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Integrated assessment of ecosystem connectivity and functioning: coastal forest avifauna of northeast Australia

Christina Amy Buelow

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Abstract

The extraordinary diversity of species-environment relationships that occur across space and time can engender a deep curiosity of their mechanistic underpinnings. Moreover, the rapid rate of ecosystem change associated with anthropogenic and climatic pressures makes information regarding species' landscape and resource use ever more important. Without this information, we will be unable to effectively protect landscapes and their constituent species. The coastal ecosystem mosaic of northeast Australia, which is comprised of a high diversity of habitat types, provides a suitable region for investigating how species respond to heterogeneity in habitat and resource availability. The present thesis examined ecosystem functioning in heterogeneous coastal landscapes of northeast Australia for forest avifauna. An array of analytical approaches were employed to establish a comprehensive understanding: 1) spatial assessment to determine relationships between regional landscape connectivity and coastal forest bird assemblages, 2) isotopic assessment to evaluate the local foraging ecology of mangrove bird assemblages, and 3) nutrient assessment of cross-ecosystem connectivity provided by a migratory coastal forest bird species (i.e. the Pied Imperial-Pigeon (*Ducula bicolor*)).

Within the coastal ecosystem mosaic, mangrove forests sit at the land-sea interface. Therefore, to effectively 'set the scene' I review how mangrove birds require and facilitate connectivity through their use of the broader coastal landscape. Next, to specifically assess regional landscape patterns and processes influencing northeast Australia's coastal forest avifauna, I surveyed the composition of bird assemblages in four of the major coastal forest types occurring throughout the region (i.e. Eucalypt, Melaleuca*,* mangrove, and rainforest). Following this, spatial patterns of habitat configuration within the coastal landscape (i.e. structural connectivity) were quantified to understand broad relationships between coastal forest bird assemblage composition and landscape heterogeneity at multiple spatial scales. Most bird species in coastal northeast Australia occurred in multiple forest types. Spatial assessment suggested that Melaleuca woodlands are a keystone structure that supports use of the entire coastal landscape mosaic by coastal forest generalist species. However, the species composition of mangrove bird assemblages was distinct relative to other coastal forest types. Therefore, to provide more detailed information regarding the response of coastal forest generalists and mangrove specialists to specific forest attributes, functionally connected forest networks were developed to assess the relative importance of forest area, availability, and connectivity to their compositional turnover. This revealed that mangrove specialists and coastal generalists differ in the forest attributes they require (i.e. area vs. availability) to maintain regional beta diversity.

Understanding landscape pattern-process relationships that drive bird assemblage composition and turnover can inform the prioritization of regional-scale landscape features for protection. However, species' responses to local-scale spatiotemporal variability in resource availability may also play a role in these relationships. I used isotopic analysis to better understand the foraging ecology of coastal forest birds in a highly dynamic mangrove forest environment. This demonstrated that flexible and opportunistic foraging strategies were prevalent among coastal forest generalist species. However, specialized foraging strategies were employed by some species, primarily for resources that were uniquely available in mangrove forests (i.e. estuarine fish and crabs).

Mobile species not only respond to landscape patterns and processes, but can also facilitate connectivity processes through their movement (e.g. nutrient transfer, pollination, genetic linking, etc.). To determine the implications of avian mobility for ecosystem functioning in northeast Australia, I focused on a migratory coastal forest bird species, the Pied Imperial-Pigeon (*Ducula bicolor*). Nutrient measurements demonstrated that Pied Imperial-Pigeons provide mainland-derived nutrient subsidies to island forests, highlighting their important role as an avian mobile-link species.

The integrated analytical approach used in this thesis has provided insight to the complexity of coastal landscapes and their use by forest avifauna. This has broadened our understanding of coastal ecosystem functioning to include a hierarchy of ecosystem components that exist at local and regional scales. The ecosystem properties that emerge from interactions across coastal ecosystem components include: vegetative connectivity, compositional turnover, avian foraging strategy, and nutrient transfer. Results from this thesis can inform the holistic conservation and management strategies that are required to maintain coastal ecosystem functioning in regional northeast Australia.

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1 General introduction

1.1 Biocomplexity and ecosystem functioning

Understanding how ecosystems function is a fundamental pursuit of ecology. The patterns and processes that underpin ecosystem functioning are often elaborate, and their intricate relationships can be referred to as 'biocomplexity' (Colwell 1998). Two philosophically opposed methodological approaches to understanding complex ecosystem functioning have evolved: reductionism and holism. Reductionism considers the collective properties of individual ecosystem components that are distinct, predictable, and can be summed across individual components (Salt 1979). In addition to collective properties, holism also considers emergent properties occurring within and among all ecosystem components that are interactive, unpredictable, and are greater than the sum of individual components (Odum and Barrett 2005, Feller et al. 2010). There is broad consensus that reductionist approaches are inadequate to fully represent biocomplexity, but holistic approaches are generally more difficult and less pragmatic to develop and use (Bergandi and Blandin 1998). To ease issues of pragmatism associated with a holistic approach, a framework has been established that considers three dimensions of biocomplexity explicitly: connectivity, heterogeneity, and historical contingency (Cadenasso et al. 2006).

The biocomplexity framework can be used to investigate ecosystem properties, such as connectivity, that arise from interactions between pattern-process relationships in spatiotemporally heterogeneous environments. Connectivity is an emergent property of the biocomplexity framework that couples habitats, ecosystems, and food webs through the movement of materials and organisms (Breckling et al. 2005, Reuter et al. 2005, Cadenasso et al. 2006, Feller et al. 2010). For example, connectivity between mangrove forests and adjacent ecosystems emerges as a result of complex interactions between structural landscape features, geomorphology, hydrology, tidal regimes, and climatic variability, with consequences for ecosystem functioning (Feller et al. 2010). The consequences are exemplified in marine protected areas, where connectivity to mangrove forests increases herbivore biomass and richness on coral reefs, enhancing protected reef functioning and resilience (Olds et al. 2012).

Individual species can both require and facilitate connectivity processes. For example, energetic demands will dictate the minimum distance that long-distance shorebird migrants require between stop over sites (Skagen 2006). Alternatively, long-distance migrants can foster indirect dispersal and connectivity between invertebrate populations among their wetland foraging sites (Green and Figuerola 2005). Regardless of whether ecological connectivity is required or facilitated by species, its disruption can have negative consequences for their survival and for ecosystem functioning. For example, compromised ecosystem functioning has been documented when pollinator mobility is limited by habitat fragmentation, resulting in reduced plant reproductive success (Aguilar et al. 2006).

Environmental heterogeneity is another key dimension of the biocomplexity framework (Cadenasso et al. 2006), and is broadly classified as diversity and variability in habitat and resource availability (Fahrig 1992). Interactions between heterogeneity and connectivity, which can occur across multiple spatial and temporal scales, result in highly complex ecosystems. For example, riverine floodplain channels are highly complex, spatially heterogeneous systems that vary by their depth, length, width and sinuosity; and their hydrological connectivity fluctuates across temporal scales ranging from inter-annual, decadal, to centennial (Amoros and Bornette 2002). In highly complex and spatiotemporally heterogeneous systems like riverine floodplains, identifying and measuring the causes and consequences of connectivity processes will be necessary to fully understand ecosystem functioning.

Historical contingency refers to how ecosystems and their component habitats change through time (Cadenasso et al. 2006). Although the historical contingency dimension of the biocomplexity framework is beyond the scope of this thesis' investigation, the rapid rate of change ecosystems are experiencing world-wide makes it an important consideration. In particular, species' interactions within an ecosystem are determined in part by the timing of their arrival in the community, and therefore assembly history is necessary to fully understand species' interactions (Fukami 2015) and ecosystem functioning (Fukami et al. 2010). Furthermore, beyond community assembly history, ecosystem restoration will only be successful if the history of ecosystem change is used to review and improve past restoration targets for better outcomes in the future (Jackson and Hobbs 2009).

1.2 Variably mobile species assemblages

Through the evolution of life-history traits, individual species are predominantly sedentary, nomadic, or migratory; and their mobility is an integral component of their landscape- and resource-use (Roshier and Reid 2003). However, mobility can be highly variable across ecological communities, species assemblages, or even a population within a species. For example, some species of pond-breeding amphibians exhibit partial migration, where only a select number of individuals within a population will migrate to terrestrial over-wintering areas (Grayson and Wilbur 2009). Alternatively, within a butterfly assemblage, the migration patterns of three specialist species using the same grassland habitat network vary by distances spanning hundreds of metres (Baguette et al. 2000). In spatiotemporally heterogeneous systems, species' mobility is likely to be variable if they are predisposed to track fluctuations in resource availability, making the development of effective management and protection strategies challenging.

The difficulties in developing effective conservation strategies, such as the establishment of protected areas, have recently been highlighted for mobile species, particularly migrants and nomads (Woinarski et al. 1992, Newmark et al. 2008, Runge et al. 2014, Runge and Tulloch 2017). Movements of migratory species are predictable in nature; however the large scale at which migrants disperse makes identifying and protecting critical habitat challenging. Furthermore, migrators often traverse protected area boundaries, placing high importance on ensuring that protected areas are properly connected for migration completion. If conservation actions are implemented at inappropriate spatial scales, or do not provide adequate connectivity, populations of highly mobile, migratory species can decline (Murray and Fuller 2015, Runge et al. 2015*b*, Polak et al. 2016). For example, a critical bottleneck has been identified in the migratory route of the migratory Mongolian Saiga (*Saiga tatarica mongolica*) and, without an alternative route, loss of the bottleneck habitat would likely result in population collapse (Berger et al. 2008).

Challenges concerning the appropriate spatial scale for effective conservation action are amplified when there is high uncertainty regarding species' movement patterns, which is typical of nomadic species. Nomads track resources across landscapes that are highly heterogeneous in habitat and resource availability, resulting in unpredictable and erratic movements following resource booms and busts (Runge et al. 2014, 2015*a*, 2016). Identifying relationships between species' movements and habitat and resource availability can provide critical information for conservation planning in areas with high spatiotemporal heterogeneity. For example, the copperbelly water snake (*Nerodia erythrogaster neglecta*) relies on spatiotemporally variable resources in ephemeral wetland pools and is highly mobile in comparison to the sympatric northern water snake (*Nerodia sipedon sipedon*) that forages primarily in stable and permanent wetland pools (Roe et al. 2004). Therefore, sympatric species can require very different conservation strategies depending on the mobility that their resource-use demands.

For sedentary species, site-level and target-based approaches to protected area planning can achieve good outcomes (Thomas et al. 2012). Conservation efforts often focus on site-level pattern-process relationships associated with specialist species, because specialists are highly sensitive to threats such as land-use and climate change, reducing their resilience to disturbance (Devictor et al. 2008, Pardini et al. 2009, Poniatowski et al. 2016, Reside et al. 2017 a). However, many nomadic species are also resource specialists, and a static protected area network will be inadequate if it does not protect key resources across spatiotemporal scales (Runge et al. 2014, 2015*b*; Runge and Tulloch 2017, Webb et al. 2017). Furthermore, placing a primary conservation focus on sedentary specialists may provide limited benefit for biodiversity and ecosystem functioning as a whole. To maintain ecosystem functioning at adequate spatiotemporal scales for many species, there is an urgent need to understand broader scale pattern-process relationships that are associated with variably mobile species assemblages. However, addressing interactions between mobility, landscape- and resource- use is a complex and formidable task.

1.3 Whole-landscape assessment of ecosystem functioning

Essential for the maintenance of functioning ecosystems is an understanding of the habitat attributes that species require for their survival. Life-history traits, such as niche width (i.e. specialists or generalists) or dispersal ability, can play a role in shaping species’ habitat requirements. For example, the survival of specialist species that also have low dispersal ability should be dependent on both the size and connectedness of suitable habitat in a landscape (Harris and Pimm 2007, Ockinger et al. 2010). Conversely, the adaptability of generalist species with high dispersal ability should mean that they are less sensitive to habitat fragmentation and isolation (Ewers and Didham 2006). However, in reality, differences in species’ habitat requirement are much more complex and can be confounded by other factors, such as the ability of species to cross or use matrix habitat (Ewers and Didham 2006, Prugh et al. 2008).

Habitat requirements for sedentary, nomadic, and migratory species will also differ across spatial and temporal scales. Therefore, static and target-based conservation approaches occurring at a site-level will not be adequate for variably mobile species responding to heterogeneous patterns and processes. The delivery of local-scale connectivity by mobile animals is often dependent on the regional-scale spatial distribution of resources, demonstrating the need for mobile species-connectivity relationships to be protected at the landscape-scale instead of at site or habitat-scales (Kremen et al. 2007). Landscape-scale conservation strategies that explicitly consider connectivity processes are increasingly being called for as recognition of the importance of maintaining biodiversity across landscapes grows (Lindenmayer et al. 2006, 2008; Boyd et al. 2008; Thrush et al. 2010; McCauley et al. 2012; Mazaris et al. 2013; Watson et al. 2017).

‘Whole-landscape’ conservation aims to protect multi-scale ecological pattern-process relationships and maintain ecosystem functioning for the persistence of all regional biota (Poiani 2000). Through the protection of regional biodiversity, whole-landscape conservation is likely to enhance the resilience of ecosystems to threatening processes, such as land-use change. Connectivity can provide a ‘spatial insurance’ against disturbance where, if there is adequate connectivity in the landscape, dispersal processes are able to maintain regional species diversity (Loreau et al. 2003). High species diversity alleviates the consequences of losing species during a disturbance, because functional redundancy within a diverse species assemblage can allow key ecosystem functions to be retained.

Biodiversity itself is an important determinant of ecosystem functioning, and encompasses the collective properties of all biota from the gene to ecosystem level, making it a difficult and impractical quality to measure (Margules et al. 2002, Tilman et al. 2014). Depending on the question, data, and assessment tools available, studies of biodiversity largely rely on surrogates to represent the majority of species, patterns, and processes occurring in an area (Lewandowski et al. 2010, Grantham et al. 2010). Once a surrogate has been chosen, measures of surrogate species’ richness and distributions can be used to assess species-environment relationships and inform conservation planning. However, measurements of species’ diversity and distributions are often analyzed as static properties of regional biodiversity, and this can undermine the overall effectiveness of the conservation strategies they are informing (Poiani et al. 2000, Margules et al. 2002). Modeling approaches have recently been used to incorporate species’ dynamic distributions into understanding their responses to changing environmental conditions, enabling better conservation prioritization (Reside et al. 2010, 2012; Runge et al. 2015*a*, 2016; Ikin et al. 2016; Webb et al. 2017). However, many approaches to understanding community-level responses still rely on relatively simple and static measures of biodiversity (i.e. species richness; Veach et al. 2017), which can fail to consider the spatiotemporal processes that underpin regional biodiversity, such as species' assemblage composition and turnover.

Beta diversity is the spatial variation in species composition, and can be measured as the rate at which species composition changes along an environmental gradient (i.e. compositional turnover; Anderson et al. 2011). Factors such as habitat area, habitat isolation, and species' dispersal are known to influence turnover (Soininen 2010), and identification of these relationships are required to ensure maintenance of biodiversity and ecosystem functioning. For example, landscape context can determine local and regional species' pools, and well-connected landscapes allow species' dispersal following disturbance (Oliver et al. 2015). This has been demonstrated in coral reef systems where spatiotemporal variation in coral reef fish beta diversity allows communities to remain stable following extreme environmental disturbances through biomass replacement (Lamy et al. 2015). Furthermore, environmental heterogeneity can increase beta-diversity, as is demonstrated by small-scale habitat heterogeneity provided by shell debris in soft-sediment coastline areas (Hewitt et al. 2005).

Although regional-scale management of environment and beta-diversity pattern-process relationships is important, there is a probable trade-off between generalizing broad-scale community-level assessment information with detailed knowledge regarding population responses to finer-scale environmental heterogeneity. Therefore, when possible, regional assessment should integrate analytical approaches that will provide the best understanding of multiple species responses to environmental heterogeneity at different spatiotemporal scales.

1.4 Case study: coastal forest avifauna of regional northeast Australia

Australia is a continent characterized by high inter-annual variability in climatic conditions and resource availability (Hobbs et al. 1988). Consequently, the movement patterns of many Australian bird species are highly variable and difficult to predict, ranging from local, regional, to intercontinental (Griffioen and Clarke 2002). Moreover, many sedentary Australian bird species are likely to be more mobile than expected (Maron et al. 2005), or exhibit partial migration (i.e. sedentary and migratory individuals or populations occur within a species; Chan 2001). The documented dynamism in Australian bird assemblages and their movements is likely associated with heterogeneous environmental conditions, such as spatiotemporally variable nectar and insect resources (Chan 2001).

Australia's northeast coast has suitable attributes for investigating interrelationships between environmental heterogeneity and connectivity, and for considering the consequences for biodiversity, ecosystem functioning and resilience. This region is comprised of a concentrated diversity of vegetation with fluctuating resource availability, and its coastal forest avifauna is an assemblage of variably mobile species (i.e. sedentary, nomadic, and migratory). Using coastal forest avifauna as a variably mobile biodiversity surrogate, I evaluate their responses and relationships to heterogeneity and connectivity, and consider the implications for ecosystem functioning. I approach this complex system with integrated analyses: spatial assessment of landscape-use, isotopic assessment of resource-use, and nutrient assessment of cross-ecosystem linkages (Figure 1-1). Using this assessment information, I consider the effectiveness of current protection measures for whole-landscape ecosystem functioning in coastal northeast Australia.

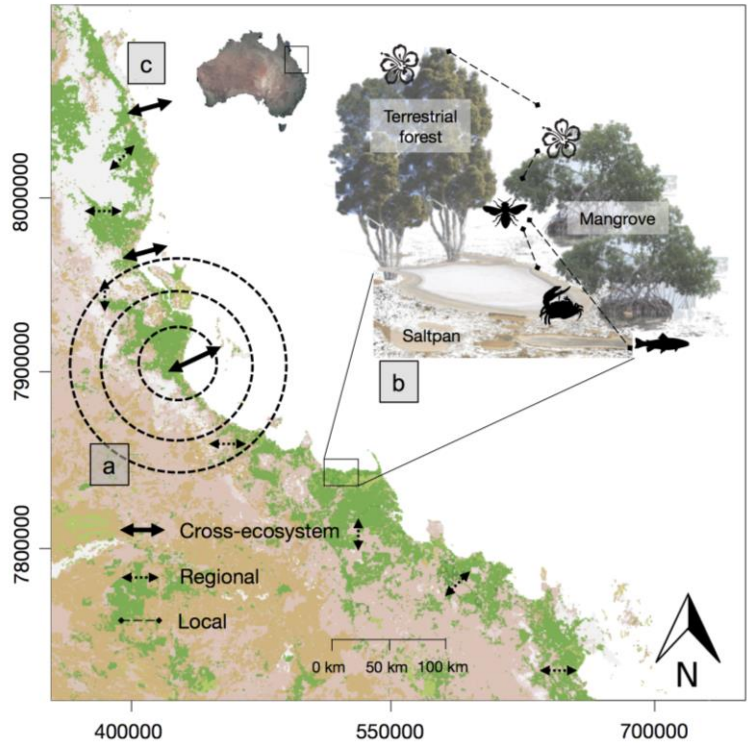


Figure 1-1 Conceptual diagram illustrating the integrated analytical approach used to inform protection of whole-landscape ecosystem functioning for coastal forest avifauna of regional northeast Australia: a) spatial assessment of landscape use, b) isotopic assessment of resource use, and c) nutrient assessment of cross-ecosystem linkages provided by a migratory species. Landscape colors represent vegetation types (NVIS 2012), and arrows indicate local, regional, and cross-ecosystem bird movements.

1.4.1 Overview of integrated approach to regional assessment of variably mobile avifauna

Acquiring a whole-landscape understanding of highly complex and heterogeneous systems that host variably mobile species will require a set of integrated assessment approaches. Here, I outline the integrated approach used in this study. Mangrove forests sit at the coastal land-sea interface; making them an ideal habitat to review how bird species require and facilitate connectivity processes in heterogeneous coastal landscapes (**Chapter 2**). Next, to specifically assess regional landscape patterns and processes influencing northeast Australia's coastal forest avifauna, I surveyed the composition of bird assemblages in four of the major coastal forest types occurring throughout the region (i.e. Eucalypt, Melaleuca*,* mangrove, and rainforest). Subsequently, spatial patterns of habitat configuration within the coastal landscape (i.e. structural connectivity) were quantified to understand broad relationships between coastal forest bird assemblage composition and landscape heterogeneity at multiple spatial scales (**Chapter 3**, Figure 1-1 a). To provide more detailed information regarding the response of coastal forest generalists and mangrove specialists to specific forest attributes, functionally connected forest networks were developed to assess the relative importance of forest area, availability, and connectivity to their compositional turnover (**Chapter 4**, Figure 1-1 a).

Understanding landscape pattern-process relationships that drive bird assemblage composition and turnover can inform the prioritization of regional-scale landscape features for protection. However, species' responses to local-scale spatiotemporal variability in resource availability may also be playing a role in these relationships. I used isotopic analysis to better understand the foraging ecology of coastal forest birds in a highly dynamic mangrove forest environment (**Chapter 5**, Figure 1-1 b).

Finally, mobile species not only respond to landscape patterns and processes, but can also facilitate processes, such as connectivity, through their movement (e.g. nutrient transfer, pollination, genetic linking, etc.). To determine the implications of avian mobility for ecosystem functioning in northeast Australia, I focused on a migratory coastal forest bird species, the Pied Imperial-Pigeon (*Ducula bicolor*). Specifically, I used nutrient measurements to assess the consequences of Pied Imperial-Pigeon daily migrations for transferring nutrients from mainland to island ecosystems (**Chapter 6**, Figure 1-1 c).

In the general discussion (**Chapter 7**), I place the results of the integrated analytical approach within a whole-landscape conservation context. I consider the effectiveness of the protected area network that is currently established in coastal northeast Australia, and provide recommendations for moving towards whole-landscape protection of variably mobile species assemblages. This is the first comprehensive work to take a broad range of approaches to better understand the functioning of this complex landscape.

2 A birds-eye view of biological connectivity in mangrove systems

2.1 Abstract

Considerable advances in understanding of biological connectivity have flowed from studies of fish-facilitated connectivity within the coastal ecosystem mosaic. However, there are limits to the information that fish can provide on connectivity. Mangrove bird communities have the potential to connect coastal habitats in different ways and at different scales than fish, so incorporation of these links into our models of coastal ecosystem mosaics affords the opportunity to greatly increase the breadth of our understanding. We review the habitat and foraging requirements of mangrove-bird functional groups to understand how bird use of mangroves facilitates biological connectivity in coastal ecosystem mosaics, and how that connectivity adds to the diversity and complexity of ecological processes in mangrove ecosystems.

Avian biological connectivity is primarily characterized by foraging behaviour and habitat/resource requirements. Therefore, the consequence of bird links for coastal ecosystem functioning largely depends on patterns of habitat use and foraging, and potentially influences nutrient cycling, top-down control, and genetic information linkage. Habitats that experience concentrated bird guano deposition have high levels of nitrogen and phosphorus, placing particular importance on the consequences of avian nutrient translocation and subsidization for coastal ecosystem functioning.

High mobility allows mangrove-bird communities to link mangrove forests to other mangrove, terrestrial and marine-pelagic systems. Therefore, the spatial scale of coastal connectivity facilitated by birds is substantially more extensive than fish-facilitated connectivity. In particular, migratory birds link habitats at regional, continental, and inter-continental scales as they travel among seasonally available feeding areas from breeding grounds to non-breeding grounds; scales at which there are few fish equivalents. Knowledge of the nature and patterns of fish connectivity have contributed to shifting the initial, historical perception of mangrove-ecosystem functioning from that of a simple

system based on nutrient and energy retention, to a view that includes fish-facilitated energy export. In a similar way, understanding the nature and implications of mangrove connectivity through bird movements and migrations affords new possibilities for revising our view of the extent of functional links between mangroves and other ecosystems.

2.2 Introduction

Many animals require multiple habitats to complete their life-histories, establishing biological connectivity as specific habitats are used at different life-history stages for different purposes. The movement of animals links habitats into an interconnected ecosystem mosaic (Sheaves 2009). The exact way different species use component habitats within ecosystem mosaics varies spatially and temporally in species-specific, daily, seasonal, ontogenetic or gender-related ways (Law and Dickman 1998, Sheaves 2005). For example, some bat species switch between their roosting and foraging habitat on a daily basis, while other species demonstrate gender-driven patterns of habitat use because females require different resources than males during lactation (Law and Dickman 1998). The necessary movement of animals between habitats is a key facilitator of biological connectivity within ecosystems, and has consequences for nutrient transport and cycling (Sheaves and Molony 2000, Clark et al. 2009), patterns of top-down control (Sheaves et al. 2006) and the transfer of genetic information (Green and Figuerola 2005).

Coastal ecosystem mosaics consist of inter-connected marine, estuarine, freshwater and terrestrial habitats (Sheaves 2009). At the center of the mosaic are a variety of shallow and intertidal habitats that occupy the interface between land and sea. Mangroves provide unique forest habitat that extend into the intertidal zone of tropical and sub-tropical latitudes, enabling terrestrial and marine organisms to interact across a broad land-sea ecotone (Sheaves 2009). Mangroves are prized for their high productivity relative to their low vegetative diversity, and for their ability to support highly diverse communities (Kathiresan and Bingham 2001, Nagelkerken et al. 2008, Alongi 2009*b*, Feller et al.

2010). Mangrove ecosystems have also been central to many of the developments in coastal connectivity understanding because of the key roles they play as nursery habitat for many marine fish species, often forming critical components of local-scale ecosystem mosaics (Nagelkerken et al. 2013).

Associated with their intertidal position is the physically-dynamic nature of mangrove forests. The dynamic nature of mangrove forests will influence biological connectivity and nutrient flow, due to a number of eco-physiological factors and processes that can influence nutrient availability and mangrove metabolism (Alongi 2009*a*). Temperature, atmospheric carbon-dioxide levels, salinity and sea-level rise affect photosynthetic and growth rates of mangrove forests (Krauss et al. 2008, Alongi 2009*a*). Additional factors such as tidal inundation, redox status, soil type, zonation, latitude and sedimentation will also influence mangrove productivity through nutrient availability (Lovelock et al. 2007, Feller et al. 2009, Reef et al. 2010). The complexity of processes regulating nitrogen and phosphorus availability in mangrove forests (nitrogen and phosphorus are nutrients documented to limit mangrove productivity; Reef et al. 2010) means that nutrient limitation will vary at both narrow and broad eco-tonal gradients (Feller et al. 2002, Feller et al. 2009). Therefore, understanding biological connectivity and nutrient flow in mangrove forests will require investigation over a broad spatio-temporal range, and will need to consider a wide-range of eco-physiological factors.

The realization that ecosystem mosaics, rather than single habitats, are important for species' survival is an emerging and important theme in coastal-ecology conservation. For example, understanding the importance of mangroves as nursery habitat for coral-reef fish has led to the development of algorithms that incorporate mangrove-coral connectivity into marine-reserve area planning (Mumby 2006). Although mangrove forests provide important habitat for many animals, they are facing destruction at an alarming rate with up to 50% already lost around the world (Feller et al. 2010), primarily due to anthropogenic factors (Kathiresan and Bingham 2001). Without carefully planned conservation much of the remaining forest area is likely to continue to suffer decreases in biodiversity, resilience to disturbance and connectivity (Beger et al. 2010). In addition to rapid degradation, the role that mangroves play in supporting a wide range of fauna and a diversity of key processes underscores the urgent need to investigate the full spectrum of ways that mangrove forests enhance coastal ecosystem connectivity.

2.2.1 Mangrove connectivity

Up to the present, coastal connectivity studies have focused on the movement of fish between mangrove forests and nearby habitats for completion of their life history migrations; a perspective that has shaped the idea of mangroves as part of an interconnected habitat mosaic (Sheaves 2005, Feller et al. 2010). Inshore fish use mangroves as nursery habitat because mangrove forests provide abundant food and shelter from predation for early juvenile stages (Sheaves 2005, Unsworth et al. 2008, Alongi 2009*b*, Feller et al. 2010). Connectivity contributes to the nursery ground value of mangroves for juvenile fish by providing ecological services such as nursery habitat, access to resources and regulating physical conditions (Sheaves et al. 2014*b*). The configuration of habitats within the coastal ecosystem mosaic influences the species and age classes of fish using these habitats due to differences in predation risk, with fish undergoing sequential ontogenetic migrations (e.g. mangrove to seagrass to coral reef) as their stage-specific requirements change (Dorenbosch et al. 2007, Unsworth et al. 2008). Therefore connectivity between mangroves and adjacent habitats due to fish ontogenetic development plays an important role in shaping fish assemblages, in ecological functioning and in supporting near-shore fish stocks and fisheries.

Fish-facilitated biological connectivity in coastal ecosystems has important food web implications. Mangrove food webs were formerly thought to be simple systems dominated by detritus and detritivores (Alongi 2009*b*), with detritivorous crabs retaining mangrove productivity within the forest (Feller et al. 2010). However, upon closer inspection, predatory fish feeding on these crabs during tidal inundation can export a considerable amount of mangrove productivity (Sheaves and Molony 2000). Consequently, the movement of fish modifies the flow of nutrients between habitats, resulting in considerable trophic coupling throughout the coastal ecosystem mosaic.

Thus, investigation of connectivity among mangroves and other components of the coastal ecosystem mosaic has brought a much fuller understanding of ecological functioning at a whole-ecosystem level.

While the fish-centric focus of mangrove connectivity studies has provided new insights, a broader range of study will build on the types and extents of connectivity that can be conceptualized. It is time to explore this concept more extensively by considering groups, such as birds, that interact with mangroves and adjacent components of the ecosystem mosaic in different ways and at more expansive spatio-temporal scales. For example, fish connectivity between mangroves and coral reefs typically spans 10′s of kilometres (Mumby 2006), while migratory birds can link mangrove systems at scales reaching 1000′s of kilometres (Barter and Hou 1990). The high mobility of birds makes them obvious candidates for extending mangrove connectivity research into a larger spatial context (Morales and Pacheco 1986), and their interaction with both terrestrial and marine environments provides possibilities for categories of interactions beyond those in which fish participate (Figure 2-1).

Depending upon the location, mangrove bird communities can be species-rich relative to their low floristic diversity (Table 2-1; Noske 1996, Mohd-Azlan et al. 2012). This is contrary to the expectation that low floristic diversity results in decreased productivity and species richness (Recher et al. 1996). Despite their diversity and abundance in mangrove systems, birds have not been incorporated into current mangrove-connectivity theory. Depending on the foraging guild they belong to, birds will use mangrove habitat for roosting, breeding, and refuge (Noske 1996, Kutt 2007), but will occupy other coastal habitats for foraging purposes (e.g. rainforest, tidal mudflat and marine-pelagic environments; Nagelkerken et al. 2008). There appears to be very few mangrove-bird species that depend solely upon mangrove habitat for survival (Nagelkerken et al. 2008), suggesting the potential for substantial and widespread connectivity with other habitat types.

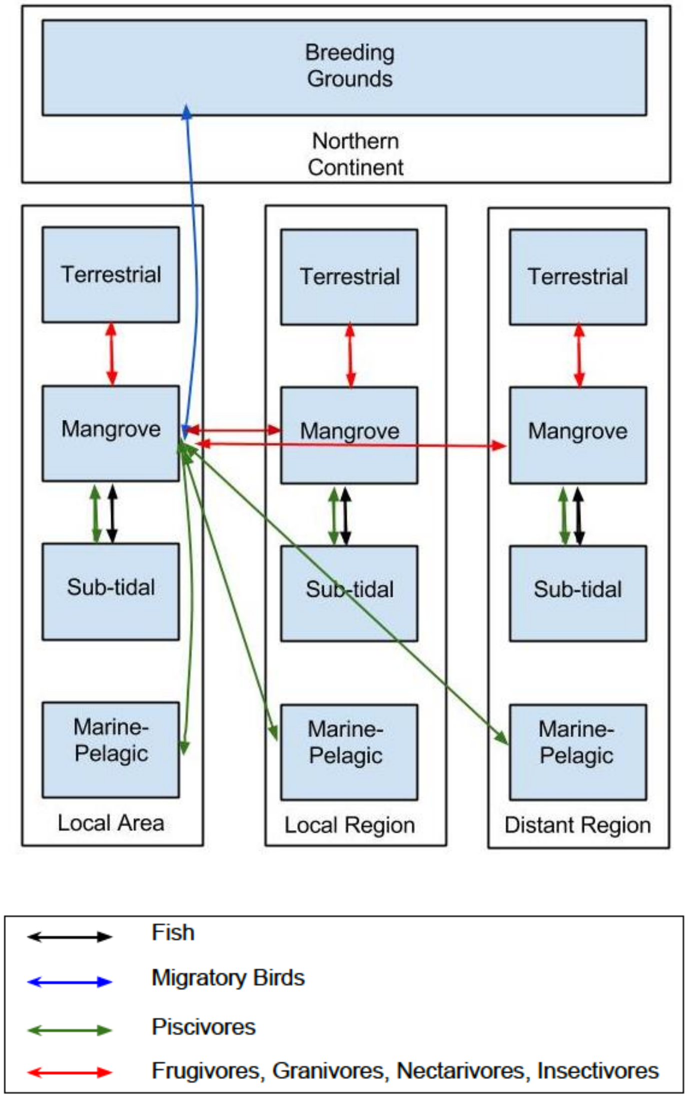


Figure 2-1 Comparison of the spatial degree of connectivity facilitated by inshore fish vs. mangrove avian functional groups (i.e. migratory birds, piscivores, frugivores, granivores, nectarivores, and insectivores).

Table 2-1 Species richness of mangrove avifaunal communities from survey locations around the world. These studies focused primarily on terrestrial birds and excluded migrants.

Survey Location	Species Richness	Reference(s)
Australia	47-70	Ford (1982), Noske (1996), Kutt (2007) Mohd-Azlan (2010)
Malaysia	47	Noske (1995)
Singapore	42	Sodhi (1997)
Brazil	59	Mestre (2007)
Puerto Rico	26	Acevedo and Aide (2008)
India	32	Kumar and Kumara (2011)
Panama[a]	104	Lefebvre and Poulin (1997)

[a]The survey in Panama was conducted at two sites on opposite coastlines, and included waterbirds and migrants (10 species) in addition to terrestrial bird species.

Their dependence on alternative foraging habitats implies that many mangrove birds are “link species” that perform ecological functions and services essential to ecosystem functioning (Lundberg and Moberg 2003). Examples of avian ecological functions include: frugivorous birds that facilitate seed dispersal to suitable nursery habitats, and piscivorous birds that translocate nutrients from aquatic ecosystems to terrestrial ecosystems (Sekercioglu 2006). Connectivity promoted by mobile link species increases the complexity of trophic structuring within ecosystem mosaics, although obligate connectivity can also increase the vulnerability of link species to habitat degradation because of their dependence on multiple habitats for survival (Sheaves 2005). In fact, there have been documented decreases in mangrove-dependent bird populations due to mangrove destruction and fragmentation (Alongi 2009*b*).

Incorporation of birds into concepts of coastal ecosystem connectivity provides the potential to expand understanding of this process in new and valuable directions. This expansion in scale and context needs to be built into coastal connectivity models and theories, as the concept of biological connectivity is primarily focused on achieving a more accurate and holistic view of ecosystem functioning. This review explores the role that avifauna play in connecting mangroves to other habitats within coastal ecosystem mosaics and the consequences for coastal ecosystem functioning.

2.3 Avian functional connectivity in mangrove ecosystems

Bird movement is an important factor for the transfer of energy within and among coastal ecosystem mosaics, which is mainly driven by daily foraging behavior, breeding/roosting requirements, and seasonal migration patterns. Functional grouping of avian species based on diet provides a useful basis for assessment of their movement in coastal interconnected habitats, providing insight to the ecological function of each bird species (Sekercioglu 2006). Functional connectivity is an important tool used when studying rainforest bird habitat fragmentation, and has demonstrated that certain ecosystem characteristics (e.g. distance to or size of adjacent habitats) are of different importance to each functional group (Awade and Metzger 2008, Martensen et al. 2008). Consequently, an examination of mangrove-bird foraging behavior provides a fruitful avenue for illuminating the consequences of mangrove-bird habitat linkage (Figure 2-2).

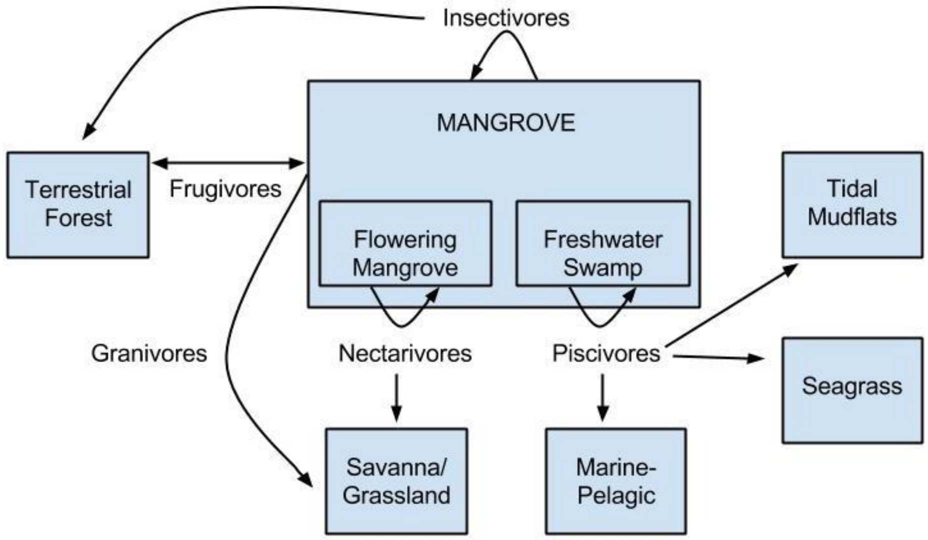


Figure 2-2 Connectivity facilitated by avian functional groups in the coastal ecosystem mosaic. Some species of each avian functional group move between mangrove forest and adjacent habitat, while other species will stay within the mangrove forest depending upon resource availability and abundance.

Avifaunal community surveys to date have revealed a diversity of avian functional groups in mangrove forests worldwide. At a rudimentary level of classification, mangrove avian functional groups include: frugivores, granivores, nectarivores, piscivores, insectivores and temporary migrants (insectivores are the most abundant group; Noske 1996, Lefebvre and Poulin 1997, Mestre et al. 2007, Acevedo and Aide 2008, Mohd-Azlan et al. 2012). Patterns of functional group assemblage in mangrove forests are influenced by mangrove zonation, habitat type surrounding the mangrove forest and seasonality; all of which determine food availability (Lefebvre and Poulin 1997, Kutt 2007, Mohd-Azlan and Lawes 2011). The following subsections illustrate the habitat requirements of each avian functional group and demonstrate how mangrove forests meet these requirements.

2.3.1 Frugivores and Granivores

Frugivores and granivores require foraging habitat with abundant fruit and seed resources (Howe and Smallwood 1982). Mangrove forests do not fulfill these foraging requirements because fruits and grains are scarce in mangrove forests, and mangrove-fruits tend not to be eaten by birds because they are not fleshy (Noske 1995, Lefebvre and Poulin 1997, Mohd-Azhlan et al. 2012). Consequently, granivores roost in mangroves with adjacent savanna or grassland habitat, while frugivores are more abundant in mangroves that have fruiting, terrestrial-forest habitat nearby (Noske 1996, Lefebvre and Poulin 1997, Trainor 2002, Kutt 2007, Mohd-Azlan et al. 2012).

Daily foraging trips by frugivores and granivores to adjacent fruit/seed abundant habitats can facilitate a high degree of coastal connectivity. For example: pigeon species in both Australia and Florida prefer to nest in island mangrove forests and fly to mainland terrestrial forests on foraging trips up to 20 kilometers in length (King 1990, Bancroft et al. 2000). Thus the configuration and identity of adjacent habitats has a substantial influence on the types of birds using mangroves, and consequently on the nature and outcomes of connectivity. The pigeon example underlines the difference in scales of fish and bird connectivity, with pigeon 'local-scale connectivity' of 20 kilometers at least an order of magnitude greater than 'local-scale' fish movements (Nagelkerken et al. 2013).

There is a lack of research exploring why frugivores and granivores choose to nest or roost in mangroves over terrestrial habitats where their food sources are abundant. Perhaps the closed-canopy of mangrove forests provides shelter, and the water surrounding the forest deters predators. However, artificial bird nests in mangrove and rainforest habitats often experience higher predation than nests in open canopy habitats (Noske et al. 2008); suggesting that protection from predation is not necessarily the reason. Alternatively, it may be that competition for space excludes some groups of frugivores and granivores from other habitats, forcing them to use mangrove forests as alternate roosts.

