More than marine: revealing the critical importance of mangrove ecosystems for terrestrial vertebrates

Stefanie M. Rog*, Rohan H. Clarke and Carly N. Cook

ABSTRACT

Aim Despite mangrove forests spanning marine, freshwater and terrestrial realms, their function as terrestrial ecosystems has been largely ignored. In the light of the rapid global decline of mangroves, it is critical to build a more holistic understanding to plan for effective management of the whole ecosystem. This study examines the importance of mangrove forests for terrestrial vertebrates.

Location Global mangrove forests.

Methods An extensive review of records of the use of global mangrove forests by the most poorly studied terrestrial vertebrate groups: mammals, reptiles and amphibians. We explored the species richness and distribution of these groups, along with their ecological characteristics. We also explored the relationship between animal and plant species richness across the distribution of mangrove forests.

Results Mangroves are used by a remarkable number of terrestrial mammal, reptile and amphibian species ($n = 464$); five times more than previously reported. The diversity of species uncovered by this study, almost half of which are of conservation concern, underscores the value of mangroves as terrestrial ecosystems. Most species were facultative users of mangroves; however, there are critical knowledge gaps in how these species interact with these ecosystems. We found a positive global correlation between animal and mangrove plant richness.

Main conclusions This study highlights that mangrove forests are considerably more important for terrestrial animals than generally acknowledged. We present the most comprehensive review of the importance of mangrove forests for terrestrial vertebrates, but also reveal significant knowledge gaps in the ecology of these ecosystems. Our study uncovers evidence that these habitats may be increasingly important as refuges for species from anthropocentric disturbance. Our findings emphasize the importance of moving beyond viewing mangroves as marine ecosystems, towards recognizing their cross-realm importance. Without such a shift, there will be significant limitations in our ability to manage and conserve these ecosystems.

Keywords biodiversity patterns, coastal forest, ecosystem function, lagoon, swamp, transboundary.

INTRODUCTION

Mangrove forests fringe intertidal zones spanning marine, freshwater and terrestrial realms in tropical, subtropical and temperate latitudes ($30^\circ$ N and $30^\circ$ S; Giri et al., 2011). They provide a wide range of ecosystem services, including coastal protection, carbon sequestration and opportunities for biodiversity (Macintosh & Ashton, 2002). These services are
being lost because of the decline in mangrove forests, with major ecological and economic implications for both the wildlife and people that depend on them (Alongi, 2002). Globally, 35% of the total area of extant mangroves forests was lost over a recent 30-year period (Giri et al., 2011) and currently, 40% of mangrove plant species are listed as Threatened on the International Union for Conservation of Nature (IUCN) Red List (Polidoro et al., 2010). A little known fact is that mangrove forests are declining faster than inland tropical forests and coral reefs, which are a strong focus for conservation (Duke et al., 2007). Despite the value of mangrove forests, aspects of their terrestrial ecology are poorly understood, limiting the capacity to effectively conserve and manage them (Nowak, 2013).

Mangrove forests occur at the interface between land and sea, and as a consequence, these forests span both aquatic and terrestrial realms, playing fundamental roles in both (Beger et al., 2010). Nevertheless, well-justified concerns about the decline in mangrove systems have focused on their value as marine environments, largely ignoring their value as terrestrial ecosystems (e.g. the provision of forest products for human benefit (Buelow & Sheaves, 2014) and habitat for terrestrial fauna (Meades et al., 2002)). As mangrove ecosystems are traditionally conceptualized as marine environments (e.g. providing nursery areas for important commercial fisheries (Mumby et al., 2004)), there is a strong bias towards research on their marine fauna, including polychaetes (Metcalfe & Glasby, 2008), molluscs (Appadoo & Roomaladowo, 2013), shrimp (Primavera, 1998), crabs (Schories et al., 2003) and fish (Faunce & Serafy, 2006). This emphasis on mangroves as marine ecosystems may explain why their value as terrestrial habitat for vertebrates remains one of the most poorly studied aspects of this ecosystem (Luther & Greenberg, 2009; Nowak, 2013).

