three habitats (cleared, average: 10.9 ± 1.70 , species, range: 6–16; mallee, average: 10.2 ± 2.26 , species, range: 7–14;

woodland: ± 2.10 , 10.3 species, 6–13). Meliphagidae assemblages with the presence of miners were characterized by exceptionally high rates of local colonization and extinction regardless of the habitat type (Figure 3). When only considering those plots without the presence of *Manorina* species, we did not find statistically significant differences among habitat types in either colonization (Kruskal-Wallis test; $H = 4.01$, $p = 0.13$) or extinction rates ($H = 2.95$, $p = 0.23$) (Table 1). Colonization and local extinction rates were highly correlated in all habitat types, indicating that assemblages with rapid (or slow) colonization rates also exhibited rapid (or slow) rates of

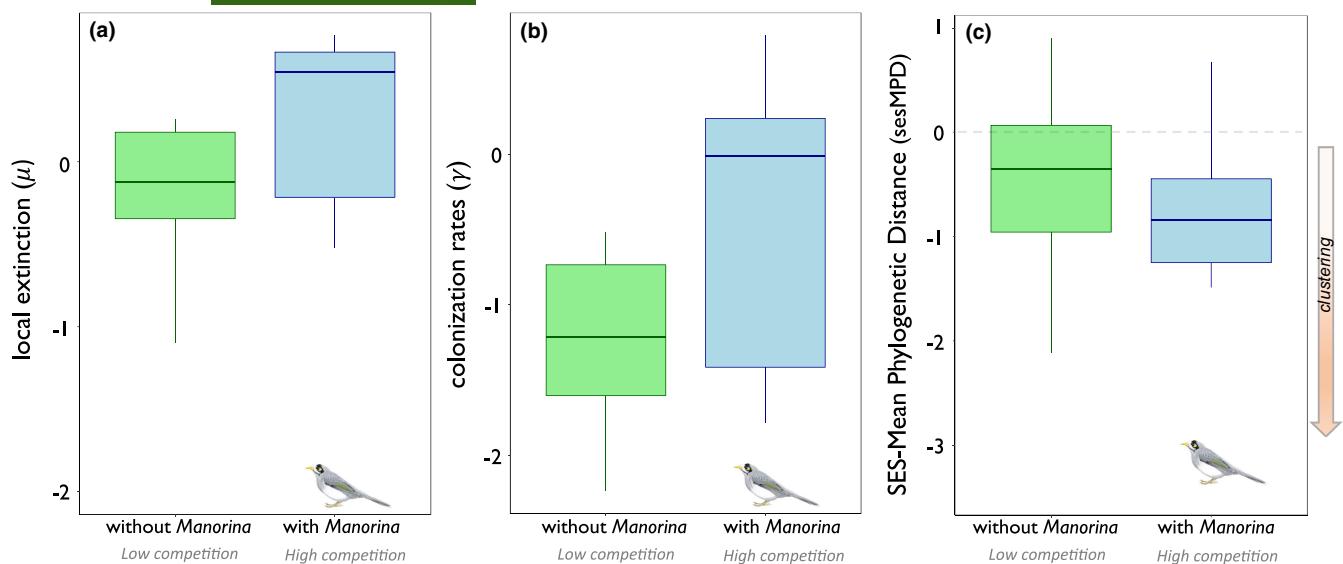


FIGURE 3 Differences in (a) colonization rates, (b) local extinction rates and (c) standardized effect size-mean phylogenetic distance [sesMPD] between assemblages with and without the presence of *Manorina* species in Southeastern Australia. Note that the values of colonization and extinction were log-transformed for illustrative purposes.

TABLE 1 Habitat differences in colonization and local extinction rates (per lineage per million years), phylogenetic structure (standardized effect size-mean phylogenetic distance [sesMPD] and standardized effect size-mean nearest taxon distance [sesMNTD]), and functional structure (standardized effect size-mean functional distance [sesMFD] and standardized effect size-mean nearest functional distance [sesMNFD]) for bird assemblages without the presence of *Manorina* species in Southeastern Australia. Means \pm SD [range] are given.