2.3.2 Nectarivores

There are few nectar-producing plant species in mangrove forests, causing foraging, nectarivorous birds to regularly link mangroves to adjacent nectar-abundant habitats (e.g. savanna/dune habitat in Australia; Noske 1996, Kutt 2007, Mohd- Azlan et al. 2012). Of particular interest to coastal ecosystem connectivity are species of Australian honeyeaters that are primarily nectarivorous. The high mobility of Australian honeyeaters may afford them the unique ability to connect flowering habitats over long distances (i.e. hundreds of kilometers) as they follow patterns of asynchronous flowering phenology (Craig and MacMillan 1985, McGoldrick and MacNally 1998).

In addition to the flowering phenology of adjacent habitats, the vegetative composition of the mangrove forest itself may also influence patterns of nectarivore foraging movement. Indo-malayan mangrove forests contain the nectar-producing mangrove genus *Bruguiera*, and some species have large, long flowers that enable birds to exploit their nectar resources (Noske 1993). The presence of bird-accommodating *Bruguiera* species will cause avian foraging patterns to differ from mangrove forests lacking these species. The consequences of vegetative composition is described in Venezuela, where nectarivores (specifically Coerebids) will move into flowering mangrove forests during the dry season when nectar resources are low in nearby habitats (Lefebvre et al. 1994). Therefore, mangrove forest community composition may play an important role in the nature and extent of avian connectivity in mangrove and coastal ecosystems.

Omnivory by nectarivorous birds complicates the idea that they rely primarily upon either nectar-producing mangroves or nearby nectar-abundant terrestrial forests. Many nectarivorous birds are not completely dependent upon nectar for food and supplement their diet with fruits or invertebrates, allowing mangrove forests to partially fulfill their foraging requirements (Feinsinger and Colwell 1978, McGoldrick and MacNally 1998, Franklin and Noske 2000). Thus, nectar feeders are able to collect substantial nutrition in mangrove forests even if nectar-producing mangroves are absent. Mangroves may provide premium habitat for nectarivores looking to supplement their diet during times of low nectar availability, due to high insect abundance in mangroves (Burrows 2003, Cannicci et al. 2008). These factors imply that the degree of omnivory within a nectarivorous species is likely to have a substantial effect on their facilitation of connectivity by foraging, and should be considered when investigating nectarivorous mangrove avifauna.

2.3.3 Piscivores

A variety of fish-eating birds use coastal habitats including: wading birds (e.g. herons, egrets, cranes), seabirds, and carnivorous forest birds (e.g. kingfishers, raptors). Three piscivorous birds have become dependent upon mangrove habitat in Australia: the Striated Heron, Collared Kingfisher, and Great-billed Heron (Table 2-2; Ford 1982, Noske 1996, Kutt 2007). Mangrove forests present unique foraging opportunities for these wading birds, providing both freshwater and marine foraging habitats (Ramo and Busto 1993, Acevedo and Aide 2008). Of particular value are freshwater mangrove swamps that retain their water continuously, providing year-round access to prey and drinking water (Ramo and Busto 1993, Woodin 1994). In addition to foraging, many wading birds use mangroves as breeding habitat, suggesting that they provide high-quality nursery habitat with access to food and shelter (Ghasemi et al. 2012). The extensive use of mangroves for feeding, breeding and roosting (Stolen 2006, Ma et al. 2010) means there is considerable potential for wading birds to contribute to connectivity among coastal ecosystems.

In contrast to wading birds, there has been no substantial study of seabird use of mangrove habitats. However, there are reports of breeding and/or roosting seabirds (such as pelicans and frigate birds) in mangroves (Onuf et al. 1977, Powell et al. 1991, Ghasemi et al. 2012). Similar to the situation for other mangrove birds that forage in adjacent habitats, it is likely that seabirds breed/roost in mangroves that are nearby high-quality, marine-pelagic foraging habitat (e.g. areas of upwelling; Butler et al. 2001, Vilchis et al. 2006). During their breeding season seabirds are confined to foraging in pelagic habitats near their colonies (Vilchis et al. 2006), making breeding sites near high-quality foraging habitats critical for reproductive success. However, some seabirds travel up to 250 kilometers on daily foraging trips if local geography requires it (e.g. Marbled

Murrelets in SE Alaska; Whitworth et al. 2000), suggesting a potential role for seabirds in connecting marine-pelagic foraging habitat to mangroves at large distances.

Table 2-2 Bird species dependent upon Australian mangroves (categorized by their functional group according to: Barker and Vestjens 1989, Barker and Vestjens 1990). Mangrove-dependence is defined broadly, ranging from mangrove as the species' principal habitat to mangrove as one of multiple woodland/forest habitats used.

Mangrove-dependent bird species	Study reference and location			
	Ford (1982) Western Australia	Noske (1996) Western Australia	Kutt (2007) Eastern Australia	Mohd-Azlan et al. (2010) Northern Territory
Insectivores				
Mangrove Fantail (*Rhipidura phasiana*)	X	X		X
Mangrove Golden Whistler (*Pachycephala melanura*)	X	X		X
Broad-billed Flycatcher (*Myiagra ruificollis*)	X	X		X
Mangrove Robin (*Peneoenanthe pulverulenta*)	X	X	X	X
Mangrove Gerygone (*Gerygone levigaster*)	X	X	X	X
Yellow White-eye (*Zosterops luteus*)		X		X
Dusky Gerygone (*Gerygone tenebrosa*)	X			
Large-billed Gerygone (*Gerygone magnirostris*)	X	X		
Kimberly Flycatcher (*Myiagra nana*)	X			
White-breasted Whistler (*Pachycephala lanioides*)	X	X		

Little Shrike-thrush (*Colluricincla megarhyncha*)	X			
Shining Flycatcher (*Myiagra alecto*)			X	
Little Bronze-cuckoo (*Chysococcyx minutillus*)			X	
Mangrove Honeyeater (*Gavicalis fasciogularis*)	X			
Varied Honeyeater (*Gavicalis versicolor*)			X	
Graceful Honeyeater (*Meliphaga gracilis*)			X	
Nectarivores				
Red-headed Honeyeater (*Myzomela erythrocephala*)	X	X		X
Brown Honeyeater (*Lichmera indistincta*)		X	X	
Piscivores				
Striated Heron (*Butorides striata*)		X		X
Great-billed Heron (*Ardea sumatrana*)	X	X		
Collared Kingfisher (*Todiramphus chloris*)		X	X	X
Omnivore				
Black Butcherbird (*Melloria quoyi*)	X	X		X
Chestnut Rail (*Eulabeornis castaneoventris*)				X
Total	14	14	8	11

2.3.4 Insectivores

Mangrove forests support large and diverse communities of insects (Burrows 2003, Cannicci et al. 2008). Consequently, mangrove bird communities are composed primarily of insectivores that do not need to leave the mangrove forest for foraging purposes (Noske 1996, Luther and Greenberg 2009). Mature mangrove forests that are separated from the direct flow of seawater retain large amounts of litter and deadwood, providing important foraging substrate for insectivorous birds such as the Mangrove Finch (Fessl et al. 2011). Additionally, wide ranges of foraging niches are available to forest birds within mangrove habitats (i.e. gleaning, poking, probing, scaling, hawking and hovering) due to the structural complexity of mangrove forests (Noske 1996, Sodhi et al. 1997).

Contrary to what would be expected in such a niche-abundant habitat, inter-specific competition does not determine mangrove-bird species assemblage because there is a lack of bird community saturation in mangrove forests (Mohd-Azlan et al. 2012). Lack of community saturation is perhaps because many insectivorous birds are not mangrove-dependent, and in fact occupy both mangrove and terrestrial forests in a transient manner (Mestre et al. 2007, Mohd-Azlan and Lawes 2011). The highest proportion of mangrove-dependent birds (~15%; Nagelkerken et al. 2008) is considerably lower than proportions of terrestrial forest-dependent birds (~61%; Watson et al. 2004). Less mangrove-dependency may foster a higher degree of biological connectivity in mangrove-bird communities compared to analogous, littoral-forest bird communities.

Insectivore presence in mangroves is driven by insect abundance, which is influenced by the following habitat characteristics: mangrove area, mangrove-plant species composition, flowering, and amount of rainfall (Lefebvre and Poulin 1997, Sodhi et al. 1997, Mohd-Azlan et al. 2014). Hydrographic characteristics, such as tidal cycles, may also provide additional foraging opportunities for generalist, mangrove insectivores that feed upon small crabs (e.g. the Mangrove Robin (Noske 1996) and the Shining Flycatcher (Sheaves, personal observation)). In comparison to terrestrial forests, small crabs are a resource uniquely available in mangroves during low tide, which may be particularly important during periods of low rainfall and reduced insect abundance. Dependence upon small crabs as a food resource would establish a daily foraging migration by generalist insectivores into the mangrove forest at low tide, and facilitate regular connectivity between mangrove and adjacent, terrestrial forest habitats.

2.3.5 Migratory Birds

Migratory birds have the potential to link mangroves and other coastal habitats at the largest geographic scales. Many temperate shorebirds, wading birds and passerines fly to tropical areas during their non-breeding seasons (Butler et al. 1997) and spend six to eleven months in tropical wintering habitats (Norris et al. 2004, Studds and Marra 2005). High-quality wintering habitat is critical for migrant survival and reproductive success, and mangrove wetlands have been identified as important winter habitat for migrating waterbirds (Ghasemi et al. 2012) and passerines (Reitsma et al. 2002).

Insectivorous, passerine migrants use mangroves as roosting and foraging habitat. Mangroves may be preferred foraging habitat due to high and consistent prey availability that is fostered by a lack of rainfall seasonality and high moisture levels (Lefebvre and Poulin 1996, Smith et al. 2010). High insect abundance in mangroves has been shown to increase the reproductive success of migratory American-redstarts that are able to overwinter in mangrove forests instead of adjacent, low-quality scrub habitat (Studds and Marra 2005). In addition to prey availability, flooding drives the daily foraging behavior of migrant insectivores that use mangrove pneumatophores as foraging substrate (Reitsma et al. 2002). Therefore, high mobility is a requirement for migrant passerines to successfully forage in physically-dynamic, mangrove habitat.

In addition to providing foraging habitat, mangroves are also selected as favorable roosting sites by passerine migrants that forage in habitats up to 2 kilometers away (Smith et al. 2008). Thermoregulatory benefits associated with warm, moist, mangrove microclimates may explain mangrove-roost fidelity. Thermoregulation is important for weight gain in migratory passerines, however Smith et al. (2010) found nightly weight loss in mangrove-roosting passerines equivalent to the weight loss of passerines roosting in temperate areas. Further investigation of weight loss in migrant passerines that roost in tropical areas is needed to establish whether mangrove roosts are preferred for the thermoregulatory benefits they provide.

Access to suitable roosting sites is a key factor determining habitat selection by migratory wading birds and shorebirds (Li and Lee 1998, Zharikov and Milton 2009), and mangroves provide preferential roosting habitat if there are adjacent, tidal mudflats for foraging (Zou et al. 2006, Acevedo and Aide 2008). The importance of the tidal-mudflat/mangrove link to migratory wading/shorebirds has been demonstrated in the Persian Gulf (Ghashemi et al. 2012), Neotropical Panama (Butler et al. 1997), China (Zou et al. 2008) and Australia (Zharikov and Milton 2009). Roosting migrants will make daily trips to foraging habitat up to 20 kilometers away (Green and Sanchez 2006), and a high degree of tidal-mudflat/mangrove landscape connectivity may allow birds to search for food over shorter distances and reduce the energetic cost of foraging (Farmer and Parent 1997). In addition to high landscape connectivity, suitable mangrove roosting sites also require shallow-water areas for access to fish prey and cooling habitat (Wong et al. 1999, Zharikov and Milton 2009, Kumar and Kumara 2011).

Wading birds and shorebirds may prefer mangrove roosting habitat due to mangrove subsidization of prey availability in adjacent, foraging habitats (but see Lee 2000; Butler et al. 1997). Alternatively, mangrove roosts may provide a refuge from predators (Zou et al. 2008) due to their structural complexity (Surman and Wooller 1995, Zharikov and Milton 2009). However, Kober and Barlein (2006) argue that mangrove forests experience a higher abundance of raptor predators, causing shorebirds to avoid foraging areas with mangroves nearby (and see Rogers et al. 2006). Discrepancies in wading/shorebird use of mangrove roosts may be remedied by survey technique, and a combination of terrestrial and aerial surveys should be employed to obtain the most accurate estimates (Rodrigues 2007).

2.4 Consequences of avian connectivity for coastal ecosystem functioning

Schmitz et al. (2014) has proposed the idea of "animating the carbon cycle", calling for more research to shed light on the role that animals play in the transfer and cycling of energy within ecosystems. In particular, top predators have been neglected when considering ecosystem energy flow, especially in comparison to the studies of microbes and plants which have traditionally been viewed as the main drivers of carbon cycling (Schmitz et al. 2010). Previous studies of energy flow have shown that secondary production in mangrove ecosystems is either: 1) not derived from mangrove plants, but instead from other nearby habitats such as seagrass or 2) mangrove carbon is of poor nutritional quality and therefore does not play a major role in supporting secondary production (but see Bui and Lee 2014; Bouillon et al. 2008, Heithaus et al. 2011, Sheaves et al. 2014*a*). In Australian mangroves, Abrantes and Sheaves (2009) describe a complex food web comprising 4 trophic levels with several pathways transferring carbon to the top of the food chain, and only one pathway was of mangrove origin. Regardless of the origin of carbon in mangrove food webs, consumers play an important role in its cycling and transfer due to their abundance and consumption rate (Kristensen et al. 2008).

Previous studies of predators in mangrove food webs have limited their scope to fish, and have disregarded birds as top predators. Birds may compete with fish as top predators and shorten the food chain by preying upon primary consumers such as detritivorous fish or crabs. Alternatively birds may prey upon top, piscivorous fish as well, thereby enhancing the rate of nutrient cycling within and out of the mangrove ecosystem. The following subsections look at the role that avian connectivity may play in coastal ecosystem functioning including: nutrient translocation, seasonal influences, top down control, and genetic information linking (Table 2-3).

Table 2-3 Ecosystem functions associated with avian functional group connectivity in mangrove forests and areas for future research.

Ecosystem Function	*Avian Functional Group*	*Consequence*	*Future Research Direction(s)*

Nutrient Translocation	Piscivorous Colonial Roosting/Breeding Birds	Provide concentrated nutrient subsidy to roosting/breeding habitat	Seabird use of mangrove habitat and the spatio-temporal degree of connectivity they facilitate
Top-down Control	Forest Insectivores	Increased mangrove productivity	1.) Avian insectivore initiation of a trophic cascade that increases mangrove productivity 2.) Daily foraging migrations by generalist insectivores to feed upon crabs at low tide
	Piscivorous Wading Birds	Spread effects of predation and transfer nutrients throughout the ecosystem mosaic (vs. fish confined to one wetland pool)	Effect of climatic conditions (i.e. drought) on wading bird foraging behaviour (may concentrate predation in small wetland pools)
Genetic Information Linking	Nectarivorous Honeyeaters	Spread nutrients and facilitate pollination across a wide array of habitats	Effect of omnivory on nectarivore-facilitated connectivity
	Migratory Waterbirds	Long-distance and regional dispersal of aquatic plants and invertebrates	Studies of wading bird movement and foraging behaviour in conjunction with propagule transport and survivorship
	Frugivores and Granivores	Long-distance and local seed dispersal	1.) Pigeon species' potential to facilitate local connectivity at a large scale (20km +) 2.) Mechanism of mistletoe infection into new mangrove host areas

2.4.1 Nutrient translocation

Mangroves can either act as nutrient sources or sinks within the coastal ecosystem mosaic, depending on the net transport of nutrients into or out of the mangrove ecosystem (Twilley and Day 1999, Sheaves 2009). Nutrient translocation and subsidization are inevitable consequences of biological connectivity due to the movement of animals between habitats, so these processes are critical to understanding how coastal ecosystems function. The role that birds play in the movement of nutrients may be of particular importance because bird guano increases the nitrogen and phosphorous levels of the habitat it is deposited in, and nitrogen and phosphorus are limiting nutrients of primary production in mangrove forests (Onuf et al. 1977, Feller 1995, Twilley and Day 1999, Josens et al. 2009). For example, egret colonies have been shown to increase the nitrogen and phosphorous levels of water in their wetland nesting sites (i.e. phosphorus: 25 mg/L in nesting wetlands vs. 2 mg/L in non-nesting wetlands, and nitrogen: 2 mg/L in nesting wetlands vs. 0.3 mg/L in non-nesting wetlands; Baxter and Fairweather 1994). The consequences of nutrient deposition by birds for mangrove productivity will depend on bird behavior (i.e. nutrient concentration through colonial breeding/nesting/foraging vs. nutrient dispersal via resource-tracking throughout the coastal ecosystem mosaic) and their food source (i.e. plant vs. animal protein; Table 2-4).

Bird movement between foraging and breeding/roosting grounds can result in considerable unidirectional translocation of nutrients (Morales and Pacheco 1986), which subsidizes mangrove productivity and affects adjacent, nutrient-recipient habitats. For example: colonial birds often roost in the same location for years (Pearse 2010) and accumulation of guano in mangrove roosts increases nutrient availability, resulting in increased growth of mangrove trees, nitrogen accumulation, and increased growth of macroalgae (Onuf et al. 1977, Lapointe et al. 1993, Feller 1995). Additionally, this mangrove nutrient enrichment can subsidize adjacent seagrass habitats. Florida-everglade mangroves support thousands of wading birds in breeding colonies, and seagrass meadows nearby support high densities of larval pink shrimp that are an important resource for fish and wading birds (Powell et al. 1991). Thus, bird-facilitated nutrient donation from mangroves to seagrass meadows may result in a positive feedback between piscivorous birds, high-quality seagrass biomass and shrimp abundance within the coastal ecosystem. Connectivity is the key to this nutrient cycle.

Table 2-4 Quantification of the annual rates of nitrogen and phosphorous nutrient deposition (g/m^2/yr) for avian nutrient transport categories (distinguished by functional group and roosting behavior). Nitrogen deposition by each avian nutrient transport category is expressed as a percentage of nitrogen needed for mangrove-forest primary production; demonstrating that nutrient transport by piscivorous birds (i.e. seabirds and wading birds) could lead to nutrient over-enrichment in mangrove forests. Examples of distances travelled by mangrove birds in each avian nutrient transport are given, and whether they are concentrating or dispersing nutrients in coastal ecosystems is indicated.

Avian nutrient transport category	*Nitrogen (g/m^2/yr)*	*Phosphorus (g/m^2/yr)*	*% nitrogen required for mangrove forest primary production**	*Example mangrove birds*	*Possible daily distances travelled by example mangrove birds*	*Nutrient concentration (i.e. roosting)*	*Nutrient dispersal (i.e. resource-tracking)*	*Reference(s)*
Roosting passerines	2.316	0.23	17%	American-redstart, White-crowned Pigeon	2 - 20	X		Fujita and Koike (2009), Smith et al. (2008), Bancroft et al. (2000)
Non-roosting passerines	0.0387	0.00307	0.003%	Brown Honeyeater	30		X	Franklin and Noske (1998), Fujita and Koike (2009)
Seabirds	103	22	763%	Lesser Noddy	250	X		Allaway and Ashford (1984), Surman and Wooller (1995), Whitworth et al. (2000)
Wading birds and seabirds (mixed flocks)	21.7	1.2	161%	Cormorants, herons, egrets, ibis	1-15	X		Powell et al. (1989), Wong et al. (1999)

* based on average nitrogen requirement (13.5 g/m^2/yr) of a mixed-species mangrove forest (*Avicennia*, *Bruguiera*, *Ceriops* and *Rhizophora*; Robertson et al. 1993).

The phenology and distribution of food resources dictates avian foraging behavior. This results in species-specific patterns of avian movement that can influence energy flows within the coastal ecosystem mosaic. Colonial, roosting/breeding birds tend to concentrate nutrients in one area, while more transient foragers (i.e. honeyeaters) can transport nutrients across a larger array of habitats within the coastal ecosystem mosaic. Nectarivorous birds are known to track nectar resources in intensely seasonal environments (Franklin and Noske 1999), and in Australia the Brown Honeyeater moves regionally at distances up to 33 kilometers (Franklin and Noske 1998). For other, less-mobile species, smaller-scale patterns of movement are dictated by adjacent foraging habitat availability. When foraging habitat is not available nearby there is potential for an ecological bottleneck. Similar controlling mechanisms have been identified in fish-mangrove connectivity, with the absence of suitable, adjacent habitat resulting in low abundances of certain fish species in mangroves (Sheaves 2005).

Birds will use mangrove forests as a refuge when their usual habitat has been damaged or saturated by influxes of birds displaced from other areas, and this behaviour can influence ecosystem nutrient retention and translocation (Kutt 2007). For example, in Western Australia, some mangrove-facultative birds have become restricted to small patches of mangroves where structurally-similar, alternative habitat types have been lost (Philips et al. 2008). Thus, because of their phytomorphological similarity, mangroves can play a critical role in providing the last bastion of suitable habitats in human-disturbed environments. If a temporary refuge becomes a permanent habitat for a population of birds (e.g. where it replaces lost terrestrial habitat resources) the rate of nutrient retention or import in the mangrove forest may increase, resulting in a mangrove sink.

Mangrove-bird nutrient translocation may also be influenced by the evolution of mangrove-dependent bird species. Mangrove forests in northwestern Australia harbor up to twenty mangrove-dependent bird species while, in stark contrast, mangrove forests in Africa and South America each accommodate only one mangrove-dependent bird species (Ford 1982, Noske 1996). To investigate the effects of avian mangrove-dependency on mangrove ecosystem functioning, the mangrove-bird communities of Australia provide a pertinent case study (Table 2-2). Mangrove forests of eastern Australia harbor fewer mangrove-dependent birds (~nine species) than mangrove forests in western Australia (~twenty species; Ford 1982, Nagelkerken et al. 2008). Differences in historical landscape connections have been hypothesized to influence the evolution of distinct, mangrove-dependent bird groups in western vs. eastern Australia (Ford 1982). A sustained mangrove-rainforest habitat link in eastern Australia may have allowed mangrove-facultative birds to travel easily between these two habitats, without creating the need to specialize to one habitat type (Mohd-Azlan et al. 2014). Mangrove-bird communities with fewer mangrove-dependent species may foster a higher degree of biological connectivity within the coastal ecosystem mosaic, as birds are able to travel more freely among habitats. This suggests that, by influencing present mangrove-bird community assemblage, historical patterns of landscape connectivity may be a determinant of avian biological connectivity within the coastal ecosystem mosaic.

2.4.2 Nutrient Translocation Influenced by Seasonality

Seasonality may influence the rate of nutrient translocation and retention in mangroves by causing shifts in connectivity patterns. Seasonality determines omnivorous-bird foraging strategies, causing them to switch between specific food sources from season to season (O'Donnell and Dilks 1994). During non-flowering seasons, retention of mangrove-productivity may increase if nectarivores choose to stay within the mangrove forest and forage on abundant insect prey instead of nectar. Alternatively, the rate of nutrient translocation outside of the mangrove forest may increase if nectarivores choose to continue feeding upon nectar in flowering habitats adjacent to mangroves. Understanding seasonal, omnivorous-bird behaviour will determine whether there is a net transfer of energy in to or out of mangrove ecosystems and how this varies with location and time.

The arrival of migrants changes bird-species composition on a seasonal basis (Acevedo and Aide 2008, Kumar and Kumara 2011). During winters in the Persian Gulf, the most abundant birds in mangrove habitat are migratory waders, while seabirds are most abundant during non-migratory summer seasons (Ghasemi et al. 2012). It is likely that the addition of migrant, wading-bird species to resident mangrove-bird communities increases nutrient concentration in mangrove forests during the winter (Josens et al. 2009). The degree of additional predation pressure and nutrient import will vary with details of the avifauna, the extent and type of resources provided by mangrove forests and connectivity strength (Webster et al. 2002). Full incorporation of migratory, wading birds into the current understanding of mangrove ecosystem functioning requires measurement of the nutritive quality (i.e. nitrogen/phosphorous levels) of migratory wader vs. resident seabird diets to determine their relative ecosystem effects.

Quantification of carbon dynamics in migratory shorebird roosting/foraging habitats has found little contribution of mangrove carbon to the foraging habitat of shorebirds (Li and Lee 1998, Lee 2000). This is corroborated by the fact that the presence of adjacent mangroves is not enough to ensure shorebird abundance in a tidal-mudflat (Butler et al. 1997), and suggests that other factors, such as up-welling, are contributing to a productive prey base in preferred tidal-mudflat foraging areas (Butler et al. 2001). It also suggests that migratory shorebirds at stopover sites are importing tidal-mudflat derived carbon into mangrove forests at a local and seasonal spatio-temporal scale.

In addition to local connectivity between foraging and roosting sites, migratory wading birds and shorebirds have the capacity to transport nutrients between stopover sites and establish biological connectivity at distances ≥1000 kilometers. Large wading birds (i.e. Bar-tailed Godwits, Great Knots and Red Knots) will travel distances of 5500-8000 kilometers between stopover sites in China and northwestern Australia (Barter and Hou 1990). The large numbers of birds (~500000 individuals) moving between stopover sites in China and northwestern Australia has the potential to create a high degree of energy transfer between these ecosystems on a seasonal basis, especially considering that migratory birds are ″refueling″ at these sites with high-energy intake rates (Tulp and Goeij 1994).

2.4.3 Top-Down Control

Insectivores are the most abundant avian functional group in mangrove forests (Noske 1996, Lefebvre and Poulin 1997, Mohd-Azlan et al. 2012) and are top predators that feed upon herbivorous insects, granting them the ability to control herbivory in mangrove forests. Controlling herbivory may be of particular importance in mangrove forests where insect-abundance fluctuation and outbreak potential is lower in comparison to terrestrial habitats, allowing insectivorous birds to exert year-round control (Sekergioclu 2006). This creates the potential for a stable trophic-cascade that will increase plant biomass, as vertebrate insectivores have been documented to reduce plant damage by 40% and increase plant biomass by 14% through their predation on insect herbivores (Mooney et al. 2010).

A trophic cascade in which insectivore control of herbivore abundance has a positive effect on plant productivity would complicate our current understanding of mangrove-ecosystem functioning. Previous investigations have found that guano accumulation in mangroves by colonial, roosting birds increases leaf growth in mangrove forests, but that this positive effect is reduced by increased herbivore abundance (Onuf et al. 1977). If insectivorous bird predators are included in studies of this food web, herbivore abundance may be reduced by predatory-bird behavioural response, allowing increased growth of mangrove forests. This trophic cascade would add a new interaction to the current understanding of mangrove food-web dynamics. The insectivorous trophic role may already be complemented in some mangrove forests by the activities of insectivorous archerfish (Simon and Mazlan 2010). This would provide the potential for unique ecological interactions, such as competition or enhanced predatory effects between very different vertebrate predators occupying contrasting media (i.e. air vs. water).

In addition to the top-down effects of insectivorous birds, piscivorous wading birds have the ability to regulate fish stocks in mangrove areas (Miranda and Collazo 1997). In a reciprocal way to insectivorous birds and archerfish, the presence of piscivorous birds in mangrove forests contributes to piscivorous-fish predation pressure on inshore fish stocks, and in particular on juvenile fish using mangrove nurseries. However, in contrast to predatory fish that can only access habitats with aquatic connections, wading birds' high mobility allows them to move rapidly between spatially-separate habitat units and exhibit a relatively rapid numerical response to high prey densities (Sheaves et al. 2006). This spreads the impact of predatory control across spatially-separated habitats, and promotes a more balanced and spatially-homogeneous regulation of fish stocks and stability across different components of coastal ecosystems.

Daily hydrographic conditions influence wading bird numerical response in a similar way to predatory fish, as tidal inundation is a requirement for access to prey. However, in addition to daily hydrographic conditions, longer time-scale climatic conditions need to be considered. For example, wading bird predation pressure in mangroves may increase if preferable wetland foraging habitat dries out during drought conditions (Halse et al. 1998). Alternatively, fish may become trapped when wetlands dry out, creating a temporary foraging area with high-prey density for piscivorous, wading birds (Sheaves et al. 2006). In addition to trapping prey, drought conditions in Everglade wetlands create pulses of secondary productivity that concentrate prey biomass for wading birds (Frederick & Ogden 2001). Evidently, large-scale climatic conditions influence the foraging behaviour of wading birds with consequences for nutrient dynamics in coastal ecosystems.

2.4.4 Genetic Information Linkers

Pollination and seed/aquatic-plant/invertebrate dispersal is an ecological function facilitated by birds that transfers genetic information within and among the coastal ecosystem mosaic (Sekergioclu 2006). Nectarivores are probably the most locally-mobile mangrove-bird functional group because of the fluctuating nature of the nectar resources they rely on, traveling up to several-hundred kilometers per year (Woinarski et al. 2002). High gene flow among Australasian mangrove forest populations of *Bruguiera gymnorrhiza* may be due to connectivity facilitated by these avian pollinators (Ge et al. 2005). Future studies could compare the genetic population structure of mangrove species with differing flower sizes (i.e *Bruguiera gymnorrhiza* (large) vs. *Bruguiera exaristata* (small)) to investigate consequences of the foraging and movement behavior of their respective avian pollinators. Large flowers may promote higher genetic connectivity among mangrove forests because they will not exclude pollination services provided by larger honeyeaters.

Invertebrate dispersal (internal and external) is another category of genetic information linkage performed by birds at large spatial scales. The role of migratory waterbirds in long-distance dispersal of aquatic invertebrates is generally understudied, but potentially facilitates genetic connectivity at distances up to 1000 kilometers (Green and Figuerola 2005). At a regional scale, mangrove-arthropod communities along the eastern coast of Australia demonstrate similar compositions and this implies a high degree of connectivity (Meades et al. 2002). Wading bird dispersal of insect larvae via internal transport may be the mechanism allowing this high degree of connectivity, as the dispersal ability of mangrove arthropods via flight and wind is limited (Green and Sanchez 2006).

Frugivores and granivores transfer genetic information through seed dispersal, which may have important consequences for plant regeneration and coastal-ecosystem functioning. For example, Australian Spiny-cheeked Honeyeaters are generalist frugivores that feed preferentially on mistletoe fruit, playing an important role in seed dispersal and establishment of mistletoe infections in new host areas (Rawsthorne et al. 2011). Mistletoe is an epiphyte associated with mangrove trees and has been identified as preferred nesting habitat for a wide range of bird species, encompassing functional groups from small insectivores to large wading birds (Noske 1996, Cooney et al. 2006). Initial infections of mistletoe in mangrove areas may require Spiny-cheeked Honeyeater dispersal of mistletoe to mangrove-adjacent woodlands, allowing less nomadic bird species (i.e. Mistletoebirds, Olive-backed Sunbirds) to transfer mistletoe seeds from woodlands to mangrove forests. Alternatively, in northern areas of Australia where the range of Spiny-cheeked Honeyeaters does not extend, long-distance dispersal of mistletoe seeds by generalist insectivores (via epizoochory) may be the dominant process facilitating mistletoe infection into mangrove forests (Watson 2013). Species-specific home ranges and foraging behaviour are likely to influence avian facilitation of mistletoe genetic-information linkage.

2.5 Bat functional connectivity in mangrove ecosystems

As highly mobile flying animals, bats that have the potential to facilitate coastal ecosystem connectivity in a similar way to birds. During the Australian dry season, large numbers of nectarivorous/frugivorous flying foxes (3000-25000 individuals) will roost in mangrove trees and track flowering/fruiting *Eucalyptus* trees at a regional scale of ~50 kilometers (Palmer and Woinarski 1999). The importance of flying foxes as mobile, genetic-information linkers in the coastal ecosystem mosaic (via pollination and seed dispersal) may be analogous to birds. Insectivorous bats are also known to use mangrove forests as both foraging and roosting habitat (McKenzie and Rolfe 1986, McConville et al. 2013). The spatiotemporal scale of bat-facilitated connectivity in coastal ecosystems requires further study; however radio-tracking has revealed that insectivorous bats roosting in mangroves will make nightly foraging trips of 1-10 kilometer distances (McConville et al. 2013). A thorough investigation into bat-facilitated coastal ecosystem connectivity is beyond the scope of this review, but should not be disregarded as a knowledge gap in coastal ecosystem functioning.

2.6 Conclusion

High mobility allows mangrove-bird communities to link spatially separate mangrove habitats, as well as link mangroves to other terrestrial and marine-pelagic habitats. Therefore, the spatial scale of coastal connectivity facilitated by birds is substantially more extensive than via fish-facilitated connectivity. In particular, connectivity facilitated by migratory birds links habitats at regional, continental and inter-continental scales as they travel among seasonally available feeding areas from breeding grounds to non-breeding grounds. Understanding the nature and patterns of fish connectivity has shifted the historical perception of mangrove ecosystem functioning from that of a simple system based on nutrient and energy retention, to a view that includes fish-facilitated energy export. In a similar way, understanding mangrove connectivity through bird movements and migrations opens a range of new possibilities for revising our view of functional links between mangroves and other ecosystems, even many that are spatially distant.

Mangrove-bird connectivity is primarily limited by the interaction between bird behaviour, bird resource requirements and the types of habitats available in surrounding areas. This contrasts with fish where connectivity is governed by the interaction between fish behavior, life-cycle needs and hydrologic-landscape connectivity. The linkage of trophic processes between systems is concomitant with connectivity among habitats, and the role that birds play in linking trophic processes varies by bird functional group. Therefore, investigation of mangrove-bird behaviour and diet are of critical significance to coastal ecosystem connectivity and conservation. In particular, avian functional connectivity as a process in carbon cycling within the coastal ecosystem mosaic has been overlooked.

Future research should investigate the consequences of mangrove-dependency in avian coastal ecosystem connectivity. Three patterns have been observed in mangrove ecosystems: 1) low numbers of mangrove-dependent bird species vs. terrestrial forest-dependent bird species, 2) mangrove-dependent bird species tend to be dietary generalists and 3) numbers of mangrove-dependent bird species vary globally. These observations suggest that the dynamic nature of mangrove forests foster transient, generalist bird communities that facilitate a high degree of biological connectivity. However, this may not apply to all foraging groups or species. For example, mangroves offer an abundant and stable supply of insect prey items for relatively rich and abundant insectivorous bird assemblages that may be relatively sedentary. Comparisons of bird movement in rainforests with high numbers of dependent, specialist birds and mangrove forests with low numbers of dependent, generalist birds would test this hypothesis. Additionally, global comparisons of mangrove-dependent bird communities would test the hypothesis that mangrove ecosystems with more mangrove-dependent insectivorous birds (i.e.

Australasia) enhance nutrient retention in comparison to those with less mangrove-dependent species (i.e. Neotropics and Africa).

Our current understanding of mangrove-connectivity theory is not yet complete without considering mangrove avifauna. Until bird-facilitated connectivity is incorporated, important links and regulating processes in mangrove-ecosystem functionality will continue to be ignored. Understanding bird linkages will provide a more complete knowledge base to support the conservation of mangrove habitat and preserve connectivity throughout the entire coastal ecosystem mosaic.

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

3.1 Abstract

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. 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.
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. 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. 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.

3.2 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 (Martin et al. 2006; Radford et al. 2005; Radford and Bennet 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 (Riffel et al. 2000; 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 (Mohd-Azlan and Lawes 2011; Kutt 2007; Woinarski et al. 2000a). 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.

3.3 Methods

3.3.1 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 (Commonwealth of Australia 2012; Figure 3-1). 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).

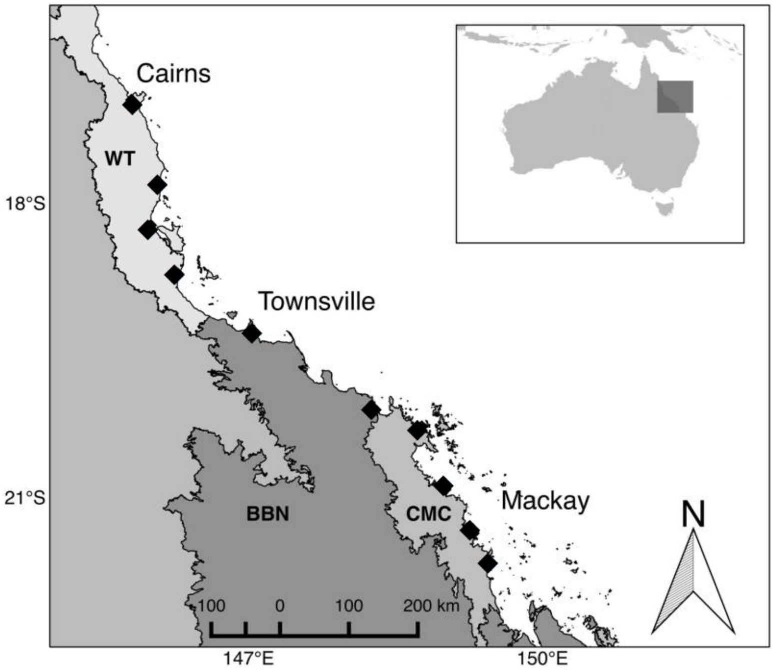


Figure 3-1 Map of survey locations (black diamonds) along the north-east coast of Queensland, Australia. Boundaries of the three biogeographic regions are displayed. WT = Wet Tropics (north-east tropical landscape context), BBN = Brigalow Belt North and CMC = Central Mackay Coast (south-east tropical landscape context).

Ten survey locations were placed sequentially along the study area coastline, 50 to 150 km apart, with six locations in the 'SE tropics' and four locations in the 'NE tropics' (Figure 3-1). 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 dominant coastal forest 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.

3.3.1 Bird assemblage data

Point count bird surveys were conducted from dawn-10:00 hours and from 14:30 hours-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 minute 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.

3.3.2 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 10 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 Appendix 1, Table A3.1). 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 3-1 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 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).

3.3.3 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 10 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).

Table 3-1 A brief description of the 11 vegetation types identified for connectivity analysis (NVIS 2012).

Connectivity variables and individual landscape metrics

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.

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).

Principal components analysis 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).

3.4 Results

3.4.1 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. The most common bird species observed were the yellow-spotted 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 (Figure 3-2 a) and by landscape context (Figure 3-2 b). Bird species composition in mangrove forests differed from other coastal forest types (Figure 3-2 a) and between north-east and south-east tropical landscape contexts (Figure 3-2 b). The variations in bird species composition were confirmed with a two-factor PERMANOVA (Appendix 1, Table A3.4). 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; Figure 3-2).

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 (Figure 3-2 a). 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; Figure 3-2 a). 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; Melaeluca, Eucalypt*:* t = 0.82, p = 0.782; Figure 3-2 a).

3.4.2 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, Figure 3-3). The correlation of connectivity variables to the bird ordination depended on the spatial scale being considered (Figure 3-3). At the 3 and 6 km spatial scales, two connectivity variables (i.e. Melaleuca and SandRockMud (Figure 3-3 a), and Melaleuca and grassland (Figure 3-3 b); 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; Figure 3-3 c).

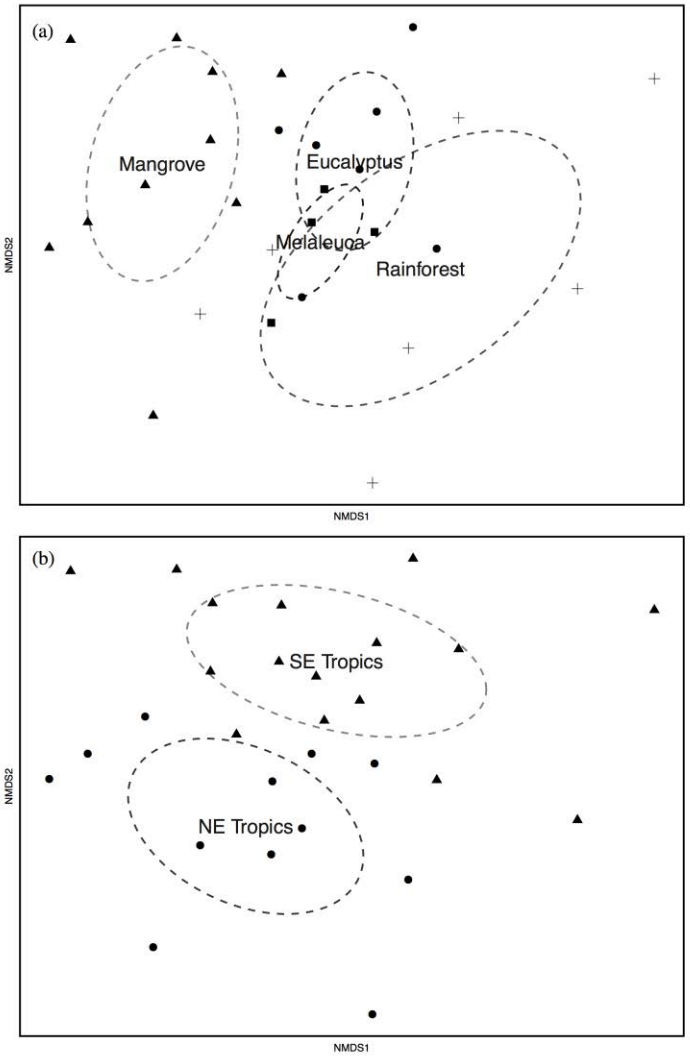


Figure 3-2 An nMDS ordination plot (stress = 0.22) of bird species presence-absence data at each survey site, pooled throughout the year, and grouped by a) coastal forest type (Melaleuca (square), Eucalypt (circle), Rainforest (plus-sign), Mangrove (triangle)) and b) landscape context (NE tropics (circle), SE tropics (triangle)). Centroid ellipses (95% confidence interval) distinguish the coastal forest and landscape context groupings.

