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RESEARCH ARTICLE

Spatial dynamics of coastal forest bird assemblages: the influence of landscape context, forest type, and structural connectivity

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Abstract
Context Complex structural connectivity patterns can influence the distribution of animals in coastal landscapes, particularly those with relatively large home ranges, such as birds. To understand the nuanced nature of coastal forest avifauna, where there may be considerable overlap in assemblages of adjacent forest types, the concerted influence of regional landscape context and vegetative structural connectivity at multiple spatial scales warrants investigation.
Objectives This study determined whether species compositions of coastal forest bird assemblages differ with regional landscape context or with forest type, and if this is influenced by structural connectivity patterns measured at multiple spatial scales.
Methods Three replicate bird surveys were conducted in four coastal forest types at ten survey locations across two regional landscape contexts in northeast Australia. Structural connectivity patterns of 11 vegetation types were quantified at 3, 6, and 12 km spatial scales surrounding each survey location, and differences in bird species composition were evaluated using multivariate ordination analysis.
Results Bird assemblages differed between regional landscape contexts and most coastal forest types, although *Melaleuca* woodland bird assemblages were similar to those of eucalypt woodlands and rainforests. Structural connectivity was primarily correlated with differences in bird species composition between regional landscape contexts, and correlation depended on vegetation type and spatial scale.
Conclusions Spatial scale, landscape context, and structural connectivity have a combined influence on bird species composition. This suggests that effective management of coastal landscapes requires a holistic strategy that considers the size, shape, and configuration of all vegetative components at multiple spatial scales.

Keywords Species composition · Avifauna · Structural connectivity · Coastal forests · Spatial scale · Landscape context · Keystone structure

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Introduction

Coastal ecosystems frequently consist of an interspersion of diverse vegetation types, resulting in a heterogeneous landscape mosaic that supports unique ecological communities (Sheaves 2009; Brittain et al. 2012). The individual habitats within this coastal ecosystem mosaic are linked in complex ways meaning that, rather than functioning as 'islands', they are influenced by processes occurring within and among adjacent habitats (Wiens 1995). Highly mobile species, such as birds, are likely to be particularly responsive to processes and patterns occurring among coastal habitats at scales of hundreds of meters to kilometers, tracking resource abundance throughout these heterogeneous landscapes. However, much of the research into processes influencing bird assemblages has focused on small-scale, within-habitat vegetation patterns (Grover and Slater 1994; Mohd-Azlan et al. 2014) rather than landscape-scale patterns and processes that are required to underpin a broader understanding (Radford et al. 2005; Martin et al. 2006; Radford and Bennett 2007; Galitsky and Lawler 2015).

Landscape-scale processes operate across local, regional, and inter-continental scales, making them inherently complex (Heffernan et al. 2014). As a result, the appropriate spatial scale for examining landscape processes will be unique to the study system being investigated, and will depend on a range of factors (Steffan-Dewenter et al. 2002; Brennan and Schnell 2005, 2007; Burgess and Maron 2016). However, the data needed to understand these factors is often limited. For instance, although understanding species' dispersal abilities is critical to determining the appropriate scales to study (Wiens 1995; Franklin and Noske 1999; Saab 1999; Westphal et al. 2003; Brennan and Schnell 2007), there is rarely sufficient knowledge of dispersal ability to allow unambiguous definition of the appropriate spatial scale. Furthermore, the distances a species is able to disperse can be different from daily movements of individuals, and therefore multiple spatial scales need to be considered when studying landscape processes and patterns. This is especially important when investigating the response of bird assemblages, where there is likely to be variation in dispersal and daily movement ability among species.

A structural connectivity view can improve understanding of the landscape-scale patterns and processes occurring within the coastal ecosystem mosaic (Luque and Saura 2012). Structural connectivity measures the size, shape, and configuration of habitats within a landscape mosaic, and can influence bird species distributions (Radford and Bennett 2007; Ziolkowska et al. 2014). Associated with structural connectivity is the concept of landscape context, which classifies the composition and structure of a study area's surrounding landscape. However, the definition of landscape context depends on the spatial extent of classification. For example, local-scale landscape contexts, defined as the number and type of habitats adjacent to a focal habitat, influence the composition, structure, and species richness of their bird assemblages (Riffell et al. 2003; Martin et al. 2006; Mohd-Azlan and Lawes 2011; Elliott et al. 2012; Galitsky and Lawler 2015). Additionally, landscape context is associated with bird species distribution when defined at smaller and larger spatial extents: within forests (interior vs. edge; Watson et al. 2004; Elliott et al. 2012) and at regional scales (vegetative patterns associated with rainfall or climate; Woinarski et al. 2000a; Shriver et al. 2004).

In northern Australia, the mix of habitats found within the coastal landscape mosaic is an important factor influencing bird species richness, abundance, and composition within individual coastal habitats (Woinarski et al. 2000a; Kutt 2007; Mohd-Azlan and Lawes 2011). Although there is some understanding of the individual importance of landscape context, spatial scale, and structural connectivity on coastal forest bird assemblages (Woinarski et al. 1988; Shriver et al. 2004; Watson et al. 2004; Kutt 2007; Mohd-Azlan and Lawes 2011; Mohd-Azlan et al. 2014), their interactive and synergistic effects have not been considered. Given the interconnected nature of forest and woodland habitats within coastal ecosystem mosaics, this study aimed to determine if: (1) the species composition of bird assemblages differ with regional scale landscape context or with forest type, (2) if bird species composition is influenced by structural connectivity patterns in the surrounding landscape, and (3) if spatial scale acts synergistically, i.e. if the influence of structural connectivity on bird assemblages depends on the spatial scale being considered.

Methods

Study area and site selection

The study area extended along approximately 630 km of north-eastern Australia's coastline and was comprised of three biogeographic regions: the Wet Tropics, the Brigalow Belt North, and the Central Mackay Coast (IBRA 2012; Fig. 1). The Wet Tropics experiences average annual rainfall of 2000–8000 mm, while both the Brigalow Belt North and Central Mackay Coast experience less at 590 and 1200–2000 mm, respectively. Vegetation in the Wet Tropics is comprised primarily of rainforest, wet sclerophyll forests and woodlands, shrublands, mangroves, grasslands, and sedges. In contrast, eucalypt and acacia woodlands, drier rainforests and sclerophyll forests, and more abundant grasslands and saltmarshes/flats characterize the Brigalow Belt North. Rainforest vegetation in the Central Mackay Coast replaces the more abundant eucalypt and acacia woodland vegetation in the Brigalow Belt North. Due to differences in vegetation patterns associated with climate in these biogeographic regions, two regional-scale 'landscape contexts' have been identified: the 'north-eastern tropics' (the Wet Tropics) and the relatively drier 'south-eastern tropics' (the Brigalow Belt North and Central Mackay Coast).

