

Mammalian herbivores in Australia transport nutrients from terrestrial to marine ecosystems via mangroves

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Abstract: Nutrient subsidies from one ecosystem to another serve a critical link among ecosystems. The transfer of materials across the terrestrial-to-marine boundary is considered to be driven by hydrological connectivity, but animal movement can provide another pathway for nutrient transfers. In two separate studies we assessed the role mammals (bats and kangaroos) play in alleviating nutrient limitation in mangrove forests in Australia. At Lizard Island, we measured tree growth and foliar elemental and isotopic composition of trees growing within and outside a large flying fox roost. In Western Australia, we measured foliar elemental and isotopic composition of trees within two forests frequented by kangaroos that feed in spinifex grasslands and shelter in the shade of the mangroves. We compared those with mangroves from adjacent forests that are not frequented by kangaroos. We show that at both locations, the mangrove forest receives terrestrial nutrient subsidies through animal movement. At Lizard Island dominant mangrove species were significantly enriched in nitrogen within the bat roost, as evidenced by higher foliar N concentrations (by up to 150%), N:P and N:C ratios in trees within the roost compared with trees outside the roost. The isotopic signature of foliar N was significantly enriched in ^{15}N by 1–3‰ within the roost, further suggesting that the source of the N enrichment was the bat roost. Growth rates of mangroves within the roost were nearly six times higher than trees outside the roost. In the arid coast of Western Australia, we show elevated foliar ^{15}N abundance of up to 3‰ in mangroves where kangaroos shelter relative to trees where they do not. Thus, this study presents two examples for mammalian herbivore mediated localized transport of nutrients from terrestrial to marine ecosystems, consequently affecting mangrove tree growth, productivity and forest structure.

Key Words: elemental composition, flying fox, kangaroos, *Macropus* spp, nutrient subsidy, *Pteropus* sp, roost, stable isotopes, tree growth, vector

INTRODUCTION

Local ecosystems are rarely isolated from neighbouring ecosystems and subsidies from one ecosystem to another are important in supporting biodiversity and productivity in the receiving ecosystem (Meyer & Schultz 1985, Polis *et al.* 1997). Theoretical works (Gravel *et al.* 2010, Loreau & Holt 2004) indicate that transfers can provide important subsidies for organisms in the receiving ecosystem that may enhance primary and secondary production.

The movement of fauna can provide an important avenue for movement of materials across habitat boundaries (Polis *et al.* 1997), including the marine

terrestrial boundary (Anderson & Polis 1998, Gende *et al.* 2002, Polis & Hurd 1996, Rose & Polis 1998). There are many examples for biotic vectors moving material from the marine to the terrestrial habitat, for example anadromous fish that breed and die in freshwater streams (Cederholm *et al.* 1999, Hocking & Reynolds 2011, Naiman *et al.* 2002) and insects that feed on marine food sources and in turn are eaten by terrestrial spiders (Polis & Hurd 1996). However, very few studies have shown fauna-driven transfer of material from land to sea.

Transfer of material from terrestrial to marine habitats is strongly influenced by physical/hydrological connectivity, e.g. riverine outflows, which enhance primary and secondary production in marine ecosystems (Baisre & Arboleya 2006, Dunton *et al.* 2006, Loneragan & Bunn 1999, Lovelock *et al.* 2007, Paerl 1997, Smith *et al.* 1999). Here we investigate whether mammalian

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herbivores can play a role as significant biotic vectors for transferring terrestrial material into a marine environment.

In the tropics and subtropics mangrove trees form forests in the intertidal zone. These forests are accessible to both marine and terrestrial fauna. Although much of the fauna does not directly feed on the trees (but see Feller 1995, Reef *et al.* 2012, Robertson & Duke 1987), the trees provide habitat for a range of invertebrates, algae and microphytobenthos, which support consumers. The role of mangroves in supporting fish and crustaceans is well established (Faunce & Serafy 2006, Fry & Ewel 2003, Mumby *et al.* 2004). They also provide key roosting habitats for birds (Nagelkerken *et al.* 2008) and flying fox species (Pierson & Rainey 1990) and provide shade and shelter for other terrestrial mammal species (Hutchings & Recher 1983, Odum *et al.* 1982).

Mangrove forests are often nutrient-limited, with trees showing enhanced growth when nutrient availability is experimentally increased (Feller *et al.* 2009, Lovelock *et al.* 2004, Naidoo 2009). Increasing nutrient availability has profound effects on mangrove forest structure, which include altered species composition and significant changes in wood production, tree size and basal area (Chen & Twilley 1999). Such changes to forest structure have significant effects on the biodiversity supported by the forest and the flow of nutrients between the mangrove and the surrounding ecosystems (Ewel *et al.* 1998, Field *et al.* 1998). Increases in soil fertility can also result in increases in the abundance of herbivores (Feller & Chamberlain 2007, Onuf *et al.* 1977), as well as increase the capacity of the soil surface to keep up with sea-level rise (McKee *et al.* 2007).

Because of the importance of nutrients to a range of ecological processes, we investigated whether two common Australian mammals, fruit bats and kangaroos, can transfer terrestrially derived nutrients into the marine environment to the extent that they influence the growth and nutrient relations of mangroves.

METHODS

Study sites

We tested the effects of terrestrial mammals on nutrient availability and mangrove productivity in two separate studies. In one, we assessed the influence of the flying fox *Pteropus alecto* on the nutrition of mangroves at Watson's Bay on Lizard Island in the Northern GBR (Figure 1). In the second, we assessed the influence of kangaroos on the nutrition of mangroves at Mangrove Bay in Western Australia (Figure 1). The sites were chosen based on their location within oligotrophic marine environments

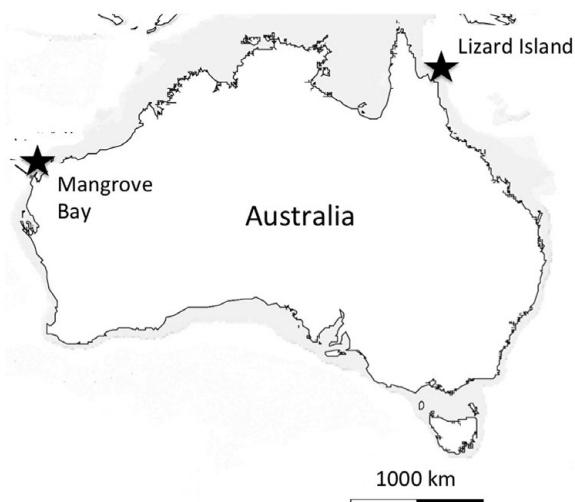


Figure 1. A map of Australia showing the two study sites (marked by stars). Lizard Island in the northern Great Barrier Reef lagoon, and Mangrove Bay, located on the upper west coast of North West Cape, Western Australia.

lacking riverine inputs and their large distance from anthropogenic nutrient sources, making the mammalian nutrient subsidy easier to quantify.