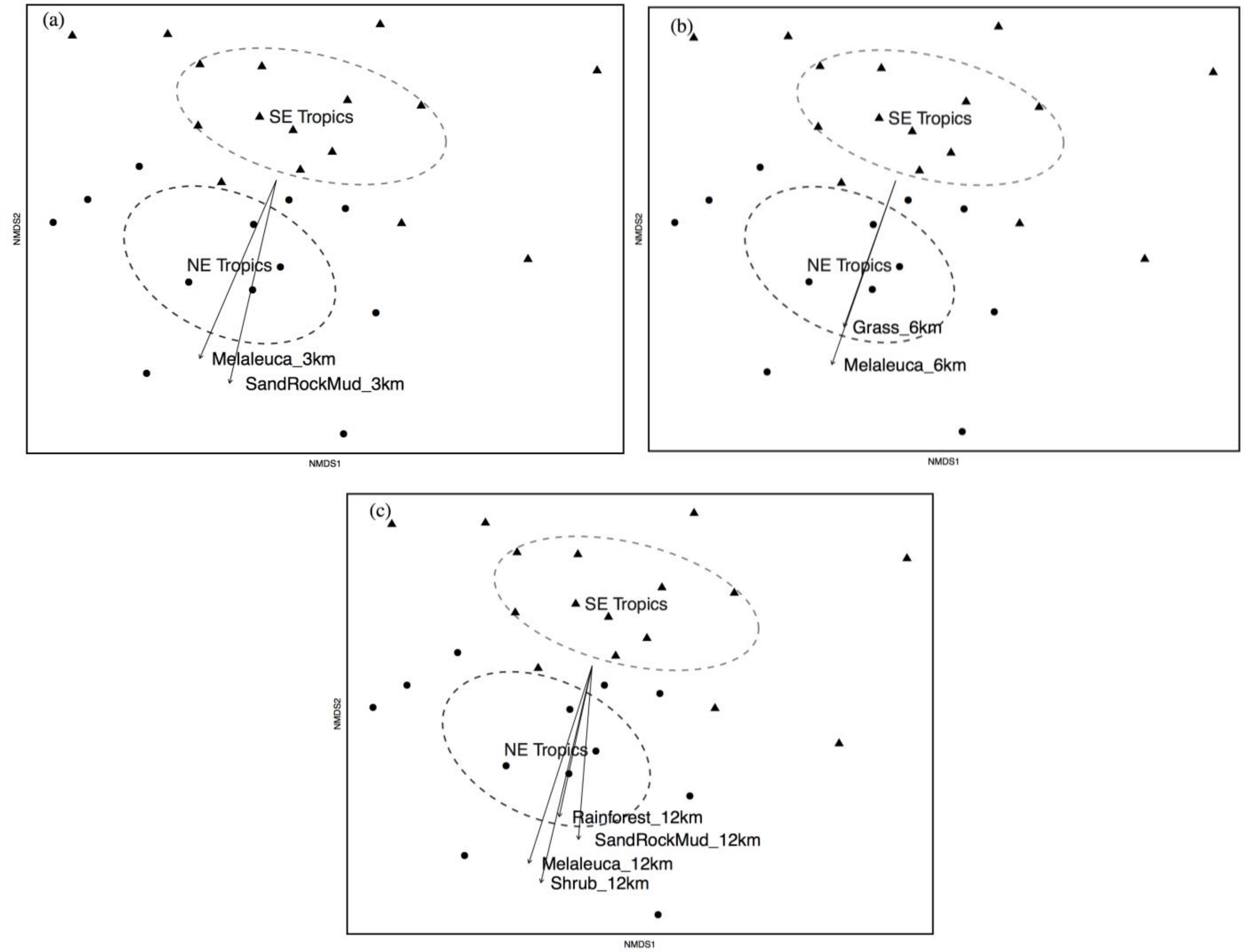


Figure 3-3 Fitted vectors of 11 connectivity variables were overlaid on an nMDS ordination plot of coastal forest bird species composition (stress = 0.22) at the: a) 3 km spatial scale, b) 6 km spatial scale, and c) 12 km spatial scale. Only connectivity variables that were correlated with the bird ordination ($p<0.05$) are displayed. Bird species

composition is grouped by landscape context (•NE tropics, ▲SE tropics). The vector arrows indicate the direction in which connectivity variable values are increasing, while the length of the vectors is proportional to the strength of the correlation between the bird ordination and the connectivity variable (Oksanen et al. 2015).

3.4.3 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 (Figure 3-3) 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; Figure 3-4 a) and SandRockMud total edge (TE; Figure 3-4 b) 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 (Figure 3-4). 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 (Figure 3-4 a). Alternatively, the lowest values of SandRockMud TE were associated with bird species composition in rainforest survey sites (Figure 3-4 b).

Principal components analysis (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 (Figure 3-5; Appendix 1, Table A3.3). Principal components 1, 2, and 3 cumulatively explained 98.5% of the variation in landscape metric R^2 values (Figure 3-5). 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 km vs. 12 km; Figure 3-5). However, landscape metric R^2 values were similar among all spatial scales for Melaleuca connectivity variables (Figure 3-5).

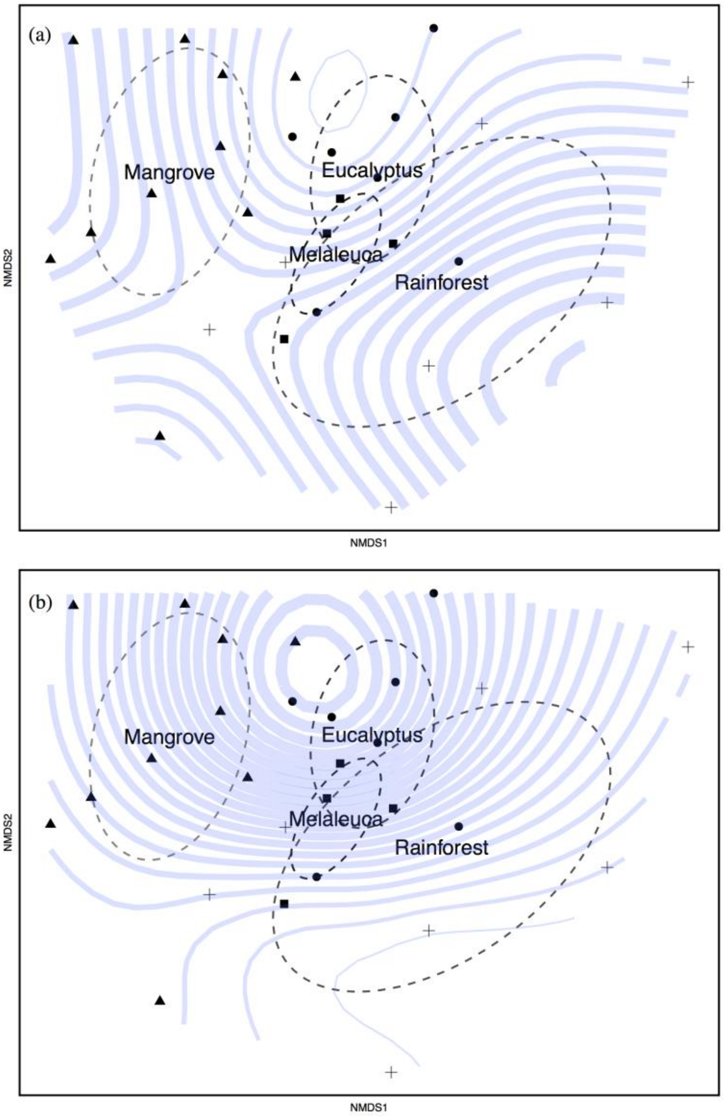


Figure 3-4 Surface fitting of individual landscape metrics at the 12 km spatial scale for a) rainforest total landscape area (TLA, R^2=0.68) and b) SandRockMud total edge (TE, R^2=0.42) to the bird ordination (stress = 0.22). The value of each metric is indicated by the thickness of the contour lines (■ = highest TLA or TE, ▬ = lowest TLA or TE), and the symbols in the plot indicate survey sites by coastal forest type (Melaleuca (square), Eucalypt (circle), Rainforest (plus-sign), Mangrove (triangle)).

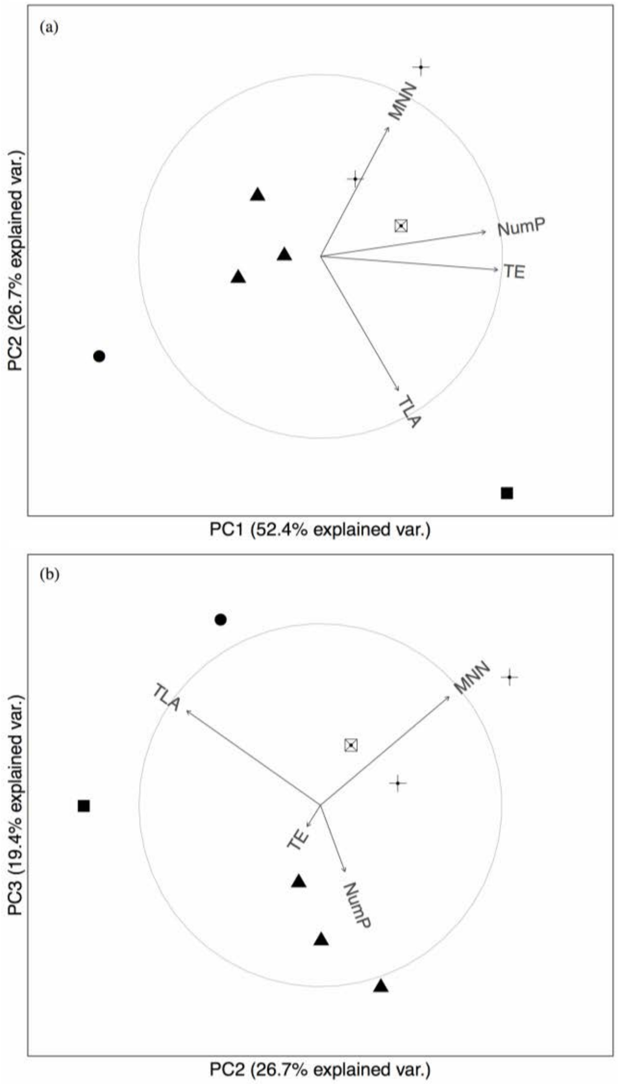


Figure 3-5 Principal components analysis demonstrates how landscape metric R^2 values (represented by vector arrows: TLA, NumP, TE, and MNN) are related to connectivity variables that were correlated to the bird ordination: (Melaleuca (3, 6, and 12 km; (triangle)), grassland (6 km; (circle)), SandRockMud (3 & 12 km; (plus-sign)), shrubland (12 km; (square with X)), and rainforest (12 km; black 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).

3.4.4 Connectivity variables and landscape context

This subsection describes the proportional comparison of landscape metric measurements in the north-east vs. south-east tropical landscape contexts for connectivity variables that were correlated to the bird ordination (Appendix 1, Figure A3.5).

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

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

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

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

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

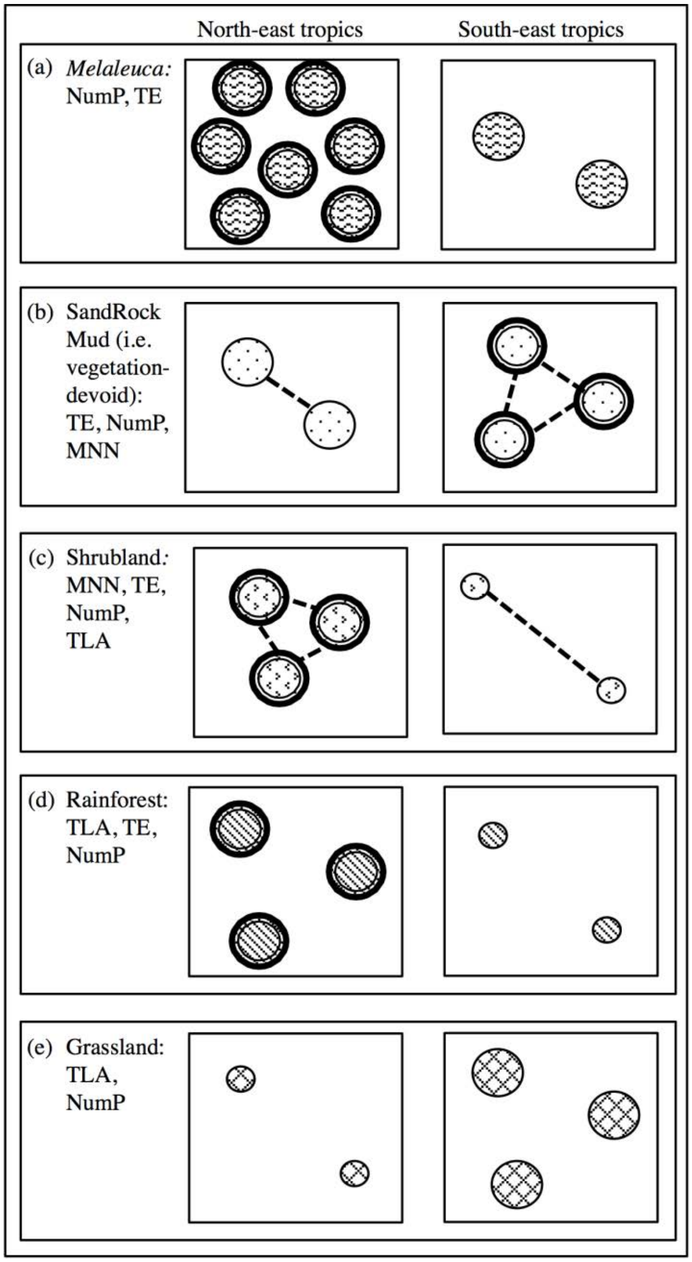


Figure 3-6 Summary figure of connectivity variables that were correlated to the bird ordination, and how their landscape metric average values (TLA, NumP, TE, and MNN) differ proportionally between north-east tropical and south-east tropical landscape contexts. Only landscape metrics of each connectivity variable that had high surface-fit R^2 values are represented as follows: circles inside boxes represent vegetation patches, and 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).

3.5 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; Riffel 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.

3.5.1 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 composition. 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 composition 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. 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 this study.

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., *Grevillia* 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 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 (Franklin and Noske 1998, 2000; Woinarksi and Tideman 1991; 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)).

3.5.2 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 modelling 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. 2007 a, 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 modelling.

3.5.3 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 ~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 2004; Woinarski 2004).

3.5.4 Conclusions

This 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. The present study provides a broad overview of the importance of landscape structural connectivity for mangrove bird assemblages. Further research is needed to examine the specific responses of foraging groups and individual species.

4 Ecological networks reveal divergent requirements for beta diversity conservation of generalists and specialists

4.1 Abstract

Networks of forests and woodlands commonly typify coastal landscapes, however species' use of these networks can differ depending on their niche specificity (e.g. habitat generalist or habitat specialist). Furthermore, whether a forest network is functionally connected depends on the distances that species are able to travel. We developed spatial models of coastal forest networks for bird assemblages of coastal northeast Australia, defined by the following attributes: forest area, forest availability, and forest connectivity. Bird species with similar daily home ranges were surveyed at ten locations along the northeast coast, and categorized as habitat generalists or specialists. Spatial models of coastal forest network attributes were then used as predictors of bird assemblage compositional turnover. Forest availability was the most important network attribute for generalists, while forest area was of greater importance to specialists. Network attributes were used to predict the compositional similarity of bird assemblages across coastal northeast Australia, finding that patterns of compositional similarity differ for specialists and generalists. Finally, current protected area coverage of important network attributes was evaluated, showing different levels of coverage in the northern and southern halves of the study region. In summary, generalist and specialist bird assemblages require different coastal forest network attributes to maintiain beta-diversity in regional northeast Australia. When divergent requirements cannot be dually protected, maintaining high amounts of forest area will benefit both groups.

4.2 Introduction

Improving understanding of the ways in which biodiversity promotes ecosystem resilience is increasingly important, especially considering the high rate of ecosystem change occurring worldwide (Tilman et al. 2014, Oliver et al. 2015, Lefcheck et al.

2015). Species are continually threatened by factors such as habitat loss, pollution, invasive species, and climate change; and protected areas can be ineffective at providing refuge if they are not well designed (Chape et al. 2005). Challenges to effective protected area planning are partly due to the complexity of processes occurring within and among ecosystems that contribute to spatial variation in species composition (i.e. beta diversity; Anderson et al. 2011). Determining how landscape attributes influence biodiversity will allow better-targeted management strategies, resulting in more effective conservation of resilient ecosystems (Oliver et al. 2015). For example, measures of landscape heterogeneity are positively correlated with species diversity in the mountain ranges of Nepal, demonstrating the need for adequate protection across the elevation gradient when designing an effective reserve network in this region (Paudel and Heinen 2017).

Since the 1970's there has been debate over which landscape attributes should be prioritised for effective conservation. This has been underpinned by island biogeography theory, examining whether reserve networks are best designed as single large or several, small protected areas (i.e. SLOSS; Diamond 1975, Higgs 1981, Margules et al. 1982). More recently, there has been debate over the importance of incorporating landscape connectivity vs. habitat area into protected area networks (Hodgson et al. 2009, Doerr et al. 2011, Hodgson et al. 2011). Connectivity patterns and processes are highly complex and variable, particularly in comparison to the relatively simpler and well-established species-area relationship. Therefore, decision-making may be more effective if habitat area requirements are prioritized over the inclusion of more complicated connectivity patterns and processes (Hodgson et al. 2009, Hodgson et al. 2011). However, the relationships underpinning habitat area, habitat quality, and connectivity requirements are likely to interact, and their relative importance will vary among species. Therefore, understanding the interactions between habitat area, quality, and connectivity is necessary (Doerr et al. 2011, Hodgson et al. 2011).

Conserving multiple species is further complicated by variation in landscape use associated with individual species' life history traits. One approach for accounting for this variability is to group species by their niche specificity, i.e. as habitat generalists or specialists. Generalists are able to use many resources across multiple habitats, while specialists are highly efficient at exploiting a specific resource in one habitat (Futuyama and Moreno 1988). Specialists are typically considered of greater conservation concern than generalists due to their higher sensitivity to habitat loss, causing high rates of population decline (Clavel et al. 2011, Buchi and Vuilleumier 2014, Poniatowski 2016). Furthermore, an abundance of generalist species is often viewed negatively for regional biodiversity because it indicates increased functional homogenization and redundancy (Clavel et al. 2011). Regardless of their perceived conservation importance, quantifying relationships between landscape features and generalist/specialist beta diversity will elucidate interactions between multi-species habitat requirements and landscape use.

Of the analytical approaches available for measuring landscape features, graph theory is a useful tool that represents landscapes as ecological networks comprised of habitat patches and linkages (Rayfield et al. 2011). Graph theory also allows information regarding species' movement abilities and habitat suitability requirements to be incorporated into the development of functionally connected ecological networks. Ecological network models based on graph theory have primarily been used to investigate the response of either single species or static measures of species diversity (e.g. species richness) to various landscape attributes. However, investigating single species' responses can be of limited value if the primary goal of conservation efforts is to protect the collective biodiversity of a region. Moreover, measures of species richness often over-simplify species' responses to environmental patterns and processes, resulting in inadequate information regarding species' habitat requirements (Veach et al. 2017). One solution lies in the use of generalized dissimilarity modelling, which determines the influence of environmental variables, such as ecological networks, to the compositional turnover of multiple species within a region (Ferrier et al. 2007). Compositional turnover is a measurement of beta diversity that determines how species' identities change in relation to spatial, temporal, or environmental gradients, and can be expressed as a rate (Anderson et al. 2011).

We developed functionally connected coastal forest networks to investigate how forest area, availability, and connectivity are related to the beta diversity of coastal forest avifauna. Specifically, we measured the compositional turnover of two coastal forest bird assemblages (coastal generalists and mangrove specialists) in response to forest area, availability, connectivity, and geographic separation. We also predicted the compositional similarity of coastal generalist and mangrove specialist bird assemblages across the study area, and evaluated the current protection of forests for avifauna.

4.3 Methods

4.3.1 Study area and bird assemblage data

The study area encompassed approximately 630 km of northeast Australia's coastline, comprising three biogeographic regions: the Wet Tropics, Brigalow Belt North, and Central Mackay Coast (Commonwealth of Australia 2012). Four major coastal forest types occur throughout these biogeographic regions: mangrove, rainforest, Eucalypt, and Melaleuca woodlands (see Figure 4-1 a for their distribution). In 2015, ten survey locations were placed sequentially along the coastline at 50-150 km distances (Figure 4-1 c). At survey locations, three replicate bird surveys were conducted in each coastal forest type (replicate surveys were at least 200 m apart, and surveyed twice in January/February, June, and October of 2015). Bird surveys were performed as 10-minute point counts from dawn-10:00 h and 14:30 h-dusk. All bird species seen or heard within a 50 m radius during the 10-minute period were recorded, while birds flying over the point count area at any distance were not recorded. Additionally, all point count surveys were audio recorded with a Sony IC Recorder to confirm difficult-to-distinguish bird calls. (Note: the same bird assemblage data were used in **Chapter 3**.)

The average daily movement ability of each bird species was identified using the Handbook of Australian, New Zealand and Antarctic birds (Marchant and Higgins 1990, 1993; Higgins and Davies 1996; Higgins 1999; Higgins et al. 2001, 2006; Higgins and Peter 2002) and the Australian Bird and Bat Banding Scheme database (ABBBS 2016). A distance of ~1000 m was representative of the average daily movement ability for the majority of bird species identified, and these species were selected from the presence-absence dataset for analysis. Thereafter, bird species were classified as either: mangrove forest specialists (> 90% of occurrences were in mangrove forest only (total = 4 species)), or coastal forest generalists (< 90% of occurrences were in only one forest type (total = 32 species)). A table displaying percentages of each bird species' occurrence among forest types, and their classification as a coastal generalist or mangrove specialist, is provided in the Appendix 2, Table A4.1.

4.3.3 Functionally connected coastal forest networks: forest area, availability, and connectivity importance

Graph theory was used to develop functionally connected forest networks for coastal generalist and mangrove specialist bird assemblages. Graph theory estimates landscape connectivity by determining links between habitat patches (i.e. nodes) with direct Euclidian distance or, if habitat suitability data is available, with least-cost paths through a resistance landscape surface (Rayfield et al. 2011). Habitat suitability data was not available for all bird species in the present study, and therefore a binary landscape surface (i.e. forest vs. non-forest) and Euclidian link distance were used.

A vegetation raster (resolution = 100 m X 100 m) was obtained from the National Vegetation Information System for development of the coastal forest networks (NVIS 2012). The NVIS raster was clipped along the length of the coastline that was surveyed, and at least 50 km inland from each survey location to avoid truncated modelling (Figure

4-1 a). The vegetation raster was reclassified as a binary landscape surface (i.e. forest vs. non-forest) separately for each forest network type (i.e. coastal generalist or mangrove specialist). For coastal generalist bird assemblages, links and nodes were based on all four forest types (i.e. mangrove, rainforest, Eucalypt, and Melaleuca). Alternatively, for mangrove specialist bird assemblages, only mangrove forests formed the basis for links and nodes in the forest network. Forest area and the links between forest patches in the binary landscape surfaces for coastal generalists and mangrove specialists were determined by construction of a minimum planar graph (MPG; inset of Figure 4-1 a). An MPG is an approximation of a complete graph, where only one link is shown between adjacent pairs of forest patches, and links do not cross each other (i.e. the graph is planar; Fall et al. 2007). The MPG method of link determination was chosen for its computational efficiency because of the relatively large raster used in the present study.

Following development of the functionally connected coastal forest networks, the area, availability, and connectivity importance of forest patches were quantified. Forest area was calculated by voronoi tessellation of the MPGs with 100 m X 100 m resolutions, meaning that forest area represented the total area of forest patches within ≤ 100 m distances from each other. The importance of forest patches to coastal forest networks was evaluated using several indices: integral index of connectivity (IIC), number of links (NL), and number of components (NC; see Table 4-1 for full description of each index and how they were calculated using Conefor 2.6 software (Saura and Torne 2009)). Importantly, indices were calculated when the Euclidian distance of links in the MPG were ≤ 1000 m, and therefore functionally linked for bird species with average daily movement abilities of 1000 m. The importance of individual forest patches for each index (I) were calculated by the Conefor 2.6 software as:

$$Importance(I) = I - I_{after}$$

where I is the overall value of the index when all forest patches are present in the landscape, and I_{after} is the overall value of the index after the removal of that forest patch from the landscape (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007). Forest patches in the vegetation rasters were reclassified with values calculated by each index, creating spatial models of forest area (A), availability (IIC), and connectivity importance (NL and NC) for coastal generalists (Figure 4-1 b_1) and mangrove specialists (Figure 4-1 b_2).

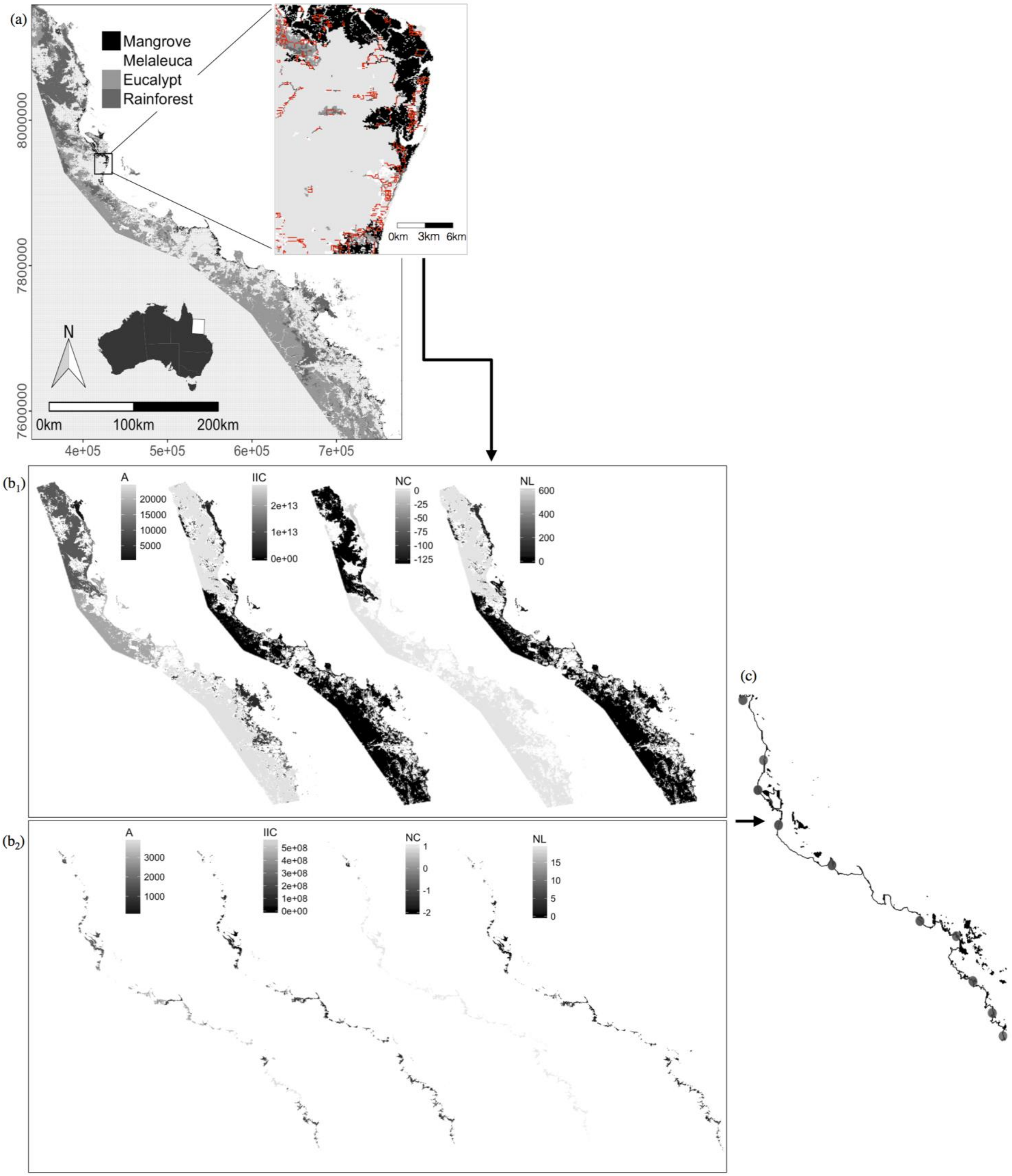

(a)
Mangrove
Melaleuca
Eucalypt
Rainforest
0km 3km 6km
N
0km 100km 200km
8000000
7800000
7600000
4e+05
5e+05
6e+05
7e+05
(b1)
A
20000
15000
10000
5000
IIC
2e+13
1e+13
0e+00
NC
0
-25
-50
-75
-100
-125
NL
600
400
200
0
(b2)
A
3000
2000
1000
IIC
5e+08
4e+08
3e+08
2e+08
1e+08
0e+00
NC
1
0
-1
-2
NL
15
10
5
0
(c)

Figure 4-1 Diagram of modelling approach, where (a) shows the distribution of four coastal forest types in northeast Australia (mangrove, Melaleuca, Eucalypt, and rainforest). The inset plot shows a network of coastal forest patches connected at a Euclidian distance threshold of ≤1000 m (links are displayed in red), forming a functionally connected forest network for bird species surveyed in the present study. Functionally connected coastal forest networks were developed for: (1) coastal generalist bird assemblages (all forest types were nodes) and (2) mangrove specialist bird assemblages (only mangrove forest patches were nodes). From these networks, forest area, availability, and connectivity were evaluated to develop predictors of compositional turnover for coastal generalists (b_1) and mangrove specialists (b_2) (See Table 4-1 for a description of each predictor (i.e. area (A), integral index of connectivity (IIC), number of components (NC), and number of links (NL)).) Finally, generalized dissimilarity models were used to evaluate the relationship between predictors and the compositional turnover of bird assemblages in coastal forests at ten survey locations (c) along the northeast coast of Australia (survey locations = grey dots).

4.3.4 Generalized dissimilarity models: relationships to compositional turnover

Generalized dissimilarity models (GDMs) were used to determine relationships between the compositional turnover of bird assemblages and predictors of forest area (A), availability (IIC), and connectivity importance (NL and NC; Figure 4-1 $b_{(1,2)}$, c)). In addition to these four predictor variables, GDMs offer the option to include Euclidean distance between survey sites (i.e. Geographic distance) as a predictor of compositional turnover (Table 4-1). GDMs perform nonlinear matrix regression using maximum likelihood estimation and flexible I-spline functions to accommodate variation in the rate of compositional turnover along a predictor gradient (Ferrier et al. 2007). GDMs also use a link function to accommodate the curvilinear relationship between composition dissimilarity (constrained between 0 and 1) and the increasing environmental/geographic distance between survey sites (Ferrier et al. 2007).

Table 4-1 Description of the forest network attributes that were used as predictors of bird assemblage compositional turnover in generalized dissimilarity models (GDMs). Minimum planar graphs (MPGs) were the basis for the calculation of A, IIC, NL, and NC (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007, Galpern and Doctolero 2016), and geographic distance was evaluated during the GDM procedure (Ferrier et al. 2007).

Predictor	Description
Forest area (A)	Total forest patch area (ha), defined by voronoi tessellation of the minimum planar graph (resolution = 100 m X 100 m).
Integral index of connectivity (IIC)	IIC is a measure of the forest patch availability that evaluates forest area and the number of links to a forest patch. High IIC value indicates that a forest patch has high importance to the availability of forest patches within a coastal forest network. IIC for a focal forest patch is calculated by: $$IIC = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} \frac{a_i a_j}{1 + nl_{ij}}}{A_L^2}$$ where a_i is the area of each forest patch and nl_{ij} is the number of links in the shortest path between patches i and j, and A_L is the total landscape area.
Number of links (NL)	The numbers of links connecting a forest patch to the network, at a Euclidian distance threshold ≤ 1000 metres. Forest patches with high NL values indicate high connectivity importance in the coastal forest network.
Number of components (NC)	A component is either an isolated forest patch, or multiple forest patches that are linked by ≤ 1000 metres. When a coastal forest network is more connected there will be less components. Therefore, low NC values indicate high connectivity importance in the coastal forest network.
Geographic distance	The Euclidian distance (m) between survey sites in the present study.

All five predictor variables (A, IIC, NL, NC, and Geographic distance) were included in construction of GDMs (using Jaccard dissimilarity matrices) for coastal generalist and mangrove specialist bird assemblages, separately. To determine the maximum deviance explained by each model, the number of I-spline basis functions per predictor was increased by an increment of one (from the default of three) until the increase in deviance explained was < 0.05%. Model significance was determined by matrix permutation (n = 500), and the relative importance of each predictor variable to the compositional turnover of bird assemblages was determined by summing their I-spline coefficients (Ferrier et al. 2007, Fitzpatrick et al. 2013).

Individual predictor relationships to compositional turnover were further investigated using partial regression fits where the effects of all other variables were held constant (i.e. the I-spline function for each individual predictor). The height of the I-spline function represents the total amount of compositional turnover associated with the predictor variable of interest, while the slope represents the rate of compositional turnover (Ferrier et al. 2007, Fitzpatrick et al. 2013).

I-spline functions of predictors that contributed to the overall deviance explained by GDMs were used to transform the original raster surfaces of each predictor. The transformed rasters were used to predict patterns of compositional dissimilarity for coastal generalists and mangrove specialists across their forest networks. Hierarchical cluster analysis of the predicted dissimilarities allowed grouping of areas that were compositionally similar (clustering method = *Wards*). Subsequently, the compositional dissimilarity between groups identified from hierarchical cluster analysis was calculated, creating a group dissimilarity matrix. Metric multidimensional scaling (MDS, k=3) of the group dissimilarity matrix was used to assign red, green, and blue (RGB) colour gradients to the 1st, 2nd, and 3rd dimension of each group, respectively (Ferrier et al. 2007). The colour of each group was defined by the combination of their three colour axes, allowing the predicted compositional dissimilarity of bird assemblages to be visualised by the

RGB colour scale. Colours that are close to each other on the scale are compositionally more similar.

Finally, the protection of coastal forest network attributes was assessed. Data providing the extent of areas protected by the Queensland government and other managers within the study area were obtained from the Collaborative Australian Protected Area Database (Commonwealth of Australia 2014). Using the extent of each protected area, the average value of forest network attributes (i.e. area, availability, or connectivity importance) that were found to be important to bird compositional turnover was calculated for each protected area.

Analyses were performed in R version 3.3.2 (R Core Team 2016) and in Conefor 2.6 software (Saura and Torne 2009). The following R packages were used during analyses: ‘raster’ for raster processing (Hijmans 2016), ‘grainscape’ for development of minimum planar graphs (Galpern and Doctolero 2016), ‘gdm’ for generalized dissimilarity modelling (Manion et al. 2016), and predictor indices were calculated with the Conefor 2.6 software (Saura and Torne 2009).

4.4 Results

4.4.1 Compositional turnover

We measured the compositional turnover of bird assemblages in response to several forest network attributes (i.e. forest area (A), availability (IIC), number of links (NL), and number of components (NC)). The observed compositional dissimilarity of bird assemblages against the linear predictor of the regression equation obtained by GDMs was plotted (i.e. predicted ecological distance; Figure 4-2). This shows the change in assemblage composition associated with the predicted distance between site pairs given their environmental dissimilarity and geographic distance, demonstrating that mangrove specialist bird assemblages had greater compositional turnover than coastal generalists in relation to the predictor variables investigated (Figure 4-2). The total deviance in the observed compositional dissimilarity of bird assemblages explained by predictors used in the GDMs was 13.2% for coastal generalists (p = 0.002) and 32% for mangrove specialists (p = 0.02).

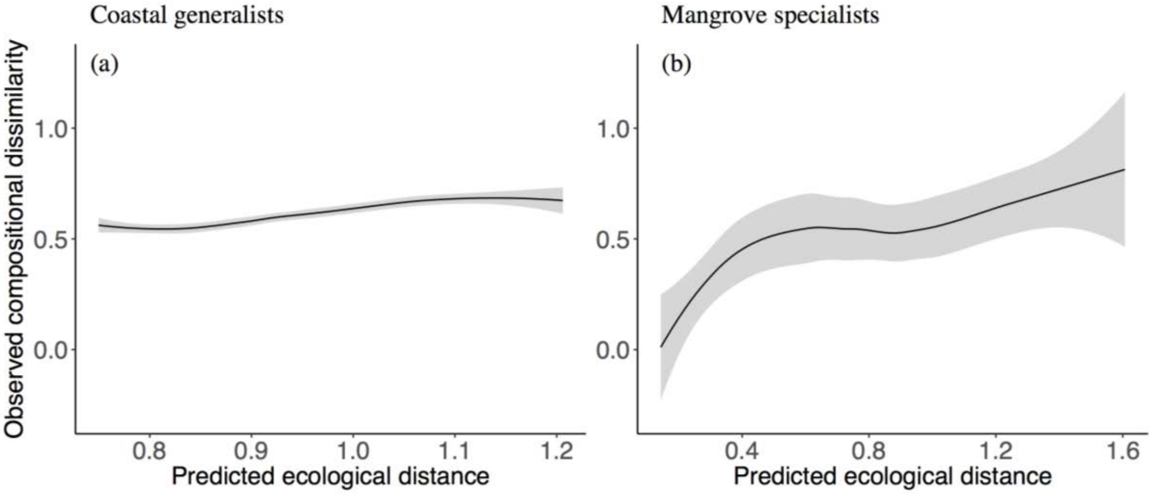


Figure 4-2 Relationship between the predicted ecological distance of site pairs and their observed compositional dissimilarity for (a) coastal generalist bird assemblages and (b) mangrove specialist bird assemblages. 'Predicted ecological distance' is the linear predictor of the regression equation from the GDM procedure (i.e. the predicted distance between site pairs given their environmental dissimilarity and geographic distance).

4.4.2 Relative importance of landscape attributes to compositional turnover

The relative importance of predictor variables to the compositional turnover of mangrove specialist and coastal generalist bird assemblages was determined by summing their I-Spline coefficients showing that, for both bird assemblages, forest area (A) and Geographic distance were related to compositional turnover, while the number of forest components (NC) and links (NL) were not (Table 4-2). The integral index of connectivity (IIC) was related only to compositional turnover of coastal generalists, while Geographic distance was the most important variable influencing compositional turnover of mangrove specialists (Table 4-2).

Table 4-2 Relative importance of predictor variables to the compositional turnover of coastal generalist and mangrove specialist bird assemblages, determined by summing their I-spline coefficients. The relative importance of the variable with the highest summed coefficients is highlighted in bold, while variables that were not related to compositional turnover are indicated by a dash.

Bird assemblage type	Model significance (p-value)	Variable importance				
		Forest area (A)	Integral index of connectivity (IIC)	Number of components (NC)	Number of links (NL)	Geographic distance
Coastal generalists	0.002	0.055	**0.387**	-	-	0.068
Mangrove specialists	0.02	0.878	-	-	-	**1.171**

4.4.3 Individual relationships between landscape attributes and compositional turnover

Partial regression fits were used to investigate the relationship between compositional turnover and each individual predictor variable, showing both the maximum compositional turnover (height of the fitted function) and the changing rate of turnover (slope of the fitted function) along each predictor variable gradient (Figure 4-3, 4-4). For predictor variables that influenced compositional turnover (i.e. A, IIC, and Geographic distance), the compositional turnover of bird assemblages increased as the predictor variable gradient increased (although relationships were not linear, Figure 4-3, 4-4). More specifically, the rate of mangrove specialist compositional turnover was highest when forest area was between 500 and 1000 ha, and lower when forest area >1000 ha (Figure 4-3 a). Mangrove specialist compositional turnover also increased continuously as Geographic distance increased (Figure 4-3 e).

