Variable nutrient stoichiometry (carbon:nitrogen:phosphorus) across trophic levels determines community and ecosystem properties in an oligotrophic mangrove system

ARTICLE *in* OECOLOGIA · JULY 2015

Impact Factor: 3.09 · DOI: 10.1007/s00442-015-3379-2 · Source: PubMed

13 AUTHORS, INCLUDING:

Robert E. Ulanowicz

University of Florida

172 PUBLICATIONS **6,986** CITATIONS

SEE PROFILE

Myrna E Jacobson

University of Southern California

31 PUBLICATIONS **436** CITATIONS

SEE PROFILE

Ilka C Feller

Smithsonian Institution

89 PUBLICATIONS **2,316** CITATIONS

SEE PROFILE

Karen L McKee

United States Geological Survey

137 PUBLICATIONS **5,200** CITATIONS

SEE PROFILE

Oecologia
DOI 10.1007/s00442-015-3379-2

ECOSYSTEM ECOLOGY - ORIGINAL RESEARCH

Variable nutrient stoichiometry (carbon:nitrogen:phosphorus) across trophic levels determines community and ecosystem properties in an oligotrophic mangrove system

U. M. Scharler[1] · R. E. Ulanowicz[2,3] · M. L. Fogel[4,5] · M. J. Wooller[6,7] · M. E. Jacobson-Meyers[8] · C. E. Lovelock[9] · I. C. Feller[10] · M. Frischer[11] · R. Lee[12] · K. McKee[13] · I. C. Romero[14] · J. P. Schmit[15] · C. Shearer[16]

Received: 4 November 2014 / Accepted: 16 June 2015

Abstract Our study investigated the carbon:nitrogen:phosphorus (C:N:P) stoichiometry of mangrove island of the Mesoamerican Barrier Reef (Twin Cays, Belize). The C:N:P of abiotic and biotic components of this oligotrophic ecosystem was measured and served to build networks of nutrient flows for three distinct mangrove forest zones (tall seaward fringing forest, inland dwarf forests and a transitional zone). Between forest zones, the stoichiometry of primary producers, heterotrophs and abiotic components did not change significantly, but there was a significant difference in C:N:P, and C, N, and P biomass, between the functional groups mangrove trees, other primary producers, heterotrophs, and abiotic components. C:N:P decreased with increasing trophic level. Nutrient recycling in the food webs was highest for P, and high transfer efficiencies between trophic levels of P and N also indicated an overall shortage of these nutrients when compared to C. Heterotrophs were sometimes, but not always, limited by the same nutrient as the primary producers. Mangrove trees and the primary tree consumers were P limited, whereas the invertebrates consuming leaf litter and detritus were N limited. Most compartments were limited by P or N (not by C), and the relative depletion rate of food sources was fastest for P. P transfers thus constituted a bottleneck of nutrient transfer on Twin Cays. This is the first comprehensive ecosystem

Communicated by Michael Madritch.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-015-3379-2) contains supplementary material, which is available to authorized users.

✉ U. M. Scharler
scharler@ukzn.ac.za

1 School of Life Sciences, University of KwaZulu-Natal, Westville Campus, Durban 4001, South Africa

2 Arthur R. Marshall Laboratory, Department of Biology, University of Florida, Gainesville, FL 32611-8525, USA

3 Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, MD 20688-0038, USA

4 Geophysical Laboratory, Carnegie Institution of Washington, 5251 Broad Branch Road NW, Washington, DC 20015, USA

5 School of Natural Science, University of California at Merced, Merced, CA 95343, USA

6 School of Fisheries and Ocean Sciences, Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, AK 99775-5860, USA

7 Alaska Stable Isotope Facility, Water and Environmental Research Center, University of Alaska Fairbanks, P.O. Box 755860, Fairbanks, AK 99775-5860, USA

8 University of Southern California Dana and David Dornsife College of Letters, Arts and Sciences, 3616 Trousdale Parkway AHF 139, Los Angeles, CA 90089-0371, USA

9 School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia

10 Smithsonian Environmental Research Center, Edgewater, MD 21037, USA

11 Skidaway Institute of Oceanography, Savannah, GA 31411, USA

12 Center for Dark Energy Biosphere Investigations, University of Southern California, AHF 209, Los Angeles, CA 90089-0371, USA

13 US Geological Survey, National Wetlands Research Center, Lafayette, LA 70506, USA

14 College of Marine Science, University of South Florida, St Petersburg, FL 33701, USA

15 National Capital Region Inventory and Monitoring Network, National Park Service, 4598 MacArthur Boulevard NW, Washington, DC 20007, USA

Published online: 18 July 2015

study of nutrient transfers in a mangrove ecosystem, illustrating some mechanisms (e.g. recycling rates, transfer efficiencies) which oligotrophic systems use in order to build up biomass and food webs spanning various trophic levels.