DAMOCLES dynamic null model				Random draw (picante)		
Within-assemblage colonization and local extinction rates		Phylogenetic structure		Functional structure		
	Extinction, μ	Colonization, γ	sesMPD	sesMNTD	sesMFD	sesMNFD
Cleared (n = 24)	0.859 \pm 0.980 [0.044–3.299]	0.086 \pm 0.087 [0.007–0.303]	0.455 \pm 0.723 [-0.506–2.116]	0.315 \pm 0.682 [-1.223–1.420]	0.448 \pm 1.169 [-2.478–2.555]	1.004 \pm 1.166 [-1.985–2.670]
Mallee (n = 18)	1.128 \pm 1.134 [0–2.929]	0.108 \pm 0.091 [0.006–0.265]	0.470 \pm 0.701 [-0.900–1.432]	0.859 \pm 0.887 [-1.505–2.016]	0.420 \pm 0.917 [-1.199–2.307]	0.240 \pm 0.881 [-1.715–1.635]
Woodland (n = 16)	1.690 \pm 1.143 [0–2.979]	0.134 \pm 0.092 [0.018–0.276]	0.429 \pm 0.831 [-0.902–2.099]	0.216 \pm 0.488 [-0.546–0.947]	0.400 \pm 0.861 [-0.900–1.775]	0.467 \pm 0.909 [-0.973–1.753]

extinction (cleared $r = 0.968$, $p < 0.001$; mallee $r = 0.968$, $p < 0.001$; woodland, $r = 0.959$, $p < 0.001$).

When we compared observed diversity to what was expected under the DAMOCLES null model, we found that virtually all assemblages presented negative ses-MPD and ses-MNTD values suggesting clustering tendencies in the phylogenetic structure of the Meliphagides. Only in a few cases the empirical values were significantly lower than expected by the DAMOCLES model, which indicates the prevalence of random patterns (Figure 4a,b). That is, with a couple of exceptions, all assemblages were consistent with the expectation from a null model of allopatric speciation and equal rates of colonization and local extinction. Those assemblages with the presence of *Manorina* species showed a higher degree of clustering than those in which no miners were detected at deep (sesMPD: $F_{1,76} = 6.17$, $p = 0.01$) (Figure 3) but not at shallow levels of the branching structure (sesMNTD: $F_{1,76} = 0.33$, $p = 0.57$). We did not

find habitat differences statistically significant for any metric (MPD, MNTD) when only considering those plots without the presence of despots (sesMNTD: $H = 3.40$, $p = 0.18$; sesMPD: $H = 0.19$, $p = 0.90$) (Table 1).

3.3 | Functional structure of Meliphagides assemblages

Similar to what was observed in terms of phylogenetic structure, only a few assemblages (8% and 13% for sesMFD and sesMNFD, respectively) were different from that expected by the random draw null model, with most of these significantly structured assemblages showing functional clustering (Figure 4c,d). About half of assemblages presented positive ses-MFD and ses-MNFD values indicating a higher preponderance of overdispersion tendencies in