The rate of coastal generalist compositional turnover was relatively inconsistent along each predictor variable's gradient (Figure 4-4 a,b,e). When forest area was greater than ~ 5000 ha the rate of coastal generalist compositional turnover increased (Figure 4-4 a). In response to Geographic distance, coastal generalist compositional turnover showed 'stepped' increases, with a maximum rate of turnover at distances > ~ 400 km (Figure 4-4 e). However, the most important predictor of coastal generalist compositional turnover was the integral index of connectivity (IIC), which showed a high rate of turnover that declined temporarily and then continued to increase gradually (Figure 4-4 b).

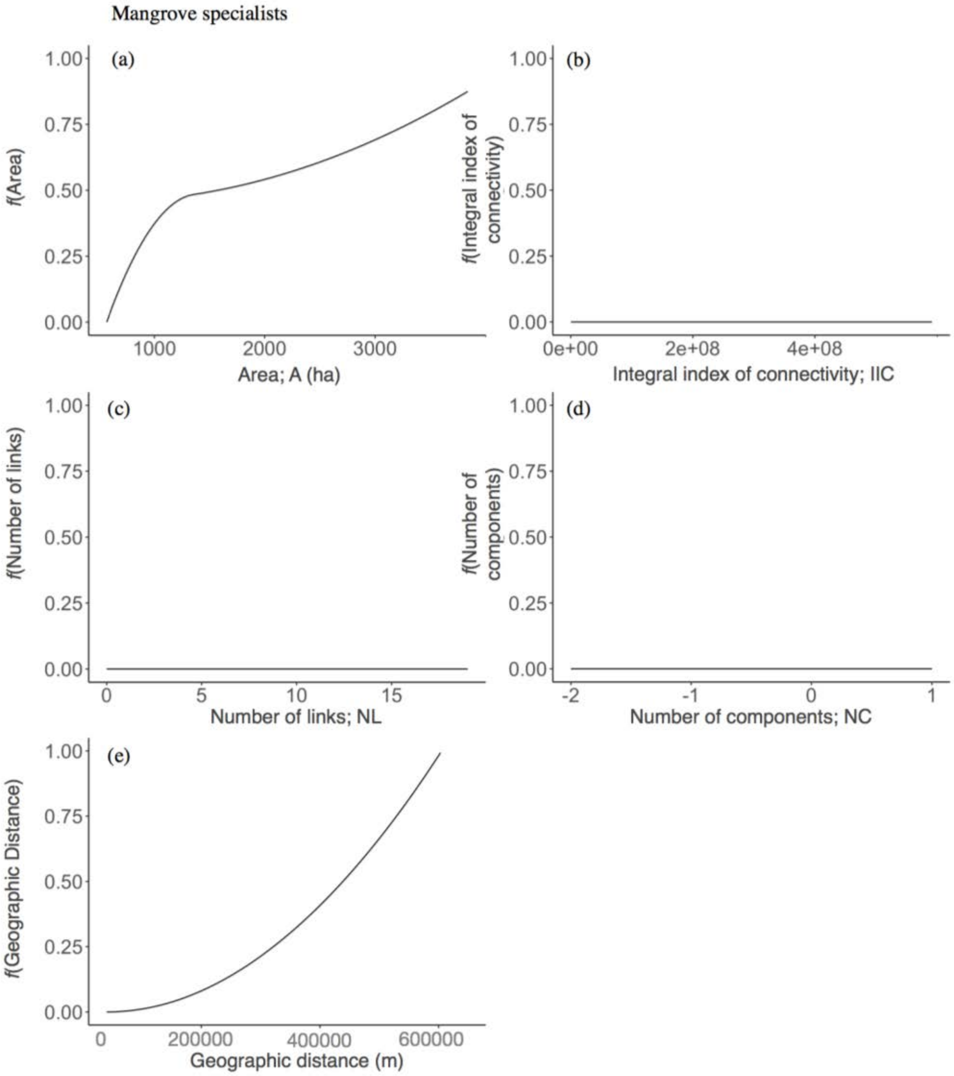


Figure 4-3 I-spline functions (i.e. partial regression fits) of each predictor variable in relation to the compositional turnover of mangrove specialist bird assemblages, while holding all other variables constant. See Table 4-1 for a full description of each predictor variable. The height of each I-spline represents the total amount of compositional turnover associated with each predictor variable, while the slope shows the changing rate of compositional turnover along the predictor's gradient.

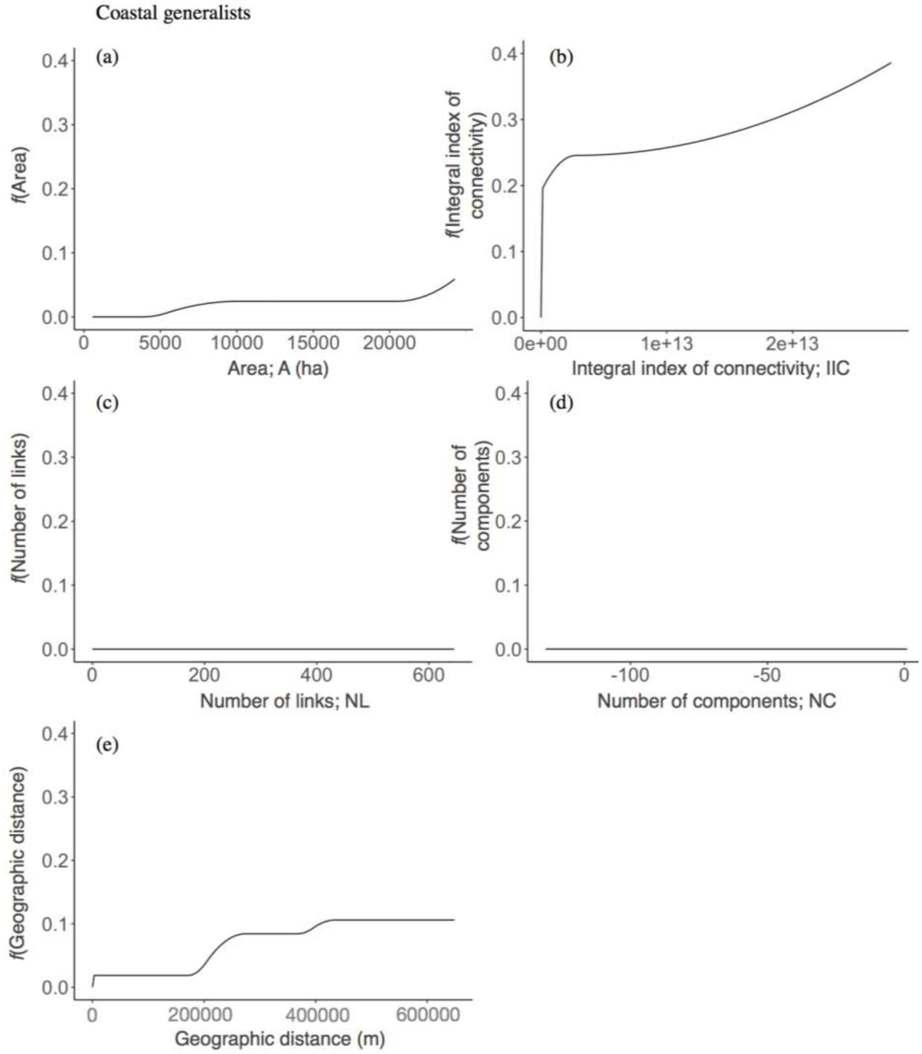


Figure 4-4 I-spline functions (i.e. partial regression fits) of each predictor variable in relation to the compositional turnover of coastal generalist bird assemblages, while holding all other variables constant. See Table 4-1 for a full description of each predictor

variable. The height of each I-spline represents the total amount of compositional turnover associated with each predictor variable, while the slope shows the changing rate of compositional turnover along the predictor’s gradient.

4.4.4 Predicted compositional similarity across northeast Australia

The predicted compositional similarity of coastal generalist and mangrove specialist bird assemblages across northeast Australia differed for mangrove specialists and coastal generalists (Figure 4-5). For coastal generalists, areas in the northern half of the study area had greater compositional similarity in comparison to the south (i.e. the northern half had dark and light blue colors that are adjacent to each other on the color scale, while the southern half had pink and yellow colors that are not directly adjacent to each other on the color scale; Figure 4-5 a). The Whitsunday region was predicted to have the most compositionally distinct coastal generalist bird assemblage relative to the rest of the study area (i.e. yellow colors; Figure 4-5 a). Alternatively, mangrove specialists showed a gradual change in composition from north to south along the coastline (i.e. green to blue to red to yellow, Figure 4-5 b).

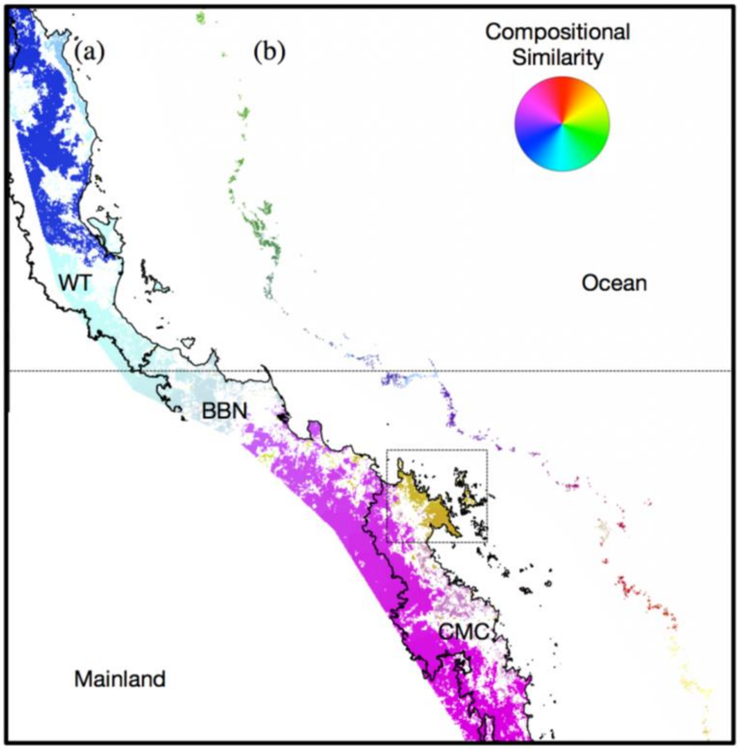


Figure 4-5 Predicted compositional similarity of: (a) coastal generalist bird assemblages and (b) mangrove specialist bird assemblages across northeast Australia. Colours that are farther apart on the red, blue, and green colour scale indicate less compositional similarity between areas. Borders designate the three biogeographic regions of the study area (WT = Wet Tropics, BBN = Brigalow Belt North, CMC = Central Mackay Coast; Commonwealth of Australia 2012). A dashed box shows the location of the Whitsunday region and, for reference, the dashed line splits the study area in to north vs. south.

4.4.5 Average values of important landscape attributes in protected areas

Given their importance for the beta diversity of coastal forest avifauna, the average value of forest area (A) and integral index of connectivity (IIC) in protected areas within the study area was evaluated (Figure 4-6). Overall, protected forests in the north were of intermediate size (pink colors in Figure 4-6 a) and well connected (yellow colors in Figure 4-6 b) compared to larger (yellow colors in Figure 4-6 a) but more disconnected forests in the south (purple colors in Figure 4-6 b). However, an exception to this overall pattern was the Whitsunday region, where protected areas contained forests that were on average small and disconnected (purple colors in Figure 4-6 a, b).

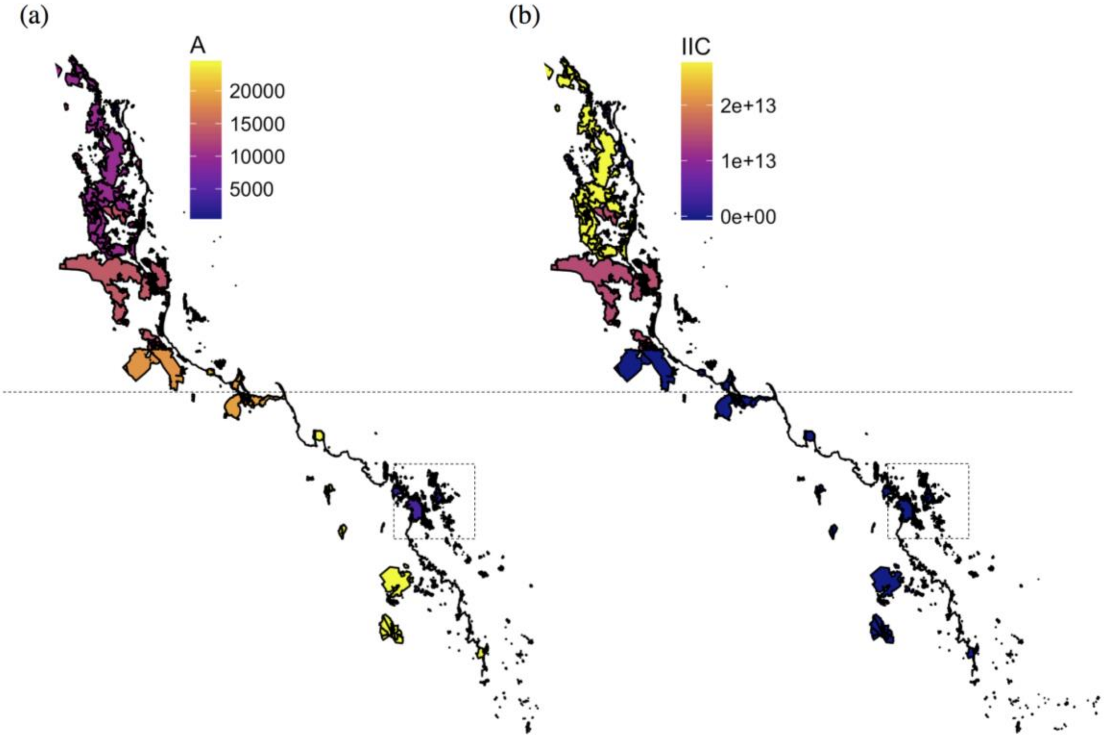


Figure 4-6 Protected areas within the study area are displayed as polygons. The colour gradient represents the average value of forest area (a) and importance to the integral index of connectivity (b) within each protected area. A dashed box shows the location of the Whitsunday region and, for reference, the dashed line splits the study area into north vs. south.

4.5 Discussion

Combining ecological network analysis with a multi-species modelling approach revealed that the importantance of forest network attributes differs depending on whether assemblages are comprised of habitat generalists or specialists, suggesting that the niche requirements of species assemblages are an important characteristic to consider when investigating compositional turnover. Furthermore, this approach demonstrates that habitat area, availability, and connectivity requirements can be considered simultaneously in regional biodiversity conservation planning.

4.5.1 Beta diversity of coastal generalists and mangrove specialists

Compositional turnover across northeast Australia was greatest for mangrove specialists. Specialists tend to exploit fewer resources and require very specific habitat requirements. Therefore, the high rate of specialist compositional turnover in the present study could be associated with spatial variability in either habitat quality or resources within the mangrove forest network. The lower overall rate of compositional turnover for coastal generalist bird assemblages is likely related to their propensity for using multiple forest types. Indeed, high variability in nectar and insect availability is characteristic of the Australian landscape and is known to encourage generalist and nomadic foraging strategies in birds (Chan 2001).

There were positive relationships between mangrove specialist beta diversity and both mangrove forest area and geographic separation. As the area or geographic separation of mangroves increased, the rate of mangrove specialist compositional turnover also increased. This suggests that spatial variability in either habitat quality or resource availability associated with mangrove extent and geographic distance contributed to the high rate of specialist compositional turnover. For example, larger mangrove forests may offer resources that small forests do not, allowing them to support a different mix of species. Prior analysis of the entire coastal forest bird assemblage (i.e. specialists and generalists) contrasts this, finding that the spatial extent and configuration of mangrove vegetation was not associated with variation in bird species composition among the four coastal forest types considered (i.e. mangrove, Eucalypt, Melaleuca, and rainforest;

Buelow et al. 2017). However, the present study provides a more specific definiton of the relationships between the compositional turnover of specialist and generalist bird assemblages and forest area.

Interestingly, the compositional turnover of mangrove specialists was not related to forest patch availability. This contrasts theory and empirical evidence that specialists are highly sensitive to habitat fragmentation due to their inability or unwillingness to use matrix habitat (Henle 2004). Therefore, including habitat suitability into the development of forest networks may help to more adequately address this unexpected result. Forest patch quality can be included ecological network development by the use of resistance (cost) landscape surfaces, instead of binary landscape surfaces. Resistance surfaces assign values to forest patches according to their quality and suitability for species, allowing these attributes to be accounted for in the measurement of forest patch availability and connectivity (Rayfield et al. 2011).

In contrast to mangrove specialists, the compositional turnover of coastal forest generalists was associated primarily with forest patch availability, and less so with forest area or geographic separation. Forest availability (measured by the integral index of connectivity; IIC) is the importance of a forest patch to the network given its area and connectivity, following the logic that connectivity occurs both within and between patches (Pascual-Hortal and Saura 2006). For this reason, and because it is highly robust to changes in spatial scale, IIC is considered among the best binary network connectivity measures (Saura and Pascual-Hortal 2007). The present study corroborates the superiority of forest availability for representing connectivity, as indices that did not explicitly account for forest area (i.e. number of components (NC) and number of links (NL)) were not related to beta diversity for either specialists or generalists. This suggests that, for coastal generalists, it is the combined influence of area and connectivity, culminating in forest availability that influences coastal generalist beta diversity.

There are likely to be factors influencing the response of generalist and specialist species' assemblages that were not captured in the present study. For example, previous research has also discovered that species' responses to area and connectivity depends on their foraging requirements, sensitivity to forest disturbance (Uezu et al. 2005, Martensen et al. 2012), and the latitude at which they occur (Bregman et al. 2014). Furthermore, response variable choice (i.e. compositional turnover, richness, or abundance) is likely to yield differences in the relative importance of patch size and connectivity for bird species assemblages. For example, the effect of connectivity was greater for species richness relative to the abundance of bird assemblages, and abundance was influenced by a combination of both patch area and connectivity (Shanahan et al. 2011). A complementary multi-species approach, using measures of both species richness and compositional turnover, could provide better information for regional conservation planning (Arponen et al. 2008).

4.5.2 Predicted compositional similarity and protection of important forest network attributes

The compositional similarity of coastal generalist and mangrove specialist bird assemblages differed across the study region. Generally, coastal generalist composition was more similar in the northern half of the study region compared to the southern half, while mangrove specialists showed a gradual transition in composition from north to south. For coastal generalists, the north-south distinction may be associated with climatic differences that result in higher average annual rainfall in the north (2000-8000 mm/year) relative to the south (590-2000 mm/year), driving differences in resource availability for birds between the two areas. Furthermore, structural differences in vegetative connectivity associated with landscape context in the present study region are known to influence the composition of coastal forest bird assemblages (Buelow et al. 2017).

The number and extent of protected areas (PAs) in the present study was also divided along the north-south boundary, with more PAs in the north relative to the south. Average forest availability (IIC) in northern PAs was relatively high, while in southern PAs forest availability was low and area was high (except for the Whitsunday region). This suggests that the existing network of protected areas may be more effective for both generalists and specialists in the north than in the south. Furthermore, the relative isolation of individual PAs in the south may reduce their effectiveness given that geographic distance was an important predictor of turnover for both bird assemblages. Given the compositional dissimilarity of assemblages in the south relative to the north, the development of more southern PAs may be warranted to ensure that these unique assemblages are able to persist (but, for discussion regarding the Whitsunday region, see below). However these are merely hypotheses, and measuring how well PAs represent the species composition of generalist and specialist bird assemblages would provide a more direct evaluation of their effectiveness.

The Whitsunday region was predicted to have the most compositionally distinct coastal generalist bird assemblage relative to the surrounding forest network. In contrast, the mangrove specialist bird assemblage of this region was not particularly unique in its composition. The Whitsunday region experiences higher than average rainfall compared to adjacent areas, and therefore hosts relatively more abundant rainforest vegetation that is disconnected from rainforest further north. Also, the PAs of the Whitsunday region consist of relatively small and disconnected forest patches. Therefore, it is likely that vegetative composition, area, and availability are all features of the Whitsunday region's coastal forest network that are contributing to the unique composition of its generalist bird assemblage. This illustrates the value of predictive modelling for PA management. Without considering the predicted effects of landscape features on compositional similarity, priority may be placed on protecting patches that are large in size and readily available within the forest network. However, this strategy would place the Whitsunday region as a low conservation priority, potentially leading to the loss of its unique avian assemblage.

4.5.3 Conclusions

The compositional turnover of coastal forest bird assemblages across northeast Australia differed for generalists and specialists, and this is likely associated with their differential landscape use. Generalists depend more heavily on forest availability to allow tracking of resources, while the forest area is more important to specialists. It is likely that the quality of mangrove patches influences specialist beta diversity as well (Mohd-Azlan et al. 2015), however this was not quantified in the present study. Forest patch quality, along with area and availability, are cornerstones of connectivity conservation, and should therefore be considered in future research of coastal avian beta diversity (Doerr et al. 2011).

Our results show that, with predictive modelling, PAs can be used to target specific areas with important forest network features for either generalist or specialist beta diversity. The current paradigm is to prioritize highly vulnerable specialist species, but this may occur at the expense of generalists. The relative importance of generalists vs. specialists for ecosystem functioning requires more research to determine what the appropriate allocation of protection will be. Theory suggests that communities with high specialist species richness enhance ecosystem functioning (Clavel et al. 2011), however the contribution of generalists should not be over-looked. Competition models have shown that, under specific conditions, generalist communities can provide greater contributions to ecosystem function than those rich with specialist species (Richmond et al. 2005). Furthermore, although generalist species tend to have large ranges and flexible landscape- and resource- use, there may be a limit to their adaptability. When possible, generalists should be included in conservation decisions. Given the importance of forest area to both generalists and specialists it seems sensible that, when area and availability cannot be dually protected, forest area requirements should take priority.

5 Stable isotopes reveal opportunistic foraging in a spatiotemporally heterogeneous environment

5.1 Abstract

Environmental heterogeneity can foster opportunistic foraging by mobile species, resulting in generalized resource and habitat use. Determining species' food web roles is important to fully understand how ecosystems function, and stable isotopes can provide insight into the foraging ecology of bird assemblages. We investigated spatiotemporal opportunism in mangrove bird assemblages by determining whether their species' carbon and nitrogen isotopic signatures corresponded to foraging group classification described in the literature. Subsequently, we evaluated the isotopic niche size and overlap of isotope-based foraging groups, and determined the probable proportions of coastal resources that contribute to their collective diets. Mangrove bird assemblages consist of foraging groups that are more opportunistic than expected by previous diet studies. Importantly, relationships between the dietary diversity of species within a foraging group and isotopic niche size are spatially inconsistent, making inferences regarding foraging strategies difficult. However, determining the probable relative contributions of coastal resources to the collective diet of isotope-based foraging groups can help to differentiate between specialised and generalised foraging strategies. We show that flexibility in their foraging strategies can occur in response to environmental heterogeneity. This is important because of the role that birds play in ecosystem functioning through processes such as nutrient transfer. A complementary approach that combines isotopic analysis with other dietary information (acquired by visual observation or gut content analyses) has provided useful insight to how highly mobile species assemblages partition resources in spatiotemporally heterogeneous environments.

5.2 Introduction

Where resource availability is patchy and unpredictable in space and time, species can survive by opportunistically consuming resources as they become abundant. This has been observed across avian taxa, including insectivorous and nectarivourous passerines (Rotenberry 1980, Brooker et al. 1990, Sherry et al. 2016), piscivorous waterbirds (Trayler et al. 1989), raptors (Stevens et al. 1990), and seabirds (Montevecchi et al. 2009). Shorebirds also forage opprotunistically when fluctuating water levels at wetland stopover sites cause high variability in prey abundance (Davis and Smith 2001, Andrei et al. 2009), and when tides or floodwaters inundate their preferred foraging areas (Skagen and Knopf 1994, Long and Ralph 2001). Therefore, in environments characterized by heterogeneous resource availability, opportunism can occur across multiple features of a species' ecological niche, resulting in generalized resource and habitat choice. Given the importance of species' food web roles for ecosystem functioning, there is a need to understand relationships between environmental heterogeneity and the niches that species are able to occupy.

Heterogeneity can manifest from the abiotic or biotic characteristics of an environment. For example, coastal mangrove forests are located at the land-sea interface, and their functioning is influenced by abiotic factors, such as tides, and biotic factors, such as the extent and configuration of adjacent vegetation. For forest birds, tidal inundation means that the availability of many mangrove resources fluctuates daily. Mangroves also offer estuarine prey items (e.g. mudskippers and crabs) that are not found in terrestrial forest types. Furthermore, mangroves are often situated in a complex mosaic of adjacent vegetation types such as grasslands, saltmarshes, and woodlands, and this could mean that flexibility in foraging strategy and choice of foraging habitat may be advantageous for highly mobile forest avifauna.

Relative to other forest types, mangroves support few bird species that are obligate habitat (mangrove) specialists and instead host many species with generalized foraging niches (Noske 1995, Mohd-Azlan et al. 2014, Buelow and Sheaves 2015). However, foraging niches have traditionally been examined through visual observation or gut content analyses and, unless individuals can be tracked or recaptured, these methods are inappropriate for determining the consistency of an individual's foraging strategy. For example, visual observation can indicate what resources are consumed by a species in a specific area, but will not provide information on whether individuals move to forage in different habitats, or if individuals consume different resources over time.

Stable isotope analysis provides complementary information to traditional measurements of foraging ecology. The carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) stable isotope ratios of resources vary depending on the photosynthetic pathway of primary producers and with trophic level, respectively, and are integrated into the tissues of consumers (Layman et al. 2012). Therefore, isotopic signatures can be used as 'tracers' of resources that are consumed, allowing consumer food webs and 'isotopic niches' to be constructed if there is sufficient variability in the isotopic signatures of basal resources (Newsome et al. 2007, Jackson et al. 2011, Layman et al. 2012, Phillips et al. 2014, Swanson et al. 2015).

An isotopic niche represents only a subset of a species' entire ecological niche (Bearhop et al. 2004, Newsome et al. 2007, Swanson et al. 2015). Bird carbon isotopic signatures represent foraging habitat choice (e.g. saltmarsh vs. forest), and nitrogen isotopic signatures represent resource choice by proxy of trophic level (e.g. insects vs. fruit). Also, bird blood and claw tissues differ in how quickly their isotopic signatures are integrated (i.e. isotopic turnover rate), providing a temporal comparison of individual foraging choice (Bearhop et al. 2002, Lourenco et al. 2015). Therefore, stable isotopes offer a unique way to quantify species' niches and food-web positions in spatiotemporally heterogeneous environments.

We investigated spatiotemporal opportunism in mangrove birds using carbon and nitrogen stable isotopes to provide insight into their foraging behavior and flexibility. Categorizing species into foraging groups is a useful way to understand how bird assemblages partition resources (Simberloff and Dayan 1991). However, species employing opportunistic foraging strategies may not necessarily fit within literatureprescribed foraging groups. Therefore, we investigated whether the isotopic signatures of bird species occupying mangrove forests corresponded to their foraging groups described in the literature. Given the inherent heterogeneity of mangrove forests, we anticipated discordance between literature-based and isotopic bird foraging groups.

Following identification of isotopic foraging groups, we measured their isotopic niche size and overlap (Jackson et al. 2011, Swanson et al. 2015) expecting patterns indicative of generalized foraging strategies (although see Appendix 3 Figure A5.1 for an illustration of some challenges in interpreting isotopic niche size). We also used tissues with different isotopic turnover rates to examine seasonal variability in resource selection, expecting that temporally opportunistic birds will have dissimilar isotopic signatures between blood and claws (Bearhop et al. 2002, Lourenco et al. 2015). Finally, we constructed the isotopic food web of mangrove bird foraging groups to determine the probable proportions of resources that contribute to their diet. Together, these findings provide insight into the complex foraging behavior of these species and thus the functioning of this system.

5.3 Methods

5.3.1 Study area

This study was conducted at two mangrove forest sites in the Brigalow Belt North bioregion of northeast Australia (Commonwealth of Australia 2012, Figure 5-1). This region has a dry tropical climate, with rainfall occurring primarily in the wet season (November to April, ~590mm/year). In addition to mangrove forest, coastal vegetation of this region includes: saltmarsh, rainforest, grassland, agricultural land, and Eucalypt, Acacia, and Melaleuca woodlands and forests.

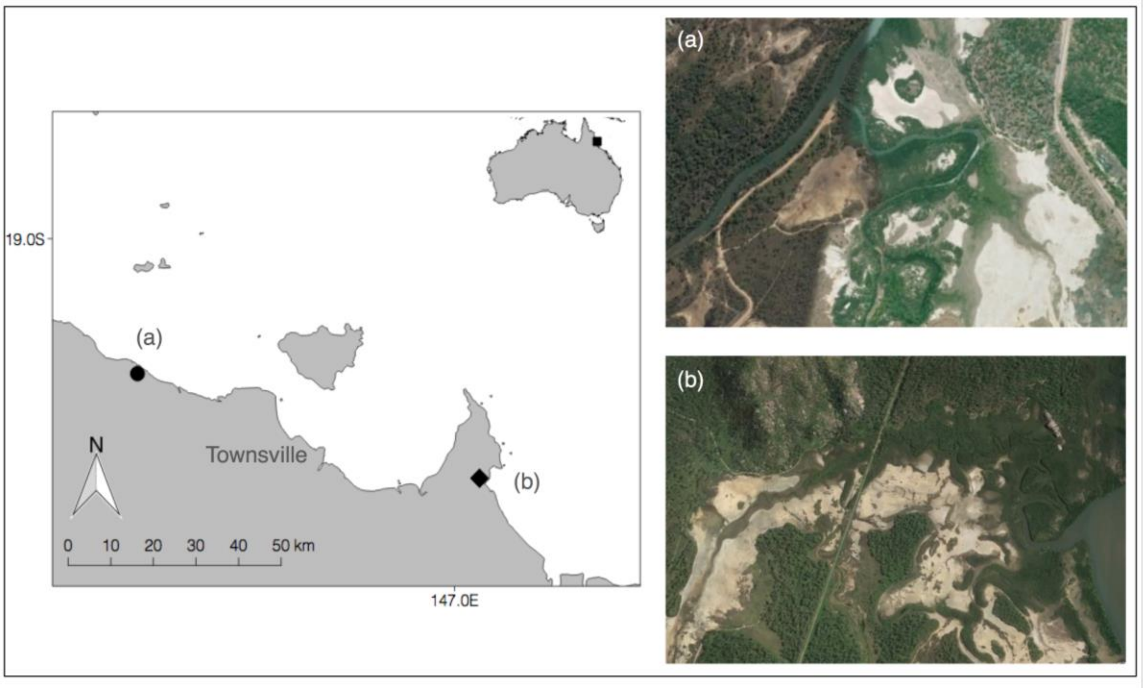


Figure 5-1 Map displaying two mangrove forest sampling sites in northeast Queensland, Australia: (a) Healy creek (circle) and (b) Cocoa creek (diamond).

5.3.2 Bird capture and foraging group classification

Bird capture and sampling occurred during the months of March-April, 2015 (wet season) and July-August, 2015 (dry season) at Cocoa creek (Figure 5-1 b), and only during the wet season months at Healy creek (Figure 5-1 a). Eight to ten nylon mist-nets (dimensions = 12 × 2.5 m, mesh-size = 16 mm) were used to catch birds on each day of sampling. Locations for mist-nets were chosen haphazardly at each site, and shifted approximately every two days. Nets were opened before dawn and closed by 12:00. Captured birds were identified to species using Pizzey and Knight (2012), and aged and sexed using ‘The Australian Bird Bander’s Manual’ (Lowe 1989) and ‘The Bander’s Aid’ (Rogers et al. 1986). Each bird was fitted with a band issued by the ABBBS (Australian Bird and Bat Banding Authority) and standard morphological measurements were taken.

Birds were classified into one of four foraging groups based on previous diet studies (Barker and Vestjens 1989, 1990): carnivores, insectivores, nectarivore-insectivores, and omnivores. Foraging groups had the following dietary compositions: carnivores = arthropods and vertebrates; insectivores = arthropods; nectarivore-insectivores = arthropods and nectar; and omnivores = seeds, nectar, fruit, arthropods, and vertebrates. Foraging group classification for each bird species caught is provided in the Supplementary Materials (Appendix 3, Table A5.2).

5.3.3 Collection and preservation of samples for isotopic analysis

Blood was sampled (20 -100 µl) from the antebrachial vein of each bird using a needle (23-27 gauge, depending on bird body size) and a heparinized capillary tube. Blood samples were transferred from the heparinized capillary tube to a glass slide, allowed to dry, and sealed with another glass slide for preservation until preparation for stable isotope analysis. Stainless steel scissors were used to cut 1-2 mm from the tips of four claws of each bird. Claw samples were placed in plastic Eppendorf tubes for preservation until preparation for stable isotope analysis. Birds were released following blood and claw tissue sampling and were not re-sampled if caught again during the same sampling trip.

Potential resource and prey items (basal food sources) for birds were collected during bird sampling periods at each mist-netting site. Plant, arthropod, and vertebrate food sources were collected in the mangrove forests where birds were sampled, and in adjacent woodlands (*Eucalyptus* and *Melaleuca* spp.) and saltmarshes (see Appendix 3 Table A5.3 for a full description of the basal food sources collected and their isotopic signatures). It should be noted that, while many birds caught may feed on nectar or fruit, these sources were not sampled directly. Instead, given their status as primary producers, leaf samples were collected with the assumption that they should have similar isotopic signatures to nectar and fruit. Comparison of isotopic signatures among different anatomical plant parts has shown that variation is generally small (between 2 and 3% for $\delta^{15}N$; Evans 2001). Furthermore, Codron et al. 2005 did not find substantial differences in the $\delta^{15}N$ and $\delta^{13}C$ signatures of leaves, flowers, and fruit in South African savannah trees. However, because anatomical differences in isotopic signatures have not been explicitly tested for in the present study, the assumption that leaves have similar isotopic signatures to nectar and fruit will be taken into consideration when interpreting results.

Plant matter and crabs were collected by hand, insects by beating and direct searching (Sutherland 1996), and fish by cast-net. Once collected, all basal food sources were immediately placed on ice, and subsequently stored frozen until preparation for stable isotope analysis.

5.3.4 Sample preparation and isotopic analysis

Five leaf samples were pooled for each species of plant in preparation for isotopic analysis. White muscle tissue was excised from chelae and legs of crabs, and from below the dorsal fin in fish. Multiple individuals from each Order or Family of insects were pooled and left whole for isotopic analysis. Subsequently, all samples were washed in distilled water, oven-dried at 60°C, and homogenized using a bead mill. Claw samples were washed in a 2:1 chloroform:methanol mixture for fifteen minutes with a magnetic stirrer, allowed to air dry for 48 hours under a fume hood, and left un-homogenized for isotopic analysis. Dried blood samples were powdered and homogenized using a metal scraper on the glass slide where samples had been smeared during collection.

Samples of blood, claws, and basal food sources were weighed into tin capsules, and carbon and nitrogen stable isotope ratios were determined using a PDZ Europa ANCA-GSL elemental analyzer connected to a PDZ Europa 20-20 isotope ratio mass spectrometer at the University of California Davis Stable Isotope Facility, USA. All stable isotope ratios were expressed in per mill (‰) using the δ notation:

$$\delta X = \left(\frac{R(\text{sample})}{R(\text{standard})} - 1\right) \times 1{,}000$$

where X refers to the element of interest (i.e. C or N) and R is the ratio of the heavier isotope to the lighter isotope of element X (i.e. $^{13}C/^{12}C$ or $^{15}N/^{14}N$). The δ values are presented relative to the international standards VPDB (Vienna PeeDee Belemnite) for $\delta^{13}C$, and Air for $\delta^{15}N$.

5.3.5 Data analysis

Foraging group identification

There are many clustering techniques (e.g. hierarchical, partitioning, etc.) available for determining statistical groups that occur within multivariate data. When prior biological knowledge is available to inform statistical clustering of data, two indexes have been developed to validate cluster algorithm choice and the number of clusters in the data: 1) the biological homogeneity index (BHI) and 2) the biological stability index (BSI) (Datta and Datta 2006). Biological validation using BHI and BSI quantify the ability of unsupervised clustering algorithms to provide biologically meaningful clusters (Datta and Datta 2006).

Given the average isotopic signature of blood tissues for each bird species, and prior knowledge of their placement in foraging groups identified from previous diet studies, the R package *clValid* was used to choose the best clustering algorithm ('hierarchical', 'k-means clustering', or 'partitioning around medoids') and to identify the number of clusters in the data (ranging from 2 to 8; Brock et al. 2008). The biological validation procedure found the 'partitioning around medoids' (PAM) clustering algorithm and three clusters to provide the most biologically meaningful grouping of bird blood isotopic signatures at both sites. Subsequently, the PAM clustering algorithm with the Manhattan distance metric was used to group species' average blood $\delta^{13}C$ and $\delta^{15}N$ signatures into three clusters at both Cocoa creek and Healy creek, separately (Kaufman and Rousseeuw 1990, Maechler et al. 2017). The R package *factoextra* was used to visualise cluster analysis results at both sites (Kassambara and Mundt 2017).

Isotopic turnover rate and application of stable isotope discrimination factors

Isotopic turnover rates measure the time required for animal tissues integrate resource isotopic signatures, and tissue discrimination factors measure the difference between resource and tissue discrimination factors that arise due to physiological processes (i.e. excretion and assimilation). Avian blood and claw tissues differ in their isotopic turnover rates and discrimination factors (Bearhop et al. 2002, Lourenco et al. 2015). Due to differences in turnover rate, whole blood integrates food source isotopic ratios from the previous 2-3 weeks (Herrera et al. 2009) and claw tissue (specifically the distal 1-2mm 'tip' of the claw) integrates isotopic ratios from the previous 2-3 months (Hahn et al. 2014). Therefore, isotopic signatures in consumer blood and claw tissues can provide a temporal comparison of individual niche size and overlap.

The majority of birds caught in the study were of the Order Passeriformes. Discrimination factors ($\Delta^{13}C$ and $\Delta^{15}N$) for passerine blood and feather tissue have been measured in multiple studies (Hobson and Bairlein et al. 2003, Pearson et al. 2003, Carleton and Martinez del Rio 2005, Herrera et al. 2007), but there are few studies quantifying passerine claw discrimination factors. Given that claws and feathers are both primarily composed of keratin, and that previous studies have found high correlation between their $\delta^{13}C$ and $\delta^{15}N$ signatures, passerine feather discrimination factors were used for claw tissue in the present study (Ferger et al. 2013).

As well as varying among tissue types, discrimination factors are likely to differ between species and foraging groups with different dietary compositions (Pearson et al. 2003, Herrera et al. 2009). However, when investigating a bird assemblage comprised of 31 species, it is not feasible to use species-specific discrimination factors. Instead, we have chosen to use discrimination factors that have been determined for multiple foraging groups within the Order Passeriformes. We have followed the approach of Ferger et al. (2013) and taken an average of discrimination factors, separately for blood and feathers, across multiple passerine foraging groups (omnivores, insectivores, frugivores, and granivores). Using average discrimination factors can provide misleading results if they deviate significantly from species-specific consumer-prey discrimination factors (Caut et al. 2008, Martinez del Rio et al. 2009). However, the main objective of the present study was to compare the relative isotopic niche size, overlap, and source contribution among foraging groups occurring within sites. Therefore, average discrimination factors may not be entirely accurate for individual bird species, but comparisons among foraging groups should be robust.

Following averaging across passerine foraging groups, discrimination factors were calculated as $\Delta^{13}C = 1.81 \pm 1.45$ and $\Delta^{15}N = 2.23 \pm 0.39$ for blood tissue, and $\Delta^{13}C = 3.04 \pm 0.9$ and $\Delta^{15}N = 3.42 \pm 0.36$ for claw tissue (re-calculated from raw data provided in the Supplementary Materials of Ferger et al. 2013). To directly compare isotopic niche size and overlap in blood and claw tissues, bird isotopic signatures were reconstituted by subtracting the $\Delta^{13}C$ and $\Delta^{15}N$ value specific to each tissue from raw $\delta^{13}C$ and $\delta^{15}N$ signatures. Discrimination factors for blood tissue were also used in stable isotope mixing models to allow bird $\delta^{13}C$ and $\delta^{15}N$ signatures to be related to basal food source isotopic signatures, and the standard deviation associated with each discrimination factor was used to incorporate natural variability into estimates of dietary composition (see 'Relative contribution of sources to foraging group diet' subsection below for further explanation).