Previous research on terrestrial vertebrates in mangroves has largely focused on birds or charismatic fauna, such as the Sumatran tiger, Panthera tigris sumatra, (Noske, 1996; Barlow et al., 2011). The assemblage of smaller mammals, reptiles and amphibians that occupy mangrove forests has, by contrast, received little attention (but see Nagelkerken et al., 2008; Luther & Greenberg, 2009; Hogarth, 2015). The literature also over-represents species that depend on mangrove forests for all their critical resources (i.e. obligate mangrove users), resulting in a narrow focus that excludes many facultative mangrove users (Hansson & Akesson, 2014). Yet, facultative users continue to provide important ecosystem services, such as pollination of mangrove plants (McKenzie & Rolfe, 1986) and the transfer of nutrients from adjacent habitats (Reef et al., 2014). In addition, the loss of primary habitats for these facultative users may mean mangrove forests are increasingly important habitat for these species in the future (Nowak, 2013; Rodrigues & Martinez, 2014). To better understand the functioning of mangrove ecosystems, it is important to understand their relationship with the fauna that uses them (both obligate and facultative users) in both the marine and terrestrial realms.

Here, we review existing knowledge of the terrestrial vertebrates known to use mangroves and document the global distribution of species richness that can serve as a baseline for future studies. We explore what is known about the ecological relationships between terrestrial vertebrates and mangrove forests, identify critical knowledge gaps and provide recommendations for improved conservation management of these vital ecosystems.

METHODS

Scope of the review

We sought records of terrestrial mammals, reptiles and amphibians that use the terrestrial component of mangrove ecosystems. We defined the terrestrial component of mangroves as those areas exposed to air at some time during the tidal cycle (e.g. branches, roots, adjacent mud flats). Semi-aquatic snakes, water rats and frogs were included as they routinely occupy terrestrial habitats (Fish & Baudinette, 1999; Gibbons, 2003; Willson et al., 2006), whereas sea turtles were excluded as they exclusively use the aquatic aspects of mangrove systems (Lutz et al., 2002). While birds are important inhabitants of mangroves, they were excluded from this study because they have previously received significant attention (e.g. Cawell, 1964; Buelow & Sheaves, 2014; Kumar & Kumara, 2014). To ensure that as many records of terrestrial vertebrates in mangroves were captured, we include species with only a single record in mangroves. It is possible that some vagrant species are included in the species list, so we have indicated how many times the species was recorded (see Table S1 in Supporting information). Both obligate and facultative users of mangrove forests were included to identify the full range of species that exploit their resources and potentially play a role in ecosystem function. We defined use of mangroves as when a species was reported to use any key resource provided by the mangrove forest (e.g. food, shelter, dispersal route – see ‘Characteristics of species reported in mangrove forests’ below for more detail).

Search strategy and inclusion criteria

We conducted a comprehensive online search of the literature published up to the end of June 2016. The publication databases Web of Science, Trove Thesis Search and Google Scholar were searched using the following terms: (fauna AND diversity AND mangrove*); (mangrove* AND mammal*; mangrove* AND biodiversity); (mangrove AND reptile; mangrove AND amphibian); (mangrove AND monitoring OR techniques AND fauna OR reptile OR mammal OR amphibian); (mangrove AND survey AND fauna OR reptile OR mammal OR amphibian OR vertebrate); (mangrove AND terrestrial AND vertebrates OR fauna OR mammal OR reptile OR amphibian). We also searched synonyms for mangrove habitat (coastal forests, swamp and coastal lagoon) together with the above search terms. The reference list of each
relevant publication was scrutinized to identify further relevant literature. All mammal, reptile and amphibian taxa reported as occurring in mangroves were documented. Taxonomy followed the IUCN Red List (IUCN, 2016).

Species records were also obtained from PhD theses and three open source databases: World Wildlife Fund (WWF, 2016), ARKive (ARKive, 2016) and IUCN Red List (IUCN, 2016). These databases were included because they focus on global species records, allow for restriction of searches to mangrove habitat and have provision for peer-review by experts. Records from guidebooks, local management plans and additional online sources were excluded because it was not possible to determine the accuracy and consistency of the records in those sources.