The influence of bats on mangrove nutrition and growth

We assessed the influence of a roosting colony of the black flying fox *Pteropus alecto* Temminck 1837 (Figure 2a) on the nutrition of mangroves at Watson's Bay on Lizard Island (14°40'00''S, 145°27'07''E, Figure 1) in the Northern Great Barrier Reef Lagoon. Mangrove area on the island is approximately 13 ha that fringes a tidal creek on the seaward edge and freshwater stream on the landward edge (Proske & Haberle 2012). The forest is dominated by *Rhizophora stylosa* Griff. but 11 other mangrove species are also present (R. Reef, pers. obs.). A colony of up to several thousand individuals (colony size varies seasonally) of *P. alecto* roost in trees at the landward edge of the forest in the canopy of tall (3–8 m) *R. stylosa*, *Ceriops tagal* (Perr.) C. B. Robinson and *Lumnitzera rosea* Gaud., making trips to the nearby mainland to forage for fruit and nectar. The bats defecate in their roosts and therefore may provide nutrients derived from the mainland to the mangrove. Lizard Island is a continental island 35 km from the coast whose underlying geology is granite, but supports an extensive fringing coral reef (Rees *et al.* 2006). Its underlying geology and isolation from the coast result in it being highly oligotrophic. In this setting, we explored the effect of the fruit bat roost on mangrove tree growth and nutrition.

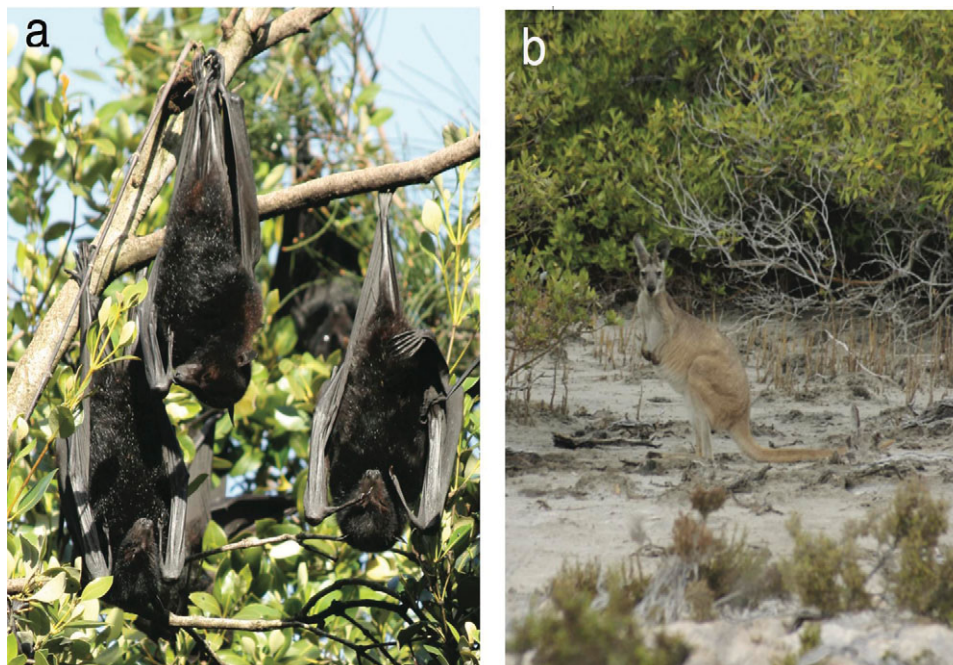


Figure 2. Mammalian herbivores in Australian mangrove forests. Individuals of the black flying fox, *Pteropus alecto* roosting in *Avicennia marina* trees in Queensland (a) (photo: R. Reef) and a euro, *Macropus robustus* in an *Avicennia marina* forest in Mangrove Bay, Western Australia (b) (photo: R. Kelley).

Tree growth rates

We assessed rates of wood growth of *R. stylosa* at Lizard Island over a 2-y period using stainless steel dendrometer bands (Hall 1944) installed at breast height on eight trees associated with the bat roost and eight that were adjacent in a forest where the bats were not present. Dendrometer bands were installed on 29 June 2008. Radius increments were measured to the nearest 0.01 mm on 8 November 2009 and on 30 July 2010. Only the radial increments recorded during the period between November 2009 and July 2010 were used to calculate basal area increment in order to ensure sufficient time for the band to settle prior to the initiation of measurements (all trees recorded radial increments between June 2008 and November 2009). Differences in increases in basal area between trees associated with the bat roost and trees not associated with the bat roost were tested statistically using a Student's *t*-test.

Lizard Island nutrient and soil analysis

Foliar nutrient analysis was conducted on fully sun-exposed green and senescent leaves of three mangrove species occurring within and outside the bat roost on 30 July 2010. At each site, leaves were collected from six individual *R. stylosa* trees, three *C. tagal* trees and three *L. rosea* trees. *Rhizophora stylosa* had no

senescent leaves at the time of leaf collection. Three green leaves and senescent leaves were collected from each tree. The difference in nutrient concentrations of green and senescent leaves indicates the plant's resorption efficiency for the tested nutrient with higher resorption efficiencies suggesting the nutrient is limiting growth. Triplicates were later pooled for analysis. Leaves were photographed alongside a ruler, and leaf area was then measured using the image analysis software ImageJ (US National Institutes of Health, Bethesda, Maryland, <http://imagej.nih.gov/ij>, ver 1.45s). Leaves were dried at 70 °C and were subsequently pulverized using a bead mill. Three samples of relatively fresh bat guano were scraped off leaves from underneath roosting *P. alecto*. Soil and bat guano samples were dried and ground.