Isotopic niche size and overlap

Boxplots of foraging group blood and claw δ^{13}C and δ^{15}N signatures at each sampling site were inspected, and extreme outliers outside of the expected range were removed. It is possible that these outliers represented individual specialists, however they were not considered representative of the entire foraging group, and their removal was necessary to meet assumptions of multivariate normality. Multivariate normality in δ^{13}C and δ^{15}N signatures is an assumption of Bayesian isotopic niche size and overlap calculations (Jackson et al. 2011, Swanson et al. 2015), and was assessed for using the function 'mshapiro.test' in the R package *RVAideMemoire* (Herve 2016). Additionally, differences in bird blood and claw δ^{13}C and δ^{15}N signatures across seasons and sites were assessed using Welch's two-sample t-tests (Appendix 3, Table A5.4.1 and A5.4.3).

Bird reconstituted δ^{13}C and δ^{15}N signatures were used to determine the isotopic niche size and overlap of bird foraging groups identified from cluster analysis. Isotopic niche size was calculated using standard Bayesian ellipse areas (hereafter referred to as 'ellipse areas' or 'SEA_B') in the R package *SIBER,* which provides an estimate of each foraging group's dietary variability and indicates their degree of generalism or specialism (Jackson et al. 2011). Subsequently, pairwise comparisons of tissue and foraging group SEA_B's determined the probability that one group's posterior distribution was smaller or larger than another (Jackson et al. 2011). Finally, the probability of isotopic niche overlap among foraging groups was calculated in the R package *nicheROVER* (Lysy et al. 2014).

Due to variability in baseline resource isotopic signatures between sites, it is often necessary to standardize measures of isotopic niche size and overlap when making direct site comparisons (Matthews and Mazumder 2004, Newsome et al. 2007, Warry et al. 2016). However, we were primarily interested in within-site comparisons of isotopic niche size and overlap among foraging groups, rather than in making direct site comparisons. Additionally, due to the capture of different species at each site, direct comparison of foraging group niche sizes between sites was not prudent. Therefore, we chose to forego site standardization, and readers should be cautious about making any between-site comparison of isotopic niche size and overlap in this study.

Relative contribution of sources to foraging group diet

For foraging group food web construction, Bayesian stable isotope mixing models were used to determine the probable relative contribution of basal food sources to the diet of mangrove bird isotope-based foraging groups at each sampling site. Mixing models require differentiation in source isotopic signatures to reach a solution, and their discriminatory power decreases as the number of sources increases (Phillips et al. 2014). Therefore, sources that are not significantly distinct in their isotopic signatures can be grouped together prior to running mixing models (Phillips et al. 2014). Biological interpretability should also be considered when grouping sources *a priori* (Phillips et al. 2005, Phillips et al. 2014). Therefore, in the present study, sources that had over-lapping error bars (± sd) and were biologically similar were grouped as follows: mangrove primary (M), woodland primary (W), mangrove fish (F), mangrove crab (C), forest insect (I), and saltmarsh crab and insect (S) (see Table 5-1 for description).

Table 5-1 A description of the basal resources grouped into sources for use in stable isotope mixing models. Detailed identification of all basal food resources collected and their isotopic signatures can be found in the Supplementary Materials (Appendix 3, Table A5.3).

Source	Description of source isotopic signatures
Mangrove primary (M)	Primary production (leaves) to represent nectar and fruit resources from mangroves
Woodland primary (W)	Primary production (leaves) to represent nectar and fruit resources from terrestrial woodlands and forests (*Eucalyptus* and *Melaleuca* spp.)
Saltmarsh crab and insect (S)	Insect and crab prey from saltmarsh*
Forest Insect (I)	Insect prey from all forest types (mangrove and terrestrial)
Mangrove crab (C)	Crab prey from mangroves
Mangrove fish (F)	Fish prey from mangroves (includes estuarine fish species and mudskippers)

*Note: Saltmarsh leaves were also collected, but were not included as a source in the stable isotope mixing models because birds are not likely to be feeding on saltmarsh primary resources.

Mixing models were run separately for each foraging group at each sampling site, and only basal food sources that are known to be consumed by birds in each foraging group were used (through consultation of previous dietary studies). Also, because basal food sources were collected when birds were sampled, only bird blood $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures were used in the mixing models because blood tissue most closely reflects diet integration at that time.

Prior to running the mixing models, mixing biplots were used to satisfy the assumption that all consumers lie within source polygons (Smith et al. 2013). Three individual consumers lay outside of the 95% mixing region (Appendix 3, Figure A5.5), and were removed prior to running the mixing models in the R package *simmr* (Parnell 2016). Bayesian stable isotope mixing models allow variability in discrimination factors across all passerine foraging groups to be incorporated (i.e. standard deviation from discrimination factor estimates), and provide a measure of how uncertain estimates of relative source contributions are in the form of posterior probability distributions (Phillips et al. 2014). To meet the assumption of complete mixing, model convergence was confirmed using Gelman convergence diagnostics (Parnell et al. 2013). Although we grouped sources *a priori* to obtain a manageable number of sources, some source pairs were still unable to be distinguished by mixing models due to similarity in their isotopic signatures. Therefore, following protocol outlined in Phillips et al. (2014), an *a posteriori* approach was used to further combine sources that had high negative correlation.

All statistical analyses were performed in R version 3.3.2 (R Core Team 2016).

5.4 Results

A total of 31 bird species comprising five literature-based foraging groups were caught during wet and dry seasons at both mangrove sampling sites (Appendix 3 Figure A5.6). Only two individuals of one granivorous bird species (*Geopelia striata*) were caught, and therefore the granivore foraging group was removed from subsequent analyses. There was no difference in blood or claw isotopic signatures across wet and dry season sampling periods at Cocoa creek, except for $\delta^{15}N$ signatures in claw tissue (Appendix 3 Table A5.4.1). Although the difference in claw $\delta^{15}N$ signatures was found to be significant at the $p<0.05$ level, the effect size was not large enough to warrant biological relevance (mean wet season $\delta^{15}N = 5.8$ vs. mean dry season $\delta^{15}N = 6.3$). Therefore, isotopic signatures were pooled across seasons at Cocoa creek, separately for blood and claw tissues, in all subsequent analyses. As noted above, birds were only sampled from Healy creek during the wet season.

5.4.1 Foraging group identification

Cluster analysis demonstrated that blood $\delta^{13}C$ and $\delta^{15}N$ signatures of mangrove bird species did not fully correspond to their foraging group classification by previous diet studies (i.e. carnivores, insectivores, nectarivore-insectivores, and omnivores; Figure 5-2). Additionally, grouping of bird species by their isotopic signatures was not the same at both mangrove sites. At Cocoa creek, two isotope groups were comprised of a mix of omnivorous, carnivorous, nectarivorous-insectivorous, and insectivorous bird species (C_1, C_2; Figure 5-2 a). However, the third isotope group (C_3) had less dietary diversity among its bird species, consisting mainly of insectivorous bird species and one omnivore (Figure 5-2 a). At Healy creek, carnivorous Sacred Kingfishers (*Todiramphus sanctus*) and Little Kingfishers (*Ceyx pusillus*) were grouped separately from all other bird species (H_1, Figure 5-2 b). The second isotope group at Healy creek was comprised of insectivorous and nectarivorous-insectivorous bird species (H_2, Figure 5-2 b), while the third isotope group was comprised of omnivorous and insectivorous bird species (H_3, Figure 5-2 b).

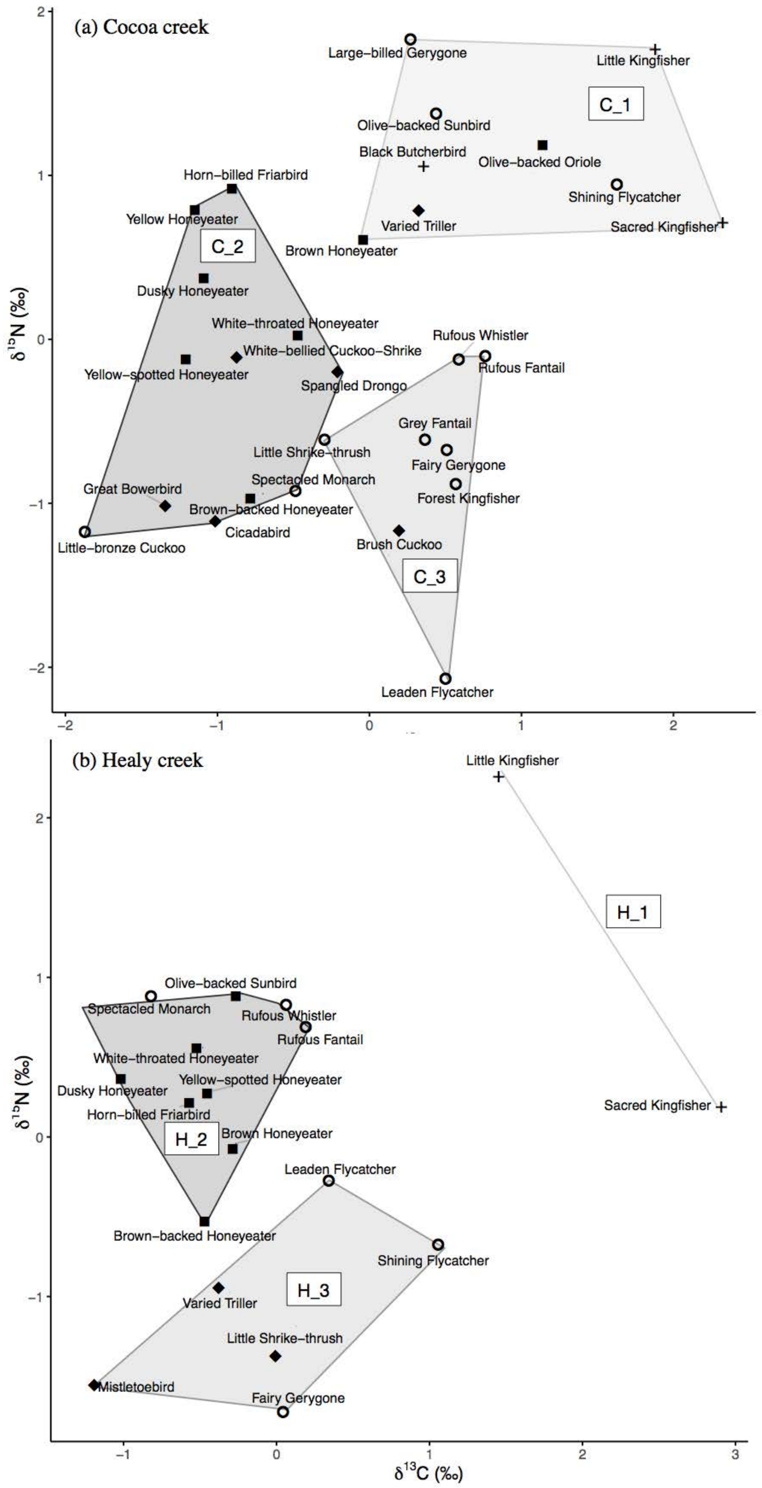


Figure 5-2 Cluster analysis showing bird species grouped by their blood $\delta^{13}C$ and $\delta^{15}N$ signatures at mangrove forest sites (a) Cocoa creek and (b) Healy creek. Symbols indicate

each species' foraging group as defined by the literature: omnivore (diamond), nectarivore-insectivore (square), carnivore (+), and insectivore (open circle). Convex hulls delineate the three isotope-based foraging groups identified by cluster analysis at Cocoa creek (C_1, C_2, C_3) and Healy creek (H_1, H_2, H_3). The axes show standardized values of bird blood $\delta^{13}C$ and $\delta^{15}N$ signatures (mean = 0, standard deviation = 1).

Isotope-based foraging groups identified from cluster analysis were used in all subsequent analyses of mangrove bird foraging group isotopic niche size, overlap, and source contribution at Cocoa creek and Healy creek.

5.4.2 Isotopic niche size and overlap

Isotopic niche measures dietary trophic diversity, and can therefore provide an indication of how generalised or specialised the collective diet of individual foraging groups are (Bearhop et al. 2004, Layman et al. 2012). The overlap of foraging group isotopic niches determines dietary similarity among groups, and therefore the degree to which individuals might be competing for resources (Swanson et al. 2015). Isotopic niches were measured by calculation of standard Bayesian ellipse areas (SEA_B) using reconstituted blood and claw isotopic signatures for isotope-based foraging groups (Figure 5-3). Reconstituted claw $\delta^{15}N$ signatures were generally of lower value than reconstituted blood $\delta^{15}N$ signatures, with an average difference across foraging groups of 1.45 ‰ ± 0.09 standard deviations and 1.64 ‰ ± 0.84 standard deviations at Cocoa creek and Healy creek, respectively (Figure 5-3). The consistently low values of reconstituted claw $\delta^{15}N$ signatures across foraging groups and sites suggest that this pattern is likely an artefact of the trophic discrimination factors used. Furthermore, this consistency indicates that discrimination did not differ among forging groups, and that our use of average discrimination factors to make comparisons of relative isotopic niche size, overlap, and source contributions among foraging groups should be robust.

The ranges of $\delta^{15}N$ isotopic signatures in blood and claw tissues were larger at Healy creek than at Cocoa creek, which corresponds to a larger range in baseline source $\delta^{15}N$ isotopic signatures at Healy creek (all $\delta^{15}N$ range differences between sites in blood, claw, and baseline isotopic source signatures were significant at $p<0.05$, Appendix 3 Table A5.4.3, Table A5.4.4). However, due to lack of site-standardization, ellipse areas cannot be directly compared between sites. Therefore, the following subsections make only within-site comparisons of isotopic niche size and probability of niche overlap. For all probabilistic pairwise comparisons of isotopic niche size (described below), see Appendix 3 Tables A5.7.1, A5.7.2.

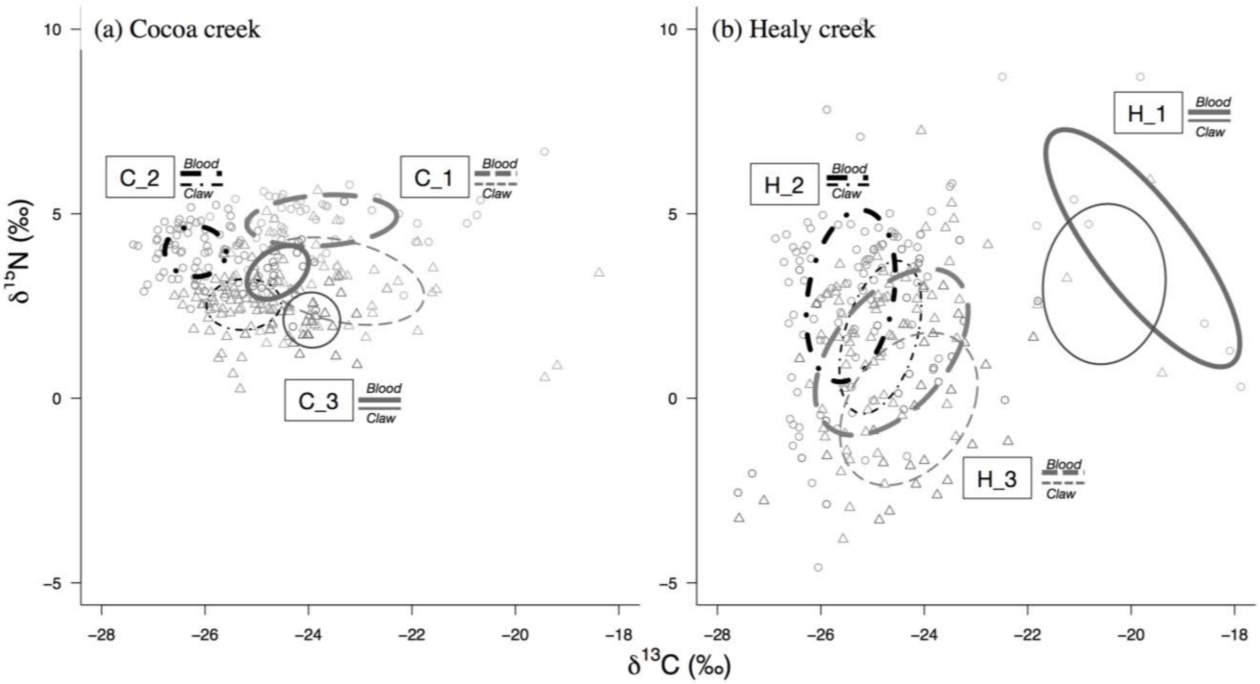


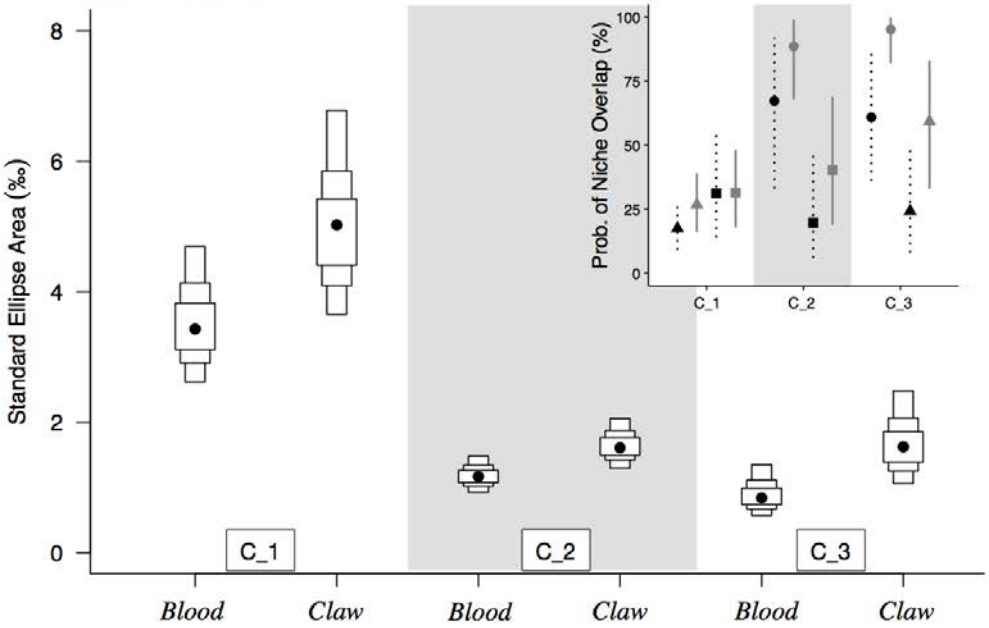
Figure 5-3 Standard Bayesian ellipse areas (SEA_B) representing the isotopic niches of mangrove bird isotope-based foraging groups at two mangrove sampling sites: Cocoa creek (a) and Healy creek (b). Line colour and type differentiates between isotope-based foraging groups, and line thickness indicates tissue type (thicker-lined ellipses show blood isotopic niches, and thinner-lined ellipses show claw isotopic niches for each group). Individual consumer isotopic signatures are also displayed (circles = blood,

triangles = claw). Note: between sites the isotope-based foraging groups are comprised of different species and therefore should not be directly compared.

5.4.3 Tissue comparisons (i.e. short-term vs. long-term isotopic integration)

Given that blood and claw integrate isotopic signatures of resources consumed over different time frames (short-term vs. long-term), comparison of their isotopic signatures can indicate whether resources consumed by each foraging group is seasonally consistent. Within each site, ellipse areas differed between blood and claw tissues of some foraging groups, suggesting temporal changes in their foraging strategies (Figure 5-4). At Cocoa creek, all isotope groups had larger claw ellipse areas in comparison to blood (probability claw > blood ranged between 95-98% for C_1, C_2, and C_3; Figure 5-4 a). Probability of isotopic niche overlap (Pr(INO)) between isotope groups C_1 and C_2 was similar in claw and blood tissues, while C_3 had lower Pr(INO) in blood tissue compared to claw tissue (Figure 5-4 a). At Healy creek, ellipse areas of blood and claw tissues were similar in most isotope groups except for H_2, which had larger blood ellipse areas in comparison to claw ellipse areas (probability blood > claw = 100%, Figure 5-4 b). Also, Pr(INO) did not differ between blood and claw tissues for any of the isotope foraging groups at Healy creek (Figure 5-4 b).

(a) Cocoa creek



(b) Healy creek

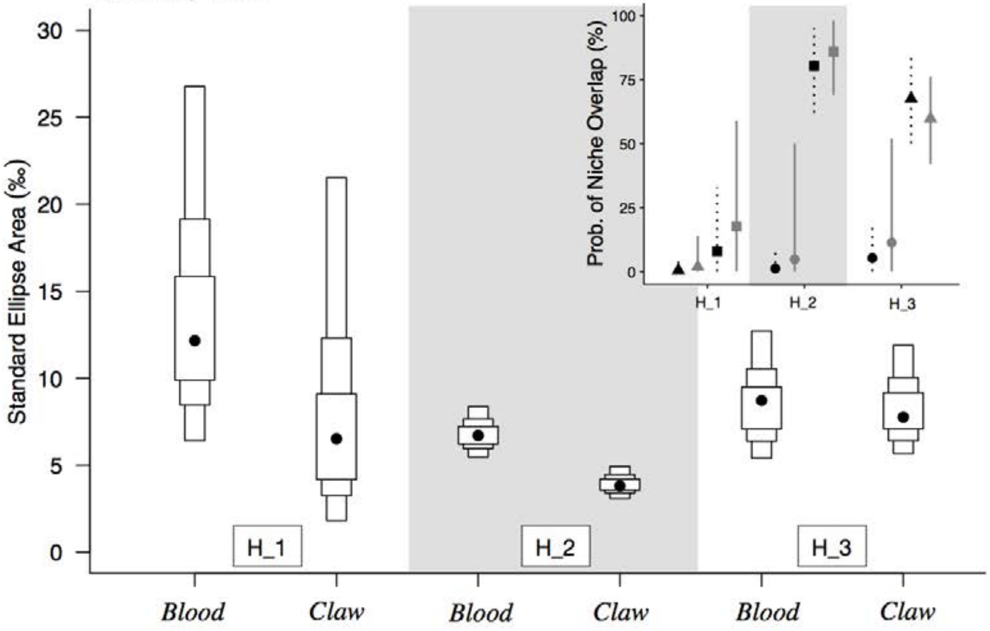


Figure 5-4 Standard Bayesian ellipse areas (SEA_B) for blood and claw tissues of mangrove bird isotope-based foraging groups at Cocoa creek (a) and Healy creek (b). Black circles are the mode SEA_B, and boxes show the 50%, 75%, and 95% credible intervals. Inset plots show the probability of isotopic niche overlap (mean ± 95% credible intervals) among the foraging groups. In the inset plots, colour indicates tissue type

(‘black’ = blood, ‘grey’ = claw), and symbols represent the foraging groups as follows: (circle) = C_1 or H_1; (triangle) = C_2 or H_2; (square) = C_3 or H_3.

5.4.4 Foraging group comparisons

At Cocoa creek, C_1 had the largest ellipse areas in comparison to other isotope foraging groups (probability C_1 > C_2 or C_3 = 100%) and had low to intermediate Pr(INO) with other foraging groups (Figure 5-4 a). Isotope group C_2 had a larger blood ellipse areas than isotope group C_3 (probability C_2 > C_3 = 87%), and these two foraging groups had low to intermediate Pr(INO) with each other (Figure 5-4 a). At Healy creek, H_1 had the largest blood ellipse areas (probability H_1 > H_2 or H_3 = 99% and 91%, respectively) and low Pr(INO) with other isotope foraging groups (Figure 5-4 b). Isotope groups H_2 and H_3 had similar ellipse areas except for H_2’s claw ellipse area, which was smaller than all other isotope groups (probability H_2 < H_1 or H_3 = 93% and 100%, respectively; Figure 5-4 b). Also, isotope groups H_2 and H_3 had intermediate to high Pr(INO) with each other (Figure 5-4 b).

5.4.5 Relative contribution of sources to foraging group diet

Bayesian stable isotope mixing models were used to determine the probable relative contribution of coastal basal resources to the diet of mangrove bird isotope-based foraging groups (Figure 5-5). However, given that mixing models for all foraging groups were underdetermined (i.e. too many sources and not enough isotopic tracers), it was not prudent to evaluate mean relative contribution values because unique solutions were not possible (Fry 2013 a,b). Therefore, the relative likelihoods of source contributions for each foraging group were reported as 95% credible interval ranges (Figure 5-5), and caution was exercised in their interpretation so that all feasible solutions were considered.

Prior to running mixing model analyses, simulated mixing regions for consumer-source biplots validated mixing models for all isotope foraging groups at both sites. Following *a* *posteriori* combination of sources that could not be distinguished by mixing model analyses (Phillips et al. 2014), mixing models demonstrated that the relative contribution of sources to isotope foraging groups differed between sites, and was dependent on their species composition (Figure 5-5). At Cocoa creek, isotope group C_1 was comprised of a mix of carnivorous, insectivorous, omnivorous, and nectarivorous-insectivorous species, and their collective diet appeared to be primarily supported by crab, fish, insect, and mangrove primary sources (Figure 5-5 a). Alternatively, isotope group H_1 at Healy creek was comprised of only carnivorous bird species, and their collective diet appeared to be primarily supported by crab, saltmarsh, and fish sources (Figure 5-5 b).

At Cocoa creek, isotope group C_2 was composed of insectivorous, omnivorous, and nectarivorous-insectivorous species that likely foraged mainly on insect and mangrove primary sources, and secondarily on crab and saltmarsh sources (Figure 5-5 c). Similarly, isotope group H_2 at Healy creek was composed of nectarivorous-insectivorous and insectivorous species whose diet appeared to be supported mainly by insect and mangrove primary sources, and relatively less crab and saltmarsh sources (Figure 5-5 d).

At Cocoa creek, isotope group C_3 consisted of primarily insectivorous bird species and one omnivorous species, and their collective diet appeared to consist primarily of insect, mangrove primary, crab, and saltmarsh sources (Figure 5-5 e). Likewise, at Healy creek, isotope group H_3 consisted of insectivorous and omnivorous species whose diet appeared to be supported primarily by insect, mangrove primary, crab, and saltmarsh sources (Figure 5-5 f).

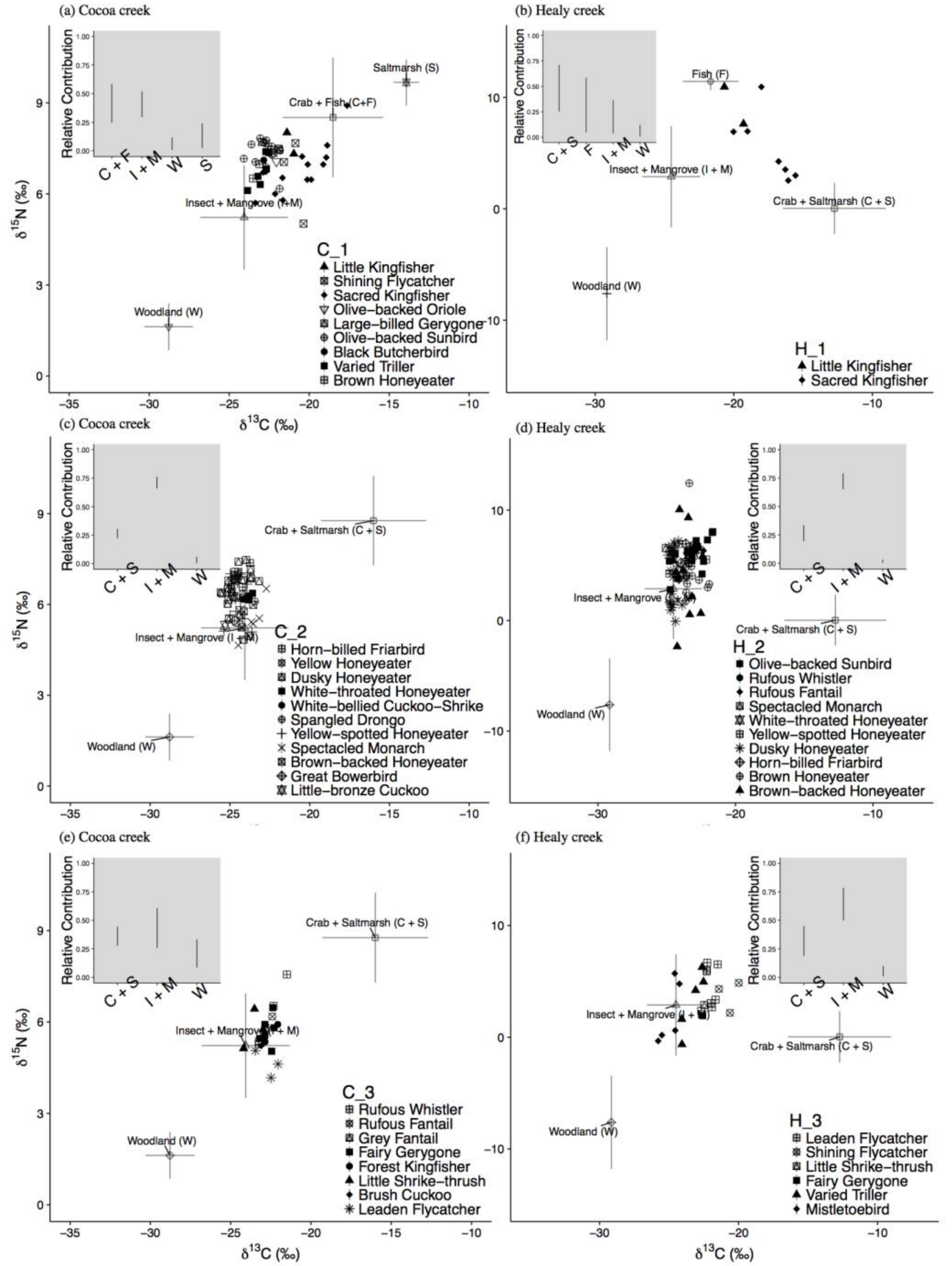


Figure 5-5 $\delta^{13}C$ and $\delta^{15}N$ signatures of sources (mean ± sd) and mangrove bird consumers at Cocoa creek and Healy creek for each isotope-based foraging group. Sources that were unable to be distinguished by mixing models were combined. Inset plots show the probable relative contribution of sources (95% credible interval ranges), as estimated by mixing models, to the diet of each foraging group.

5.5 Discussion

Environmental heterogeneity in resource availability can cause opportunistic and generalised foraging by resident species (Rotenberry 1980, Yang et al. 2008, Blanchette et al. 2014). The present study has provided insight into the foraging strategies and food webs of birds inhabiting a complex and dynamic coastal mangrove environment. The isotopic signatures of mangrove bird assemblages suggest that bird foraging strategies are more opportunistic and generalised than expected by previous diet studies.

5.5.1 Isotopic insights to mangrove bird foraging ecology

Two sites were used in the present study to determine if bird foraging patterns were spatially consistent. The baseline $\delta^{13}C$ ranges were similar at both mangrove sites, however Healy creek had depleted $\delta^{15}N$ source signatures resulting in a larger baseline $\delta^{15}N$ range. Despite differences in $\delta^{15}N$ range, carnivorous, nectarivorous-insectivorous, and insectivorous bird species occupied similar positions relative to sources in isotope spaces at Cocoa creek and Healy creek. However, between sites, there were differences in the organization of bird species into isotopic foraging groups and their respective foraging strategies.

5.5.2 Correspondence between literature- and isotope-based foraging groups

The organization of mangrove forest bird species into isotope-based foraging groups implied opportunistic resource use, as isotopic foraging clusters did not strictly correspond to bird species' foraging group classification by previous diet studies (i.e. their observed diet). The only isotope group that did correspond to literature-based classification was a Healy creek cluster that was comprised of two carnivorous bird species (i.e. H_1), and they had higher isotopic separation from each other relative to species within other clusters. The overall prevalence of opportunism in mangrove forest birds corroborates previous research of their foraging ecology, which has been well studied in the Northern Territory of Australia using visual observation to describe a bird assemblage that is dominated by opportunistic insect foragers (Noske 1996, Mohd-Azlan et al. 2014). However, until now, similar research has been limited for mangrove bird assemblages of northeastern Australia, which contain a higher abundance of facultative bird species that are known to forage in adjacent coastal woodlands and wetlands seasonally (Kutt 2007). Furthermore, the utility of an isotopic approach in this system has not been previously investigated.

5.2.3 Isotopic niche size and overlap as an indicator of dietary diversity

At Cocoa creek, the dietary diversity of birds within isotope groups was associated with isotopic niche size and overlap, meaning that isotope groups with greater observed dietary diversity among their species (i.e. carnivorous, omnivorous, insectivorous, or nectarivorous-insectivorous) had larger isotopic niche sizes. Isotope group C_1 was comprised of bird species with all four observed diets, and had the largest isotopic niche size relative to other foraging groups at Cocoa creek. Notably, carnivores were grouped with other insectivorous and omnivorous bird species in C_1 (e.g. the Shining Flycatcher (*Myiagra alecto*) and Olive-backed Oriole (*Oriolus sagittatus*)), revealing that these species may opportunistically forage on crab and fish sources as well (corroborated by visual observation of Shining Flycatcher crab foraging; C.A. Buelow 2015, pers. comm., June). Alternatively, insects may also support carnivore diets at Cocoa creek. In contrast to the observed dietary diversity of C_1, isotope group C_3 was comprised primarily of insectivorous species (with one omnivore) and had the smallest isotopic niche size, which is likely congruent with a smaller resource base.

Isotope groups at Cocoa creek had primarily low to intermediate probability of isotopic niche overlap, which suggests that, as a whole, isotope groups at this site are foraging on different resources from one another. Supporting this suggestion, mixing models show that all three isotope groups forage to some extent on forest insect and mangrove primary sources, and differ by probable relative contribution of crab, fish, and saltmarsh sources to their collective diets. Not surprisingly, mangrove primary and forest insect sources had the highest probable contribution to isotope group C_2 (~ 70-76%), which had a high abundance of nectarivorous and insectivorous bird species.

In comparison to Cocoa creek, isotope groups at Healy creek did not show similarly high observed dietary diversity among their constituent species. Also, further in contrast to Cocoa creek, higher observed dietary diversity was not consistently associated with larger isotopic niche size; rather, the opposite was true. Isotope groups H_2 and H_3, each comprised of species with two different diets, had smaller isotopic niche sizes than H_1, which was comprised of carnivorous species only. Isotope groups H_2 and H_3 also had intermediate to high probability of niche overlap with each other, suggesting that species within these groups forage on similar resources (i.e. insect and mangrove sources, as indicated by mixing models).

The lack of a clear observed dietary diversity-isotopic niche size relationship at Healy creek may indicate that two different specialist foraging strategies occur within isotope groups at this site. For example, isotope group H_1 may be comprised of individual specialists with different preferences for fish, crab, or saltmarsh resources. This is corroborated by the relatively similar contribution of fish, crab, and saltmarsh resources to the collective diet of carnivores in isotope group H_1. Alternatively, isotope groups H_2 and H_3 may be comprised of individuals employing specialized foraging strategies with similar resource preferences, as mixing models confirm that these groups appear to be supported primarily by forest insect and mangrove primary sources. However, generalist and specialist foraging strategies can be challenging to interpret using isotope data; see Appendix 3 Figure A5.1 for additional scenarios possible.

There are several ecological mechanisms that could underpin the divergent dietary diversity-isotopic niche size relationships observed between sites. Landscape heterogeneity, resource availability, habitat fragmentation, species interactions (e.g. competition), and individual specialisation are factors that may influence these relationships (Darimont et al. 2009, Araujo et al. 2011). Quantifying these factors at each site would further our understanding of the processes shaping the observed patterns, and requires more attention in the future.

5.2.4. Temporal changes in foraging strategies: tissue comparisons

The claw isotopic niches of all isotope groups at Cocoa creek were consistently larger relative to their blood isotopic niches, suggesting either temporal opportunism in their foraging strategies, or dietary-switching as resource availability and abundance changes seasonally. For example, seasonally shifting foraging strategies may reflect an increase in insect availability during the wet season in mangrove forests. However, at Healy creek, blood and claw isotopic niche sizes were similar (except for H_2, which had a relatively larger blood isotopic niche size). Because seasonal diet shifting was not consistent between sites, further research is needed to make concrete conclusions regarding seasonal and spatial differences in resource availability for mangrove forest birds in these areas.

5.5.2 Limitations and recommendations

It should be noted that using isotopic niche size to evaluate generalist vs. specialist foraging strategies could in part be driven by the degree of isotopic distinction between sources. For example, insect resource partitioning by birds may occur at a finer scale than can be examined by stable isotopes. In fact, observational studies have found that mangrove insectivores will select insects by size (Mohd-Azlan et al. 2014), demonstrating the importance of using a combination of methods (i.e. observational and gut content analyses) when investigating foraging ecology. Future studies should also consider using sulphur stable isotopes to improve isotopic discrimination in coastal environments (Mancinelli and Vizzini 2015), and have more mangrove sites for comparison. Finally, larger sample sizes of each bird species would allow the evaluation and comparison of species-specific isotopic niche sizes, and better determine the degree to which individual species exhibit specialized vs. generalized foraging strategies.

It is important to consider that any solution within a range of possible solutions (i.e. 95% credible interval ranges) is potentially the real solution (Fry 2013 a,b). To obtain the most well constrained mixing model contribution estimates, we used prior information to include only sources that are known to be consumed by bird species in each foraging group (Semmens et al. 2013), and our interpretations reflect a combination of the prior information and mixing model outputs. Despite this, our models remained underdetermined and so other solutions in the source-consumer mixing model spaces should not be disregarded. For example, the solution for C_2 (Figure 5-5 c) suggests that Woodland primary sources are unimportant, yet it is possible they could contribute more substantially to C_2's collective diet than is suggested by the mixing model outputs (Fry 2013 a, b). Greater confidence in relative source contribution estimates could be garnered by inclusion of more consumer data and the use of additional prior information (Semmens et al. 2013). However, for the objectives of our study, the mixing model outputs combine with other information to better understand the foraging ecology of mangrove bird assemblages.

5.5.3 Conclusions

Due to the unpredictably of Australian climate systems and their inter-annual variability, Australian bird species often survive by tracking resources (Reside et al. 2010). Most of the bird species in the present study are mangrove-facultative (except the Little Kingfisher (*Ceyx pusillus)*), and are likely to also use adjacent forests and woodlands (Kutt 2007). Additionally, many species have broad distributions, either along the length of the east coast or across the tropical north of Australia. With large flexibility and range in habitat choice, we would expect diets of these bird species to differ spatially, and foraging groups to shift accordingly. A comparative approach using both isotopic and traditional diet studies has provided insight to the foraging ecology and food webs of coastal forest bird assemblages, however more research is required to understand the limits to their foraging flexibility to ensure their persistence in Northern Australia.

6 Nutrient subsidy indicators predict the presence of an avian mobile-link species

6.1 Abstract

Island ecosystems can be inordinately dependent on avian nutrient subsidies because of their isolation from external nutrient pools. We investigated relationships between several nutrient subsidy indicators and the presence of Pied Imperial-Pigeon (*Ducula bicolor*) breeding colonies in island forests of northeast Australia. The following nutrient subsidy indicators were measured in island forest soil and leaf samples: nutrient origin (δN^{15} and δC^{13}); total carbon (C), nitrogen (N), and phosphorus (P) levels; and nutrient quality (C:N:P ratios). Random forest models were used to determine the relative importance of nutrient subsidy indicators for classifying island forests as 'PIP colony present' or 'PIP colony absent'. Total P was the most important soil nutrient subsidy indicator, while δN^{15} was the most important leaf nutrient subsidy indicator. Furthermore, in both soil and leaves, δN^{15} enrichment and N and P levels increased as the probability of PIP colony presence increased. Measures of nutrient quality also implied plant growth rates were higher in island forests with increased likelihood of PIP colony presence. Pied Imperial-Pigeons should be classified as an avian mobile-link species that have an important role in island ecosystem functioning, encouraging further investigation of the direct and indirect effects associated with PIP nutrient subsidies. This research highlights the importance of understanding the local-scale connectivity processes that underpin the longer distance movements of highly mobile species for effective ecosystem management.

6.2 Introduction

Ecosystem resilience is defined as the ability to withstand perturbation and is dependent on myriad factors, such as nutrient availability (Holling 1973, Gunderson 2000). Nutrient availability directly influences ecosystem productivity, and *in situ* nutrient production is often supplemented by subsidies from other ecosystems through transport by wind, water, or mobile organisms (Polis et al. 1997). Island ecosystems are relatively isolated from other landmasses, meaning that external nutrient subsidies provided by mobile organisms may play a critical role in their functioning and resilience. Information regarding the origin, quantity, and quality of island nutrient subsidies is needed to evaluate the importance of mobile link species for island ecosystem functioning.