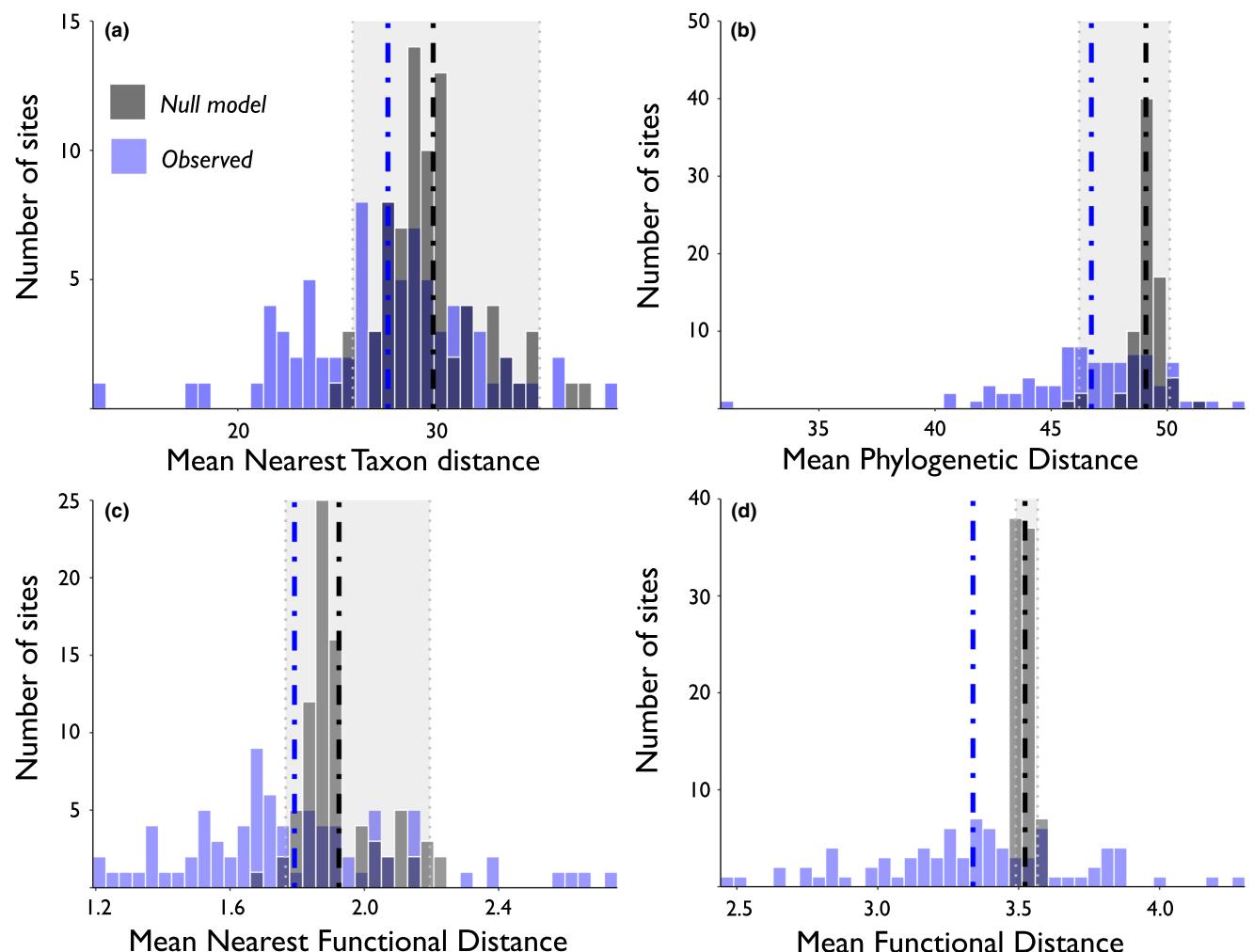


FIGURE 4 Observed (blue) and expected values under a null model (black) across the 82 study sites (bird assemblages) in Southeastern Australia for: (a) (tip-level) Mean nearest taxon phylogenetic distance [MNTD]; (b) (root-level) Mean phylogenetic distance [MPD]; (c) (tip-level) Mean nearest taxon functional distance [MNFD] and (d) (root-level) Mean functional distance [MFD]. Vertical dot-dashed lines indicate mean distribution for observed (blue) and null model (black) values. Grey background area represents 95% confidence intervals for null expectations. For MNTD and MPD, we used a dynamic model of community assembly (DAMOCLES) as null model. For MNFD and MFD, we used the 'sample.pool' null model available in the *picante* package.

the functional structure of the Meliphagidae in comparison with that observed from a phylogenetic perspective.