Ten survey locations were placed sequentially along the study area coastline, 50–150 km apart, with six locations in the 'SE tropics' and four locations in the 'NE tropics' (Fig. 1). Mangrove forests were chosen as the center-point for survey locations due to their location in the coastal intertidal, and their shared edge with other coastal forest types that are not restricted to the coastline (e.g. rainforest, eucalypt and *Melaleuca* woodlands). The survey locations were chosen for their similarity in mangrove patch size and shape (~500 ha in size and ~30,000 m of mangrove forest edge). The dominant coastal forest

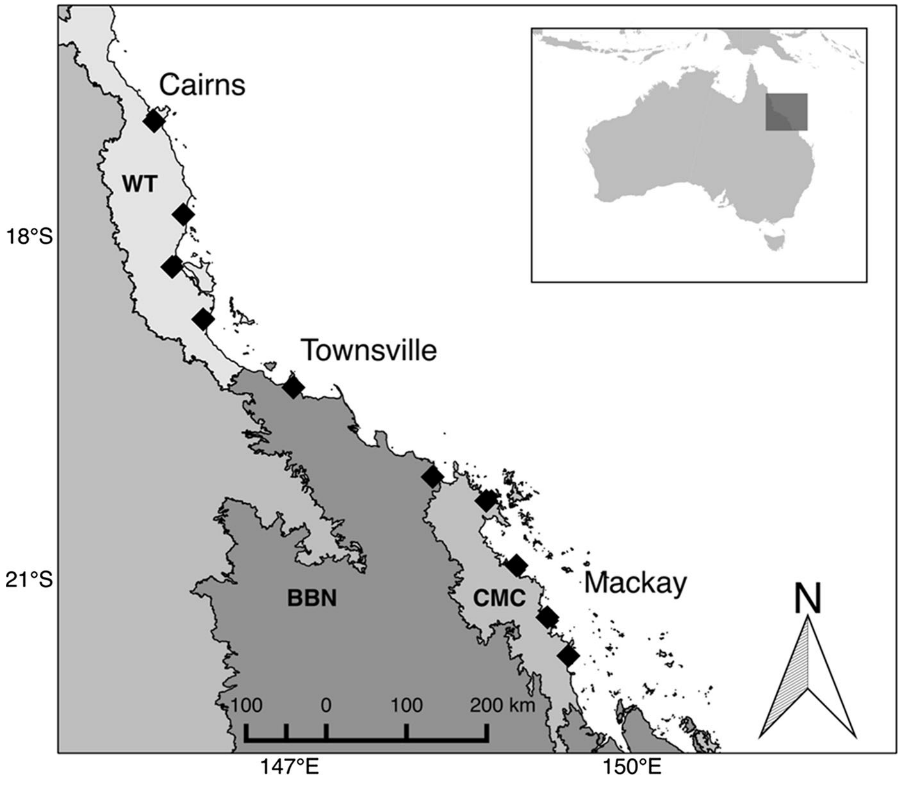


Fig. 1 Map of survey locations (*black diamonds*) along the north-east coast of Queensland, Australia. Boundaries of the three biogeographic regions are displayed. *WT* Wet Tropics (north-east tropical landscape context); *BBN* Brigalow Belt North and *CMC* Central Mackay Coast (south-east tropical landscape context)

types within a 2 km radius surrounding each focal mangrove patch were identified in ArcGIS (v.10.2). Within the mangrove patch, and in each adjacent, dominant coastal forest type, three points were haphazardly chosen for replicate point count bird surveys. This resulted in the following survey hierarchy: survey location, forest type (mangrove, eucalypt woodland, *Melaleuca* woodland, and rainforest), and point count survey (three within each coastal forest unit, total = 84).

Bird assemblage data

Point count bird surveys were conducted from dawn-10:00 h and from 14:30 h-dusk to determine bird species presence–absence in coastal forests throughout the year (each replicate point count was surveyed twice during each of the following time periods: January/February, June, and October 2015). Replicate point counts were at least 200 m apart, and all bird species seen or heard within a 50 m radius during a 10 min period were recorded. Birds flying over the point count area were not recorded, and all point count surveys were audio recorded with a Sony IC Recorder to confirm difficult-to-distinguish bird calls.

Structural connectivity patterns

Structural connectivity patterns (referred to from this point as 'connectivity') were quantified at three nested spatial scales (3, 6, and 12 km) at each of the ten survey locations using ArcGIS (v.10.2) with the Patch Analyst extension (Rempel et al. 2012). The range of spatial scales was chosen due to the sedentary/locally migratory nature of the majority of the coastal forest bird species considered in this study (for species list, see Supplementary material Appendix 1, Table A1). At each survey location, the center point for connectivity quantification was placed in a central position relative to point counts in all forest types and 1 km from the nearest coastline.

Eleven vegetation types in the coastal ecosystem mosaic were identified for connectivity analysis: eucalypt woodland, freshwater, mangrove, *Melaleuca* woodland, rainforest, vegetation-devoid ('SandRockMud'), shrubland, grassland, *Casuarina*/*Allocasuarina* forest, cleared urban/agricultural land, and *Acacia* forests and woodlands (see Table 1 for description). Four standard FRAGSTATS landscape metrics were measured for each vegetation type present at each nested spatial scale (TLA: total landscape area of patches (ha); NumP: number of patches; TE: total edge

Table 1 A brief description of the 11 vegetation types identified for connectivity analysis (NVIS 2012)

Habitat	Description
Eucalypt woodland	Open forests and woodlands comprised primarily of *Eucalyptus* trees, with grassy or shrubby understories.
Freshwater	Freshwater features, both natural and artificially constructed, that are generally devoid of vegetation.
Mangrove	Intertidal forests, ranging in height from shrublands to tall forests.
Melaleuca woodland	Open forests and woodlands comprised primarily of *Melaleuca* tree species, and found in coastal and sub-coastal areas near wetlands, rivers, or swamps.
Rainforest	Closed forests including: dry rainforest, tropical rainforest, vine thickets, and warm temperate rainforest types.
Vegetation-devoid ('SandRockMud')	Areas naturally devoid of vegetation including: bare ground, sand dune, claypan, and saltmarsh/flat.
Shrubland	Includes a broad range of shrub species (e.g. *Banksia*, *Bursaria*, *Grevillea*, *Nitraria*, etc.), primarily less than 3 m in height.
Grassland	Dry and wet grasslands, including tussock grasslands, herblands, and sedgelands.
Casuarina/*Allocasuarina* forest	Open forests of *Casuarina* and *Allocasuarina* trees that are primarily associated with coastal foredunes in eastern Australia.
Cleared urban/agricultural land	Areas with all or most native vegetation removed including urban areas, cropland, grazing land, and areas dominated by introduced species.
Acacia forests and woodlands	Open and closed forests and woodlands composed primarily of *Acacia* tree species, with understory species comprised primarily of low shrubs and herbaceous plants.