Due to their high mobility and colonial roosting or nesting behaviour, seabirds are key vectors in the transportation of marine-derived nutrients to island ecosystems (Lundberg and Moberg 2003, Ellis 2005, Sekercioglu 2006). Concentrated marine nutrient subsidies delivered by seabirds can influence island plant growth and species composition, food web structure, and ecosystem productivity (Polis and Hurd 1996, Sanchez-Pinero and Polis 2000, Croll et al. 2005, Vizzini et al. 2016). When nutrient subsidies are inhibited or interrupted, the consequences for ecosystem functioning can be far-reaching. For example, when changes in habitat availability or predation prevent nesting birds from providing marine nutrient subsidies, recipient terrestrial ecosystems become nutrient depleted and experience shifts in their ecosystem states (Maron et al. 2006, Fukami et al. 2006, Jones 2010, Young et al. 2010). The extreme consequences of precluding nutrient subsidies has been demonstrated on islands of the Aleutian Archipelago, where fox predation of seabirds has caused these ecosystems to shift entirely from grassland to tundra (Croll et al. 2005).

While there is a substantial understanding of the role of seabirds in ocean-island nutrient flows, there has been considerably less investigation of nutrient subsidies from mainland ecosystems to islands. To our knowledge, the only mainland-island nutrient flow that has been quantified is nutrient transfer to an island mangrove forest by fruit bats that forage in mainland terrestrial forests (Reef et al. 2014). However, also in northeast Australia, Pied Imperial-Pigeons (*Ducula bicolor*) make daily fruit-foraging migrations to mainland rainforests from islands where they breed colonially, providing an opportunity to further explore mainland-island nutrient subsidies.

The northeast Australian Pied Imperial-Pigeon (PIP) population undertakes annual migrations from southern Papua New Guinea to breed on islands along the northeast coast of Australia (Winter et al. 2016). During the breeding season, PIPs make daily forging migrations between island nesting habitat and mainland rainforest foraging habitat. The high degree of localized connectivity facilitated by the daily movements of PIPs is potentially an important process whereby large amounts of nutrients are exported from mainland coastal rainforests to nesting islands. The large size and range of the northeast Australian PIP population (1000 to > 10,000 breeding pairs in medium or large breeding colonies on islands along ~1300 km of coastline; King 1990, Brothers and Bone 2012) also means that the localized connectivity they provide may extend to a regional scale. Although the northeast Australia PIP population has rebounded following declines linked to hunting, clearing of mainland rainforest foraging habitat, and cyclones; the carrying capacity of the region may be permanently reduced since ~60% of lowland coastal rainforest was cleared prior to the 1980s (Winter et al. 1987, Thorsborne et al. 1988, King 1990, Winter et al. 2016). As coastal development continues, there is a need to understand the role of PIPs in connecting mainland coastal and island ecosystems.

Maintenance of ecosystem function and resilience is dependent on understanding the ecosystem linkages that are facilitated by mobile animals, particularly when defining spatial boundaries for effective ecosystem-based management (Toonen et al. 2011). For example, connectivity processes occurring outside of protected areas (PAs) can influence ecosystem functioning within PA boundaries, and therefore disregarding linkages can undermine effective PA management (Pringle 2001). Many islands along the northeast coast of Australia are protected as National Parks (Queensland Government 2017), and quantifying the daily, cross-ecosystem nutrient flow facilitated by Pied Imperial-Pigeons is a first step towards understanding their role in the functioning of island ecosystems. Nitrogen and carbon isotopic signatures (δN^{15} and δC^{13}), and nitrogen (N) and phosphorus (P) levels, measure the origin and quantity, respectively, of avian nutrient subsidies in recipient ecosystems (Vizzini et al. 2016). While the quantity of nutrient subsidies can influence nutrient limitation and plant growth, nutrient quality is often over-looked and can have equally important effects on ecosystem processes (Sitters et al. 2015). The quality of nutrient subsidies is determined through ecological stoichiometry (ES) by measurement of carbon, nitrogen, and phosphorus ratios in either detrital matter or in organisms (C:N:P; Sterner and Elser 2002, Sitters et al. 2015).

This study aimed to assess the relationships between Pied Imperial-Pigeon breeding colony presence and indicators of nutrient subsidy quantity and quality. Specifically, this research quantified several key indicators of nutrient subsidization in forest soil and leaf samples from islands with and without PIP colonies: 1) nutrient origin, as indicated by δN^{15} and δC^{13}, 2) nutrient quantity, as indicated by total carbon (C), nitrogen (N), and phosphorus (P) levels, and 3) nutrient quality and limitation, as indicated by C:N:P ratios.

6.3 Methods

6.3.1 Island forest study areas

Forest areas of eight northeast Australian islands were selected and categorised as following: 'PIP colony absent' (three island forests) or 'PIP colony present' (five island forests; Figure 6-1). Nest searches were conducted to confirm PIP colony presence or absence in forest sampling areas during the breeding season. In addition to PIP colony presence/absence, island forests also differed by their geomorphology (continental or cay island type; Figure 6-1). Sedimentary differences between these two island types could confound assessment of nutrient origin, quantity, and quality in soil and leaf samples. Therefore, island type has been included as an additional variable when analysing the results of the present study (see *Data Analysis* subsection below).

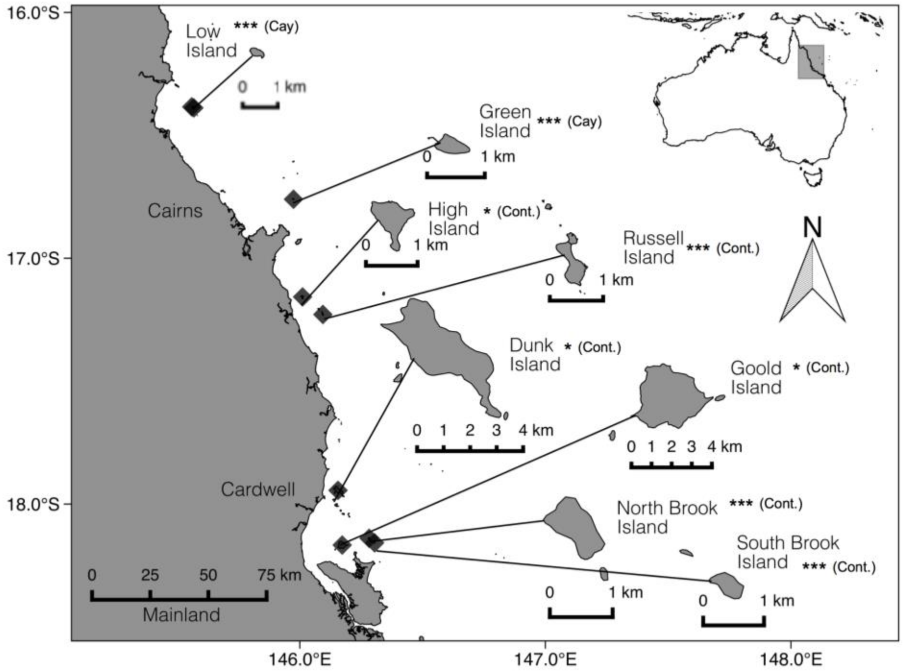


Figure 6-1 Map of the eight study islands located along the northeast coast of Australia. Diamonds show island position relative to the mainland, and each island is enlarged to show individual size and shape. Asterisks indicate PIP colony presence (***) or absence (*) in island forest sampling areas. Islands also differed by their geomorphology: Cay vs. Continental (Cont.).

6.3.2 Soil and leaf collection

All island forests were sampled at the end of the TIP breeding season (post-breeding season, February-March 2016). Four locations were randomly selected from within each island forest sampling area, and the closest suitable trees (*Mystrica muelleri*) and soil areas to each location were sampled. Soil samples were collected with a soil core (diameter = 3 cm, depth = 5 cm; total = 4 samples/island forest) and five leaves from each tree were collected (total = 4 trees/island forest). *Mystrica muelleri* was chosen for leaf sampling due to its common presence in rainforests of northeast Queensland, Australia. Following collection, all soil and leaf samples were stored frozen until further analysis.

6.3.3 δN^{15}, δC^{13}, carbon, nitrogen, and phosphorus measurement

Soil samples were oven-dried at 60°C for 24 hours. Samples from five leaves of each tree were pooled together, washed in distilled water, and then oven-dried at 60°C for 24 hours. Dried soil and leaf samples were homogenized with a bead mill and weighed into tin capsules. Subsequently, δN^{15}, δC^{13}, total carbon (C mg/g), and total nitrogen (N mg/g) were measured in parallel using a PDZ Europa ANCA-GSL elemental analyzer connected to a PDZ Europa 20-20 isotope ratio mass spectrometer at the University of California Davis Stable Isotope Facility, USA. All nitrogen and carbon stable isotope ratios were expressed in per mill (‰) using the δ notation:

$$\delta X = \left(\frac{R(\text{sample})}{R(\text{standard})} - 1\right) \times 1{,}000$$

where X refers to the element of interest (i.e. C or N) and R is the ratio of the heavier isotope to the lighter isotope of element X (i.e. $^{13}C/^{12}C$ or $^{15}N/^{14}N$). The δ values are presented relative to the international standard VPDB (Vienna PeeDee Belemnite) for $\delta^{13}C$, and Air for $\delta^{15}N$.

For total phosphorus levels (P mg/kg), dried soil and leaf samples were analysed for total acid extractable P at the Environmental Analysis Laboratory (Southern Cross University, Australia). Samples were digested on a hotblock digestor using an Aqua Regia solution (1:3) Nitric acid/Hydrochloric acid, and then read on an ICP-MS (EPA3050B and APHA 3125 ICPMS).

6.3.4 Data analysis

Forest categorisation

Principal components analysis (PCA) on a correlation matrix was used to visualise the relationships among variables measured in soil and leaf samples (i.e. δN^{15}, δC^{13}, and total N, P, and C) from island forests categorized as ‘PIP colony present’ or ‘PIP colony absent’ on the basis of nest searches.

Importance of nutrient subsidies

Random Forest is a non-parametric technique that is derived from classification and regression trees (CARTs), but uses an ensemble learning algorithm to build a ‘forest’ of un-pruned trees for improved predictive accuracy (Breiman 2001, Cutler et al. 2007). Trees are grown using bootstrap samples of the original data, where a third is left out for validation (i.e out-of-bag (OOB)) (Breiman 2001, Cutler et al. 2007). The Gini index splitting rule (Breiman et al. 1984) finds the most homogeneous subgroups of the data given a randomised subset of the predictor variables, and the misclassification rate for OOB observations is aggregated across all trees in the ‘forest’ (Breiman 2001, Cutler et al. 2007). The relative importance of each predictor variable to the predictive accuracy of the Random Forest is determined by randomly permuting OOB values, and then calculating the difference between OOB error estimates for actual vs. randomly permuted values and dividing by the standard error (Cutler et al. 2007). Finally, variable dependence plots can be used to visualise variable relationships by plotting the predicted response as a function of a predictor variable of interest (Friedman 2000).

Random forest models were used to determine the relative importance and relationship of individual variables measured in soil and leaf samples to the classification of island forests as ‘PIP colony present’ or ‘PIP colony absent’. In addition to nutrient subsidy indicators, island type (i.e. continental or cay) was included as a variable to determine its importance in forest classification. Random forests of 1000 trees in size were grown using the Gini index splitting rule, and out-of-bag (OOB) error estimates were calculated to obtain a measure of model fit for each random forest.

The importance of each variable to the predictive accuracy of soil and leaf random forest models was calculated. Variable importance is determined by randomly permuting the variable's values, and then calculating the difference between OOB error estimates for actual vs. randomly permuted values. High variable importance values indicate that the variable of interest increases the predictive accuracy of the random forest model, while values ≤ 0 indicate that the variable of interest either does not contribute, or detracts, from the predictive accuracy.

The relationship between individual nutrient subsidy variables and the probability of island forest classification as 'PIP colony present' was further investigated with variable dependence plots. Variable dependence plots show the probability of classifying island forests as 'PIP colony present' as a function of each variable measurement. Loess smoothers with 95% confidence intervals were overlaid on the variable dependence plots to aid in visualization of the relationship between nutrient subsidy variables and the probability of PIP colony presence.

All statistical analyses were performed in R version 3.3.2 (R Core Team 2016). PCA plots were created with the package 'ggbiplot' (Vu 2011), and random forest models were analysed and displayed with the packages 'randomForestSRC' and ggRandomForests', respectively (Ishwarhan and Kogalur et al. 2017, Ehrlinger 2016). Raw variable measurements (± standard error) are displayed in the supplementary materials (Appendix 4).

6.4 Results

6.4.1 Forest categorisation

PCA showed that, for soil samples, principal components one (PC1) and two (PC2) explained 78.2% of the variability in δN^{15}, δC^{13}, total C (mg/g), total N (mg/g), and total P (mg/g) among island forest areas sampled in the present study (Figure 6-2 a). Soil total N and C, and δC^{13} variables were primarily correlated with PC1, with highest values in forest areas where PIP colonies were present (Figure 6-2 a). Soil total P and δN^{15} variables were not primarily correlated with either principal component, and their highest values were also in forest areas with PIP colonies present (Figure 6-2 a).

For leaf samples, principal components one (PC1) and two (PC2) explained 70.2% of the variability in δN^{15}, δC^{13}, total C (mg/g), total N (mg/g), and total P (mg/g) among island forest areas sampled in the present study (Figure 6-2 b). Leaf total C, N, and P variables were primarily correlated with PC1, with highest values in forest areas with PIP colonies present (Figure 6-2 b). Conversely, δN^{15} and δC^{13} were oppositely correlated along PC2, with the highest values of δN^{15} in forest areas with PIP colonies present (Figure 6-2 b).

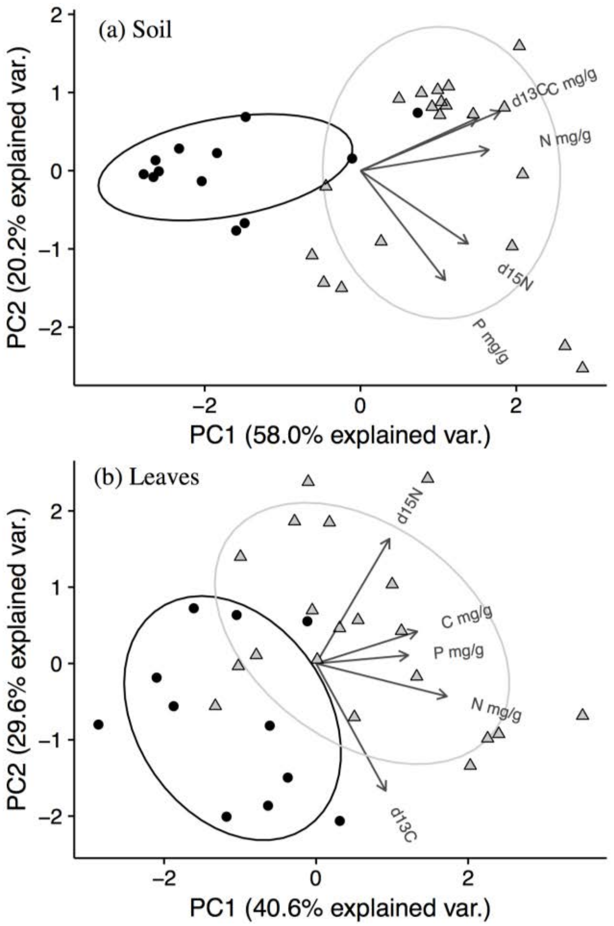


Figure 6-2 Principal components analysis showing the relationship between island forests categorized as ‘PIP colony present’ (grey triangles) or ‘PIP colony absent’ (black circles) and the following soil (a) and leaf (b) nutrient subsidy indicators: δN^{15} (d15N), δC^{13} (d13C), total nitrogen (N mg/g), total phosphorus (P mg/g), and total carbon (C mg/g).

6.4.2 Importance of nutrient subsidies

Model fit

The soil random forest model had high predictive accuracy with an overall OOB error rate of 9.68%, while the leaf random forest model had relatively lower predictive accuracy overall OOB error rate of 17.24%.

Variable importance

When soil nutrient subsidy measurements were used to classify island forests as ‘PIP colony present’ or ‘PIP colony absent’, all variables except for island type contributed to the predictive accuracy of the random forest model (Figure 6-3 a). Total phosphorus, N:P, and δC^{13} were the three most important soil nutrient subsidy indicators in island forest classification (Figure 6-3 a). Alternatively, when leaf nutrient subsidy measurements were used to classify island forests as ‘PIP colony present’ or ‘PIP colony absent’, δN^{15} was the only substantially important variable (Figure 6-3 b). ‘Island type’ also had low variable importance in the leaf random forest model (Figure 6-3 b), and therefore ‘island type’ was not included in further analysis of variable dependence (see subsections below).

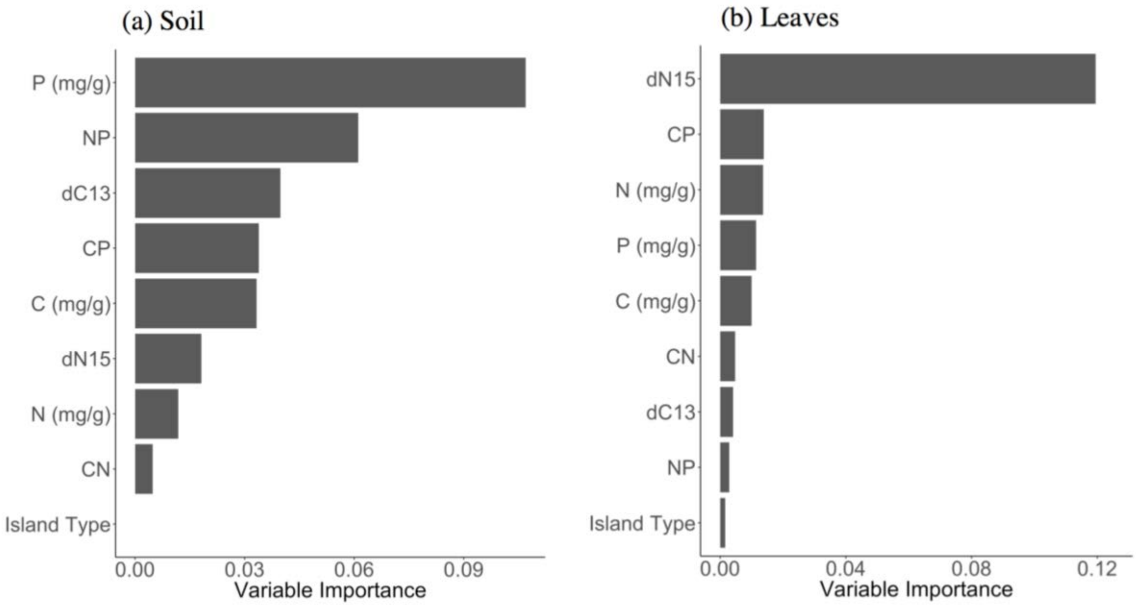


Figure 6-3 Importance of variables measured in (a) soil and (b) leaf samples for classifying island forests as ‘PIP colony present’ or ‘PIP colony absent’. Variables with high importance values contribute to the predictive accuracy of the random forest model

used for classification, while a value of zero indicates that the variable does not contribute to the predictive accuracy. (Note: dN15 = δN^{15} and dC13 = δC^{13}.)

Variable dependence: nutrient origin (δN^{15} and δC^{13})

Variable dependence plots show how individual variable measurements are related to the probability of island forests being classified as 'PIP colony present'. Soil δC^{13} values increased as the probability of PIP colony presence increased (Figure 6-4 a). In contrast, there was no clear relationship between leaf δC^{13} values and the probability of PIP colony presence (Figure 6-4 b). For δN^{15}, values in soil and leaves increased as the probability of classification as 'PIP colony present' increased (Figure 6-4 c, d).

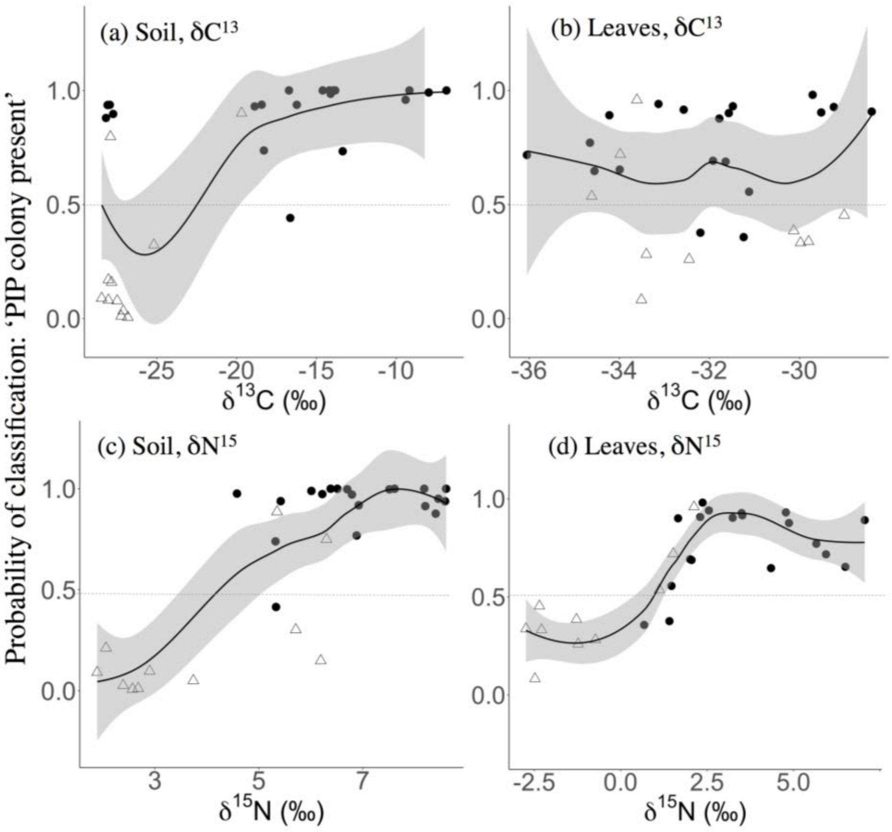


Figure 6-4 Variable dependence plots for carbon (δC^{13}) and nitrogen (δN^{15}) stable isotope signatures in soil (a & c) and leaf (b & d) samples. A loess smoother (with a 95%

confidence interval) shows the relationship between the isotopic signature (δC^{13} or δN^{15}) and probability of classification as ‘PIP colony present’ by the random forest model. Symbols represent the category to which individual measurements belong (‘PIP colony absent’ = white triangles, and ‘PIP colony present’ = black circles). The grey-dashed line indicates 50% probability of classification as ‘PIP colony present’.

Variable dependence: total nutrient levels (C, N, P) and ratios (C:N:P)

Total C, N, and P levels increased as the probability of classification as ‘PIP colony present’ increased, for both soil and leaf samples (Figure 6-5). In contrast, soil N:P and C:P nutrient ratios increased with decreasing probability of classification as ‘PIP colony present’ (Figure 6-6 a, e), and there was no clear relationship with soil C:N nutrient ratios (Figure 6-6 c). For leaves, there was also no clear relationship between N:P and probability of classification as ‘PIP colony present’ (Figure 6-6 b), while leaf C:N and C:P ratios decreased as the probability of classification as ‘PIP colony present’ increased (Figure 6-6 d, f).

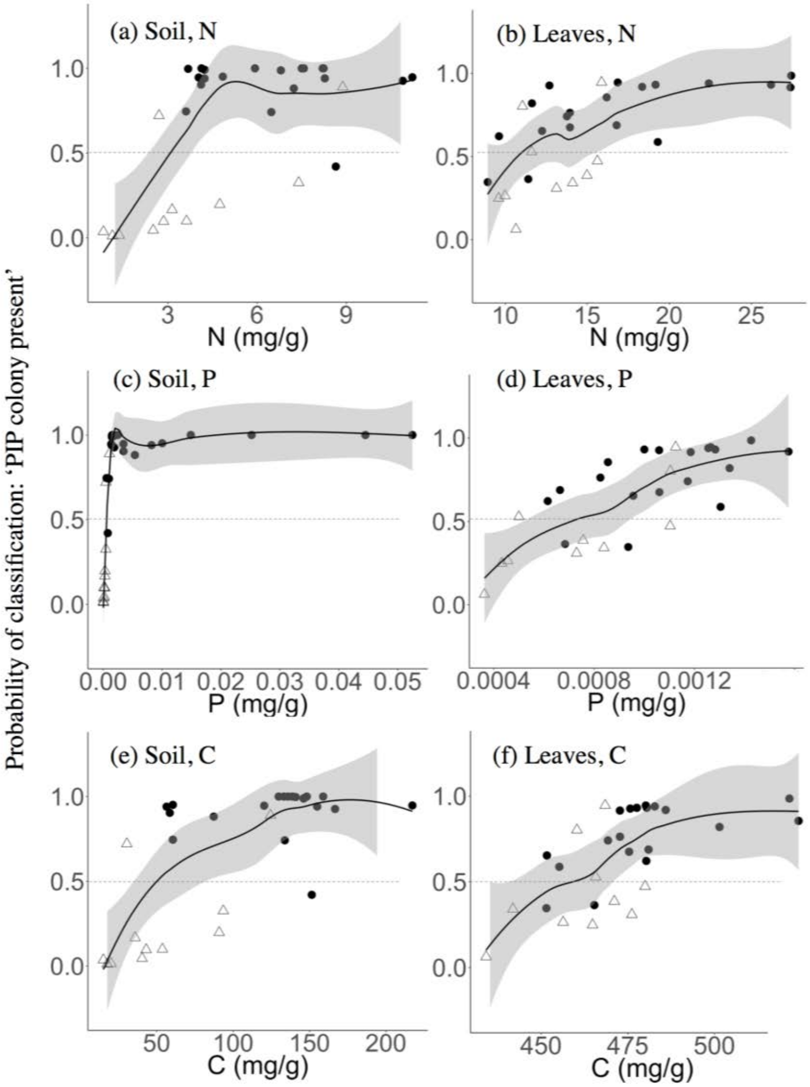


Figure 6-5 Variable dependence plots for total nitrogen (mg/g), phosphorus (mg/g), and carbon (mg/g) in soil (a, c, e) and leaf (b, d, f) samples. A loess smoother (with a 95% confidence interval) shows the relationship between the variable measurement and probability of classification as 'PIP colony present' by the random forest model. Symbols represent the category to which individual measurements belong ('PIP colony absent' = white triangles, and 'PIP colony present' = black circles). The grey-dashed line indicates 50% probability of classification as 'PIP colony present'.

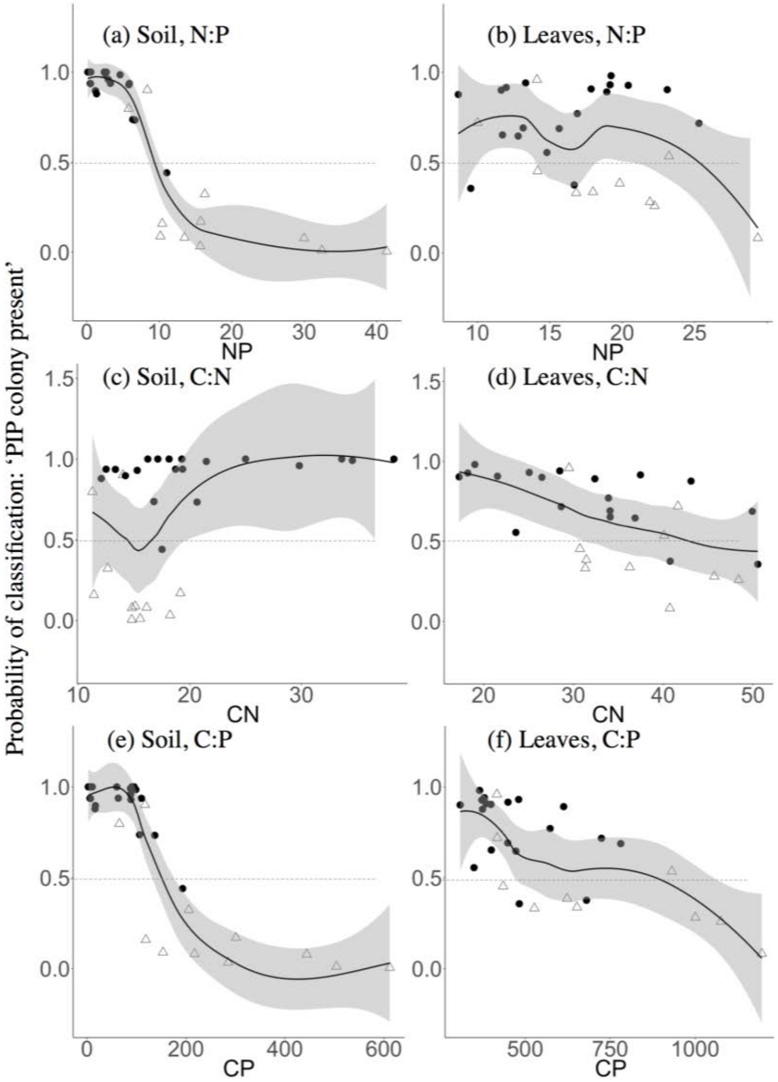


Figure 6-6 Variable dependence plots for N:P, C:N, and C:P in soil (a, c, e) and leaf (b, d, f) samples. A loess smoother (with a 95% confidence interval) shows the relationship between the variable measurement and probability of classification as 'PIP colony present' by the random forest model. Symbols represent the category to which individual measurements belong ('PIP colony absent' = white triangles, and 'PIP colony present' = black circles). The grey-dashed line indicates 50% probability of classification as 'PIP colony present'.

6.5 Discussion

The results from this study suggest that Pied Imperial-Pigeons (*Ducula* bicolor) provide a nutrient subsidy to island forests of northeast Australia where they breed colonially. The foraging behaviour of Australia's northeast PIP population has been well studied, so much so that the standard method for estimating colony size is counting individuals as they return to their island nesting sites from foraging in mainland rainforests (Atherton and Greeves 1985, Thorsborne et al. 1988, King 1999, Brothers and Bone 2012, Winter et al. 2016). This suggests that a high proportion of the nutrients they deliver to islands will be rainforest-derived, supporting the growing body of literature acknowledging the importance of cross-ecosystem nutrient flows (Sitters et al. 2015) and building a case for classifying PIPs as a mobile-link species in facilitating these processes. However, in addition to foraging in mainland rainforests, it is possible that individuals may also forage in island forests with fruiting tree species. Tracking studies would provide a better understanding of the localized foraging movements of PIPs and determine what proportion of the nutrients that they deliver to their island nesting grounds are derived from mainland rainforests. Further research is also warranted to determine the spatial extent to which the PIP colonies deliver nutrient subsidies within individual islands (i.e. measure nutrient levels within nesting forests and outside of nesting forests) and the influence of PIP colony size on nutrient loads.

6.5.1 Breeding colonies enrich $\delta N^{15}$and elevate nutrient levels

Nutrient subsidies by Pied Imperial-Pigeons are clear from soil and plant enrichment of δN^{15} and elevated soil and plant nitrogen and phosphorus levels in island forests where PIP colonies are likely to be breeding. This is consistent with guano's value as an ecosystem service that has been mined for its high concentrations of phosphorus and nitrogen (for use in fertilizer, explosives, etc.), causing wars over claims to seabird islands in the 1800's (Whelan et al. 2008, 2015). In the present study, total phosphorus was the most important soil nutrient subsidy indicator of PIP colony presence, while δN^{15}

was the most important leaf nutrient subsidy indicator. Pied Imperial-Pigeons feed primarily on fruit, meaning their guano is likely not as highly enriched in δN^{15} in comparison to piscivorous seabirds. Therefore, levels of δN^{15} enrichment by PIP colonies would not be expected to be as high as those found in areas near seabird colonies (e.g. δN^{15} values of ~22 have been found in terrestrial plants near seabird colonies; Wainright et al. 1998). However species analogous to PIPs, such as herbivorous geese and frugivorous bats, also transfer nutrients from terrestrial foraging areas that enrich δN^{15} and elevate nutrient levels in their roosting areas (Kitchell et al. 1999, Olson et al. 2005, Reef et al. 2014).

The presence of PIP breeding colonies was also related to island forest δC^{13} enrichment, however the effect differed for soil and leaf samples. In soil samples both δC^{13} values and total carbon levels increased in island forests with high likelihood of PIP colony presence. High total carbon levels in soil samples were expected in response to PIP colony presence (Garcia et al. 2002, Ellis 2005), and soil δC^{13} enrichment could be related to higher biomass of δC^{13}-enriched leaf litter below PIP colonies. However, there was no relationship between leaf δC^{13} values and the probability of PIP colony presence. This contrasts other studies that have found leaf δC^{13} enrichment in areas near bird colonies, likely due to higher leaf nitrogen levels and plant growth rates (Wainright et al. 1998, Cordell et al. 1999, Adame et al. 2015). It is possible that variation in leaf δC^{13} enrichment could be related to differential light availability for individual plants that were sampled in the present study (Buchmann et al. 1997), something worth controlling for in future studies.

Due to seasonality in the timing of breeding, nutrient deposition by colonial birds can be temporally variable and may result in a seasonal nutrient pulse to recipient ecosystems (Hahn et al. 2008, Adame et al. 2015). Pied Imperial-Pigeons breed on islands of Australia's northeast coast only during the summer months, however slight intra-annual variability in total nutrient levels may not be of great consequence for the overall functioning of these island forest ecosystems. Instead, the annual return of PIP colonies may counter-balance the short-term loss of nutrient subsidies during the non-breeding season (~ 6 months).

6.5.2 Nutrient limitation and enhanced nutrient quality in response to PIP nutrient subsidies

Nitrogen and phosphorus are often limiting nutrients in terrestrial ecosystems (Tessier and Raynal 2003, Gusewell 2004, Vitousek et al. 2010). Nutrient limitation can be inferred from increased leaf nutrient uptake in response to increased availability in soil, and also by leaf N:P ratios (Vitousek et al. 2010). Soil nitrogen and phosphorus levels were elevated in island forests with high probability of PIP colony presence and, if plants were limited by either of these nutrients, leaf nutrient levels should show similar relationships (Tessier and Raynal 2003). Indeed, leaf nitrogen and phosphorus levels increased as the probability of PIP colony presence increased, suggesting that island forests in the present study may be co-limited by both nitrogen and phosphorus.

Leaf N:P ratios provide additional support for nutrient co-limitation in island forests of the present study. Generally, low leaf N:P ratios mean that plants are nitrogen limited while high leaf N:P ratios demonstrate phosphorus limitation (Tessier and Raynal 2003). However, leaf N:P ratios did not show a clear increase or decrease with probability of PIP colony presence, suggesting either a lack of limitation or, alternatively, co-limitation by both nutrients. When nitrogen or phosphorus are not limiting other factors can influence leaf N:P ratios, such as: light, soil water, and temperature (Aerts and Chapin 2000, Tessier and Raynal 2003). Future research that includes measurement of potential confounding variables and larger sample size would improve our understanding of leaf N:P ratios and nutrient limitation. Although soil N:P ratios are not indicative of plant nutrient limitation, soil N:P decreased with increasing probability of PIP colony presence. This relationship is similar to low soil N:P ratios that were measured on islands subsidized by cormorant breeding colonies (Kolb et al. 2013).

Nutrient subsidization by PIP breeding colonies appears to enhance island forest nutrient quality and plant growth. Nutrient quality is directly related to plant growth rate, and can be inferred from C:nutrient ratios. The growth rate hypothesis states that low leaf C:N and C:P ratios are diagnostic of high plant nutrient quality and growth rate (Agren 2004, 2008; Rong et al. 2015). Additionally, low soil C:N and C:P ratios have been measured in areas that receive nutrient subsidization by seabirds (Maron et al. 2006, Jones 2010, Kolb et al. 2013). In the present study, soil C:P ratios decreased as probability of PIP colony presence increased; however, soil C:N ratios did not show a definitive trend. Additionally, leaf C:N and C:P ratios decreased as the probability of PIP colony presence increased. Overall, these relationships suggest that nutrient quality and plant growth rates increase in island forests where PIP breeding colonies are likely to occur.

Although enhanced plant growth in response to Pied Imperial-Pigeon breeding colony presence is likely, plant growth rate should be measured directly in future studies. Furthermore, this was not a comprehensive study of all effects of PIP nutrient transfer for island ecosystem functioning. For example, further research is needed to better understand why enriched soil δC^{13} values were associated with PIP colony presence. Moreover, the consequences of island nutrient subsides can extend beyond those examined here. For example, seabird nutrient subsidies can increase the abundance of island invertebrates, such as soil nematodes (Towns et al. 2009). Additionally, concentrated bird nutrient subsidies can leach from islands to adjacent marine ecosystems, elevating nitrogen and phosphorus levels in algae, or increasing seagrass biomass (Powell et al. 1991, Kolb et al. 2010, 2013). This merely hints at the great multitude of possibilities for further investigation of PIP nutrient flows, such as primary/secondary production and species composition in recipient island forests, and nutrient leaching to adjacent marine areas.

6.5.3 Implications

The cross-ecosystem nutrient subsidies provided by Pied Imperial-Pigeons argues for their classification as an avian mobile-link species that is necessary for the maintenance of island ecosystem functioning and resilience. Therefore, effective conservation of PIP's mainland foraging habitat and island forest nesting habitat is needed to maintain the nutrient flows that they provide.

The availability and connectivity of mainland and island habitats is likely to be necessary not only for the breeding success of the northeast Australian PIP population, but also for sustaining its annual migration from southern Papua New Guinea. The migratory breeding behaviour of the northeast Australian PIP population is unique in comparison to other PIP populations of northern Australia, such as in north-western Australia where PIP populations are resident (King 1990). The abundance of fruit in coastal lowland rainforests of northeast Australia, and the availability of nearby islands that may offer protection from nest-predation, likely create ideal conditions for PIPs to form dense breeding colonies and make daily foraging migrations (King 1990). Some of the breeding island forests sampled in the present study are protected as National Parks (e.g. North Brook Island and Green Island; Queensland Government 2017), and the present study illustrates that these island protected areas do not function as 'closed ecosystems'. This supports the need for an ecosystem-based perspective that considers connectivity processes when making management decisions in coastal areas, where interactions and linkages between different ecosystems are common (Stoms et al. 2005).

These insights underscore the need to consider both the habitat requirements and the processes facilitated by long-distance migrants at multiple spatial scales: local, regional, and inter-continental. Similar arguments have been made when investigating the importance of stopover sites for shorebirds during their long-distance migrations. Connectivity between roosting and foraging areas within stopover sites is needed for shorebirds to acquire enough energy for the broader success of their long-distance migration (Farmer and Parent 1997, Dias et al. 2006, Oberneufemann 2013). Therefore, although long-distance movements are perhaps more obvious, there is a need to understand the localized movements of migrants, and the drivers and consequences of the connectivity they may require or facilitate.

The preservation of Pied Imperial-Pigeon nutrient flows is not solely dependent on the availability of suitable habitat in northeast Australia. It has been acknowledged that a cooperative effort by Australia and Papua New Guinea is necessary to ensure effective conservation of migratory PIPs (King 1990, Winter et al. 2016). A cautionary example demonstrating the need for conservation initiatives to provide global scale habitat protection for migratory species is demonstrated by shorebird declines in the East Asian-Australian Flyway (EAAF). Although there are international treaties to protect migratory shorebirds in the EAAF, rapid loss of critically important tidal mudflat stopover sites has likely contributed substantially to their overall population declines (Murray and Fuller 2015). Therefore, a bilateral conservation strategy may be appropriate for Pied Imperial-Pigeon breeding and non-breeding areas. Moreover, if a bilateral agreement between Papua New Guinea and Australia were extended to include all migratory species, it would further protect 56% of Australia's migratory species that are not currently listed in Australia's Environment Protection and Biodiversity Act (Runge et al. 2017).

7 General discussion

Investigating biocomplexity in coastal northeast Australia, with an explicit focus on environmental heterogeneity and connectivity, identified several ecosystem properties that arise from species-environment interactions in this region. Given the variable mobility of the coastal forest avifauna, a comprehensive understanding of these ecosystem properties required that interactions occurring across a hierarchy of coastal mainland-island ecosystem components be explored (Figure 7-1 a). An integrated analytical approach provided insight to the landscape attributes and resources that coastal forest bird assemblages require, and likewise how they are involved in ecosystem functioning and resilience.