Carbon (C) and nitrogen (N) concentrations (presented as % mass) in dried leaf tissue and bat guano were determined using mass spectrometry (UC Davis Stable Isotope Facility). The total phosphorus (P) concentration (% mass) in the ground material was determined using the methods described in Reef *et al.* (2010a). Briefly, an acidified persulphate autoclave digestion of the organic compounds (Menzel & Corwin 1965) was followed by quantification of the released orthophosphate in a colorimetric assay with ammonium molybdate and malachite green (van Veldhoven & Mannaerts 1987).

The relative abundance of the stable isotope of ¹⁵N increases with trophic level, allowing for the quantification of the amount of nutrition plants derive

from higher trophic levels (e.g. from animal sources). We measured relative abundance of the stable isotopes of ^{15}N in leaves and bat guano in order to assess nutrient sources.

Soil porewater salinity was measured at the five locations within the bat roost and five locations in the mangrove outside the roost. Porewater was extracted from 30-cm depth using a suction device (McKee *et al.* 1988) and analysed using a handheld refractometer (model 300011, Sper Scientific, Scottsdale AZ, USA). Soil organic matter content was measured in five shallow (0–3 cm deep) soil cores collected from within the bat roost area and from the mangroves outside the roost. Soil organic matter content was measured using the weight-loss-on-ignition method by heating the dried soil sample to 450 °C for 4 h.

Five soil redox potential measurements were made in the bat roost and five in the mangrove forest outside the roost using custom-built platinum probes along with an Ag/AgCl reference probe (IJ14, Ionode Pty Ltd, Brisbane, QLD, Australia). In this system, observed E values were converted to standard reduction potential (E_{H}) by adding 200 mV to each measurement. Probes were pre-tested in freshly prepared saturated quinhydrone solutions of pH 4.01 and pH 7.00, yielding E_{H} values of 269 mV \pm 5 mV and 94.1 mV \pm 1.52 mV, respectively. Six measuring probes and a reference probe were inserted 5 cm into the soil and allowed to equilibrate for a few minutes before a measurement was made. Each measurement was an average of the readings made from each of the six measuring probes.

The influence of kangaroos on mangrove nutrition

We assessed the influence of kangaroos on the nutrition of mangroves in Mangrove Bay, Western Australia. Mangrove Bay and Ningaloo Reef are on the North West Cape of Western Australia (21°58'S, 113°57'E, Figure 1), which is the most arid coastal region in Australia, where evaporation (3200–4200 mm y^{-1}) greatly exceeds rainfall (<200–700 mm y^{-1}), which occurs mostly between November and May during cyclones (Alongi *et al.* 2000). Air temperatures range from 14 °C to 40 °C. Here, fringing coral reefs are adjacent to spinifex grasslands growing on coastal dunes. The red kangaroo (*Macropus rufus* Desmarest 1822) and euro (*M. robustus* Gould 1841, Figure 2b) are the major mammalian herbivores in this ecosystem. Mangrove vegetation on the Ningaloo coast is restricted to a few patches that occur in association with tidal creeks and lagoons formed in the swales of sand dunes and associated with fossil coral reef limestone. In these settings, they form stands of low trees (<5 m tall) in an essentially tree-less landscape. Although kangaroos are tolerant of high temperatures and low humidity, they use trees for shade, making resting nests under the

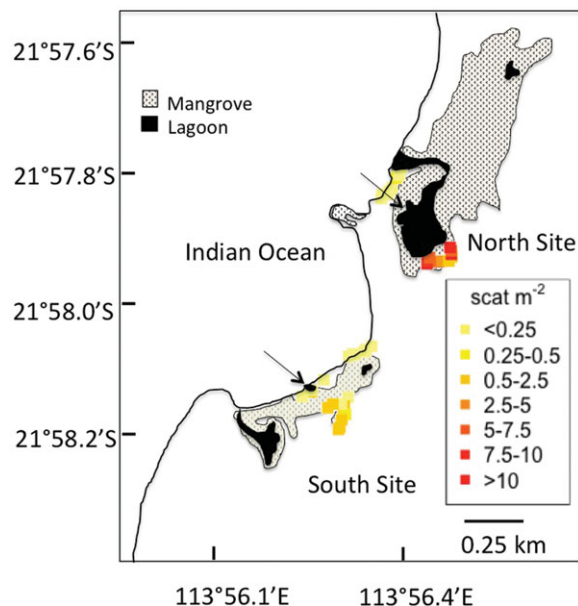


Figure 3. A detailed map of Mangrove Bay shows the two mangrove forests (North Site and South Site) and the arrows point to the North Lagoon (within the North Site) and South Lagoon (within the South Site). Kangaroos rest in the trees on the landward edge of the forests, but less so in those on the seaward edge. Coloured points indicate the density of kangaroo scat at each of the 40 transects.

canopy during the day (Newsome 1975). In Mangrove Bay, both *M. robustus* and *M. rufus* rest during the heat of the day in the landward regions of the mangrove forest. Additionally, carcasses of kangaroos are found within the forests, which may represent a transfer of nutrients from the terrestrial environment. Mangrove Bay has two distinct mangrove forests composed mainly of the mangrove *Avicennia marina* (Alongi *et al.* 1996). The northern forest is associated with a fossil coral reef formation that gives rise to a shallow lagoon fringed by mangroves while the southern forest occurs within depressions between sand dunes (Figure 3). The relative abundance of kangaroos at the landward and seaward sections of the northern and southern mangrove forests was estimated indirectly by counting faecal pellets. Faecal pellets were counted in ten 20-m² belt transects laid at each of the four locations.

The relative abundance of ^{13}C is different among plants that utilize different photosynthetic pathways (e.g. C3 or C4 photosynthesis) and thus distinguish between mangroves and grasses on which kangaroos might feed. We used ^{13}C abundance in kangaroo scat in order to establish whether kangaroos fed on terrestrial sources of vegetation (e.g. C4 *Spinifex* grasses) or rather on C3 mangrove vegetation. The isotopic relative abundances were measured using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the UC

Davis Stable Isotope Facility. The ^{13}C delta values are presented relative to the international standard V-PDB. ^{15}N delta values are presented relative to air.

Nutrient analysis – Mangrove Bay

We assessed the impact of kangaroos on the nutrition of the mangroves in two forest sites, one around the north lagoon, in the forest frequented by kangaroos and one around the south lagoon, where kangaroo activity was less frequent.