of patches (m); and MNN: mean nearest neighbour distance between patches (m); McGarigal et al. 2012). Together, these landscape metrics represent connectivity in the landscape that occurs at nested spatial scales surrounding each survey site. At the 3 km spatial scale only 1–2 sites had freshwater and *Casuarina/Allocasuarina* forest vegetation, and therefore these vegetation types were removed from further analysis at this spatial scale. Vegetation data used for quantifying connectivity were sourced from the National Vegetation Information System (NVIS 2012).

Data analysis

Coastal forest bird species composition

A Jaccard distance matrix of bird species presence–absence data (pooled over all three sampling periods) was used in non-metric multidimensional scaling (nMDS) to create an ordination plot of bird species presence–absence data at each survey site. Centroid ellipses (95% confidence interval) were used to display site groupings by coastal forest type and landscape context. A two-factor permutational multivariate analysis of variance (PERMANOVA) and subsequent pairwise comparisons were used to determine differences in bird species composition associated with coastal forest type and landscape context (Anderson 2001).

Connectivity variables and bird species composition

Principal components analysis (PCA) was used to reduce the four landscape metrics measured (TLA, NumP, MNN, and TE) into one connectivity variable for each of the 11 vegetation types, while simultaneously eliminating multi-collinearity. The landscape metrics were normalized prior to conducting the PCAs. The first principal component of each PCA became the connectivity variable for each vegetation type, explaining the majority of the variability in structural connectivity among the ten survey locations, at each spatial scale (see Supplementary material Appendix 2, Table A2 for the proportion of variance in structural connectivity explained by the first principal component of each PCA). Fitted vectors of the 11 connectivity variables for each spatial scale (3, 6, and 12 km) were overlaid onto the ordination surface to determine if they were correlated with bird species composition (Oksanen et al. 2015).

Connectivity variables and individual landscape metrics

Surface fitting was used to determine the strength of the relationship between bird species composition and individual landscape metrics (MNN, NumP, TE, and TLA) of the connectivity variables that were correlated with the ordination surface ($p < 0.05$). The fitted smooth surfaces were calculated using generalized additive models (GAM) with thin-plate splines (Oksanen et al. 2015).

PCA was used to provide a summary figure relating the R^2 values from the fitted smooth-surfaces of individual landscape metrics to the connectivity variables with which they were associated. This allowed visualization of the relationship between landscape metric importance (i.e. the R^2 value) and the vegetation type and spatial scale of the connectivity variables that were correlated to the bird ordination.

Connectivity variables and landscape context

To understand how connectivity variables that were correlated to the bird ordination differed between landscape contexts, the average values of their individual landscape metrics (TLA, NumP, TE, and MNN) were calculated and their proportions were compared between north-east and south-east tropical landscape contexts.

Statistical analyses were performed in R (v 3.1.2, R Core Team 2015) with the package 'vegan' (Oksanen et al. 2015) and in PRIMER statistical software (v 6, Clarke and Gorley 2006).

Results

Coastal forest bird species composition

Ninety-three bird species were observed during the study, however species with less than two observations were considered unrepresentative of the bird assemblages as a whole and were not retained for analysis (Supplementary material Appendix 1, Table A1). The most common bird species observed were the yellowspotted honeyeater (*Meliphaga notata*), mistletoebird (*Dicaeum hirundinaceum*), and olive-backed sunbird (*Nectarinia jugularis*). A two-dimensional nMDS ordination (stress = 0.22) with 95% confidence interval ellipses around group centroids shows bird species composition by coastal forest type (Fig. 2a) and by landscape context (Fig. 2b). Bird species composition in mangrove forests differed from other coastal forest types (Fig. 2a) and between north-east and south-east tropical landscape contexts (Fig. 2b). The variations in bird species composition were confirmed with a two-factor PERMANOVA (Supplementary material Appendix 4, Table A4). There was no interactional effect between landscape context and coastal forest type on bird species composition (pseudo-$F_{3,20} = 1.05$, $p = 0.34$). However, individually, both landscape context and coastal forest type influenced bird species composition (landscape context: pseudo-$F_{1,20} = 2.06$, $p = 0.002$; habitat: pseudo-$F_{3,20} = 2.09$, $p = 0.001$; Fig. 2).

Pairwise comparisons further examined differences in bird species composition between coastal forest types, and corroborated the patterns that were visually identified with 95% confidence interval ellipses in the bird ordination (Fig. 2a). Pairwise comparisons indicated that mangrove bird assemblages were distinct from nearby rainforest ($t = 1.65$, $p = 0.002$), eucalypt woodland ($t = 1.54$, $p = 0.002$), and *Melaleuca* woodland bird assemblages ($t = 1.54$, $p = 0.003$; Fig. 2a). Eucalypt woodland and rainforest bird assemblages were also distinct from each other ($t = 1.30$, $p = 0.031$). In comparison, the species composition of *Melaleuca* woodland bird assemblages were similar to both rainforest and eucalypt woodland bird assemblages (*Melaleuca*, rainforest: $t = 1.21$, $p = 0.121$; *Melaleuca*, *Eucalyptus*: $t = 0.82$, $p = 0.782$; Fig. 2a).

Connectivity variables and bird species composition

Vector fitting at each spatial scale demonstrated that connectivity variables were primarily correlated to the second axis of the bird ordination, which differentiates coastal bird species composition by landscape context (i.e. NE tropics vs. SE tropics, Fig. 3). The correlation of connectivity variables to the bird ordination depended on the spatial scale being considered (Fig. 3). At the 3 and 6 km spatial scales, two connectivity variables (i.e. *Melaleuca* and SandRockMud (Fig. 3a), and *Melaleuca* and grassland (Fig. 3b); respectively) were correlated to the bird ordination. Alternatively, at the 12 km spatial scale, four connectivity variables were correlated to the bird ordination (i.e. SandRockMud, *Melaleuca*, rainforest, and shrubland; Fig. 3c).