We did not find significant differences in terms of functional structure between bird assemblages with ($\text{sesMFD} = -0.693 \pm 1.010$; $\text{sesMNFD} = -0.619 \pm 1.054$) and without ($\text{sesMFD} = -0.426 \pm 0.998$; $\text{sesMNFD} = -0.281 \pm 1.192$) *Manorina* species ($F_{1,81} = 1.20, p = 0.27$ and $F_{1,81} = 1.62, p = 0.20$, respectively). After excluding those plots with the presence of miners, we found that assemblages from cleared plots exhibited a higher degree of terminal ($\text{sesMNFD} = F_{2,57} = 3.15, p = 0.05$), but not basal, functional clustering than those from eucalypt woodlands and mallee habitat ($\text{sesMFD} = F_{2,57} = 0.01, p = 0.98$) (Table 1).

Values of Pagel's λ for the analysed traits suggested that the evolution of these functional traits is conserved (Table 2). Both community-weighted body mass and dispersal capacity were greater in communities with the presence of miners in comparison with communities where these were not recorded (log-mass: $F_{1,81} = 23.73$,

TABLE 2 Quantification of the phylogenetic signal using Pagel's λ values for each selected trait.

	λ	p-value
Body mass (log)	1	<0.001
HWI	0.952	<0.001
Beak size (residual)	0.970	<0.001
PC1 _{diet}	0.848	<0.001
PC2 _{diet}	0.877	<0.001
PC1 _{foraging}	0.880	<0.001
PC2 _{foraging}	0.890	<0.001

$p < 0.001$; HWI: $F_{1,81} = 7.70, p = 0.006$) (Figure 5). There were no significant differences in community-weighted beak size between the two categories ($F_{1,81} = 0.54, p = 0.46$).

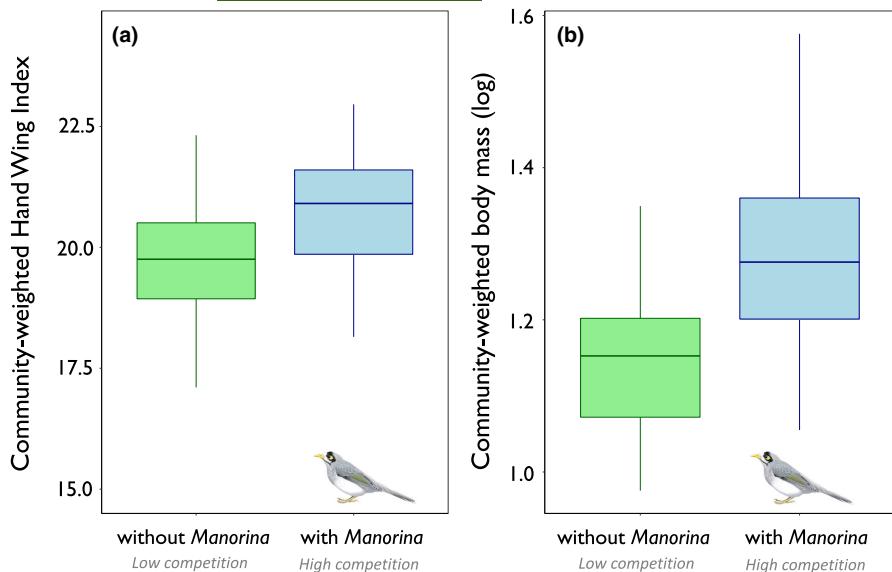


FIGURE 5 Differences in dispersal capacity (quantified using the Hand Wing Index, HWI) and community-weighted body mass (log-transformed) between bird assemblages with and without the presence of *Manorina* species in Southeastern Australia.

3.4 | Untangling the contribution of different community assembly processes

We found differences between assemblages with and without the presence of despotic species when fitting STEPCAM to the trait distributions of the study plots. We observed a lower contribution of stochastic assembly (17.5 vs. 23.8%; $F_{2,76} = 5.67, p = 0.02$) and a trend towards a higher contribution of filtering steps in assemblages with the presence of miners (15.3 vs. 11.4%; $F_{1,76} = 3.14, p = 0.08$). We did not find significant differences between plots with the presence of miners (*Manorina* spp.) and those in which these were not recorded in terms of contribution of limiting similarity ('competition') steps (3.4 vs. 2.3%; $F_{1,76} = 2.17, p = 0.14$).