Foliar nutrient analysis was conducted on fully sun-exposed green leaves of *A. marina* (the most common mangrove species at the site) in September 2009. Three green leaves were collected from each tree for the analysis.

Leaves and fresh kangaroo scat were dried and ground prior to analysis. The three leaves from each tree were pooled together. Carbon and N concentrations (presented as % mass) and stable isotopes of N in leaf tissue and kangaroo scat and stable isotopes of C in kangaroo scat and were analysed using a SerCon elemental analyser coupled with a 20–22 stable isotope ratio mass spectrometer (Sercon, Crewe, UK) at the West Australian Biogeochemistry Centre.

Statistical analysis

Data were analysed using R for Mac OS X ver. 3.0.2. Student's *t*-tests were used to compare between tree variables within and outside the main mammalian impact area for each species. The distribution of the data was tested for normality using the Shapiro-Wilks normality test. Percentage data were arcsine-transformed prior to further analysis. *Rhizophora stylosa* $\delta^{15}\text{N}$ values were logarithmically transformed to conform to normality.

RESULTS

The influence of bats on mangrove nutrition and growth

Rhizophora stylosa trees within the bat roost at Lizard Island had significantly higher growth rates than those outside the colony (*t*-test, $t_{(7.1)} = 2.46$, $P = 0.04$). Stem basal area of eight *R. stylosa* trees within the bat roost increased on average (\pm SD) by $1.47 \pm 1.54 \text{ cm}^2 \text{ y}^{-1}$, which was nearly six times faster than growth rates for *R. stylosa* trees growing outside the bat roost (which increased by only $0.25 \pm 0.24 \text{ cm}^2 \text{ y}^{-1}$). Trees of all species within the bat roost were taller (3–8 m) than trees outside the roost (where adult tree height was 1–3 m).

Rhizophora stylosa and *L. rosea* had significantly higher N:C mass ratios within the roost relative to outside the

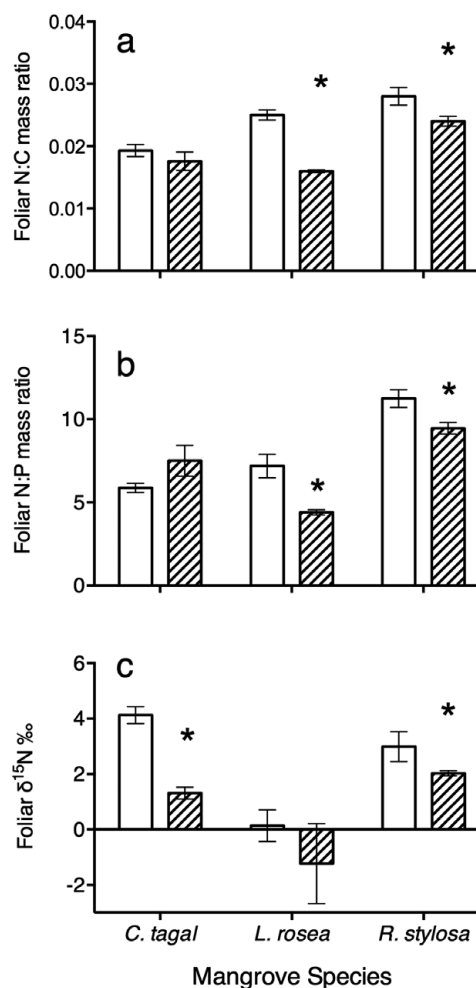


Figure 4. Mean (\pm SE) N:C dry mass ratios (a), N:P dry mass ratios (b) and N stable isotope ratios (c) for three mangrove species: *Ceriops tagal*, *Lumnitzera rosea* and *Rhizophora stylosa* within (open bars) and outside (hatched bars) the roosting area of a *Pteropus alecto* colony. $N = 3$ for *C. tagal* and *L. rosea* and 6 for *R. stylosa* at each site. Asterisk indicates significant difference between the trees within and outside the roosting area (*t*-test, $\alpha = 0.05$).

roost (*t*-test, $t_{(6.5)} = -2.6$, $P = 0.04$ and $t_{(2.6)} = -12$, $P = 0.002$ respectively, Figure 4a). The observed increase in foliar N:C within the bat roost was not significant for *C. tagal* ($t_7 = -1$, $P = 0.33$). *Rhizophora stylosa* and *Lumnitzera rosea* leaves from trees in the bat colony also had significantly higher N:P mass ratios than leaves from trees outside the roost (*t*-test, $t_{(7.2)} = -3.3$, $P = 0.01$ and $t_{(2.4)} = -4.7$, $P = 0.03$ respectively, Figure 4b). N:P mass ratios in green leaves of *C. tagal* were not significantly affected by the bat roost ($t_6 = 1.7$, $P = 0.15$, Figure 4b). *Ceriops tagal* was the only tree species for which foliar phosphorus concentrations were significantly higher in trees within the bat roost ($t_{(6.5)} = -4.2$, $P = 0.004$), increasing from an average (\pm SD) of $0.11\% \pm 0.018\%$ of dry mass to $0.15\% \pm 0.012\%$ within the bat roost.

Table 1. Soil and porewater properties of soil cores collected within the bat roost and outside the roost (N = 5 for each site). Soil organic matter was calculated using the weight loss on ignition method.

Soil properties	Soil within bat colony (Mean ± SD)	Soil outside bat colony (Mean ± SD)	P-value (t-test)
Porewater salinity (PSU)	1.7 ± 1.8	9.4 ± 6.6	0.03 *
Soil organic matter (%)	22.4 ± 10.9	49.9 ± 23	0.04 *
Redox potential (E _H , mV)	-94 ± 23	-100 ± 43	0.61 ns

The observed increase in foliar $\delta^{15}\text{N}$ ratios in trees within the bat roost than for trees outside the bat roost was statistically significant in *C. tagal* and *R. stylosa* trees (t-test, $t_{(4)} = 7.6$, $P = 0.002$ and $t_{(5,2)} = 0.9$, $P = 0.049$ respectively; Figure 4c).