Connectivity variables and individual landscape metrics

Surface fitting revealed that most landscape metrics had a linear relationship to the bird ordination, and therefore the linear vector fitting procedure (Fig. 3) was appropriate for overlaying their connectivity variables to the bird ordination. However, at the 12 km spatial scale, the relationship between the bird ordination and rainforest total landscape area (TLA; Fig. 4a) and SandRockMud total edge (TE; Fig. 4b) was not linear. Therefore, the surface fitting procedure was applied to these variables at the 12 km spatial scale, showing their association with bird species composition in different coastal forest types (Fig. 4). The highest values of rainforest TLA were associated with bird species composition in mangrove, rainforest, and *Melaleuca* survey sites, whereas the lowest values of rainforest TLA were associated primarily with eucalypt woodland survey sites (Fig. 4a). Alternatively, the lowest values of SandRockMud TE were associated with bird species composition in rainforest survey sites (Fig. 4b).

PCA provided a summary figure of the importance of individual landscape metrics (i.e. their R^2 values) to the connectivity variables that were correlated to the bird ordination (Fig. 5; Supplementary material Appendix 3, Table A3). Principal components 1, 2, and 3 cumulatively explained 98.5% of the variation in landscape metric R^2 values (Fig. 5). For SandRockMud connectivity variables, R^2 values of the MNN landscape metric (i.e. the distance between SandRockMud patches) differed depending on spatial scale (i.e. 3 vs. 12 km; Fig. 5). However, landscape metric R^2 values were similar among all spatial scales for *Melaleuca* connectivity variables (Fig. 5).

Connectivity variables and landscape context

This subsection describes the proportional comparison of landscape metric measurements in the north-east versus south-east tropical landscape contexts for connectivity variables that were correlated to the bird ordination (Supplementary material Appendix 5, Fig. A5).

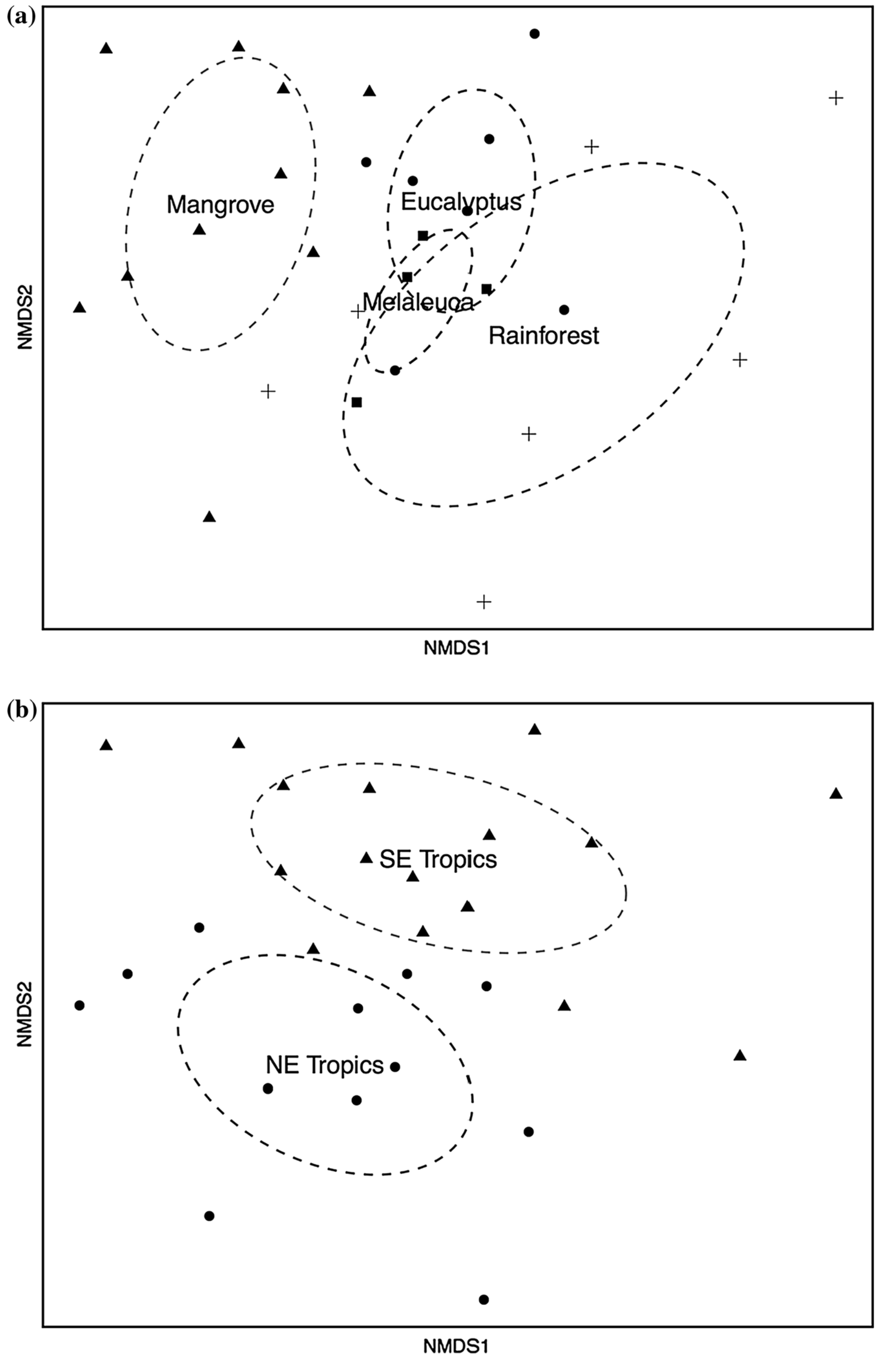


Fig. 2 An nMDS ordination plot (stress = 0.22) of bird species presence–absence data at each survey site, pooled throughout the year, and grouped by **a** coastal forest type (*square Melaleuca*, *circle* Eucalypt, + Rainforest, *triangle* Mangrove) and **b** landscape context (*circle* NE tropics, *triangle* SE tropics). Centroid ellipses (95% confidence interval) distinguish the coastal forest and landscape context groupings