The average contribution of stochastic assembly steps was lower in the cleared habitat (19.3%) in comparison with that of the remaining habitat categories after excluding those plots with the presence of miners (mallee: 27.3%; woodland: 26.8%) ($F_{2,54} = 3.69, p = 0.03$). There were no statistically significant differences among habitat types in contribution of habitat filtering (cleared: 14.4; mallee: 9.0%; woodland: 9.6%) ($F_{2,54} = 1.86, p = 0.16$) or limiting similarity steps (cleared: 2.6; mallee: 1.9%; woodland: 2.0%) ($F_{2,54} = 0.28, p = 0.75$).

4 | DISCUSSION

Community assembly occurs on a continuum between a niche-based perspective and a neutral (stochastic) perspective. Within this continuum, different factors including lineage history, biotic interactions and abiotic conditions among others act additively or interactively over different temporal and spatial scales (Emerson & Gillespie, 2008). Consequently, unravelling the influence of each of these components on the functional and phylogenetic structure of biotic communities constitutes a challenge. Here, we applied recently developed methods to ascertain the influence of historical contingencies in driving the structure and composition of local

assemblages and explicitly examine the relative contribution of deterministic and stochastic processes in community assembly. We focused on communities of Meliphagidae, which represents one of the largest and most conspicuous Australasian bird radiations. We found evidence for phylogenetic clustering in the studied local assemblages using DAMOCLES (i.e. after accounting for assembly history) for which we could not reject neutral processes of community assembly. However, we also noticed the existence of exceptionally high rates of colonization and local extinction, and a higher degree of basal phylogenetic clustering in assemblages with the presence of *Manorina* honeyeaters, which suggests that species interactions may also play an important role as drivers of community structure.

4.1 | Patterns of overrepresentation in Meliphagidae assemblages

The clade-level (node-based) analysis did not detect any node with a GND score > 0.6 indicating that our assemblages are not overrepresented by descendant species of particular sister clades. In other words, local assemblages from different habitats (cleared, eucalypt woodland or mallee) are not composed exclusively of certain subclades, but include species from several lineages (i.e. they are phylogenetically unstructured). This can explain the absence of significant differences in phylogenetic structure among habitat categories (see more below). The GND scores revealed that significant intranodal differences in environmental preferences were limited to a relatively small number of nodes. The most basal of these nodes corresponds to the split between the meliphagids, which tend to occupy more xeric habitats, and the acanthizids (Australian warblers), which inhabit colder and wetter environments. Within the Meliphagidae, we found moderate node allopatry in the split between the two major subclades. The clade comprising *Gavicalis*, *Lichenostomus*, *Ptilotula*, *Anthochaera* is mostly dominated by forest and woodland species though it does include open habitat genera such as *Manorina* and



dry country genera such as *Acanthagenys*. The clade comprising *Philemon*, *Sugomel*, *Plectorhyncha* and *Phylidonyris* is more arid and open country adapted though some members of *Melithreptus* are forest species. We also found substantial distributional change in a node that separates *Lichenostomus* and *Manorina* species suggesting that these two subclades are more segregated in geographical or environmental space than expected by chance. *Lichenostomus cratitius* and *L. melanops* show a preference for woodlands with dense shrubby understory and their populations have declined following clearing and degradation of habitat (Higgins et al., 2020a, 2020b). With the exception of the geographically restricted black-eared miner (typical of mature intact tracts of semi-arid woodlands and mallee), *Manorina* species have less restrictive habitat preferences. For instance, the widely distributed noisy miner occupy dry open forests and woodlands, especially grassy associations with few or no shrubs in understory. Thus, the presence of *Manorina* species is one of the factors that exerts a greater influence on the structure of assemblages.