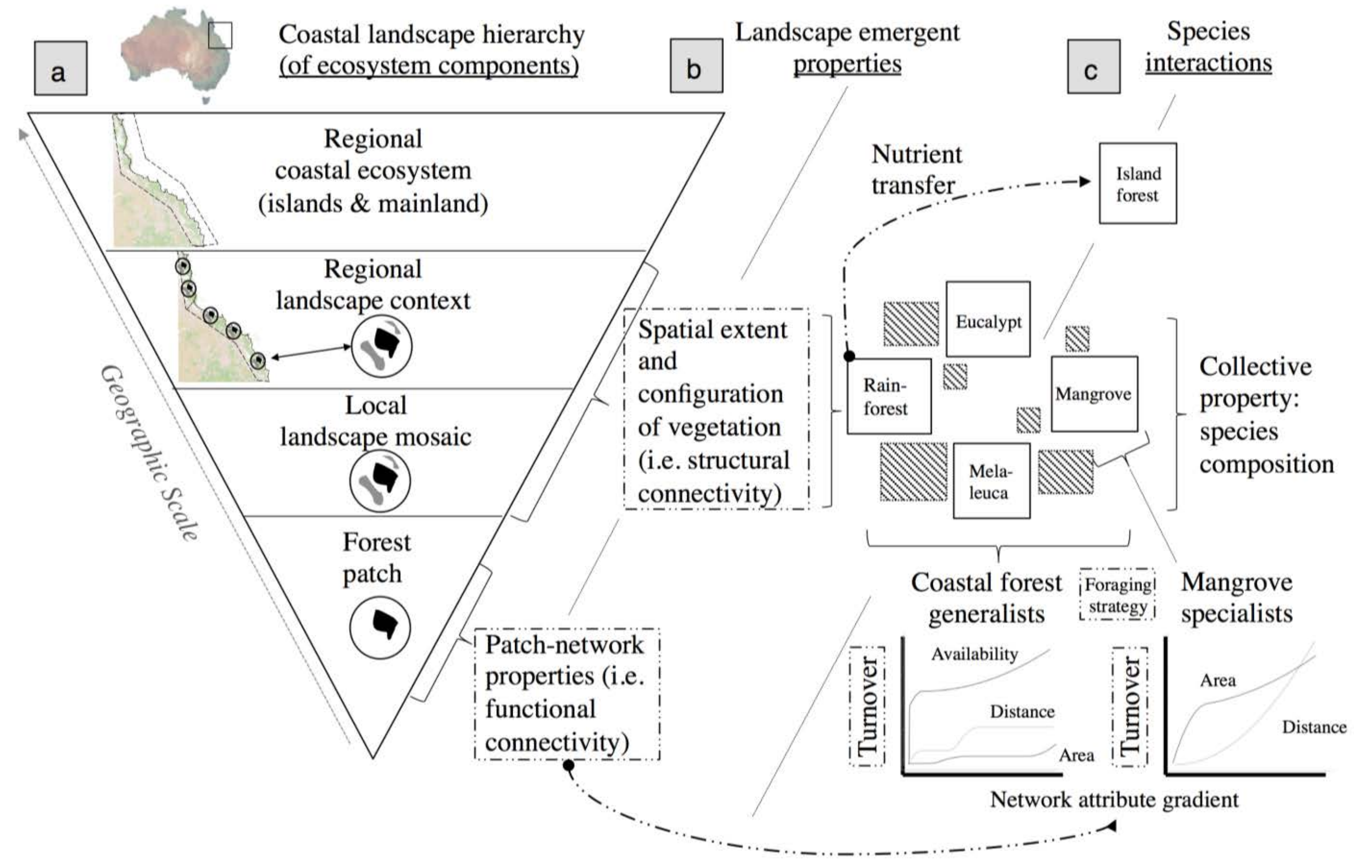


Figure 7-1 Ecosystem properties emerging from within the coastal landscape hierarchy of regional northeast Australia, and from interactions with variably mobile coastal forest

bird assemblages. The coastal landscape hierarchy (a), landscape emergent properties (b), and collective and emergent properties arising from species interactions (c) are displayed. Emergent properties are indicated by dashed boxes and dashed arrows (i.e. landscape emergent properties, nutrient transfer, foraging strategy, and compositional turnover). Patterned boxes indicate matrix vegetation within the coastal landscape mosaic.

7.1 Emergent properties: avian landscape- and resource-use in spatiotemporally heterogeneous environments

7.1.1 Spatial assessment: regional landscape heterogeneity and coastal forest avifauna

Structural relationships

While species diversity is a collective ecosystem property, there are also ecosystem properties emerging from pattern-process relationships that occur across a hierarchy of ecosystem components (i.e. emergent properties; Breckling et al. 2005, Feller et al. 2010). Emergent properties are prevalent in complex systems. For example, while zonation is an emergent property of mangrove forests (Feller et al. 2010), the spatial configuration of vegetation in the surrounding coastal landscape mosaic is a property that emerges at a broader spatial scale (i.e. a landscape emergent property, Bennett et al. 2006) (Figure 7-1 b). The present thesis determined the species composition of coastal forest bird assemblages as a collective property of the regional ecosystem (Figure 7-1 c), showing that many species use more than one forest type (i.e. are coastal forest generalists). Habitat generalists are known to rely on matrix habitats (Matthews et al. 2014), and the species composition of northeast Australia’s coastal forest avifauna was associated with the emergent structural connectivity of both forest and matrix vegetation (Figure 7-1 b, c).

Functional relationships

In addition to the structural connectivity of forest and matrix vegetation, specific attributes of functionally connected forest networks (i.e. area, availability, connectivity, and distance) were also an emergent property of the coastal landscape mosaic (Figure 7-1 b). Coastal forest generalist and mangrove specialist bird assemblages differed in the network attributes they require to maintain high rates of compositional turnover, which emerges from interactions between species composition and network attributes (Figure 7-1 c). Forest availability (which evaluates forest area and connectivity) was the most important network attribute for generalist compositional turnover, while geographic distance and forest area were the most important network features for specialist compositional turnover (Figure 7-1 c**)**. This is consistent with the paradigm that generalists' use of and movement among multiple habitats requires habitats to be adequately connected (Dennis et al. 2013). In contrast, specialists are primarily dependent on resources within a habitat that they have high fidelity to, making habitat area important for their ability to access resources (Matthews et al. 2014).

Structural and functional approaches to the assessment of relationships between landscape heterogeneity and bird assemblage composition in coastal northeast Australia provided complementary information for regional, whole-landscape conservation planning. Notably, a structural approach highlighted the importance of the landscape matrix and the spatial scale at which relevant landscape patterns occur. While it is also possible for a functional approach to include landscape matrix information and multi-scale assessment in the development of ecological networks, this requires specific data concerning species' dispersal ranges and matrix habitat preferences to be available. If these data are available, a functional approach is likely to provide a more realistic interpretation landscape-use. However, the present case study demonstrates that when limited data are available, a combined structural and functional spatial assessment approach can provide corresponding information regarding spatial configuration of the landscape matrix and specific forest attributes.

Spatial assessment would be further improved by direct measurement of habitat quality and resource availability for coastal avifauna of northeast Australia, and by incorporating future predictions of environmental change. Habitat quality is a critical component of landscapes that may be more important to species' persistence than habitat configuration (Hodgson et al. 2011). This has been demonstrated for vertebrates, where the quality of riparian forest corridors is critical for their ability to host complete species' assemblages (Lees and Perez 2008). Additionally, to provide information for long-term conservation planning, land-use and climate change predictions should be incorporated into assessment procedures to ensure adequate protection of coastal forest avifauna into the future. There is great promise in using graph theory for this purpose; allowing assessment of protected area network performance under projected land-use and climate scenarios to demonstrate how connectivity within the network is likely to change (Mazaris et al. 2013).

7.1.2 Isotopic assessment: local resource use in a spatiotemporally heterogeneous coastal environment

Foraging strategy is a property that emerges from species' interactions with their local environment (Figure 7-1 c). Isotopic analysis demonstrated that coastal forest avifauna using mangrove forests exhibit opportunistic foraging, likely in response to variable resource availability. Many of the birds caught for isotopic analysis were coastal forest habitat generalists, and their flexible foraging strategies likely contribute to their ability to use the entire coastal landscape mosaic. This is further supported by the finding that forest availability was the most important driver of coastal generalist turnover (Figure 7-1 c).

Coastal forest bird species with flexible foraging strategies will require a range of habitats and resources to be available within a region in order to adapt to increasing landscape change associated with anthropogenic and climate pressures. Whole-landscape management strategies that preserve spatiotemporal environmental heterogeneity, and therefore a breadth of foraging opportunity, will be able to provide spatial insurance for mobile, flexible foragers like coastal forest avifauna. Coupling information from spatial assessment of coastal forest avifauna's habitat and connectivity requirements with local resource use may be used to militate against the effects of habitat and connectivity loss.

In addition to using isotopic analysis to determine local-scale patterns of resource-use, this approach can provide a greater breadth of information if applied to nomadic and migratory species whose landscape- and resource- use can occur at regional and inter-continental spatial scales. For example, estimating avian migratory connectivity with hydrogen stable isotopes from feathers has enabled optimal conservation planning to protect migrators across their entire range (Martin et al. 2007). Similarly, isotopes have been used in marine systems to determine the connectivity that large mobile predators facilitate, highlighting implications for whole-ecosystem management (McCauley et al. 2012). In systems with variably mobile species and high environmental heterogeneity, isotopes can illuminate multi-scale pattern-process relationships.

7.1.3 Nutrient assessment: cross-ecosystem connectivity by a migratory species

Nutrient assessment revealed that daily migrations by a coastal forest bird species provided a nutrient subsidy to island ecosystems (an emergent property of the regional coastal ecosystem, Figure 7-1 c). Although the direct and indirect effects associated with Pied Imperial-Pigeon nutrient subsidies require further investigation, it is likely that these nutrients play an important role in island ecosystem functioning. For Pied Imperial-Pigeons to continue facilitating this connectivity process, their island breeding and mainland rainforest foraging habitat will need to be protected. Therefore, in coastal northeast Australia, whole-landscape conservation action may need to expand to protect habitats across ecosystems as well (see discussion below). Conservation planners will need to consider the spatial arrangement of island breeding and mainland foraging habitat to ensure their adequate connectivity.

The results from this thesis can help inform the development of whole-landscape management strategies for maintaining coastal ecosystem functioning in northeast Australia. Given that the Queensland Government is in the process of expanding its protected area network (Queensland Government 2016), the following discussion outlines how results from this thesis could be incorporated into plans for PA expansion. However, it should be noted that these are suggestions and that decision making should also rely on systematic conservation planning analyses to determine the most cost-effective strategies.

7.2 Protected area network in coastal northeast Australia: moving toward whole-landscape protection

Spatiotemporally heterogeneous environments operate under multi-scale pattern-process relationships, and coastal northeast Australia is no exception. An integrated analytical approach to assessing regional landscape- and resource- use by coastal forest avifauna has provided reciprocal information showing that interactions between variable mobility, landscape- and resource- use can result in divergent protection priorities. Ultimately, a whole-landscape conservation strategy is needed in coastal northeast Australia. Planning will require additional assessment of future threats (i.e. climate and land-use change) and social, economic, and political factors within the region. Action at multiple levels of government and collaboration with other stakeholders could lead to successful implementation of whole-landscape protection at multiple spatiotemporal scales. However, conservation action will not occur without evaluation of the current conservation and management strategies in place to develop a plan for implementing improvements that are informed by integrated assessment. Therefore, a challenge resides in determining how best to incorporate assessment information into effective protected area management.

7.2.1 Current protected area network evaluation and suggestions for improvement

Protected area (PA) boundaries are used to separate biota from threatening processes, and individual PAs can form networks to ensure the persistence of regional biodiversity over the long-term (Margules and Pressey 2000, Margules and Sarkar 2007, Gaston et al. 2008). The establishment of individual PAs are often planned through a target-based approach that focuses on site-level pattern-process relationships, ignoring relationships operating at larger spatial scales (Di Minin and Moilanen 2012). In regions where PAs are already established, the network should be evaluated so that expansions can be designed and implemented to further protect biodiversity (Kukkula and Moilanen 2013). Queensland currently has the lowest percentage of PA coverage relative to other states in Australia (Reside et al. 2017b), and the Queensland Government has been working to expand current coverage from 7.92% to the IUCN target of 17% (Queensland Government 2016). Data are required to inform these expansions, and results from this thesis suggest that taking a network perspective to PA planning is needed to protect patterns and processes occurring at larger spatial scales.

In taking a protected area network perspective for whole-landscape protection, the notion of ensuring ‘spatial insurance’ within the network is intuitive. Providing spatial insurance maintains the appropriate composition and configuration of habitats within a landscape to allow species to disperse and respond to disturbance (Loreau 1993), and this is consistent with the concept of complementarity in PA network design. Complementarity considers that, within a network, individual PAs or areas outside of PAs can together maintain pattern-process relationships for biodiversity persistence (Ferrier and Drielsma 2010, Williams et al. 2012, Drielsma et al. 2014). Adequate connectivity underpins the success of complementarity for biodiversity by allowing species to disperse within the PA network (Ferrier and Drielsma 2010, Williams et al. 2012). However, adequate connectivity and complementarity within a PA network will differ for species, and will be dependent on the spatiotemporal scale being considered (Mazaris et al. 2013, Maciejewski and Cumming 2016). The Great Barrier Reef (GBR) marine reserve network provides an example of effective large-scale network design that has benefited marine ecosystem health and resilience by providing adequate protection for relatively sedentary species, but has been less effective for highly mobile species, such as sharks and turtles (McCook et al. 2010).

Due to seasonal shifts in resource availability and species' ranges, designing protected area networks for nomadic and migratory avifauna is difficult (Woinarski et al. 1992; Runge et al. 2014, 2015*a*, 2016; Runge and Tulloch 2017). However, many forests and woodlands in Queensland are already degraded through land use, and deforestation is still a major threat (McAlpine et al. 2002, Bradshaw 2012, Evans 2016, Reside et al. 2017b). Therefore, it is imperative that an effective PA network exists to protect important forest attributes and connectivity for coastal forest avifauna in regional northeast Australia. Incorporating knowledge of coastal forest bird assemblage landscape- and resource- use into PA network design may help to maintain regional ecosystem functioning. Spatial assessment suggests that Melaleuca woodlands will offer high complementarity to other coastal forest types, regardless of spatial scale, and should therefore be prioritized in network design (**Chapter 3**). Furthermore, coastal generalists show flexible foraging strategies that allow them to utilize the coastal landscape when forest patches are relatively large and well-connected (i.e. have high availability; **Chapter 4, 5**). Mangrove specialist bird assemblages will also benefit from the protection of large forest patches (**Chapter 4**). Areas where protected areas could be developed/expanded for better representation of these forest network attributes have been nominated, demonstrating that the greatest opportunity for expansion occurs in the southern half of the study region (Figure 7-2).

It is important to consider that processes occurring outside of the PA network will influence functioning within the network. The degradation or loss of habitat outside of the PA network may reduce the ability of species to disperse and result in PA isolation, which is associated with biodiversity losses (Newmark et al. 2008). Given the importance of the landscape matrix for coastal forest avifauna, delineation of a protected area-centered ecosystem (PACE) (also called a 'greater ecosystem', or ecosystem-based management) may be appropriate to allow for landscape surrounding protected areas to be included in conservation assessment and planning (Hansen and DeFries 2007, Hansen et al. 2011). This may be of particular importance in the southern half of the coastal region considered in the present case study, where there is already considerable isolation of individual PAs (Figure 7-2). Furthermore, connectivity processes provided by Pied Imperial-Pigeons in coastal northeast Australia occur across protected area boundaries (**Chapter 6**), exemplifying the fact that PAs should not be considered as stand-alone, static conservation units. Instead, delineation of PACE boundaries could include island ecosystems within the PA network of coastal northeast Australia, allowing managers to account for processes such as mainland-island nutrient transfer.

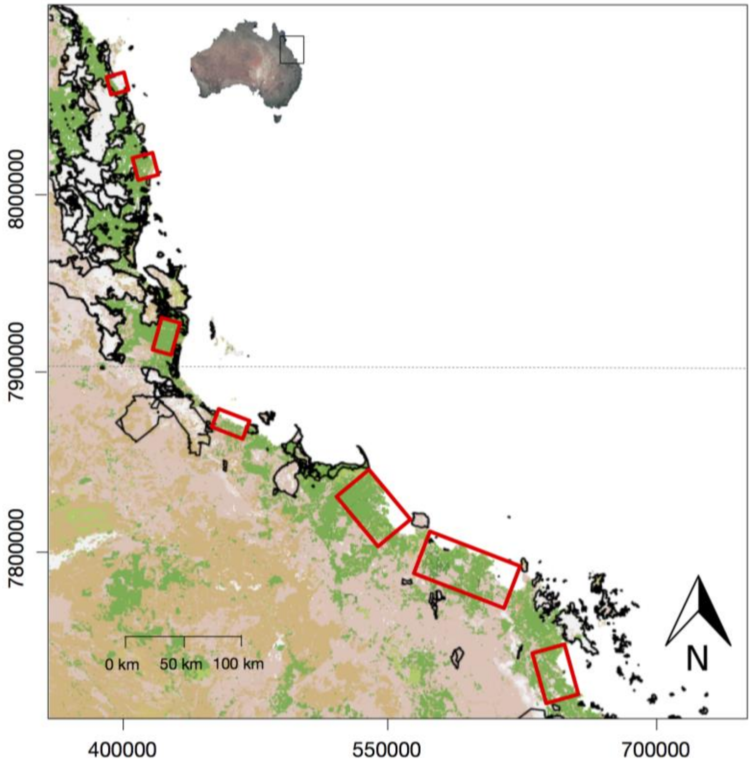


Figure 7-2 Current protected areas in the study region of northeast Australia (protected areas are black polygons), and areas where protected area expansion could occur (red

rectangles). Landscape colors represent vegetation types (NVIS 2012), and a black dashed line splits the region into northern and southern halves for reference.

Although this discussion focuses primarily on the use of protected area networks, other strategies for improving whole-landscape management should also be considered. This may be of particular importance in Australia because a relatively low population density means that the resource-base for managing protected areas is also low. A logical alternative is to link local-scale land management with regional natural resource management (NRM) groups. For example, good management outcomes have been achieved in Australia through regional Catchment Management Committees, which provide the institutional mechanism required to organize and support local Landcare groups (Curtis and Lockwood 2000). Private management by landholders may be another feasible alternative in very remote areas. For example, the fragmented nature of small mammal refuges in dryland Australia makes targeted protected area strategies difficult, and voluntary cat and fox control by landholders may be a socially and financially viable solution (Addison and Pavey 2017). Individual landholder and local community participation in regional landscape management is likely to be a necessary supplement to protected area management in coastal northeast Australia.

7.2.2 Implementation of adaptation

Implementing expansions to the current PA network in coastal northeast Australia, which could include the development of PACE boundaries, will require further assessment for determining economic, social, and political constraints (Knight and Cowling 2007, Cumming et al. 2015). At the broad spatial scale required for establishment of PACE boundaries, social and economic constraints will play highly important roles in the likelihood of success, perhaps even more than political factors (Cumming et al. 2015). To address socio-economic issues, costing of various action scenarios will need to occur. Optimistically, although landscape conservation strategies are difficult to implement, they are likely to result in both ecological and economic benefits that can foster the alignment of funding sources (Chabot et al. 2016).

Following completion of cost-effective and whole-landscape scenario assessment, implementation will require action. Unfortunately, as is the case here, there is often a high focus on conservation assessment, but little on implementation (dubbed an ‘implementation crisis’, Knight 2006a, 2006b, 2008; Arlettaz et al. 2010). Overcoming the planning-implementation hurdle will involve innovative actions such as market-based incentives (Williams et al. 2012), good-governance (Lockwood 2010), and time to establish collaboration with land-users and multiple stakeholders. Finally, following successful implementation, adequate monitoring will be required to ensure that whole-landscape protection continues to provide adequate biodiversity protection through adaptation.

7.3 Concluding remarks

Coastal landscapes have experienced high rates of habitat loss and degradation world-wide (Vitousek et al. 1997, Lotze et al. 2006), and yet human populations rely on the functioning of these coastal ecosystems for the services they provide (Barbier et al. 2011). Global estimates of coastal habitat loss are particularly high: wetland losses estimated at 62-63% (Davidson 2014), saltmarsh losses estimated at 25-50% (Deegan et al. 2012), and mangrove losses estimated at 50% (Feller et al. 2010). With the continued loss and degradation of coastal habitats, holistic conservation and management strategies are essential to ensure that coastal ecosystems remain functional. The integrated analytical approach presented in this thesis can be applied to other coastal ecosystems or faunal groups to better understand the complex relationships that underpin their ecosystem functioning.

In particular, this assessment may assist in monitoring the consequences of rapid ecosystem change occurring along Australia's Gulf of Carpentaria coastline where an unprecedented rate and extent of mangrove forest dieback occurred in 2015-2016 (6% of Queensland's mangrove vegetation; Duke et al. 2017). The consequences of these extreme events have yet to be fully understood, but it is likely that this will reduce the resilience of these coastal ecosystems for coastal forest avifauna and other taxa. Given that many locations along Australia's northern coastline have been identified as key biodiversity areas (BirdLife Australia 2017), integrated assessment is urgent to ensure adequate protection of ecosystem function.

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Appendices

*Appendix 1: Supplementary material for **Chapter 3***

Table A3.1 Bird species presence (+) and absence (-) in coastal forest types and landscape contexts at survey locations along the north-east coast of Queensland, Australia.

Bird species		Coastal forest type				Landscape context	
Common name	Scientific name	Mangrove	Melaleuca woodland	Rain forest	Eucalypt woodland	NE Tropics	SE Tropics
Australian Figbird	*Sphecotheres vieilloti*	-	+	+	+	+	+
Australian White Ibis	*Threskiornis molucca*	+	-	-	-	-	+
Brown-backed Honeyeater	*Ramsayornis modestus*	+	+	+	+	+	+
Black-faced Cuckoo-shrike	*Coracina novaehollandiae*	+	+	+	+	+	+
Blue-faced Honeyeater	*Entomyzon cyanotis*	-	+	-	+	+	+
Black-faced Monarch	*Monarcha melanopsis*	+	+	+	+	+	+
Black Butcherbird	*Cracticus quoyi*	+	+	+	+	+	+
Brown Cuckoo-dove	*Macropygia amboinensis*	-	-	-	+	-	+
Brush Cuckoo	*Cacomantis variolosus*	-	+	+	+	+	+
Brown Gerygone	*Gerygone mouki*	-	-	+	+	-	+
Brown Honeyeater	*Lichmera indistincta*	+	+	+	+	+	+
Australian Brush-turkey	*Alectura lathami*	+	-	-	+	-	+
Bar-shouldered Dove	*Geopelia humeralis*	+	+	+	+	+	+
Blue-winged Kookaburra	*Dacelo leachii*	-	-	-	+	-	+
Cicadabird	*Coracina tenuirostris*	+	+	-	+	+	+

Collared Kingfisher	*Todiramphus chloris*	+	-	-	-	+	-
Dusky Honeyeater	*Myzomela obscura*	+	+	+	+	+	+
Eastern Koel	*Eudynamys orientalis*	-	-	+	+	+	+
Emerald Dove	*Chalcophaps indica*	-	-	+	-	+	-
Eastern-yellow Robin	*Eopsaltria australis*	-	+	+	+	+	+
Fan-tailed Cuckoo	*Cacomantis flabelliformis*	+	-	+	+	+	+
Fairy Gerygone	*Gerygone palpebrosa*	+	+	+	+	+	+
Forest Kingfisher	*Todiramphus macleayii*	+	+	+	+	+	+
Golden Whistler	*Pachycephala pectoralis*	-	+	+	+	+	+
Great Bowerbird	*Chlamydera nuchalis*	+	-	+	+	+	+
Grey Fantail	*Rhipidura albiscapa*	+	+	+	+	+	+
Grey Shrike-thrush	*Colluricincla harmonica*	+	-	+	-	-	+
Grey Whistler	*Pachycephala simplex*	-	+	-	+	+	-
Horn-billed Friarbird	*Philemon yorki*	+	+	+	+	+	+
Laughing Kookaburra	*Dacelo novaeguineae*	+	-	-	+	-	+
Little-bronze Cuckoo	*Chrysococcyx minutillus*	+	-	+	+	+	+
Large-billed Gerygone	*Gerygone magnirostris*	+	-	-	-	+	+
Leaden Flycatcher	*Myiagra rubecula*	+	+	+	+	+	+
Lewin's Honeyeater	*Meliphaga lewinii*	+	+	+	+	+	+
Little Friarbird	*Philemon citreogularis*	-	+	+	-	-	+
Little Kingfisher	*Ceyx pusillus*	+	-	-	-	+	+
Little Shrike-thrush	*Colluricincla megarhyncha*	+	+	+	+	+	-
Lovely Fairy-wren	*Malurus amabilis*	+	-	+	+	+	-
Mangrove Gerygone	*Gerygone levigaster*	+	-	-	-	+	+
Mangrove Honeyeater	*Gavicalis fasciogularis*	+	-	-	-	-	+

Australian Magpie	*Cracticus tibicen*	-	-	+	+	+	+
Mangrove Robin	*Peneoenanthe pulverulenta*	+	-	-	-	+	-
Mistletoebird	*Dicaeum hirundinaceum*	+	+	+	+	+	+
Northern Fantail	*Rhipidura rufiventris*	+	+	-	-	+	-
Noisy Friarbird	*Philemon corniculatus*	+	+	-	-	+	+
Orange-footed Scrub-fowl	*Megapodius reinwardt*	-	-	+	-	+	-
Olive-backed Oriole	*Oriolus sagittatus*	+	+	+	+	+	+
Olive-backed Sunbird	*Nectarinia jugularis*	+	+	+	+	+	+
Pale-headed Rosella	*Platycercus adscitus*	-	-	-	+	-	+
Peaceful Dove	*Geopelia striata*	+	+	+	+	+	+
Pheasant Coucal	*Centropus phasianinus*	+	+	+	+	+	+
Pied Butcherbird	*Cracticus nigrogularis*	-	-	+	+	-	+
Pied Currawong	*Strepera graculina*	-	+	+	+	-	+
Pied Imperial-pigeon	*Ducula bicolor*	+	+	+	-	+	+
Rainbow Bee-eater	*Merops ornatus*	+	+	-	+	+	+
Red-backed Fairy-wren	*Malurus melanocephalus*	+	+	+	+	+	+
Rufous Fantail	*Rhipidura rufifrons*	+	+	+	+	+	+
Rufous Whistler	*Pachycephala rufiventris*	+	+	+	+	+	+
Red-winged Parrot	*Aprosmictus erythropterus*	+	-	+	-	+	+
Sacred Kingfisher	*Todiramphus sanctus*	+	-	+	+	+	+
Scarlet Honeyeater	*Myzomela sanguinolenta*	-	+	+	+	+	+
Shining Flycatcher	*Myiagra alecto*	+	-	+	+	+	+
Silvereye	*Zosterops lateralis*	+	-	-	-	+	-
Spangled Drongo	*Dicrurus bracteatus*	+	+	+	+	+	+

Spectacled Monarch	*Symposiarchus trivirgatus*	+	+	+	+	+	+
Striated Pardalote	*Pardalotus striatus*	-	-	-	+	-	+
Superb Fruit-dove	*Ptilinopus superbus*	-	+	+	-	+	+
Varied Honeyeater	*Gavicalis versicolor*	+	-	-	-	+	-
Varied Triller	*Lalage leucomela*	+	+	+	+	+	+
White-bellied Cuckoo-shrike	*Coracinapapapuensis*	+	+	+	+	+	+
White-browed Robin	*Poecilodryas superciliosa*	-	-	+	+	+	+
White-browed Scrubwren	*Sericornis frontalis*	-	-	+	-	-	+
White-eared Monarch	*Carterornis leucotis*	+	-	+	+	-	+
Whimbrel	*Numenius phaeopus*	+	-	-	-	+	+
Willie Wagtail	*Rhipidura leucophrys*	+	-	-	+	+	+
White-throated Honeyeater	*Melithreptus albogularis*	+	+	+	+	+	+
Yellow Honeyeater	*Lichenostomus flavus*	+	+	+	+	+	+
Yellow Oriole	*Icterus nigrogularis*	+	+	+	+	+	-
Yellow-faced Honeyeater	*Lichenostomus chrysops*	+	-	-	+	+	-
Yellow-spotted Honeyeater	*Meliphaga notata*	+	+	+	+	+	+
Yellow-throated Scrubwren	*Sericornis citreogularis*	-	+	-	-	+	-

Table A3.2 Connectivity variables derived from principal components analysis (PCA) of four landscape metrics (TLA, NumP, TE, and MNN) measured for 11 vegetation types at each survey location and at three spatial scales (3, 6, and 12 km). The first principal component (PC1) of each PCA became the connectivity variable for each vegetation type, and the proportion of variance in connectivity explained by each PC1 is provided.

Connectivity variable	Spatial scale	Proportion of variance explained by PC1 (%)
Eucalypt woodland	3km	59%
	6km	61%
	12km	60%
Freshwater	6km	67%
	12km	70%
Mangrove	3km	48%
	6km	54%
	12km	68%
Melaleuca woodland	3km	68%
	6km	70%
	12km	70%
Rainforest	3km	73%
	6km	71%
	12km	76%
SandRockMud	3km	75%
	6km	63%
	12km	70%
Shrubland	3km	66%
	6km	45%
	12km	64%
Casuarina/Allocasuarina forest	6km	65%
	12km	72%
Cleared urban/agricultural land	3km	51%
	6km	57%
	12km	65%
Acacia forests and woodlands	3 km	96%
	6 km	76%
	12 km	70%
Grassland	3 km	85%
	6 km	95%
	12 km	79%

Table A3.3 Summary of vector and surface fitting procedures for connectivity variables that were correlated to the bird ordination (individual landscape metrics with $p<0.05$ are highlighted in bold; MNN = mean nearest neighbour distance between vegetation patches, NumP = number of vegetation patches, TE = total edge of vegetation, and TLA = total landscape area of vegetation).

Structural connectivity variable	Spatial scale	Vector-fit p-value	Vector-fit R^2 value	Landscape metric	Surface-fit P-value	Surface-fit R^2 value	Deviance explained (%)
Melaleuca	3km	0.004	0.39	TLA	0.07	0.16	23%
				NumP	**<0.001**	**0.39**	**43%**
				TE	**0.002**	**0.31**	**37%**
				MNN	0.248	0.03	5%
Vegetation-devoid (labelled: ‘SandRockMud’)	3km	0.001	0.45	TLA	0.056	0.23	31%
				NumP	**<0.001**	**0.53**	**62%**
				TE	**0.004**	**0.43**	**53%**
				MNN	**<0.001**	**0.82**	**87%**
Grassland	6km	0.032	0.25	**TLA**	**0.001**	**0.39**	**45%**
				NumP	**0.026**	**0.20**	**26%**
				TE	0.168	0.08	12%
				MNN	0.053	0.15	19%
Melaleuca	6km	0.004	0.40	TLA	0.071	0.13	17%
				NumP	**<0.001**	**0.47**	**50%**
				TE	**0.002**	**0.34**	**38%**
				MNN	0.265	0.03	5%
Melaleuca	12km	0.008	0.33	TLA	0.394	0.00	0.2%
				NumP	**<0.001**	**0.47**	**51%**
				TE	**0.004**	**0.31**	**35%**
				MNN	0.234	0.04	6%
Rainforest	12km	0.027	0.26	**TLA**	**<0.001**	**0.68**	**76%**
				NumP	**<0.001**	**0.58**	**67%**
				TE	**<0.001**	**0.61**	**69%**
				MNN	0.292	0.02	4%
Shrubland	12km	0.001	0.54	**TLA**	**0.020**	**0.31**	**41%**
				NumP	**<0.001**	**0.46**	**50%**
				TE	**<0.001**	**0.52**	**61%**
				MNN	**0.004**	**0.44**	**54%**
Vegetation-devoid (labelled: ‘SandRockMud’)	12km	0.021	0.27	TLA	0.058	0.21	30%
				NumP	**0.001**	**0.47**	**57%**
				TE	**0.003**	**0.42**	**51%**
				MNN	**0.004**	**0.43**	**54%**

Table A3.4 Results of a two-factor multivariate PERMANOVA based on a Jaccard dissimilarity matrix of bird species presence-absence data in relation to main and interactive effects of landscape context and coastal forest type. Subsequent pairwise comparisons of individual coastal forest types are also listed. Factors influencing bird species assemblage at $p<0.05$ are highlighted in bold.

Factor	DF	SS	MS	Psuedo-*F*	*P*(perm)
Landscape context	1	4074.4	4074.4	2.062	**0.002**
Coastal forest type	3	12417	4139	2.095	**0.001**
Landscape context X coastal forest type	3	6236.9	2079	1.052	0.338
Pairwise habitat comparisons				t	P(perm)
Eucalyptus X Mangrove				1.540	**0.002**
Eucalyptus X Melaleuca				0.822	0.782
Eucalyptus X Rainforest				1.301	**0.031**
Mangrove X Melaleuca				1.535	**0.003**
Mangrove X Rainforest				1.645	**0.002**
Melaleuca X Rainforest				1.211	0.121

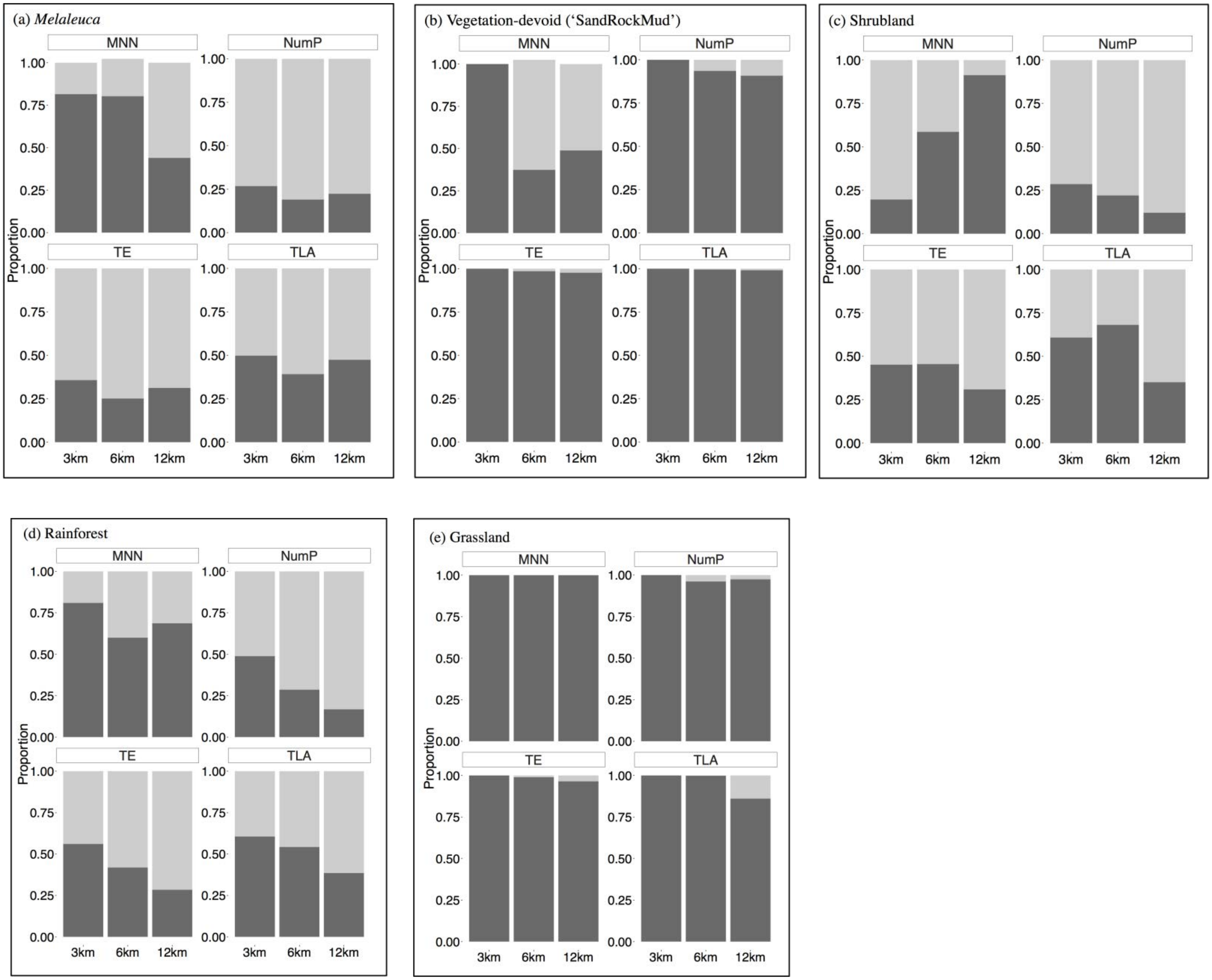

Figure A3.5 The proportions of landscape metric measurements in the ■ SE tropics and ▨ NE tropics, for connectivity variables that were correlated to the bird ordination, and displayed by spatial scale (3, 6, and 12 km). The significantly correlated connectivity variables include: a) Melaleuca*,* b) vegetation-devoid, c) shrubland, d) rainforest, e) grassland; and landscape metrics include: MNN (mean nearest neighbour distance between vegetation patches), NumP (number of vegetation patches), TE (total edge of vegetation), and TLA (total landscape area of vegetation).

Appendix 2: Supplementary material for ***Chapter 4***

Table A4.1 Percentage of bird species' occurrence in four coastal forest types (i.e. Eucalypt, mangrove, Melaleuca, and rainforest). The highest occurrence percentages for each species are highlighted in bold. Species with highest % occurrence less than 90% in any forest type were classified as 'coastal generalists', while species with highest % occurrence greater than 90% in mangrove forests only were classified as 'mangrove specialists' .

Species		% Occurrence			
Common name	Scientific name				
Coastal generalists		Eucalypt	Mangrove	*Melaleuca*	Rainforest
Brown-backed Honeyeater	*Ramsayornis modestus*	23.4%	14.9%	**55.3%**	6.4%
Black-faced Cuckoo-shrike	*Coracina novaehollandiae*	**57.1%**	14.3%	14.3%	14.3%
Black-faced Monarch	*Monarcha melanopsis*	**37.5%**	**37.5%**	12.5%	12.5%
Black Butcherbird	*Cracticus quoyi*	2.7%	**70.3%**	10.8%	16.2%
Brush Cuckoo	*Cacomantis variolosus*	27.8%	5.6%	33.3%	33.3%
Brown Honeyeater	*Lichmera indistincta*	21.0%	**58.0%**	16.0%	5.0%
Bar-shouldered Dove	*Geopelia humeralis*	33.3%	**37.5%**	18.8%	10.4%
Cicadabird	*Coracina tenuirostris*	**40.0%**	**40.0%**	20.0%	0.0%
Dusky Honeyeater	*Myzomela obscura*	20.6%	**44.1%**	11.8%	23.5%
Fan-tailed Cuckoo	*Cacomantis flabelliformis*	**50.0%**	37.5%	0.0%	12.5%
Fairy Gerygone	*Gerygone palpebrosa*	8.7%	21.7%	13.0%	**56.5%**
Forest Kingfisher	*Todiramphus macleayii*	33.3%	5.6%	**50.0%**	11.1%
Great Bowerbird	*Chlamydera nuchalis*	**54.5%**	18.2%	0.0%	27.3%
Grey Fantail	*Rhipidura albiscapa*	30.2%	**32.6%**	25.6%	11.6%
Little-bronze Cuckoo	*Chrysococcyx minutillus*	35.7%	**50.0%**	0.0%	14.3%
Leaden Flycatcher	*Myiagra rubecula*	**47.5%**	22.0%	23.7%	6.8%
Little Shrike-thrush	*Colluricincla megarhyncha*	**38.2%**	26.5%	8.8%	26.5%
Mistletoebird	*Dicaeum hirundinaceum*	26.6%	**31.2%**	25.7%	16.5%
Olive-backed Oriole	*Oriolus sagittatus*	**33.3%**	22.2%	**33.3%**	11.1%
Olive-backed Sunbird	*Nectarinia jugularis*	21.3%	**60.2%**	8.3%	10.2%
Peaceful Dove	*Geopelia striata*	**65.0%**	15.0%	15.0%	5.0%
Red-backed Fairy-wren	*Malurus melanocephalus*	**45.0%**	25.0%	25.0%	5.0%
Rufous Fantail	*Rhipidura rufifrons*	12.5%	25.0%	12.5%	**50.0%**
Rufous Whistler	*Pachycephala rufiventris*	**44.4%**	5.6%	**44.4%**	5.6%
Spangled Drongo	*Dicrurus bracteatus*	**37.7%**	34.8%	15.9%	11.6%
Spectacled Monarch	*Symposiarchus trivirgatus*	16.7%	33.3%	8.3%	**41.7%**
Varied Triller	*Lalage leucomela*	**23.5%**	20.6%	**23.5%**	32.4%

White-eared Monarch	*Carterornis leucotis*	41.7%	**50.0%**	0.0%	8.3%
White-throated Honeyeater	*Melithreptus albogularis*	**62.7%**	7.2%	**22.9%**	7.2%
Yellow Honeyeater	*Lichenostomus flavus*	**50.0%**	27.8%	7.4%	14.8%
Yellow Oriole	*Icterus nigrogularis*	14.3%	19.0%	28.6%	**38.1%**
Yellow-spotted Honeyeater	*Meliphaga notata*	12.8%	23.1%	28.2%	**35.9%**
Mangrove specialists		Eucalypt	Mangrove	*Melaleuca*	Rainforest
Collared Kingfisher	*Todiramphus chloris*	0.0%	**100.0%**	0.0%	0.0%
Mangrove Gerygone	*Gerygone levigaster*	0.0%	**100.0%**	0.0%	0.0%
Mangrove Robin	*Peneoenanthe pulverulenta*	0.0%	**100.0%**	0.0%	0.0%
Shining Flycatcher	*Myiagra alecto*	3.0%	**90.9%**	0.0%	6.1%

Appendix 3: Supplementary material for ***Chapter 5***

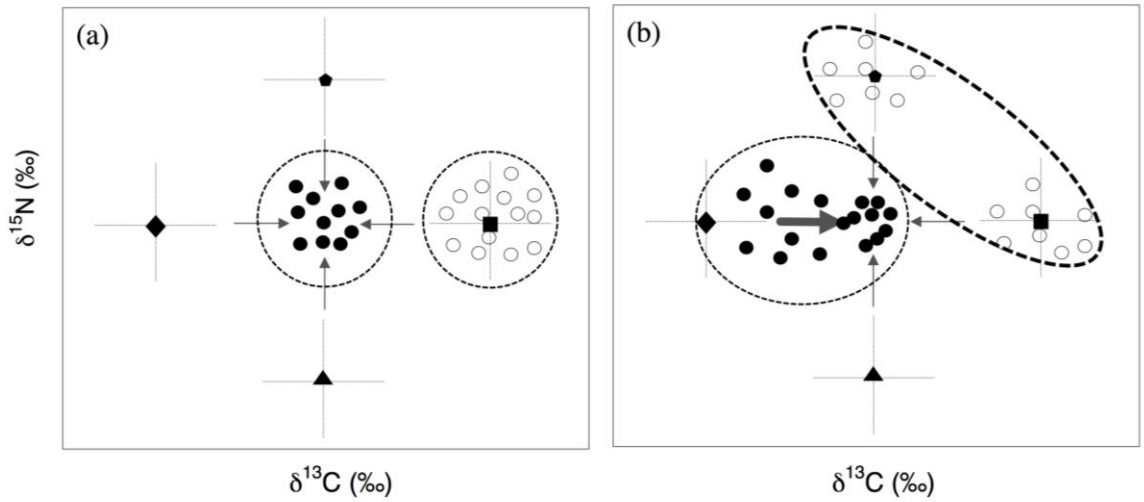

Figure A5.1 Interpreting isotopic niche size as an indicator of consumer populations having generalised or specialised foraging strategies. Plots (a) and (b) show hypothetical $\delta^{13}C$ and $\delta^{15}N$ isotope space with individuals in generalist consumer populations represented by black dots, and individuals in specialist consumer populations represented by white dots. Four different resources are available to consumers (represented by diamond, triangle, square, and pentagon symbols; with vertical and horizontal lines to indicate variability, and arrows to indicate the relative contributions of each source to generalist populations). Dashed circles or ellipses around consumer populations represent their isotopic niche size. In (a), consumers from a generalist population forage consistently on all four resources, and isotopic averaging results in an isotopic niche that is of similar size to a specialist population foraging on only one resource (square). In (b), some consumers from a generalist population forage more heavily on one resource (diamond), resulting in a larger isotopic niche compared to generalists in (a). Finally, in (b), individual consumers of a specialist population feed separately on two different resources, resulting in a larger isotopic niche relative to specialists in (a). This is not a complete illustration of all isotopic niche size scenarios that are possible, and only provides an indication of the challenges associated with interpretation.