Phosphorus resorption efficiency was on average $13.2\% \pm 23.5\%$ and $24.7\% \pm 11.7\%$ for *C. tagal* and *L. rosea* respectively and was not affected by the presence of the bat roost for either species (t-test, $t_{(5,6)} = -1.88$, $P = 0.11$ and $t_{(3,8)} = 0.27$, $P = 0.8$, respectively). No senescent leaves were present on *R. stylosa* trees. Nitrogen resorption efficiency was calculated for *C. tagal* and *L. rosea* and was not found to be significantly different between trees within and outside the bat colony roosting area (t-test, $t_{(5,3)} = -1.5$, $P = 0.2$ and $t_{(2,2)} = -0.06$, $P = 0.95$ for *C. tagal* and *L. rosea* respectively) averaging (\pm SD) $64.7\% \pm 7.4\%$ and $67.2\% \pm 3.5\%$ for *C. tagal* and *L. rosea* respectively.

Guano of *P. alecto* was composed on average (\pm SD) of $43.8\% \pm 1.7\%$ C, $2.7\% \pm 0.2\%$ N and $0.12\% \pm 0.05\%$ P as proportions of dry mass. Nitrogen in the bat guano had a $\delta^{15}\text{N}$ of $2.8\text{‰} \pm 0.3\text{‰}$. Carbon had a $\delta^{13}\text{C}$ of $-27.7\text{‰} \pm 0.42\text{‰}$. Nutrient excretion via urine was not measured in this study.

Some edaphic properties were different between soils collected under the bat roost and soil collected among the trees in the forest outside the bat roost (Table 1). Outside the bat roost, soil porewater was slightly more saline, and there was a significantly larger proportion of organic matter in the soil cores.

The influence of kangaroos on mangrove nutrition

In our study site in Mangrove Bay, *A. marina* is the most common mangrove species present. Kangaroo abundance was estimated indirectly by counting faecal pellets along ten 20-m² belt transects at each site and kangaroos were significantly more abundant in the landward forests (ANOVA, $F_{(1,36)} = 41.8$, $P < 0.001$) especially around the northern lagoon (ANOVA, $F_{(1,36)} = 26.9$, $P < 0.001$, Figure 3). In the southern lagoon, kangaroo faecal pellets were significantly more abundant on the landward side, $0.84 \pm 0.65 \text{ m}^{-2}$ (SD) than on the seaward side ($0.08 \pm 0.22 \text{ m}^{-2}$). At this site, the

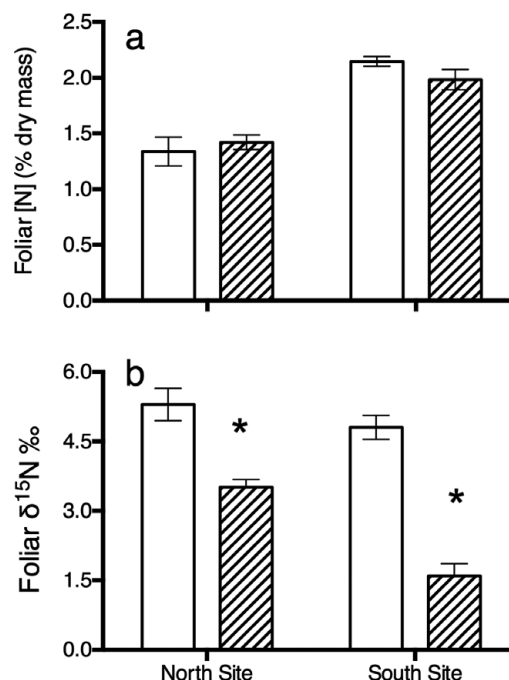


Figure 5. Mean (\pm SE) foliar N concentration (a) and N stable isotope ratios (b) for *Avicennia marina* within (open bars) and outside (hatched bars) the areas where kangaroos aggregate at two replicate sites (North and South). N = 3 at each site. Asterisk indicates significant difference between the trees within and outside the areas frequented by kangaroos at each location ($\alpha = 0.05$).

lagoon is nestled within the seaward trees. In the northern lagoon, kangaroo faecal pellets were also significantly more abundant on the landward side, $7.03 \pm 3.72 \text{ m}^{-2}$ than on the seaward side ($0.05 \pm 0.12 \text{ m}^{-2}$). At this site, the lagoon is nestled within the landward side trees.

Kangaroo presence did not significantly influence %N in *A. marina* leaves (Figure 5a) at both the north (t-test, $t_{(2,9)} = 0.6$, $P = 0.6$) and south ($t_{(2,9)} = -1.6$, $P = 0.2$) sites, but the $\delta^{15}\text{N}$ isotopic ratio in the leaves of mangroves growing in areas visited by kangaroos were significantly higher than those of leaves from adjacent sites where kangaroos were not present (Figure 5b) at both sites (t-test, $t_{(2,7)} = -4.6$, $P = 0.02$ and $t_{(4)} = -8.7$, $P < 0.001$ for north and south respectively).

Fresh kangaroo scat collected from the ground in the mangroves was composed of 34.8% C, 1.3% N and 0.35% P as proportions of dry mass. Nitrogen in the kangaroo scat had a $\delta^{15}\text{N}$ of $5.02\text{‰} \pm 0.4\text{‰}$ and a $\delta^{13}\text{C}$ of $-14.1\text{‰} \pm 0.7\text{‰}$.

DISCUSSION

Terrestrial mammals frequenting the mangrove forests provided a nutrient subsidy for mangrove trees at both study sites. Due to the high connectivity between

mangrove forests and the surrounding marine environment, terrestrial subsidies of nutrients into mangrove forests may in turn influence marine nutrient availability.

The influence of bats on mangrove nutrition and growth

At Lizard Island, the nutrient subsidy by the bat roost led to a significant increase in both the quantity and quality of mangrove vegetation. *Rhizophora stylosa* trees within the bat colony at Lizard Island had significantly higher growth rates than those outside the colony. Foliar N:C of two of the three dominant mangrove species (*R. stylosa* and *Lumnitzera rosea*) increased significantly relative to outside the roost, suggesting a significant N subsidy from the bat roost at this site. Increases in foliar N:C ratios are usually indicative of an increased investment in Rubisco and other components of the chloroplast that leads to higher rates of CO₂ assimilation (reviewed in Evans 1989).