Characteristics of species reported in mangrove forests

All literature studies that met the above criteria were read in full, and records of terrestrial vertebrate species in mangroves were collated. For each species record, we noted the following: (1) countries in which the species was reported to use mangroves; (2) the total native range; (3) IUCN conservation status (including ‘not evaluated’); and (4) feeding guild (i.e. carnivore (including insectivore and piscivore), herbivore, omnivore). If these characteristics were not mentioned, we undertook targeted literature searches to ensure the dataset was comprehensive (e.g. consulting the IUCN Red List database for the total native range (when a species was not evaluated by IUCN, we used Arkive and/or guidebooks to determine its range) and conservation status and Arkive for feeding guild).

A species’ dependence on mangrove forests was classified as obligate, facultative or not reported based on information in the studies. Obligate users included those species described as found primarily in mangroves or with a life history tied to mangrove habitat, whereas facultative users were those species that occupied both mangrove and adjacent terrestrial habitats. Facultative users were further categorized by their resource use: (1) feeding; (2) breeding; (3) dispersal route between primary habitats; (4) shelter from biotic (e.g. predators, competitors) and abiotic stressors (e.g. temperature extremes; desiccation); (5) use and increased frequency of use as refugia from human disturbance; and vi) novel use of mangroves as a result of human disturbance.

Species distribution and richness

In many instances, species records were specifically focused on a subset of countries from within the species’ broader native range (e.g. snakes in a mangrove patch in Singapore; Voris (2002)). To estimate the global species richness of terrestrial vertebrates, if a species was reported to use mangroves in part of its range, we inferred that it may do so wherever its distribution overlapped with mangrove forest. For example, the Mexican Mouse Possum, *Marmosa mexicana*, occupies mangrove forest in Mexico (WWF, 2016), thus, based on the intersection of the species’ range and extant mangrove forest, we inferred that it also uses mangroves in Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua and Panama. With this approach, the alpha diversity of terrestrial vertebrate species that occupy mangroves was calculated for each country. As Brazil and Australia span >20 degrees of latitude and are substantially larger than other countries that support mangrove habitat, outputs are presented at the state level for these two countries. Species ranges followed Hutchings & Recher (1981); Uetz (1995) and Wilson & Reeder (2005). Mangrove richness followed Spalding et al. (2010), and mangrove distribution followed Giri et al. (2011). Pearson’s correlation coefficient was calculated to determine whether there was a relationship between global mangrove plant and terrestrial animal richness. In an attempt to explain biogeographic patterns of species richness, we also calculated the correlation coefficient for regional groupings of countries (Africa, Asia, Americas, Middle East and Oceania). While the world can be divided into regions in many different ways, we followed the United Nations (2014) macro-geographical global regions as it is a commonly used source.

RESULTS

We identified 464 terrestrial vertebrate species reported to occur in mangrove forests: 320 mammals, 118 reptiles and 26 amphibians (including 22 subspecies; Table S1). This is a fivefold increase in the number of terrestrial vertebrate species previously reported to use mangroves (excluding birds), including representatives of 14 additional families to those in previous reviews (Kathiresan & Bingham, 2001; Nagelkerken et al., 2008; Luther & Greenberg, 2009; Hogarth, 2015). Of the species reported, 34 were reported fewer than five times or were stated to be rare in mangroves. Of the 391 vertebrate species whose conservation status has been assessed by the IUCN, 35% were classified as threatened. Fewer than 41% of the published species records we found (\( n = 186 \) of 464) were derived from or could be directly linked to published field studies. As such, reports, many of which were reviews, of the overwhelming majority of species occurring in mangroves did not reference the field study or observation on which this species being present in mangrove habitat was based. Therefore, the origin of these records is uncertain and separate records may not be independent, suggesting more field studies on terrestrial vertebrates in mangroves are important to improve our understanding of these ecosystems.