Table A5.2 δ^{13}C and δ^{15}N signatures (mean ± sd) and sample size (n) of blood and claw tissues for bird species caught at each sampling site. Bird species are organised by their literature-based foraging group membership: carnivores, insectivores, nectarivore-insectivores, and omnivores.

Bird species		Stable isotope signatures					
Common name	Scientific name	Site	Season	Tissue	n	δ^{13}C (‰) ± sd	δ^{15}N (‰) ± sd
				Carnivores			
Black Butcherbird	*Cracticus quoyi*	Cocoa creek	Dry	Blood	1	-22.84	7.11
				Claw	1	-20.47	6.67
Little Kingfisher	*Ceyx pusillus*	Cocoa creek	Wet	Blood	1	-20.96	7.32
				Claw	1	-22.40	6.72
			Dry	Blood	1	-21.39	8.02
				Claw	1	-20.82	9.03
		Healy creek	Dry	Blood	2	-19.99 ± 0.98	9.28 ± 2.35
				Claw	2	-21.24 ± 3.44	14.95 ± 12.76
Sacred Kingfisher	*Todiramphus sanctus*	Cocoa creek	Wet	Blood	10	-20.81 ± 1.99	6.83 ± 0.91
				Claw	8	-19.38 ± 1.87	5.87 ± 0.95
			Dry	Blood	7	-18.45 ± 2.45	5.14 ± 2.06
				Claw	6	-18.35 ± 1.83	5.56 ± 1.25
		Healy creek	Dry	Blood	4	-18.45 ± 1.39	7.26 ± 2.76
				Claw	3	-17.09 ± 1.00	6.68 ± 2.62
				Insectivores			
Fairy Gerygone	*Gerygone palpebrosa*	Cocoa creek	Wet	Blood	5	-22.57 ± 0.28	5.76 ± 0.52
				Claw	4	-20.77 ± 0.47	4.42 ± 1.17
			Dry	Blood	1	-23.19	5.46
				Claw	4	-20.9 ± 0.56	5.06 ± 0.46
		Healy creek	Dry	Blood	1	-22.59	1.93
				Claw	2	-21.08 ± 0.11	1.39 ± 0.45
Forest Kingfisher	*Todiramphus macleayii*	Cocoa creek	Wet	Blood	3	-22.61 ± 0.47	5.55 ± 0.32
				Claw	2	-20.85 ± 0.24	5.41 ± 0.41
Grey Fantail	*Rhipidura albiscapa*	Cocoa creek	Dry	Blood	1	-22.84	5.81
				Claw	2	-21.005 ± 0.90	6.81 ± 0.80
Large-billed Gerygone	*Gerygone magnirostris*	Cocoa creek	Dry	Blood	1	-22.95	7.71
				Claw	1	-20.85	7.55
		Healy creek	Dry	Claw	3	-21.61 ± 0.40	2.01 ± 1.49
Little-bronze Cuckoo	*Chrysococcyx minutillus*	Cocoa creek	Wet	Blood	1	-25.30	5.31
				Claw	1	-22.68	4.60
Leaden Flycatcher	*Myiagra rubecula*	Cocoa creek	Dry	Blood	3	-22.66 ± 0.72	4.61 ± 0.45
				Claw	3	-20.99 ± 0.50	5.51 ± 0.20

		Healy creek	Dry	Blood	8	-22.07 ± 0.38	4.57 ± 1.86
				Claw	8	-20.70 ± 0.49	3.50 ± 2.31
Rufous Fantail	*Rhipidura rufifrons*	Cocoa creek	Wet	Blood	1	-22.41	6.18
				Claw	1	-21.74	5.25
			Dry	Claw	1	-20.41	6.70
		Healy creek	Dry	Blood	1	-22.32	6.33
				Claw	1	-20.32	6.07
Rufous Whistler	*Pachycephala rufiventris*	Cocoa creek	Wet	Blood	3	-22.66 ± 1.01	6.06 ± 1.30
				Claw	2	-18.93 ± 2.17	5.69 ± 1.63
			Dry	Blood	1	-22.33	6.53
				Claw	1	-20.60	6.55
		Healy creek	Dry	Blood	1	-22.70	6.61
				Claw	1	-20.85	6.18
Shining Flycatcher	*Myiagra alecto*	Cocoa creek	Wet	Blood	3	-21.45 ± 0.54	7.40 ± 0.32
				Claw	2	-19.75 ± 0.03	6.38 ± 0.69
			Dry	Blood	3	-21.48 ± 1.00	6.60 ± 1.38
				Claw	3	-19.92 ± 0.93	6.61 ± 1.25
		Healy creek	Dry	Blood	3	-20.68 ± 0.72	3.79 ± 1.42
				Claw	3	-19.36 ± 0.46	3.86 ± 1.46
Spectacled Monarch	*Symposiarchus trivirgatus*	Cocoa creek	Wet	Blood	3	-23.86 ± 0.99	5.55 ± 0.94
				Claw	3	-22.06 ± 1.03	4.97 ± 0.46
			Dry	Blood	4	-23.68 ± 0.51	5.5 ± 0.18
				Claw	3	-21.61 ± 0.40	5.91 ± 0.17
		Healy creek	Dry	Blood	1	-25.07	6.56
				Claw	1	-23.68	6.83
Nectarivore-Insectivores							
Brown-backed Honeyeater	*Ramsayornis modestus*	Cocoa creek	Wet	Blood	2	-23.83 ± 0.42	5.87 ± 0.15
				Claw	2	-22.4 ± 0.07	6.37 ± 0.44
			Dry	Blood	3	-24.12 ± 0.27	5.28 ± 0.34
				Claw	3	-22.27 ± 0.38	5.93 ± 0.24
		Healy creek	Dry	Blood	10	-23.58 ± 0.74	4.05 ± 3.91
				Claw	8	-22.26 ± 0.83	3.58 ± 2.06
Brown Honeyeater	*Lichmera indistincta*	Cocoa creek	Wet	Claw	1	-20.34	6.74
				Blood	2	-23.30 ± 0.29	6.74 ± 0.33
			Dry	Claw	2	-21.75 ± 0.23	6.75 ± 0.74
		Healy creek	Dry	Blood	24	-23.21 ± 0.51	4.99 ± 2.09
				Claw	20	-21.73 ± 0.51	5.34 ± 2.91
Dusky Honeyeater	*Myzomela obscura*	Cocoa creek	Wet	Blood	17	-24.35 ± 1.00	6.74 ± 0.32
				Claw	13	-22.22 ± 0.99	6.16 ± 0.32

			Dry	Blood	12	-24.54 ± 0.59	6.27 ± 0.66
				Claw	15	-22.85 ± 0.43	5.85 ± 0.95
		Healy creek	Dry	Blood	22	-24.49 ± 0.28	5.485 ± 5.64
				Claw	18	-22.56 ± 0.35	5.47 ± 6.37
Horn-billed Friarbird	*Philemon yorki*	Cocoa creek	Wet	Blood	3	-24.20 ± 0.47	7 ± 0.41
				Claw	3	-21.29 ± 0.12	5.91 ± 0.73
			Dry	Claw	1	-21.49	7.15
		Healy creek	Dry	Blood	4	-23.75 ± 0.36	5.45 ± 1.31
				Claw	5	-21.49 ± 0.43	5.39 ± 1.23
Olive-backed Sunbird	*Nectarinia jugularis*	Cocoa creek	Wet	Blood	3	-22.77 ± 0.73	7.49 ± 0.17
				Claw	4	-21.57 ± 0.66	7.84 ± 0.18
			Dry	Blood	10	-22.75 ± 0.67	7.31 ± 0.51
				Claw	10	-21.51 ± 0.66	7.76 ± 0.61
		Healy creek	Dry	Blood	17	-23.13 ± 0.99	6.72 ± 3.31
				Claw	16	-21.42 ± 1.03	7.77 ± 3.54
White-throated Honeyeater	*Melithreptus albogularis*	Cocoa creek	Wet	Blood	3	-23.72 ± 0.13	6.26 ± 0.11
				Claw	4	-21.91 ± 0.13	5.94 ± 0.15
		Healy creek	Dry	Blood	7	-23.61 ± 0.67	6.09 ± 0.22
				Claw	7	-21.89 ± 0.65	6.23 ± 0.41
Yellow Honeyeater	*Lichenostomus flavus*	Cocoa creek	Wet	Blood	1	-24.51	6.90
				Claw	1	-21.93	6.07
Yellow-spotted Honeyeater	*Meliphaga notata*	Cocoa creek	Wet	Blood	9	-24.47 ± 0.33	6.29 ± 0.60
				Claw	7	-21.85 ± 0.51	5.95 ± 0.38
			Dry	Blood	9	-24.64 ± 0.50	6 ± 0.77
				Claw	9	-22.62 ± 0.34	6.32 ± 0.76
		Healy creek	Dry	Blood	3	-23.59 ± 1.36	5.57 ± 1.34
				Claw	2	-22.10 ± 0.44	5.73 ± 1.56
Omnivores							
Great Bowerbird	*Chlamydera nuchalis*	Cocoa creek	Wet	Blood	1	-24.71	5.46
				Claw	1	-22.29	4.50
Mistletoebird	*Dicaeum hirundinaceum*	Healy creek	Dry	Blood	5	-24.94 ± 0.67	2.19 ± 1.56
				Claw	5	-23.61 ± 0.71	2.6 ± 2.51
Olive-backed Oriole	*Oriolus sagittatus*	Cocoa creek	Wet	Blood	1	-22.05	7.07
				Claw	1	-20.94	6.47
Brush Cuckoo	*Cacomantis variolosus*	Cocoa creek	Wet	Blood	1	-23.10	5.22
				Claw	1	-14.43	5.19
Cicadabird	*Coracina tenuirostris*	Cocoa creek	Wet	Blood	2	-24.37 ± 0.03	5.37 ± 0.09
				Claw	1	-21.70	5.39
Little Shrike-	*Colluricincla*	Cocoa creek	Wet	Blood	3	-23.56 ± 0.61	5.77 ± 0.65

thrush	*megarhyncha*			Claw	3	-21.33 ± 0.77	5.57 ± 0.43
		Healy creek	Dry	Blood	1	-22.48	2.89
				Claw	1	-20.48	3.62
Spangled Drongo	*Dicrurus bracteatus*	Cocoa creek	Wet	Blood	1	-23.43	6.10
				Claw	1	-20.98	5.65
Varied Triller	*Lalage leucomela*	Cocoa creek	Wet	Blood	4	-23.03 ± 0.58	6.79 ± 0.68
				Claw	4	-21.34 ± 0.64	5.88 ± 0.86
			Dry	Blood	2	-22.93 ± 0.37	6.7 ± 0.17
				Claw	2	-21.09 ± 1.19	5.96 ± 1.06
		Healy creek	Dry	Blood	5	-23.28 ± 0.76	3.28 ± 2.77
				Claw	6	-21.19 ± 0.51	3.66 ± 2.38
White-bellied Cuckoo-shrike	*Coracina papapuensis*	Cocoa creek	Wet	Blood	1	-24.19	6.17
				Claw	1	-21.70	5.44
Granivores							
Peaceful Dove	*Geopelia striata*	Cocoa creek	Wet	Blood	2	-18.07 ± 1.81	4.89 ± 0.47
				Claw	1	-16.38	5.04

Table A5.3 δ^{13}C and δ^{15}N signatures (mean ± sd) and sample size (n) of basal food sources at each sampling site during wet and dry seasons. Sources are grouped by their vegetation type: mangrove, woodland, or saltmarsh.

Site	Source	Season	n	δ^{13}C (‰) ± sd	δ^{15}N (‰) ± sd
		Mangrove			
Cocoa creek	Crabs (*Sesarma* spp.)	Wet	4	-21.54 ± 2.04	4.80 ± 0.61
		Dry	5	21.33 ± 3.71	5.1 ± 1.33
	Fish (Family Mugilidae, Lutjanidae, Leiognathidae, Sparidae, Gobiidae)	Wet	6	-20.51 ± 2.1	7.26 ± 0.99
		Dry	5	-18.52 ± 0.62	6.7 ± 1.78
	Insects (Order Coleoptera, Lepidoptera, Phasmatodea, Blattodea; and Family Salticidae, Flatidae, Deinopidae, Thomisidae, Formicidae)	Wet	4	-25.35 ± 2.36	2.94 ± 2.18
		Dry	5	25.04 ± 0.74	2.02 ± 2.19
	Leaves (*Rhizophora* spp.)	Wet	4	-28.99 ± 0.23	2.57 ± 0.09
		Dry	5	-29.45 ± 0.31	2.53 ± 0.37
Healy creek	Crab (*Sesarma* spp.)	Dry	4	-19.9 ± 1.32	-0.58 ± 2.72
	Fish (Family Gobiidae)		4	-23.48 ± 2.00	9.2 ± 0.79
	Insects (Order Coleoptera, Lepidoptera, Phasmatodea, Blattodea; and Family Salticidae, Flatidae, Deinopidae, Thomisidae, Formicidae)		5	-24.55 ± 1.13	1.37 ± 5.68
	Leaves (*Rhizophora* spp.)		5	-28.90 ± 0.08	3.69 ± 1.29
		Woodland			
Cocoa creek	Insects (Order Coleoptera, Lepidoptera, Phasmatodea, Blattodea; and Family Salticidae, Flatidae, Deinopidae, Thomisidae, Formicidae)	Wet	9	-24.1 ± 1.9	3.86 ± 1.57
		Dry	10	25.08 ± 2.95	3.3 ± 2.13
	Leaves (E*ucalyptus* spp., *Melaleuca* spp.)	Wet	4	-29.8 ± 1.66	-0.08 ± 1.56
		Dry	10	-30.8 ± 1.49	-0.77 ± 0.37
Healy creek	Insects (Order Coleoptera, Lepidoptera, Phasmatodea, Blattodea; and Family Salticidae, Flatidae, Deinopidae, Thomisidae, Formicidae)	Dry	5	-25.50 ± 0.99	-3.1 ± 2.91
	Leaves (E*ucalyptus* spp., *Melaleuca* spp.)		10	-30.96 ± 0.35	-9.84 ± 4.19
		Saltmarsh			
Cocoa creek	Insects (Family Formicidae) and crabs (*Uca* spp.)	Wet	4	-15.97 ± 0.76	7.44 ± 0.56
		Dry	10	-15.64 ± 0.85	7.45 ± 0.88
Healy creek	Insects (Family Formicidae) and crabs (*Uca* spp.)	Dry	10	-12.4 ± 1.21	-2.84 ± 1.89

Table A5.4.1 Results of Welch's two-sample t-tests determining differences in bird blood and claw δ^{13}C and δ^{15}N signatures between seasons at Cocoa creek. P-values less than, or equal to, 0.05 are highlighted in bold.

	Comparison	*t*-test statistic	degrees of freedom	p-value
	Consumer tissues			
Tissue				
Blood	Wet season δ13C vs. Dry season δ13C	0.07	129.9	0.95
	Wet season δ15N vs. Dry season δ15N	0.47	108.14	0.64
Claw	Wet season δ13C vs. Dry season δ13C	0.56	130.2	0.58
	Wet season δ15N vs. Dry season δ15N	-3.25	111.95	**0.002**

Table A5.4.2 Results of Welch's two-sample t-tests determining differences in source δ^{13}C and δ^{15}N signatures between seasons at Cocoa creek. P-values less than, or equal to, 0.05 are highlighted in bold.

Comparison	*t*-test statistic	degrees of freedom	p-value
Source signatures			
Wet season δ13C vs. Dry season δ13C	-0.45	96.93	0.66
Wet season δ15N vs. Dry season δ15N	1.99	89.3	**0.05**

Table A5.4.3 Results of Welch's two-sample t-tests determining differences in bird blood and claw δ^{13}C and δ^{15}N signatures between sites. P-values less than, or equal to, 0.05 are highlighted in bold.

	Comparison	*t*-test statistic	degrees of freedom	p-value
	Consumer tissues			
Tissue				
Blood	Cocoa creek δ13C vs. Healy creek δ13C	-1.35	224.97	0.18
	Cocoa creek δ15N vs. Healy creek δ15N	6.67	141.94	**<0.001**
Claw	Cocoa creek δ13C vs. Healy creek δ13C	0.59	231.55	0.56
	Cocoa creek δ15N vs. Healy creek δ15N	6.34	135.08	**<0.001**

Table A5.4.4 Results of Welch's two-sample t-tests determining differences in source δ^{13}C and δ^{15}N signatures between sites. P-values less than, or equal to, 0.05 are highlighted in bold.

Comparison	*t*-test statistic	degrees of freedom	p-value
Source signatures			

Cocoa creek δ13C vs. Healy creek δ13C	-0.74	74.92	0.46
Cocoa creek δ15N vs. Healy creek δ15N	6.49	54.57	**<0.001**

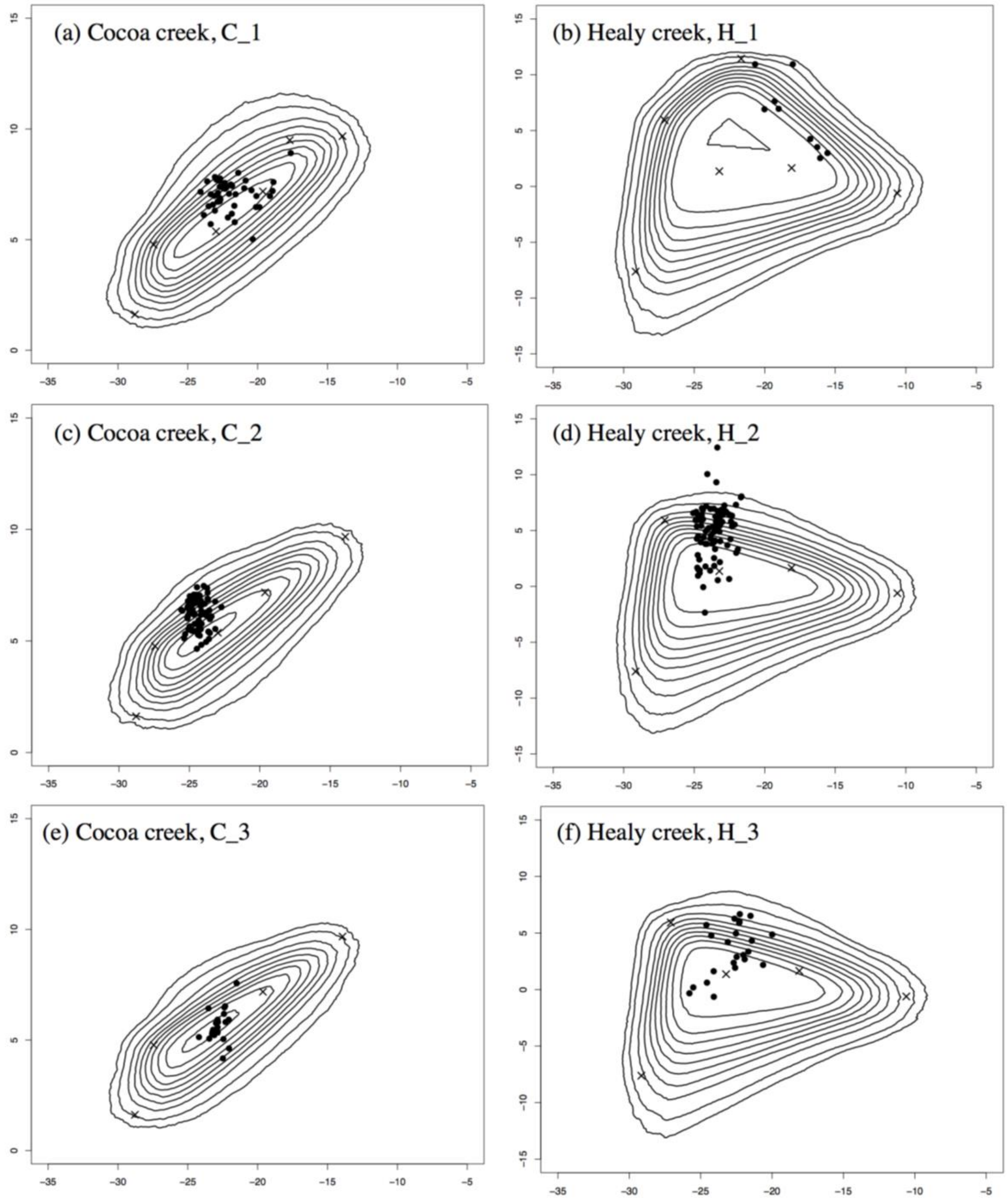

Figure A5.5 Simulated mixing regions for source-consumer biplots, categorized by isotope-based foraging group and sampling site. Sources are marked by an ‘x’ and consumers are displayed as black dots. The outer-most contour delineates where 5% of the simulated polygons have a solution (i.e. satisfy point-in-polygon) for each consumer (Smith et al. 2013). Consumers outside of the 95% mixing polygons were removed prior to mixing model analysis (i.e. three consumers in Healy creek isotope group 2 (H_2; d).

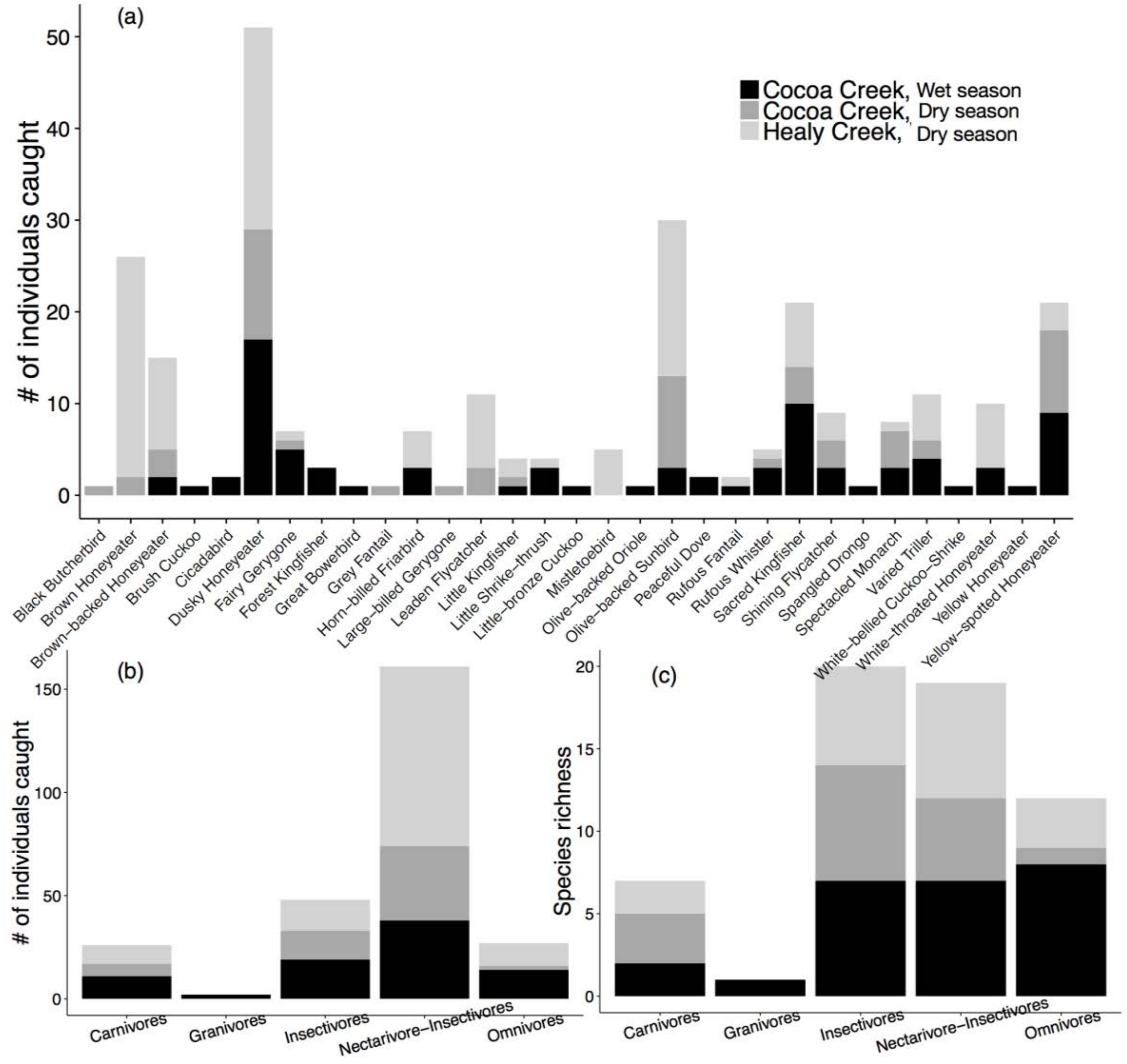

Figure A5.6 Plots showing (a) abundance of mangrove bird individuals caught by species, (b) abundance of mangrove bird individuals caught in each literature-based foraging group, and (c) richness of mangrove bird species caught in each literature-based foraging group. Species' allocation into literature-based foraging groups is shown in Table A5.2.

Table A5.7.1 Pairwise comparisons of standard Bayesian ellipse areas (SEA_B) in blood vs. claw tissues of mangrove bird isotope-based foraging groups at Cocoa creek and Healy creek. Probabilities that the SEA_B of foraging group claw tissue in rows are smaller than foraging group blood tissue in columns are provided. Highlighted in bold are probabilities that are greater than 0.85 or less than 0.15.

Site	Tissue	Pairwise comparisons			
			Blood		
		p(row<column)	H_1	H_2	H_3
Healy creek	Claws	H_1	0.81		
		H_2		**1.00**	
		H_3			0.55
		p(row<column)	C_1	C_2	C_3
Cocoa creek	Claws	C_1	**0.05**		
		C_2		**0.03**	
		C_3			**0.02**

Table A5.7.2 Pairwise comparisons of standard Bayesian ellipse areas (SEA_B) of mangrove bird isotope-based foraging groups at Cocoa creek and Healy creek in either blood or claw tissues. Probabilities that the SEA_B of foraging groups in rows are smaller than foraging groups in columns are provided. Highlighted in bold are probabilities that are greater than 0.85 or less than 0.15.

Site	Tissue	Pairwise comparisons			
		p(row<column)	H_1	H_2	H_3
Healy creek	Blood	H_1	-	**0.01**	**0.09**
		H_2		-	0.84
		H_3			-
	Claws	H_1	-	**0.07**	0.54
		H_2		-	**1.00**
		H_3			-
		p(row<column)	C_1	C_2	C_3
Cocoa creek	Blood	C_1	-	**0.00**	**0.00**
		C_2		-	**0.13**
		C_3			-
	Claws	C_1	-	**0.00**	**0.00**
		C_2		-	0.53
		C_3			-

Appendix 4: Supplementary material for ***Chapter 6***

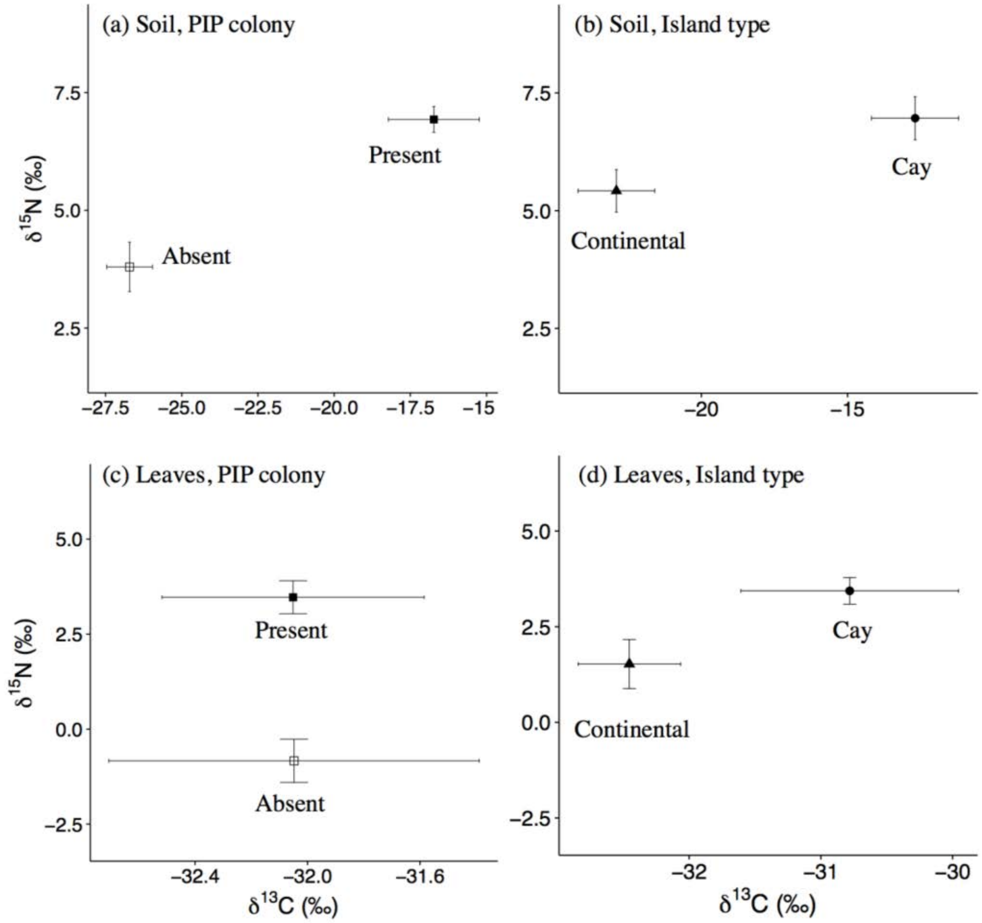

Figure A6.1 Carbon (δC^{13}) and nitrogen (δN^{15}) stable isotope biplots for soil (a & b) and leaves (c & d) from island forests grouped by PIP colony category: ‘Absent’ (open square) or ‘Present’ (closed square), and by island type: continental (triangle) or cay (circle). The data are presented as mean ± standard error.

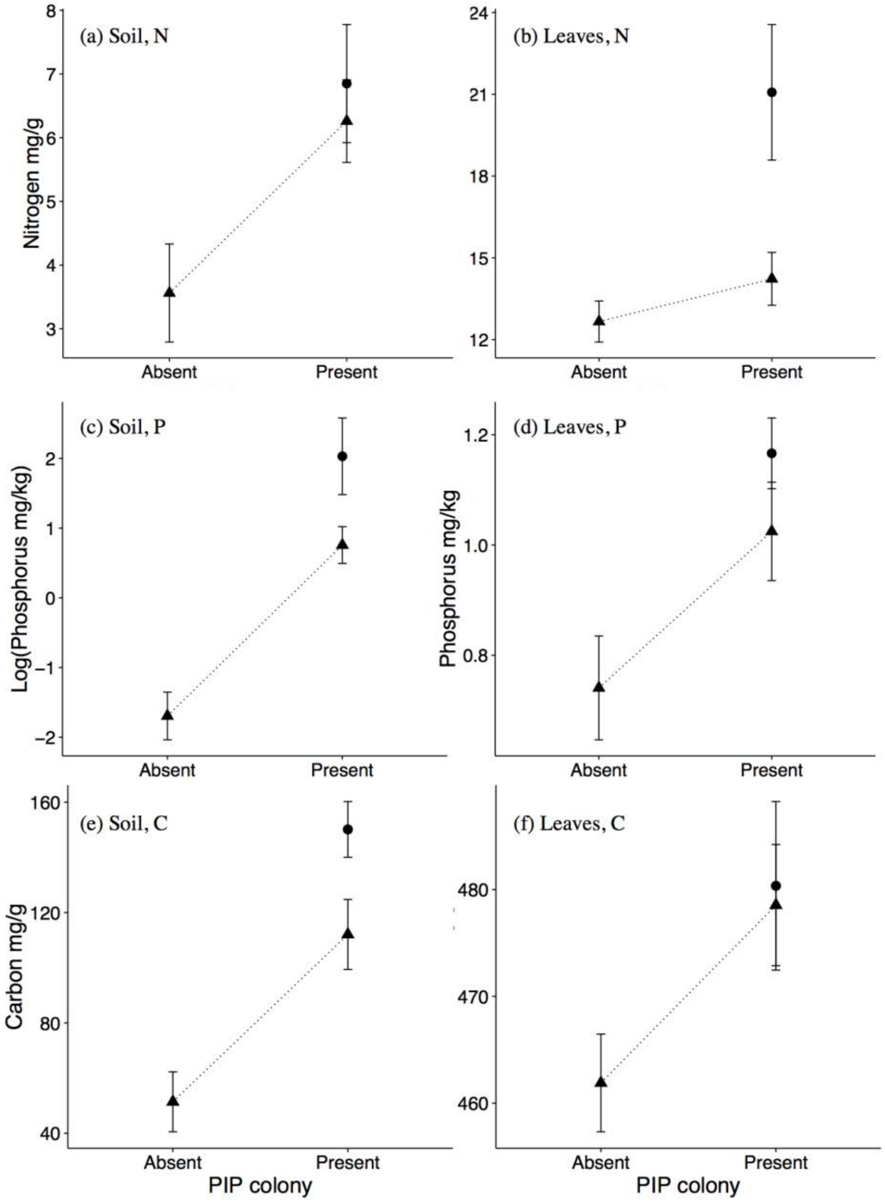

Figure A6.2 Total nitrogen (N mg/g), total phosphorus (P mg/kg), and total carbon (C mg/g) levels in soil and leaves sampled in island forests with PIP colonies either absent or present. Island forests with PIP colonies absent were all continental islands, while island forests with PIP colonies present were either continental (triangle) or cay islands (circle). The data are presented as mean ± standard error.

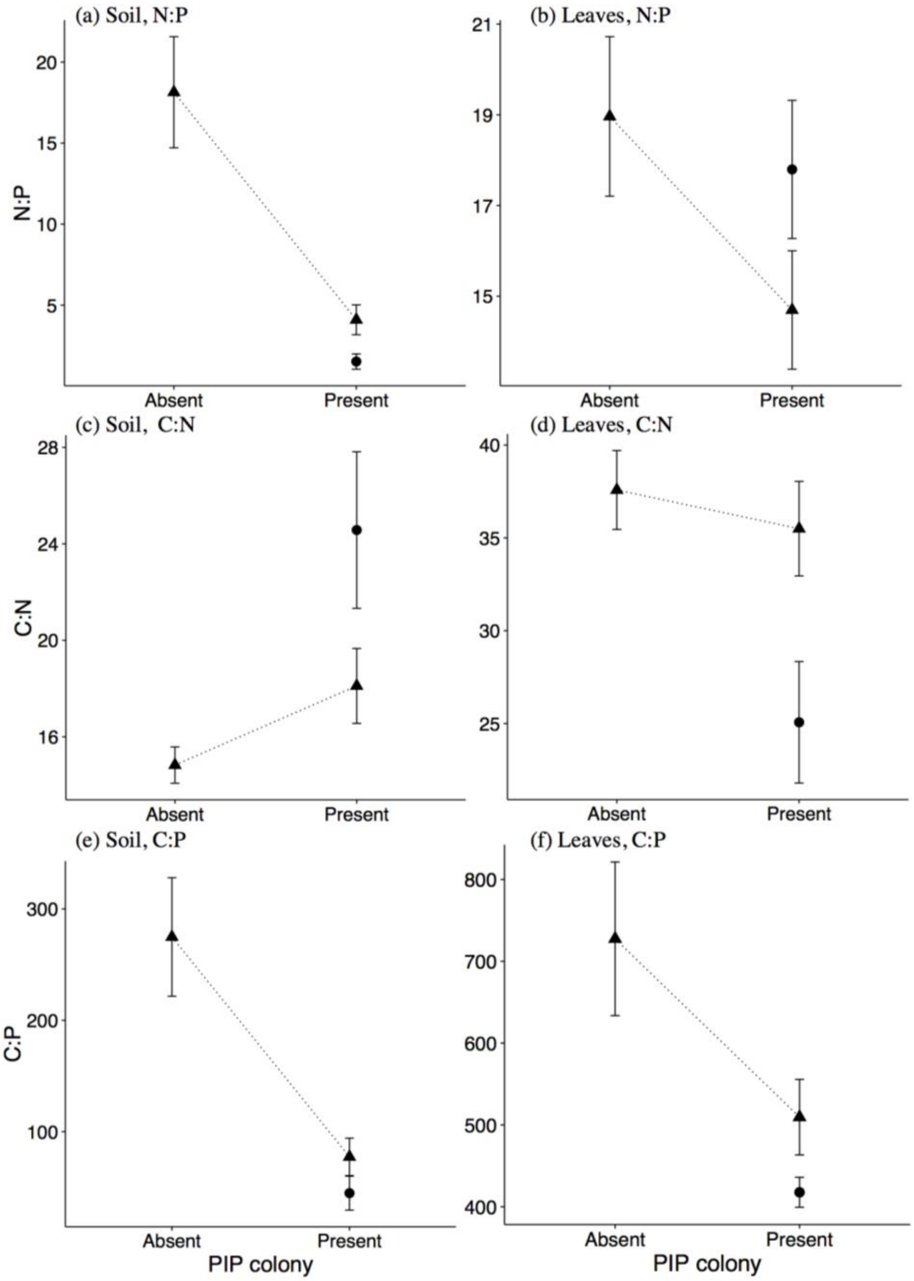

Figure A6.3 N:P, C:N, and C:P ratios in leaf and soil samples in island forests with PIP colonies either absent or present. Island forests with PIP colonies absent were all continental islands, while island forests with PIP colonies present were either continental (triangle) or cay islands (circle). The data are presented as mean ± standard error.