Apart from nutrient availability, soil salinity and soil redox potential are both factors that can have a significant negative effect on mangrove productivity (Krauss *et al.* 2008). Redox potential did not significantly vary between the bat and non-bat sites. Salinity of soil porewater was relatively low at the site (<10 ppt) due to the presence of groundwater. Salinity of porewater was significantly lower outside the roost (1.7 ppt) compared with within the bat roost (9.4 ppt), however previous experimental studies on this species suggest that growth rates of *R. stylosa* are expected to be similar within the range of salinities measured in this study (Ball & Pidsley 1988, Clough 1984). Higher-salinity conditions within the bat colony were associated with higher growth rates of trees, which may reflect higher transpiration rates and water use of the canopy (Passioura *et al.* 1992). Given the similarity in salinity and redox potential of soils within and outside the bat roost areas of the forest it is highly likely that the enhanced growth in *R. stylosa* trees within the bat roost was due to nutrient subsidies from bats and that bats have altered the structure of the forest over time. *Pteropus alecto* is a widespread bat species in Australia, Papua New Guinea and Indonesia and forms roosts that can exceed 10 000 animals, often in mangrove forests (Vardon *et al.* 2001). A recent survey along the east coast of Australia (May 2013) has recorded 161 000 *P. alecto* at 108 roosting sites, with the largest roosts in coastal areas (Australian Government, Department of Environment). In two separate surveys from different areas in the Northern Territory, between 20% (Palmer & Woinarski 1999) and 33% (Tidemann *et al.* 1999) of the roosting sites of *P. alecto* were found in mangrove forests, despite mangrove forests comprising only a small area in the species distribution. Furthermore, other *Pteropus* species are found in coastal environments, similarly forming

large roosting colonies in mangrove forests throughout the Old World tropics. It can thus indirectly be assumed that *P. alecto* colonies might be contributing significant nutrient subsidies to a large number of mangrove forests throughout their range.

Nutrient limitation in many mangrove ecosystems is primarily due to N limitation (Reef *et al.* 2010b). Our findings of low resorption efficiency for P in conjunction with the high resorption efficiency for N during senescence at Lizard Island suggests that mangrove growth at this site is limited by N availability, especially for *R. stylosa* and *L. rosea*. The high N resorption efficiencies (>65%) for the mangroves at Lizard Island (relative to resorption efficiencies calculated in mangroves elsewhere, Feller *et al.* 2007) suggest N limitation to growth both inside and outside the bat roost. The low (<14, Koerselman & Meuleman 1996) foliar N:P mass ratios measured further support N limitation to growth at this site. Nitrogen limitation to growth in mangroves develops partly due to the low fraction of inorganic N that is useable for plant growth within the total N pool in the soil (Robertson & Phillips 1995). Nitrogen provided by bat excretion is in the form of urea and ammonia (Herrera *et al.* 2011), which in flooded soils are rapidly hydrolysed by soil micro-organisms to ammonium (Alongi 1994). Ammonium is the primary form of N used by mangrove trees (Reef *et al.* 2010b). Thus, bat excretion (also as urine, which was not measured in this study) provides an N subsidy that is in a form that is readily available for mangrove growth.

The organic matter content (and % C) of soils was lower in the bat colony than outside the bat colony (Table 1). Reduction in C content of peat soils was observed when trees were fertilized with N in Belizean mangroves (McKee *et al.* 2007). This is likely due to reduced allocation to roots by nutrient-enriched trees (Giardina *et al.* 2003, Haynes & Gower 1995) and also possibly due to enhanced decomposition of soil C with N fertilization (McKee *et al.* 2007).

Ceriops tagal and *R. stylosa* trees within the bat roost had elevated foliar $\delta^{15}\text{N}$ isotopic signatures. $\delta^{15}\text{N}$ is used to measure the trophic structure of communities because of trophic enrichment (a predictable increase in the abundance of ^{15}N from resource to consumer). An elevation in $\delta^{15}\text{N}$ suggests that the source of foliar [N] could be in part from an N source from a higher trophic level (i.e. from bat guano or bat carcasses from the large roosting colony). The isotopic composition of guano is dependent on the food source and can vary seasonally as different foods become available, especially in a species like *P. alecto* that exhibits a high level of diet diversity (Palmer *et al.* 2000). The guano composition presented here represents a single time point and might not represent the average isotopic composition of bat-derived N. The roosting colony can also have indirect

effects on the isotopic composition of available N in the soil by enhancing microbial nutrient cycling through fertilization, resulting in ^{15}N enrichment (Natelhoffer & Fry 1988).

The influence of kangaroos on mangrove nutrition

In our Western Australian site, kangaroos had similar effects on stable isotope composition as bats had on the mangroves of Lizard Island, but foliar N was not significantly enhanced. *Avicennia marina* trees where kangaroos rest during the heat of the day had significantly higher $\delta^{15}\text{N}$ ratios than *A. marina* trees in areas less frequented by kangaroos. Although kangaroos have been reported to feed on mangrove seedlings (Smith 1987), the high (less negative) $\delta^{13}\text{C}$ value in kangaroo scat (-14.1‰) indicates C4 grasses were likely a main component of kangaroo diets (Iles *et al.* 2010) and it is unlikely that mangroves contributed significantly to the diet of kangaroos at this site (mangrove $\delta^{13}\text{C}$ values ranged between -26‰ and -29.3‰). Thus, the contribution of N to the mangrove forest is of terrestrial origin, offering an avenue for new, allochthonous N to enter the system.

In conclusion, mangrove habitats provide important structure for resting sites for birds, bats and other mammals, including kangaroos. Here, we provide evidence that these terrestrial organisms provide a nutrient subsidy that is taken up by mangrove trees, enhancing growth and productivity and may be exported further into adjacent marine environments. The importance of mangroves in nutrient cycling in the coastal zone is well recognized, but our study indicates that through their importance to terrestrial fauna, they may be sites of localized nutrient enrichment, which may enhance productivity and diversity.