Keywords Oligotrophic environment · Recycling · Nutrient limitation · Mangrove food web · Transfer efficiency

Introduction

Nutrient dynamics in aquatic ecosystems have been studied in recent decades mainly due to concerns over eutrophication, resulting algal blooms and their impacts on other biotic communities. As such, eutrophic systems have gained much attention, especially with regards to the nutrient-algae link (e.g. Smith et al. 1999; Anderson et al. 2014). However, there are two areas regarding nutrient dynamics that have received less consideration. Higher trophic levels are rarely included in studies, and oligotrophic systems are relatively unrepresented in the literature. Nutrient dynamics in oligotrophic systems differ from those in eutrophic systems by having considerably lower availability of nutrients in their dissolved and non-living particulate form (e.g. Zhang et al. 2007). This lower nutrient availability implies that in order to satisfy nutrient demands of higher trophic levels, recycling rates should be high and transfers of nutrients efficient across trophic levels.

Studies of elemental stoichiometry in ecosystems, especially that of macronutrients [i.e. carbon (C), nitrogen (N) and phosphorus (P)], have become important to explain a wide range of community and ecosystem properties. Such properties include taxa-specific variability and ontogenetic shifts, effects of consumer-driven nutrient cycling, and the integration of stoichiometric and metabolic theory to explain ecosystem functioning and stability (e.g. Sterner and Elser 2002; Vanni et al. 2002; Cross et al. 2005; Allen and Gillooly 2009; Hillebrand et al. 2009; Persson et al. 2010). In this regard, ecological stoichiometry is an integral part of community and food web ecology. In this paper we use C:N:P stoichiometry to infer both ecosystem and community-level properties of recycling, transfer efficiency and nutrient limitation of a mangrove forest.

In the past, aquatic ecosystems have generally been divided into those that are limited, sensu Liebig, by N (marine) or P (freshwater). These generalisations were mostly derived from nutrient limitations investigated in growth experiments, or nutrient concentrations of algae which were assumed to reflect their nutrient environment (Redfield 1934). However, nutrient limitations are not confined to primary producers, and can be exacerbated and sometimes switched at higher trophic levels. For example, algae may be N limited in a particular ecosystem, whereas fish in the same ecosystem may be P limited due to their higher requirement of P for bone synthesis (Ulanowicz and Baird 1999; Sterner and George 2000; Vanni et al. 2002). Limiting nutrients may vary between ecosystem components and it is difficult, if not impossible, to label an entire ecosystem as limited by one particular nutrient.

The overall aim of our study was to investigate the nutrient dynamics in an oligotrophic mangrove ecosystem. We established the stoichiometry (C:N:P) of biotic and abiotic ecosystem components and then used these data to calculate nutrient transfer efficiencies between trophic levels, stoichiometry at the various trophic levels and extent of recycling. We hypothesised that the nutrient stoichiometry changes between trophic levels and that recycling rates are higher for the limiting nutrients. Lastly, we investigated the changes of nutrient limitations of ecosystem components.

Materials and methods

We established the stoichiometry (C:N:P) of the biotic and abiotic ecosystem components, and nutrient flows between them for three different forest zones on the mangrove islands Twin Cays, Belize. Data were gathered during a 5-year USA-National Science Foundation Biocomplexity programme, which included ten research groups focussing on biochemistry, physiology and ecology of various ecosystem components (Table 1). Data emanating from this research served to establish the C:N:P stoichiometry of various abiotic and biotic components, and to build trophic-flow networks for three tree growth zones by quantifying standing stocks and trophic links.

Study site

This study was conducted on Twin Cays (16°50′N, 88°06′W), Belize, a 92-ha pair of mangrove islands situated about 12 km offshore (MacIntyre et al. 2004) that is part of a system of mangrove islands between the Belizean mainland and the Mesoamerican barrier reef. In the 1990s, fertilisation experiments examined nutrient limitations of the mangrove trees in each of three forest zones (fringe, transition, dwarf) (Feller et al. 2002). These studies demonstrated that mangrove trees were N limited in the fringe zone, N+P limited in the adjacent transition zone, and P limited in the interior dwarf zone (Feller et al. 2002). The fringe zone on Twin Cays is composed primarily of *Rhizophora mangle* L. (red mangrove), with lesser amounts of

[16] Department of Plant Biology, University of Illinois at Urbana-Champaign, Room 265 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801, USA

Table 1 Data sources for stocks and flows used to build the carbon (C), nitrogen (N) and phosphorus (P) networks for the fringe, transition and dwarf mangrove forest zones