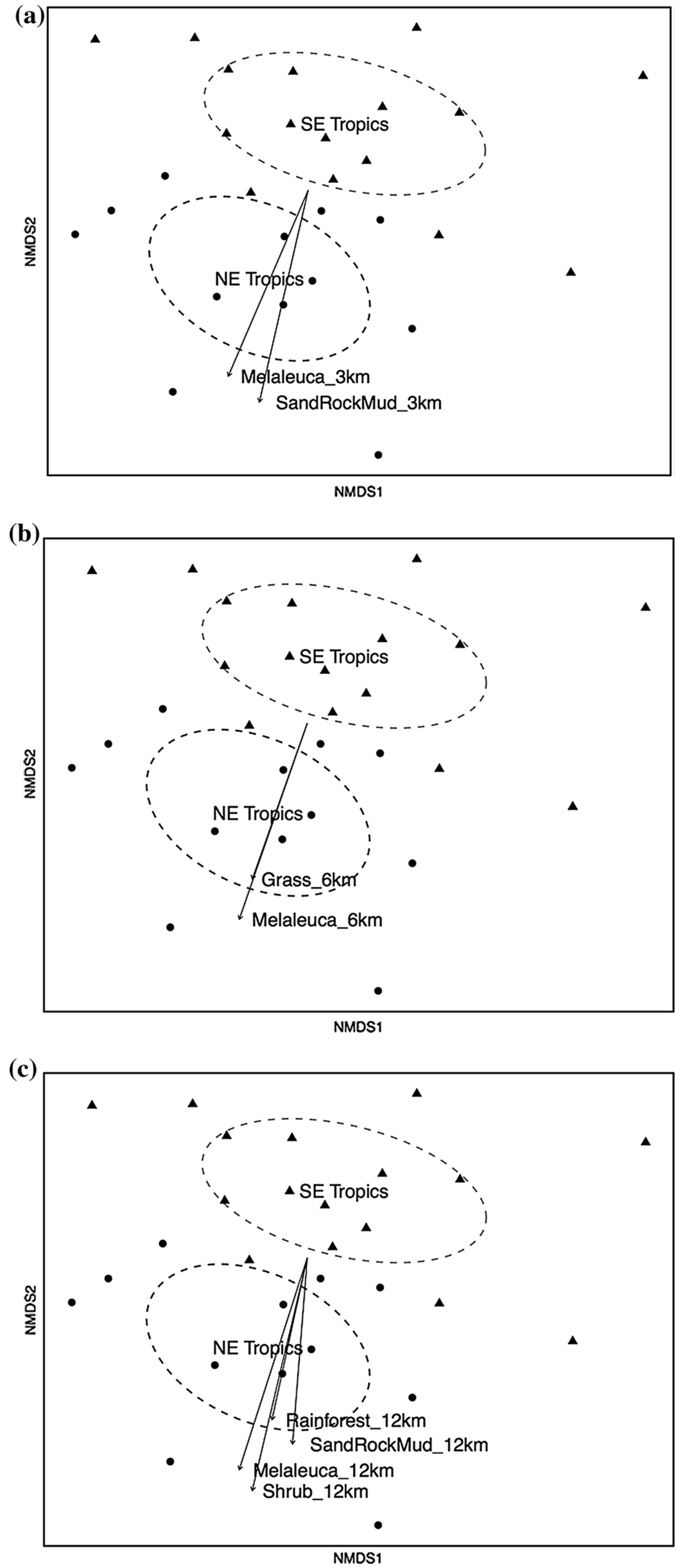
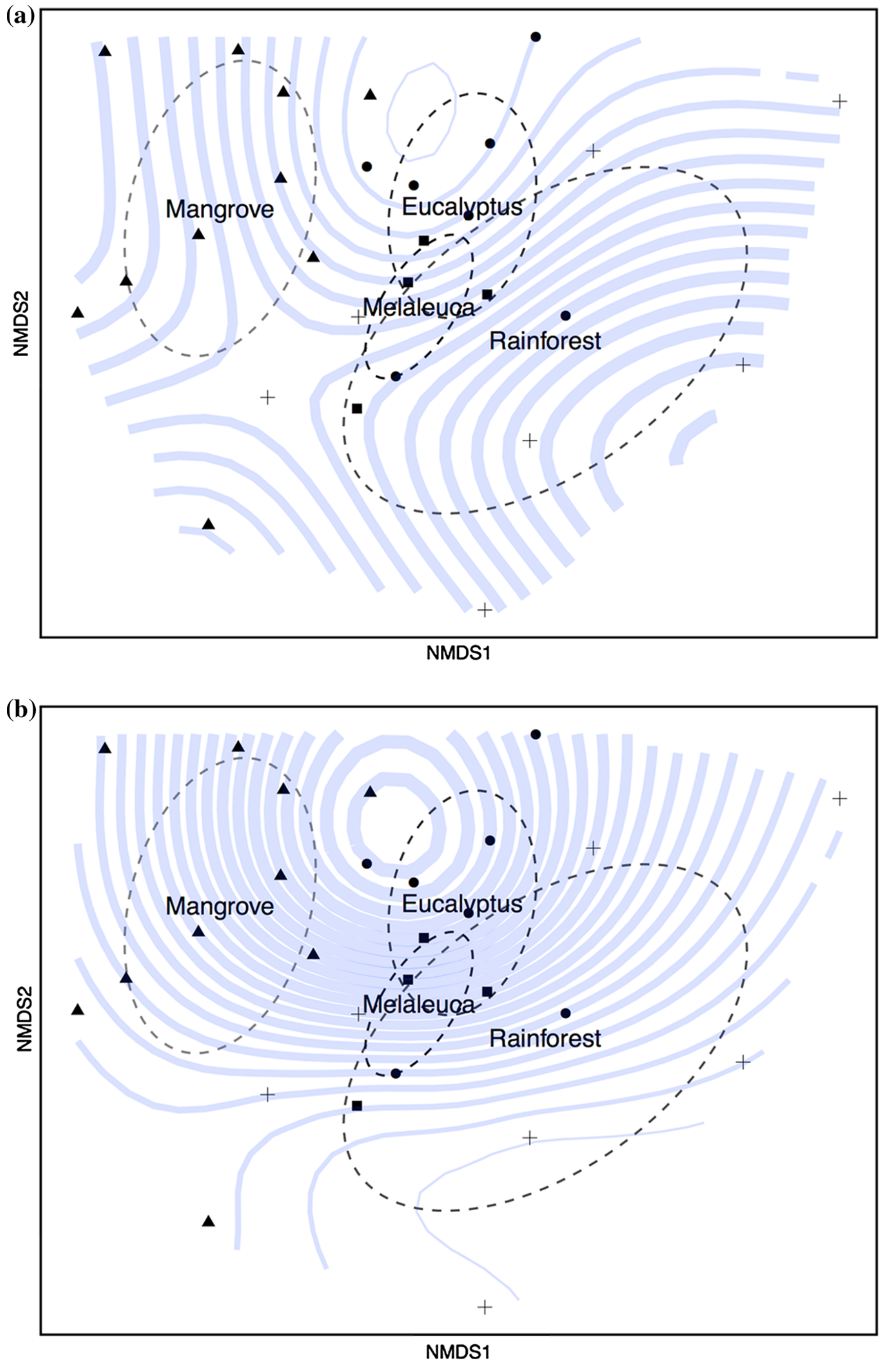