4.2 | Patterns of phylogenetic and functional structure in Meliphagidae assemblages

According to our results, phylogenetic and functional structure measures showed a random pattern. The greater incidence of negative MPD/MFD and MNTD/MNFD scores indicates that Meliphagidae assemblages of southeastern Australia tend towards a clustered structure. The observed phylogenetic signal for all the analysed traits can explain the congruence between phylogenetic and functional structure measures. Our findings agree with previous studies carried out exclusively on honeyeaters where the existence of phylogenetic and phenotypic underdispersion was attributed to ecological processes such as environmental filtering (Miller et al., 2013; Miller, Wagner, et al., 2017). The results we obtained using DAMOCLES indicate that a priori species-neutral processes considered in this dynamic model may be enough to explain the existence of such a pattern (Pigot & Etienne, 2015). Community assembly can be affected by historical events in the form of speciation and extinction, dispersal and colonization, and, for example it has been proposed that rapid speciation and/or slow extinction rates would produce a phylogenetic clustering structure (Cardillo, 2011). However, our results do not exclude the potential effect of other processes (interspecific interactions) on community assembly and species co-occurrence.

DAMOCLES yielded extremely rapid extinction rates in those communities with the presence of *Manorina* species, which suggests that this model is not only sensitive to species-neutral factors. Regarding this, Mortelliti et al. (2016) previously showed that noisy miners increased extinction risk and decreased colonization probability of the species they exclude, concluding that this species is interfering with long-term spatial population dynamics (i.e. colonization/extinction) of other birds. The estimates we obtained in this study indicate that strong species negative interactions (i.e. ecological contemporary

processes) can also influence rates of colonization and local extinction across species. Thus, the ability of DAMOCLES to tease apart the influence of local species interactions from that of historical (evolutionary) processes in driving assemblage structure is limited as previously suggested (see also Pinto-Ledezma et al., 2019). Our results showed that the presence of *Manorina* species increases the level of phylogenetic clustering across the community (tree-wide), which means that these aggressive competitors lead to an impoverishment of communities in terms of lineage diversity of deep-branching clades. Conversely, when performing tip-wise comparisons, sesMNTD values were closer to the null expectation; the absence of terminal clustering indicates that the presence of *Manorina* honeyeaters has a weaker effect across close relatives in local communities. The existence of basal phylogenetic clustering in those assemblages where at least one *Manorina* species was detected shows the relevance of miners as drivers of community composition in southeastern Australia even at small phylogenetic scale. Since clustering patterns tend to be more prevalent at large scales and a deep phylogenetic depth (Parmentier et al., 2014; Puga-Caballero et al., 2022), we hypothesize that had we expanded our analysis to include other bird families (e.g. robins Petroicidae, whistlers Pachycephalidae, woodswallows Artamidae and finches Estrildidae), we would have obtained a stronger effect of miners on the phylogenetic structure of assemblages. Thus, these despotic competitors not only reduce taxonomic diversity as previously shown (Howe et al., 2013), but also the variation in evolutionary history among species.

Although we did not find statistically significant differences between plots with and without the presence of *Manorina* species in terms of functional structure, we observed using CWM that communities with the presence of despots are made up of species with greater dispersal capacity and larger in size. These findings support what was reported by Howe et al. (2013), who observed that increased densities of noisy miners result in a loss of species diversity and homogenization of morphological characteristics of bird assemblages.

When removing the effect of interference competition by excluding those assemblages with the presence of miners, we did not find significant habitat differences in terms of phylogenetic structure. This suggests that differences in prevailing environmental conditions among the three habitat types are not very pronounced. Thus, habitat-specific conditions may have only a limited influence on the phylogenetic structure of bird communities across the study area. This corroborates results from the DAMOCLES dynamic null model and suggests that neutral processes could be driving homogenization of species diversity across open and semi-open habitats in southeastern Australia. In terms of functional structure, we found that assemblages from cleared plots (rangelands) exhibited a higher degree of terminal clustering than those from the remaining two habitat types. This finding suggests that some species that exclusively depend on trees for nesting and/or feeding (i.e. canopy species) are filtered out from these treeless environments. In open woodlands and woody pastures, just a few trees can provide the conditions for a significant increase in species as scattered trees provide nesting



habitats (e.g. tree holes), enhance the structural complexity of the environment and may have a positive effect on food resources (e.g. insects) for birds. Thus, farmland (open-habitat) and forest specialists can coexist in (semi-open) savannah-like ecosystems where trait diversity is expected to be highest (e.g. Flynn et al., 2009; Jakobsson & Lindborg, 2017).