Species distribution and alpha diversity

Mammals, reptiles and amphibians were reported to occur in mangroves in 73 of the 120 countries (60%) in which mangroves occur (Figure 1b,d), more than doubling previous...
estimates (Figure 1a). When accounting for the potential global distribution of these terrestrial vertebrates in mangrove habitat, this estimate increases to 113 of 120 countries (93%) (Figure 1c), more than trebling previous reports (Figure 1a). Our findings suggest that the highest alpha diversity of terrestrial vertebrates in mangroves occurs...
within Asia, northern Australia, West Africa and the Central American land bridge (Figure 1). In contrast, alpha diversity is lowest on the east coast of Africa, southern Australia, New Zealand, the Middle East, Brazil and small island nations (Figure 1). There were 24 countries that support extant mangroves where terrestrial vertebrates have yet to be documented as using this ecosystem as habitat; of these, 20 were island nations with a total land area of less than 2535 km² (Figure 1b indicated in black).

**Relationship between mangrove plant and terrestrial vertebrate alpha diversity**

Globally, there was a positive correlation between terrestrial vertebrate alpha diversity and mangrove plant richness for both the recorded and the potential distributions (Table 1; reported: \( r = 0.55, n = 120, P < 0.001 \); extrapolated: \( r = 0.58, n = 120, P \leq 0.001 \)). When separating the world into macrogeographical regions, the strength of the relationship varied, with the strongest correlations in Asia and Oceania for both the reported data (Asia: \( r = 0.72, P = 0.001, n = 17 \); Oceania: \( r = 0.58, P = 0.005, n = 22 \) ) and extrapolated data (Asia: \( r = 0.78, P \leq 0.001, n = 17 \); Oceania: \( r = 0.81, P \leq 0.001, n = 22 \) ). For the Americas, the correlation between mangrove plant and animal richness was significant only when using the extrapolated data (\( r = 0.47, P = 0.002, n = 42 \)). No relationship was found in Africa (reported: \( r = 0.12, P = 0.556, n = 27 \); extrapolated data \( r = 0.13, P = 0.528, n = 27 \) ) and the Middle East (reported \( r = -0.24, P = 0.941, n = 12 \); extrapolated data \( r = -0.04, P = 0.902, n = 12 \) ).

**Use of mangrove forests by terrestrial vertebrates**

For the 464 terrestrial vertebrate species reported in mangroves, 147 (31%) had information about the specific resources they were using. Species were most often reported to use mangrove forests as foraging grounds (Figure 2). Terrestrial vertebrates were also reported to use mangrove forests as refuges from human disturbance, shelter from stressors (both biotic and abiotic), to disperse between primary habitats and for breeding (Figure 2). If species were reported to use mangrove forests as refuges, most (19) were considered to be increasing their existing use of mangroves rather than using mangrove forests as a novel habitat (1).

![Figure 2](image_url)  
**Figure 2** Mangrove use by facultative terrestrial vertebrates (\( n = 147 \)). Reported uses are not mutually exclusive. Obligate users (\( n = 24 \)) are not shown in this figure as by definition, these species use mangroves for all their resources.

**DISCUSSION**

**Species distribution and richness**

We found mangrove forests to be substantially more important for terrestrial vertebrates than previously reported, supporting a remarkable richness of terrestrial mammals, reptiles and amphibians globally. This finding underscores the view that the emphasis on mangroves as marine ecosystems has led to the importance of the terrestrial components of mangrove forests being undervalued (Luther & Greenberg, 2009; Nowak, 2013).

In addition to extending our knowledge of the global richness of terrestrial vertebrates in mangrove ecosystems, our

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remained unchanged with the extrapolation suggests that any relationship between floral and faunal richness improved or human disturbance or other pressures. The fact that the cor-
distribution, in marginal habitat or areas experiencing this may overestimate species occurrences. In particular, spe-
found in mangroves across their entire range (Figure 1c),
A species intersects with the global distribution of mangroves; the extrapolated data assume that species
were derived from previous reviews, this review or the maxi-
mangrove regions was consistent regardless of whether data
subsequently discussed these regions), possibly because of political unrest (Reddy & Dávalos, 2003), as opposed to a genuinely lower results also reveal a wider range of countries in which these species use mangroves than previously reported (Figure 1b, c). There were few places in the world where terrestrial vertebrates have not been reported to use mangrove forests, mainly small islands (Figure 1b). The biogeographic patterns indicate a higher richness of species in the tropics (especially in Asia) and lower richness in temperate regions, which is one of the most well-established patterns in macroecology and biogeography (Koch, 2000). Mammals and amphibians conform to the pattern of highest diversity in the tropics (Wiens et al., 2006; Schreier et al., 2009), and our findings demonstrate this pattern extends to mangrove forests. We can think of no reason why the key processes that drive biogeographic patterns (speciation, extinction and dispersal (Wiens et al., 2009)) should differ in mangrove ecosystems, but this could be a focus of further study.