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LITERATURE CITED

- ALONGI, D. M. 1994. The role of bacteria in nutrient recycling in tropical mangrove and other coastal benthic ecosystems. *Hydrobiologia* 285:19–32.
- ALONGI, D. M., TIRENDI, F. & GOLDRICK, A. 1996. Organic matter oxidation and sediment chemistry in mixed terrigenous-carbonate sands of Ningaloo Reef, Western Australia. *Marine Chemistry* 54:203–219.
- ALONGI, D. M., TIRENDI, F. & CLOUGH, B. F. 2000. Below-ground decomposition of organic matter in forests of the mangroves *Rhizophora stylosa* and *Avicennia marina* along the arid coast of Western Australia. *Aquatic Botany* 68:97–122.
- ANDERSON, W. B. & POLIS, G. A. 1998. Marine subsidies of island communities in the gulf of California: evidence from stable carbon and nitrogen isotopes. *Oikos* 81:75–80.
- BAISRE, J. A. & ARBOLEYA, Z. 2006. Going against the flow: effects of river damming in Cuban fisheries. *Fisheries Research* 81:283–292.
- BALL, M. C. & PIDSLEY, S. M. 1988. Seedling establishment of tropical mangrove species in relation to salinity. Pp. 123–134 in Larson, H., Hanley, R. & Michie, M. (eds.). *Darwin Harbour: proceedings of a Workshop on Research and Management in Darwin Harbour*. Australian National University Press, Canberra.
- CEDERHOLM, C. J., KUNZE, M. D., MUROTA, T. & SIBATANI, A. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries* 24:6–15.
- CHEN, R. & TWILLEY, R. 1999. Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River estuary, Florida. *Estuaries and Coasts* 22:955–970.
- CLOUGH, B. 1984. Growth and salt balance of the mangroves *Avicennia marina* (Forsk.) Vierh. and *Rhizophora stylosa* Griff. in relation to salinity. *Functional Plant Biology* 11:419–430.
- DUNTON, K. H., WEINGARTNER, T. & CARMACK, E. C. 2006. The nearshore western Beaufort Sea ecosystem: circulation and importance of terrestrial carbon in arctic coastal food webs. *Progress in Oceanography* 71:362–378.
- EVANS, J. 1989. Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia* 78:9–19.
- EWEL, K. C., TWILLEY, R. R. & ONG, J. E. 1998. Different kinds of mangrove forests provide different goods and services. *Global Ecology and Biogeography Letters* 7:83–94.
- FAUNCE, C. H. & SERAFY, J. E. 2006. Mangroves as fish habitat: 50 years of field studies. *Marine Ecology Progress Series* 318:1–18.
- FELLER, I. C. 1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). *Ecological Monographs* 65:477–505.
- FELLER, I. C. & CHAMBERLAIN, A. 2007. Herbivore responses to nutrient enrichment and landscape heterogeneity in a mangrove ecosystem. *Oecologia* 153:607–616.
- FELLER, I. C., LOVELOCK, C. E. & MCKEE, K. L. 2007. Nutrient addition differentially affects ecological processes of *Avicennia germinans* in nitrogen versus phosphorus limited mangrove ecosystems. *Ecosystems* 10:347–359.
- FELLER, I. C., LOVELOCK, C. E. & PIOUS, C. 2009. Growth and nutrient conservation in *Rhizophora mangle* in response to fertilization along latitudinal and tidal gradients. *Smithsonian Contributions to the Marine Sciences* 38:345–358.
- FIELD, C. B., OSBORN, J. G., HOFFMAN, L. L., POLSENBERG, J. F., ACKERLY, D. D., BERRY, J. A., BJORKMAN, O., HELD, A., MATSON, P. A. & MOONEY, H. A. 1998. Mangrove biodiversity and ecosystem function. *Global Ecology and Biogeography Letters* 7:3–14.

