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Review

A birds-eye view of biological connectivity in mangrove systems

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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 behavior 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.

1. 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).

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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, 2009b; 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, 2009a). Temperature, atmospheric carbon-dioxide levels, salinity and sea-level rise affect photosynthetic and growth rates of mangrove forests (Krauss et al., 2008; Alongi, 2009a). 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 ecotonal gradients (Feller et al., 2002, 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 several 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.

1.1. 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, 2009b; 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., 2014b). 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, 2009b), 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. 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 (Fig. 1).

Depending upon the location, mangrove bird communities can be species-rich relative to their low floristic diversity (Table 1; Noske, 1996; Mohd-Azlan et al., 2012). However, despite their diversity and abundance, 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, suggesting the potential for substantial and widespread connectivity with other habitat types.

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-