The observed pattern of high animal richness in tropical mangrove regions was consistent regardless of whether data were derived from previous reviews, this review or the maximum possible richness of terrestrial vertebrates based on our extrapolation (the countries where the known distribution of a species intersects with the global distribution of mangroves; Figure 1). Because the extrapolated data assume that species found in mangroves in one part of their range could also be found in mangroves across their entire range (Figure 1c), this may overestimate species occurrences. In particular, species may not occupy habitat at the edges of their predicted distribution, in marginal habitat or areas experiencing human disturbance or other pressures. The fact that the correlation between floral and faunal richness improved or remained unchanged with the extrapolation suggests that any overestimation of richness is unlikely to be significant. Nevertheless, the extrapolated data provide a worst case scenario about the knowledge gaps associated with the species richness and distribution of terrestrial vertebrates in mangrove forests that can help target future research towards areas of potentially high richness but few records. To be able to make more detailed predictions and identify important mangrove areas for terrestrial vertebrates, it is necessary that future studies report characteristics (e.g. total mangrove area, source of disturbance, adjacent habitat) about the mangrove region where a species was observed.

**Relationship between mangrove plant and terrestrial vertebrate alpha diversity**

Mangrove plant richness was not always a consistent predictor of animal richness, although correlations suggest that this relationship is stronger when the data were extrapolated to the possible extent of recorded species (Figure 1c,d, Table 1). Further fieldwork may reveal a higher richness of terrestrial vertebrates in mangrove forests in areas where there is a mismatch between floral and faunal diversity. Mangrove plant diversity is an order of magnitude higher in the Indo-West Pacific (IWP) than it is in the Atlantic, Caribbean and Eastern Pacific (ACEP) (Ellison et al., 1999), and plant richness may directly influence richness of other taxa by determining the variety of food items or habitat structural elements that create niches for other organisms (Hawkins & Porter, 2003). A global concordance of plant and animal richness has been shown for our three species groups (Qian & Ricklefs, 2008). However, we found some areas of low mangrove plant richness, such as Mexico and parts of South America, where vertebrate richness was high and similar to that of parts of Asia where mangrove plant richness is far higher (Figures 1b,c,d).

This suggests that factors other than low mangrove plant richness, such as the influence of adjacent habitat (e.g. deserts have lower animal diversity than tropical rain forests and could affect the number of facultative species using mangroves) or the availability of prey species to support carnivores and omnivores, may also strongly influence animal richness in some key mangrove ecosystems. The large proportion of species that rely on animal protein instead of mangrove plant material (Figure 3) provides some support for the latter hypothesis, but a deeper understanding of the community ecology of these ecosystems is needed. Temperate regions in Oceania (e.g. New Zealand and southern Australia) showed both low floral and faunal richness in line with global biogeographic patterns (Wiens et al., 2009). However, we note that there has been limited survey effort in temperate areas of these regions where diversity would be expected to be lower. The weak correlations between animal and mangrove plant richness in Africa and the Middle East may be a product of these regions having received little study (fewer than 10% of the studies we found specifically discussed these regions), possibly because of political unrest (Reddy & Dávalos, 2003), as opposed to a genuinely lower

![Feeding guild of terrestrial vertebrates in mangroves, including both facultative and obligate mangrove users (mammals, n = 320; reptiles, n = 118; amphibians, n = 26). Insectivores and piscivores are included in the carnivore guild.](image-url)
animal richness. The discrepancy between predicted and observed richness was highest in East Africa, a biodiversity hotspot (Myers et al., 2000) and with similar mangrove richness to that of West Africa where a higher animal richness was observed. One reason for lower than predicted animal richness in Africa may be the prevalence of threats, such as hunting pressure for the bushmeat trade, which can be high in East Africa (Cawthorn & Hoffman, 2015), depleting local populations to levels that make detection of some species less likely, especially when combined with lower survey effort in the region. The variability or lack of research effort across regions, lack of insight into regional differences and a somewhat inconsistent relationship between mangrove plant richness and animal richness suggests that additional field studies are needed to achieve a more complete understanding of the occurrence of terrestrial vertebrates in mangroves.