- FRY, B. & EWEL, K. C. 2003. Using stable isotopes in mangrove fisheries research – a review and outlook. *Isotopes in Environmental and Health Studies* 39:191–196.
- GENDE, S. M., EDWARDS, R. T., WILLSON, M. F. & WIPFLI, M. S. 2002. Pacific salmon in aquatic and terrestrial ecosystems. *BioScience* 52:917–928.
- GIARDINA, C. P., RYAN, M. G., BINKLEY, D. & FOWNES, J. H. 2003. Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. *Global Change Biology* 9:1438–1450.
- GRAVEL, D., GUICHARD, F., LOREAU, M. & MOUQUET, N. 2010. Source and sink dynamics in meta-ecosystems. *Ecology* 91:2172–2184.
- HALL, R. C. 1944. A vernier tree-growth band. *Journal of Forestry* 42:742–743.
- HAYNES, B. E. & GOWER, S. T. 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. *Tree Physiology* 15:317–325.
- HERRERA, L. G., OSORIO, J. & MANCINA, C. A. 2011. Ammonotely in a neotropical frugivorous bat as energy intake decreases. *Journal of Experimental Biology* 214:3775–3781.
- HOCKING, M. D. & REYNOLDS, J. D. 2011. Impacts of salmon on riparian plant diversity. *Science* 331:1609–1612.
- HUTCHINGS, P. A. & RECHER, H. F. 1983. The faunal communities of Australian mangroves. Pp. 103–110 in Teas, H. J. (ed.). *Biology and ecology of mangroves*. Dr W. Junk, The Hague.
- ILES, J., KELLEWAY, J., KOBAYASHI, T., MAZUMDER, D., KNOWLES, L., PRIDDEL, D. & SAINTILAN, N. 2010. Grazing kangaroos act as local recyclers of energy on semiarid floodplains. *Australian Journal of Zoology* 58:145–149.
- KOERSELMAN, W. & MEULEMAN, A. F. M. 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* 33:1441–1450.
- KRAUSS, K. W., LOVELOCK, C. E., MCKEE, K. L., LÓPEZ-HOFFMAN, L., EWE, S. M. L. & SOUSA, W. P. 2008. Environmental drivers in mangrove establishment and early development: a review. *Aquatic Botany* 89:105–127.
- LONERAGAN, N. R. & BUNN, S. E. 1999. River flows and estuarine ecosystems: implications for coastal fisheries from a review and a case study of the Logan River, southeast Queensland. *Australian Journal of Ecology* 24:431–440.
- LOREAU, M. & HOLT, R. D. 2004. Spatial flows and the regulation of ecosystems. *American Naturalist* 163:606–615.
- LOVELOCK, C. E., FELLER, I. C., MCKEE, K. L., ENGELBRECHT, B. M. J. & BALL, M. C. 2004. The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. *Functional Ecology* 18:25–33.
- LOVELOCK, C. E., FELLER, I. C., ELLIS, J., SCHWARZ, A., HANCOCK, N., NICHOLS, P. & SORRELL, B. 2007. Mangrove growth in New Zealand estuaries: the role of nutrient enrichment at sites with contrasting rates of sedimentation. *Oecologia* 153:633–641.
- MCKEE, K. L., MENDELSSOHN, I. A. & HESTER, M. W. 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *American Journal of Botany* 75:1352–1359.
- MCKEE, K. L., CAHOON, D. R. & FELLER, I. C. 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography* 16:545–556.
- MENZEL, D. & CORWIN, N. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. *Limnology and Oceanography* 10:280–282.
- MEYER, J. L. & SCHULTZ, E. T. 1985. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. *Limnology and Oceanography* 30:146–156.
- MUMBY, P. J., EDWARDS, A. J., ERNESTO ARIAS-GONZALEZ, J., LINDEMAN, K. C., BLACKWELL, P. G., GALL, A., GORCZYNSKA, M. I., HARBORNE, A. R., PESCOD, C. L., RENKEN, H., WABNITZ, C. C. & LLEWELLYN, G. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427:533–536.
- NAGELKERKEN, I., BLABER, S. J. M., BOUILLON, S., GREEN, P., HAYWOOD, M., KIRTON, L. G., MEYNECKE, J. O., PAWLIK, J., PENROSE, H. M., SASEKUMAR, A. & SOMERFIELD, P. J. 2008. The habitat function of mangroves for terrestrial and marine fauna: a review. *Aquatic Botany* 89:155–185.
- NAIDOO, G. 2009. Differential effects of nitrogen and phosphorus enrichment on growth of dwarf *Avicennia marina* mangroves. *Aquatic Botany* 90:184–190.
- NAIMAN, R. J., BILBY, R. E., SCHINDLER, D. E. & HELFIELD, J. M. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* 5:399–417.
- NATELHOFFER, K. J. & FRY, B. 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. *Soil Science Society of America Journal* 52:1633–1640.
- NEWSOME, A. E. 1975. An ecological comparison of the two arid-zone kangaroos of Australia, and their anomalous prosperity since the introduction of ruminant stock to their environment. *Quarterly Review of Biology* 50:389–424.
- ODUM, W. E., MCIVOR, C. C. & SMITH, T. J. 1982. *The ecology of the mangroves of south Florida: a community profile*. United States Fish and Wildlife Service, Office of Biological Services, Washington, DC. 144 pp.
- ONUF, C. P., TEAL, J. M. & VALIELA, I. 1977. Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. *Ecology* 58:514–526.
- PAERL, H. W. 1997. Coastal eutrophication and harmful algal blooms: importance of atmospheric deposition and groundwater as “new” nitrogen and other nutrient sources. *Limnology and Oceanography* 42:1154–1165.
- PALMER, C. & WOJNARSKI, J. C. Z. 1999. Seasonal roosts and foraging movements of the black flying fox (*Pteropus alecto*) in the Northern Territory: resource tracking in a landscape mosaic. *Wildlife Research* 26:823–838.
- PALMER, C., PRICE, O. & BACH, C. 2000. Foraging ecology of the black flying fox (*Pteropus alecto*) in the seasonal tropics of the Northern Territory, Australia. *Wildlife Research* 27:169–178.
- PASSIOURA, J. B., BALL, M. C. & KNIGHT, J. H. 1992. Mangroves may salinize the soil and in so doing limit their transpiration rate. *Functional Ecology* 6:476–481.
- PIERSON, E. D. & RAINEY, W. E. 1990. The biology of flying foxes of the genus *Pteropus*: a review. Pp. 1–17 in Wilson, D. E. & Graham,

- G. L. (eds.). *Pacific Island Flying Foxes: Proceedings of International Conservation Conference*. U.S. Fish and Wildlife Service, Washington, DC.
- POLIS, G. A. & HURD, S. D. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist* 147:396–423.
- POLIS, G. A., ANDERSON, W. B. & HOLT, R. D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- PROSKE, U. & HABERLE, S. G. 2012. Island ecosystem and biodiversity dynamics in northeastern Australia during the Holocene: unravelling short-term impacts and long-term drivers. *The Holocene* 22:1097–1111.
- REEF, R., BALL, M. C., FELLER, I. C. & LOVELOCK, C. E. 2010a. Relationships among RNA:DNA ratio, growth and elemental stoichiometry in mangrove trees. *Functional Ecology* 24:1064–1072.
- REEF, R., FELLER, I. C. & LOVELOCK, C. E. 2010b. Nutrition of mangroves. *Tree Physiology* 30:1148–1160.
- REEF, R., BALL, M. C. & LOVELOCK, C. E. 2012. The impact of a locust plague on mangroves of the arid Western Australia coast. *Journal of Tropical Ecology* 28:307–311.
- REES, S., OPDYKE, B., WILSON, P., KEITH FIFIELD, L. & LEVCHENKO, V. 2006. Holocene evolution of the granite based Lizard Island and MacGillivray Reef systems, Northern Great Barrier Reef. *Coral Reefs* 25:555–565.
- ROBERTSON, A. I. & DUKE, N. C. 1987. Insect herbivory on mangrove leaves in North Queensland. *Australian Journal of Ecology* 12:1–7.
- ROBERTSON, A. I. & PHILLIPS, M. J. 1995. Mangroves as filters of shrimp pond effluent: predictions and biogeochemical research needs. *Hydrobiologia* 295:311–321.
- ROSE, M. D. & POLIS, G. A. 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. *Ecology* 79:998–1007.
- SMITH, T. J. 1987. Effects of light and intertidal position on seedling survival and growth in tropical tidal forests. *Journal of Experimental Marine Biology and Ecology* 110:133–146.
- SMITH, V. H., TILMAN, G. D. & NEKOLA, J. C. 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environmental Pollution* 100:179–196.
- TIDEMANN, C. R., VARDON, M. J., LOUGHLAND, R. A. & BROCKLEHURST, P. J. 1999. Dry season camps of flying-foxes (*Pteropus* spp.) in Kakadu World Heritage Area, north Australia. *Journal of Zoology* 247:155–163.
- VAN VELDHoven, P. P. & MANNAERTS, G. P. 1987. Inorganic and organic phosphate measurements in the nanomolar range. *Analytical Biochemistry* 161:45–48.
- VARDON, M. J., BROCKLEHURST, P. S., WOINARSKI, J. C. Z., CUNNINGHAM, R. B., DONNELLY, C. F. & TIDEMANN, C. R. 2001. Seasonal habitat use by flying-foxes, *Pteropus alecto* and *P. scapulatus* (Megachiroptera), in monsoonal Australia. *Journal of Zoology* 253:523–535.