Fig. 3 Fitted vectors of 11 connectivity variables were overlaid on an nMDS ordination plot of coastal forest bird species composition (stress = 0.22) at the: **a** 3 km spatial scale, **b** 6 km spatial scale, and **c** 12 km spatial scale. Only connectivity variables that were correlated with the bird ordination ($p < 0.05$) are displayed. Bird species composition is grouped by landscape context (*circle* NE tropics, *triangle* SE tropics). The *vector arrows* indicate the direction in which connectivity variable values are increasing, while the length of each vector is proportional to the strength of the correlation between the bird ordination and the connectivity variable (Oksanen et al. 2015)

Fig. 4 Surface fitting of individual landscape metrics at the 12 km spatial scale for **a** rainforest total landscape area (TLA, $R^2 = 0.68$) and **b** SandRockMud total edge (TE, $R^2 = 0.42$) to the bird ordination (stress = 0.22). The value of each metric is indicated by the thickness of the contour lines (*thick lines* highest TLA or TE, *thin lines* lowest TLA or TE), and the *symbols in the plot* indicate survey sites by coastal forest type (*square Melaleuca*, *circle* Eucalypt, + Rainforest, *triangle* Mangrove)



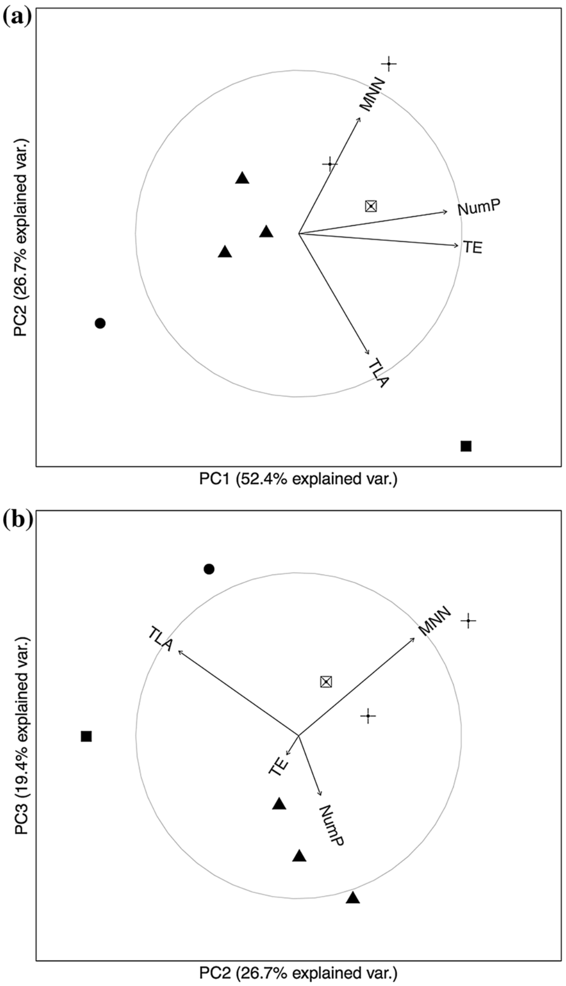


Fig. 5 Principal components analysis demonstrates how landscape metric R^2 values (represented by *vector arrows*: TLA, NumP, TE, and MNN) are related to connectivity variables that were correlated to the bird ordination: *Melaleuca* (3, 6, and 12 km; *triangle*), grassland (6 km; *circle*), SandRockMud (3 and 12 km; *plus sign*), shrubland (12 km; *X in box*), and rainforest (12 km; *square*). Principal components 1 and 2 explain 79.1% of the variation in landscape metric R^2 values (**a**), and principal components 2 and 3 explain 46.1% of the variation in landscape metric R^2 values (**b**)

Melaleuca connectivity variables were correlated to the bird ordination at all three spatial scales (3, 6, and 12 km; Fig. 3). Number (NumP) and total edge (TE) of patches were the most important landscape metrics of *Melaleuca* connectivity in explaining bird species composition (Fig. 5), and the proportion of their average values were higher in the NE tropics than in the SE tropics (Fig. 6a).

SandRockMud connectivity variables were correlated to the bird ordination at the 3 and 12 km spatial scales (Fig. 3a, c). At both spatial scales, TE, NumP, and distance between (MNN) patches were the most important landscape metrics of SandRockMud connectivity in explaining bird species composition (Fig. 5). The average values of TE and NumP were proportionally lower in the NE tropics versus the SE tropics, while the average value of MNN was similar in both landscape contexts (Fig. 6b).

Shrubland connectivity was correlated to the bird ordination at the 12 km spatial scale (Fig. 3c). NumP, distance between (MNN), TLA, and TE of patches were important landscape metrics of shrubland connectivity in explaining bird species composition (Fig. 5). The average values of NumP, TLA, and TE were proportionally higher in the NE tropics versus the SE tropics, while the average value of MNN was lower in the NE tropics (Fig. 6c).

Rainforest connectivity was correlated to the bird ordination at the 12 km spatial scale (Fig. 3c). TLA, NumP, and TE of patches were the most important landscape metrics of rainforest connectivity in explaining bird species composition (Fig. 5), and the proportions of their average values were higher in the NE tropics than in the SE tropics (Fig. 6d).

Grassland connectivity was correlated to the bird ordination at the 6 km spatial scale (Fig. 3b). TLA and NumP of grassland patches were the most important landscape metrics of grassland connectivity to bird species composition (Fig. 5), and their average values were proportionally lower in the NE tropics versus the SE tropics (Fig. 6e).

Discussion

To our knowledge, the present study is the first to identify a combined influence of landscape context and structural connectivity on coastal forest bird species composition. The structural connectivity patterns of specific vegetation types (i.e. shrubland, rainforest, *Melaleuca*, vegetation-devoid, and grassland) are associated with differences in bird species composition between regional landscape contexts. Previous studies have established landscape context as an important factor influencing bird species richness, abundance, and occurrence (Woinarski et al. 2000a; Riffell et al. 2003; Shriver et al. 2004; Watson et al.

2004; Martin et al. 2006). However, the present study also demonstrates the role of spatial scale, vegetation and landscape metric type in determining these associations, and highlights the nuanced nature of their interactions. Thus, a conservation strategy that considers regional landscape context and structural connectivity at broad spatial scales is essential for maintaining coastal bird species diversity.