Although we present the most comprehensive review of terrestrial vertebrates in mangroves, and have identified significantly more terrestrial vertebrate species using mangrove forests than previously reported, our findings probably still underestimate species richness. There was limited direct evidence of species occurrence from published field studies, and most of the records we found did not report the origin of the record, suggesting many come from unpublished data. The small number of field studies carried out in mangroves could be due to the combination of challenges associated with accessing these environments and the difficulty of sampling tidal environments due to regular inundation. New approaches may be needed to facilitate faunal surveys in mangroves. Our results provide a valuable starting point from which to target survey effort. Similarly, our findings highlight the importance of clearly reporting the source of species records to help identify where research effort is genuinely low.

**Use of mangrove forests by terrestrial vertebrates**

Understanding habitat use might help explain why biogeographic patterns differ from predictions associated with floral richness. Our results highlight that facultative users of mangroves substantially outnumber specialists, as is predicted by theory (Wilson & Yoshimura, 1994). This suggests that the tendency of previous studies to focus on obligate users of mangrove forests (Nagelkerken et al., 2008; Luther & Greenberg, 2009) has distorted our understanding of the faunal species types that use mangroves and contributed to the perception that vertebrate species richness is low in these environments. A striking finding from our study is how little is known about the interaction between terrestrial vertebrate species and mangroves. For example, the relationships between seasonality and timing in mangrove use are rarely studied. We only found 10 records in which seasonality or tidal phase was reported, including lemurs feeding on mangrove flowers in the dry season (Gardner, 2016) and varanids feeding in mangroves during low tide (Kutt, 1997). Understanding the resources consumed by facultative users of mangrove forests, and when these resources are available, is a particularly important area for future study because habitat destruction and environmental change is likely to lead to changes in resource availability (Nowak, 2013).

Our results support the suggestion that at least some terrestrial vertebrates are using mangrove forests as a refuge from anthropocentric disturbance of their primary habitat (Nowak, 2013; Figure 2). Although the number of species reported to be using mangrove forests as refuges is low, this has been reported for many different species groups (e.g. felids, Barlow et al., 2011; Nowak, 2013; snakes, Nagelkerken et al., 2008; monkeys, Nowak, 2013) in much of the world (e.g. Asia, Nowak, 2013; Africa, Nagelkerken et al., 2008; South America, Rodrigues & Martinez, 2014), suggesting it is a relatively widespread and possibly underestimated phenomenon. Much of the evidence for the increasing use of mangroves is anecdotal, with just a few examples in which empirical data document a novel expansion into mangrove forests (e.g. Wied’s marmosets, Callithrix kuhlii (Rodrigues & Martinez, 2014)). Some new records may also reflect a lack of historical data rather than evidence of a genuine expansion. It is also unclear whether mangrove forests are acting as population sinks or constitute important habitat for self-sustaining populations. Understanding this relationship may help predict the likely future impact of increased use by current mangrove inhabitants.

Knowledge gaps on vertebrate use of mangroves are particularly concerning for the many species that are of conservation significance. Given the high probability that species classified as ‘Data Deficient’ or ‘Not Assessed’ by the IUCN Red List are actually of conservation concern (Bland et al., 2014; 72 species in this review), there is a pressing need to better understand the importance of mangroves as a resource for endangered species. Better information about the dependence of terrestrial vertebrates on mangrove forests could help identify the regions of the world in which mangrove conservation should be given highest priority.