4.3 | Relative importance of community assembly processes

Although it is widely accepted that both deterministic and non-deterministic processes act simultaneously to shape community assembly (Vellend, 2010), the number of studies that have explicitly tested the contribution of each is still anecdotal. In this study, we used the STEPCAM approach for this purpose. The results obtained suggest that Meliphagidae communities are mainly structured by both environmental filtering and dispersal limitation. The relative contribution of dispersal assembly steps was substantially lower in comparison with previous studies on cichlid and gastropod communities where the average importance of this process (i.e. restricted specimen exchange) was 72% and 80%, respectively (Hauffe et al., 2016; Janzen et al., 2017). In the cleared habitat, the relative importance of stochastic assembly was significantly lower than in the remaining habitat categories. It agrees with previous studies that have shown that stochastic factors (ecological drift, priority effects) play a less important role in shaping community assembly as environmental stress increases. That is, the contribution of deterministic factors (e.g. niche-selection) is higher in unpredictable and less productive habitats (Chase, 2007; Chase, 2010; García-Navas et al., 2021).

When comparing communities with and without the presence of *Manorina* species, we did not find differences in terms of contribution of 'limiting similarity' steps to community composition, but we found a trend towards a greater importance of filtering in those plots in which one of these despotic species was detected. Although the aggression of miners has been referred to as 'indiscriminate' (Davitt et al., 2018), some bird species are more adversely affected than others. Small passerines (<60 g) are excluded from the sites that they occupy and only large-bodied species remain in the presence of these strong interactors (Kutt et al., 2016; Thomson et al., 2015). It suggests that the presence of miners acts as a sieve and the composition of bird assemblages is homogenized where they occur (Hingee et al., 2022). In turn, these results evince that it is not straightforward to differentiate between patterns arising from environmental filtering processes from those arising from species interactions since, in some circumstances, the existence of strong competition (widespread community-level displacement) generates an imprint similar to that expected if the environment exerts an overwhelming influence on community assembly. That is, species of a community show similar morphological traits because (i) environmental conditions only allow for the establishment of species that are adapted to the specific habitat or (ii) only species with certain traits are able to avoid being displaced by competitors.

5 | CONCLUSIONS

Although interspecific competition is frequently evoked as a pervasive mechanism responsible for observed patterns of community assembly (overdispersion), demonstrating the existence of competition is quite difficult. Here, we take advantage of an extreme and well-documented case of competition to show that the imprints of this phenomenon on the structure of communities are hard to spot. Overall, our study supports the notion that interspecific interactions can give rise to patterns (clustered assemblages) identical to those caused by environmental filtering (Cadotte & Tucker, 2017; Mayfield & Levine, 2010).

The lack of an overwhelming overdispersion structure in our study may have to do with the fact that it is focused on a highly localized system where rates of local extinction may be high and the regional species pool is formed through colonization events rather than allopatric speciation (Pigot & Etienne, 2015). This coupled to the despotic effect of *Manorina* species can explain the observed patterns in this region. Our results add to the existing evidence on the exceptional power of this genus as controller of the constitution of avian assemblages. This study shows that this group of hyper-aggressive honeyeaters can also undermine the evolutionary potential of communities which has important consequences for stability and resilience of these ecosystems (Ford, 2011).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in: <https://doi.org/10.5061/dryad.g4f4qrfv0>.

ORCID

Vicente García-Navas <https://orcid.org/0000-0002-9362-2663>

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Les Christidis's research interests are mainly focused on the evolution and systematics of Australian birds.

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BIOSKETCHES

Vicente García-Navas is an evolutionary ecologist with broad interests in the evolutionary and ecological processes that shape patterns of occurrence and phenotypic variation in the wild.

Carlos Martínez-Núñez is a community ecologist. His research aims to understand how global change drivers shape the multiple dimensions of biological communities.

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