Landscape context, structural connectivity, and bird species composition

Overall, the species composition of forest and woodland bird assemblages varied across different forest types within the coastal ecosystem mosaic of north-eastern Australia. In particular, rainforest, eucalypt woodland, and mangrove forest types largely differed in their species compositions. In contrast, bird species composition in *Melaleuca* woodlands overlapped substantially with eucalypt woodlands and rainforests. This corroborates previous research in northern Australia, where monsoonal rainforest and riparian bird assemblages were found to be distinct from those of adjacent eucalypt woodlands, whereas *Melaleuca* woodland bird assemblages were similar (Woinarski et al. 1988, 2000a; Woinarski 1993; Kemp and Kutt 2005). Because *Melaleuca* woodlands hosted bird species found in both eucalypt woodlands and rainforests, they are likely to play an important role in the coastal ecosystem mosaic as connective or refuge habitat.

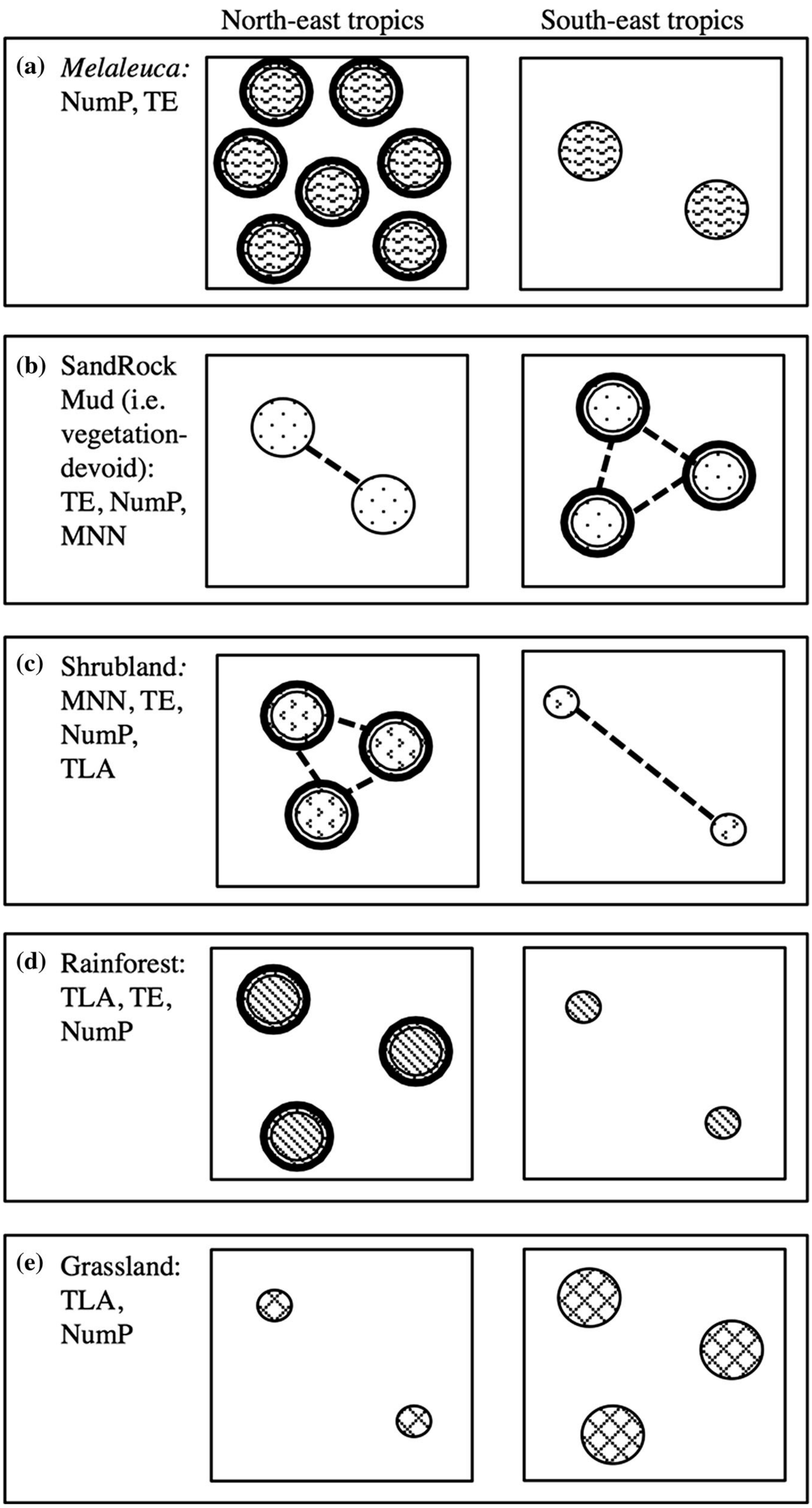
The similarities in bird species composition of *Melaleuca* woodlands with rainforest and eucalypt woodlands demonstrates that many bird species do not rely solely on individual coastal forests but instead use the entire ecosystem mosaic. This likely indicates the presence of necessary temporal functional redundancy within the coastal ecosystem mosaic, allowing birds to track highly seasonal resources, particularly nectar. Further research should be extended to consider coastal island ecosystems, and broader categories of landscape context, such as western and eastern regions of northern Australia that differ markedly in landscape pattern.

Mangrove bird assemblages were strikingly distinct in their species composition from all other coastal forest types. This may be resultant of relatively scarce nectar and fruit resources in mangrove forests (Noske 1996; Kutt 2007). Also, the unique structure, resources, and micro-climate of mangrove forests may lead to a higher richness of bird species that are confined and adapted to mangrove forests (e.g. specialist bird species that forage on crabs and mudskippers; Noske 1996). Indeed, Australian mangrove forests have the highest number of bird species restricted to mangrove forests worldwide (Ford 1982).

Mangrove survey sites with distinct bird species compositions were found in coastal landscapes with substantial amounts of rainforest in the surrounding area. In the Northern Territory of Australia, the within-forest and local-scale landscape patterns that influence mangrove bird assemblages are mangrove flowering phenology, within-patch habitat heterogeneity, and the number and type of adjacent habitats (Mohd-Azlan and Lawes 2011; Mohd-Azlan et al. 2012, 2014). However, in the Wet Tropics biogeographic region (within the present study area), the type of adjacent habitats was more important than within-patch habitat heterogeneity to mangrove bird assemblage (Kutt 2007), and rainforest is considered a ‘keystone’ habitat that increases bird species richness in nearby mangroves (Mohd-Azlan and Lawes 2011; Mohd-Azlan et al. 2014). Together, these findings suggest that local-scale landscape context, in particular the presence of rainforest vegetation, is an important factor determining which bird species will occupy mangrove forests.