The high proportion of carnivorous and omnivorous vertebrates in mangrove forests (Figure 3) is likely to be due to the marked seasonality of other food sources, such as fruit and nectar (Fernandes, 1999), and the low palatability of mangrove leaves given their high salt content (Kathiresan & Bingham, 2001). This finding also accords with the general prevalence of carnivores among reptiles and amphibians (Huey, 1982). Given that animal protein appears to be the most important source of nutrition for terrestrial vertebrates in mangrove forests, this may account for some of the variability we found in the relationship between mangrove plant and animal richness (see Species distribution and richness).

While vertebrate species were most often reported to use mangrove forests for feeding (Figure 2), for the majority of species there was no information about how they use mangroves. We found few primary records of field studies that documented habitat use by terrestrial vertebrates in mangroves. Given that most animals spend the majority of their time feeding, it is not surprising that opportunistic reports...
of species in mangroves often report individuals to be using mangroves as feeding grounds. However, we did find evidence that facultative users of mangroves rely on these areas for critical stages in their life cycles as well, using these areas to breed (e.g. the Estuarine Crocodile, Crocodylus porosus, Hutchings & Recher, 1981; and the Sea Krait, Laticauda colubrina, Hogarth, 2015). There were also records of species using mangroves to shelter from heat stress (e.g. bat species and kangaroos in Australia; Reef et al., 2014) and to disperse between primary habitats (e.g. the marsh rabbit, Sylvilagus palustris, in the United States; Kathiresan & Bingham, 2001) (Figure 2). A better understanding of the dependence of both obligate and facultative users on mangrove ecosystems will enable the implications of anthropogenic disturbances on ecosystem function of these forests to be better understood.

Importance of terrestrial vertebrates for mangrove ecosystems

The roles of terrestrial vertebrates in the health of mangrove ecosystem have been poorly studied, leaving another substantial gap in our understanding of mangrove ecosystem functioning. Terrestrial vertebrates can play an important role in mangrove forests through the provision of essential ecosystem services, such as pollination of mangroves (Ashraf & Habjoka, 2013) and nutrient transfer (e.g. Kristensen, 2008; Reef et al., 2014). The ecosystem services provided by terrestrial vertebrate fauna associated with the health of mangrove forests should therefore be explored as an important precursor to more effective conservation of these ecosystems.

CONCLUSIONS AND RECOMMENDATIONS

Our data demonstrate that mangrove forests support a considerably higher diversity of terrestrial animals than previously recognized. In spite of this, the terrestrial components of mangroves are generally ignored, overlooking a large part of this transboundary ecosystem. Our findings highlight a wide range of knowledge gaps in relation to the diversity, distribution and ecology of species using the terrestrial components of these systems. Future research should focus on undertaking field assessments of terrestrial vertebrates, particularly in regions where our findings suggest animal richness is low relative to floral richness (e.g. small islands and East Africa). Greater attention to reporting the source of species records could help identify where research effort should be directed. There is also an urgent need to understand better the ecological relationships between mangroves and terrestrial vertebrates to plan for effective conservation of these forests. In particular, it is important to understand better the role mangrove forests are playing in providing a refuge for species suffering from the loss of their primary habitat. This knowledge will help identify regions where patterns of habitat loss and human disturbance may elevate remaining mangrove forests to an indispensable status, while also identifying areas where current users of mangroves may find resources under increasing pressure. In summary, we recommend a more holistic view of mangrove forests, as only when this is realized will it be possible to effectively conserve these vital ecosystems.

ACKNOWLEDGEMENTS

We thank Julie Groce and Guillaume Latombe for helpful comments on previous versions of the manuscript and Rebecca Valkan for her assistance with the global maps.

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Diversity and Distributions, 23, 221–230, © 2016 John Wiley & Sons Ltd


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

Table S1 Terrestrial vertebrates reported to occur in mangroves (mammals, reptiles and amphibians).

Data S1 Supplementary references with Table S1.

**BIOSKETCHES**

**Stefanie M. Rog** is a conservation biologist with interests in management, monitoring, ecology and terrestrial biodiversity.

**Rohan Clarke** is an ecologist with interests in marine and terrestrial vertebrates and their conservation management.

**Carly N. Cook** is a conservation biologist interested in evidence-based conservation and the development of decision tools that integrate the best available science into conservation management.

Editor: Robert Cowie