Interestingly, mangrove structural connectivity was not correlated with bird species composition at any of the spatial scales considered. This may be related to survey location selection, as locations were chosen to have standardized mangrove patches of similar size and shape. In the coastal Northern Territory of Australia, small mangrove forest patches had higher bird species diversity than larger, more continuous mangrove patches (Mohd-Azlan and Lawes 2011). Therefore, patch size may also be an important factor in determining bird species composition in mangroves of north-eastern Australia, but was not able to be detected in our study design.

Shrubland structural connectivity demonstrated the strongest correlation to coastal forest bird species composition at the 12 km spatial scale. Shrubland vegetation may be particularly important for birds due to the flowering shrub species it contains (e.g. *Banksia* spp., *Grevillea* spp., etc.). *Banksia* shrub species in particular provide more abundant, dense, and reliable nectar resources than eucalypt forests, causing nectarivorous birds to aggregate in these flowering


North-east tropics
South-east tropics
(a) *Melaleuca:* NumP, TE
(b) SandRock Mud (i.e. vegetation-devoid): TE, NumP, MNN
(c) Shrubland: MNN, TE, NumP, TLA
(d) Rainforest: TLA, TE, NumP
(e) Grassland: TLA, NumP

◀**Fig. 6** Summary figure of connectivity variables that were correlated to the bird ordination, and how their landscape metric average values (TLA, NumP, TE, and MNN) differ proportionally between north-east tropical and south-east tropical landscape contexts. Only landscape metrics of each connectivity variable that had high surface-fit R^2 values are represented as follows: *circles inside boxes* represent vegetation patches, *thick lines* represent patches with higher total edge (TE), the *dashed line* represents distance between vegetation patches (MNN), the *size of the circles* represent the total landscape area (TLA) of vegetation patches, and a *higher number of circles* indicate a higher number of vegetation patches (NumP)

habitats (Franklin and Noske 1998; Woinarski et al. 2000b). This aligns with conclusions from previous research in northern Australia indicating that a diversity of nectar-producing habitats is critical to supporting avifauna in landscape mosaics, particularly due to seasonal changes in resource abundance (Woinarski and Tidemann 1991; Franklin and Noske 1998, 2000; Woinarski et al. 2000b; Kutt 2007).

Melaleuca woodland structural connectivity was correlated with coastal forest bird species composition at all spatial scales considered. In particular, the number and total edge of *Melaleuca* patches are important components of coastal ecosystem structural connectivity for avifauna. The importance of *Melaleuca* woodlands for coastal avifauna corroborates research in south-east Queensland that identified *Melaleuca* remnants as highly important for avian conservation (Grover and Slater 1994). Additionally, *Melaleuca* woodlands have been identified as a 'keystone resource' for nectarivorous birds in the Northern Territory of Australia because of their highly abundant nectar resources, and their wet season flowering phenology that opposes that of eucalypt woodlands typically flowering in the dry season (Woinarski et al. 2000b; Woinarski 2004; Kemp and Kutt 2005). The high importance of *Melaleuca* woodland structural connectivity to bird species composition at all spatial scales considered in this study suggests that these woodlands are a 'keystone structure' in the coastal ecosystem mosaic (i.e. a spatial structure that provides functions essential for the maintenance of biodiversity within a system (Tews et al. 2004)).

Spatial scale and structural connectivity

Spatial scale and vegetation type influenced the association between structural connectivity and bird species composition, suggesting the need to consider their combined effects. At the largest spatial scale examined (12 km), the structural connectivity of rainforest, *Melaleuca* woodland, vegetation-devoid, and shrubland vegetation patches were associated with differences in coastal bird species composition between landscape contexts. *Melaleuca* woodland and vegetation-devoid connectivity patterns were also correlated at the 3 km spatial scale, whereas grassland structural connectivity was only correlated at the 6 km spatial scale. The dependence of connectivity variable correlation on spatial scale may be related to how the measurement of individual landscape metrics changes with spatial extent. It is known that as the spatial extent of measurement increases or decreases, the value of landscape metrics can change either unpredictably or proportionally (Wu 2004). In the present study, as the spatial extent at which vegetation-devoid landscape metrics were measured increased, the importance of distance between vegetation-devoid patches (i.e. the MNN landscape metric) decreased. However, in contrast, the spatial extent of measurement did not change the importance of individual landscape metrics for *Melaleuca* woodland structural connectivity, which was correlated at all three spatial scales. The inability of the present study to find a consistent pattern in how spatial extent influences landscape metric importance reinforces the need for spatial investigations to be conducted at multiple scales.

It is likely that the importance of individual landscape metrics, such as the distance between vegetation patches, is related to the movement of individual bird species. Complex modeling approaches allow the dispersal and daily movement ability of birds (i.e. functional connectivity) to be incorporated when predicting bird response to landscape connectivity (Drielsma et al. 2007a, b). Although this is certainly an area for further research, the present study provides a first step that lays the foundation for more detailed exploration using complex modeling.

Implications for conservation

This study clearly shows the importance of conserving shrubland and *Melaleuca* structural connectivity to maintain functional landscapes for coastal avifauna. Due to high rates of clearing, *Melaleuca* vegetation falls within regional ecosystem groups that have been identified as ‘endangered’ or ‘of concern’ in all three biogeographic regions investigated, whereas some shrubland species, such as *Grevillea* spp., are ‘endangered’ in the Brigalow Belt North region (Sattler and Williams 1999). Pre-clearing investigations of the coastal lowlands in the Wet Tropics biogeographic region have also found that native vegetation has been reduced by two-thirds, of which *Melaleuca* woodlands and forests are a major component (up to $\sim$65% loss in some areas; Johnson et al. 2000; Kemp et al. 2007). The present study supports the growing body of evidence indicating that *Melaleuca* woodland remnants are highly important to the health of ecosystem mosaics in tropical and sub-tropical Australia, and efforts for their preservation should be prioritized (Grover and Slater 1994; Woinarski 2004).

Conclusions

Our research highlights the need to consider multiple aspects of structural connectivity when planning for conservation, such as how the spatial dynamics of vegetation patterns and connectivity relate to species use of coastal ecosystem mosaics. Research regarding landscape processes tends to focus on patterns that occur within, or directly adjacent to, focal habitat patches (Radford et al. 2005), perhaps due to logistical and funding constraints. However, a holistic perspective that considers interactions among components of the coastal ecosystem mosaic is necessary for effective avian conservation.

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