Compartment no.	Compartment	Parameter	References
1	*Rhizophora mangle*	Leaf biomass, production, respiration, wood biomass, wood production, C content, prop-root biomass, proportion of belowground root biomass, belowground root production, prop-root production *P*:*B*, C:N, nutrient sources, N:P	This study; CARICOMP data; Cintrón and Schaeffer Novelli (1984); Jin-Eong et al. (1995); Feller and Mathis (1997); Koltes et al. (1998); McKee et al. (2007); McKee (2011)
2	*Avicennia marina*	Wood/leaf biomass, *P*:*B*, *P*:*R*, wood biomass, C content, wood litterfall, root biomass, C:N, nutrient sources, N:P	This study; CARICOMP data; Koltes et al. (1998); Cintrón and Schaeffer Novelli (1984); McKee et al. (2007); McKee (2011)
3	*Laguncularia racemosa*	Wood/leaf biomass, *P*:*B*, *P*:*R*, wood litterfall, root biomass, C:N, nutrient sources, N:P	This study; CARICOMP data; Koltes et al. (1998); Cintrón and Schaeffer Novelli (1984); McKee et al. (2007); McKee (2011)
4	Lichen	Aerial coverage, tree surface, weight, C content, photosynthetic C gain, mean diel C loss, %N, N:P	This study; Lange et al. (2000)
5	Macroalgae—submerged	*P*:*B*, % cover, production, perimeter of island, size of fringe zone, C:N, N:P, exudates	This study; Taylor et al. (1986); Littler et al. (1985); Rodriguez and Feller (2004); Lapointe et al. (1992)
6	Macroalgae—*Bostrychia*	Biomass, photosynthetic O_2 production/consumption, respiration, C:N, N:P	This study; Zuccarello et al. (2001)
7	Microbial mats	Biomass, production, respiration, coverage, N fixation, denitrification, biomass	This study; Joye and Lee (2004); Lee (2006); Lee and Joye (2006); Lee et al. (2008)
8	Heterotrophic microfauna	*B*, *P*, *R*, *E*, *C*, C:N, N:P	This study; ATLSS; Ulanowicz et al. (1999)
9–12	Crabs—*Uca* spp. (9), *Ucides* sp. (10), *Goniopsis* sp. (11), *Aratus pisonii* (12)	Density, dry weight, *P*:*B*, *R*:*B*, diet, C:N, %P	This study; McKeon and Feller (2004); McKeon personal communication; Koch and Wolff (2002); Kathiresan and Bingham (2001); Nordhaus (2004); McKee (1995)
13–15	Larger gastropods—*Cerithidea* sp. (13), *Littorina angulifera* (14), *Melampus coffeus* (15)	Density, dry weight/C content, assimilation efficiency, *P*:*B* ratio, diet, C:N, N:P	This study; Kohlmeyer and Bebout (1986); ATLSS; Ulanowicz et al. (1999)
16-28	Fauna associated with leaf litter—harpacticoid copepods (16), Copepoda (17), Amphipoda (18), Tanaidacea (19), Isopoda (20), Ostracoda (21), Bivalvia (22), Gastropoda (23), Plychaeta (24), Oligochaeta (25), Nematoda (26), flatworms (27), mites (28).	Density, dry weight/C content, assimilation efficiency, *P*:*R*, C:N, N:P	This study; Jørgensen et al. (1991); ATLSS; Ulanowicz et al. (1999)
29–36	Fauna associated with submerged *R. mangle* roots—hydroids (29), serpulids (30), tunicates (31), sponges (32), sea slugs (33), sea urchins (34), wood-boring isopods (35), Leptostraca (36)	Ingestion rate/body weight, coverage, length of coastline, daily ingestion rate, respiration rate, excretion rate, C:N, %P	Coma et al. (1998); Ellison and Farnsworth (1992); Rodriguez and Feller (2004); Gili and Coma (1998); Clark and DeFreese (1987); McClanahan (1998); Jørgensen et al. (1991); Perry (1988); Schwinghamer et al. (1986); Kensley and Schotte (1989); Modlin (1996); this study
37–41	Herbivores and inquilines associated with *R. mangle*—leaf miners (37), stem miners (38), stem girdlers (39), twig borers (40), inquilines (41)	Density, dry weight, %C, assimilation efficiency, density per tree, tree density, *P*:*B*, *P*:*R*, C:N, N:P	This study; Feller and Mathis (1997); Feller (2002); ATLSS; Ulanowicz et al. (1999)
42–46	Herbivores and inquilines associated with *A. marina*—leaf miners (42), stem miners (43), stem girdlers (44), twig borers (45), inquilines (46)	Biomass, assimilation efficiency, *P*:*B*, *P*:*R*, C:N, N:P	Same as for *R. mangle*, adjusted for *A. marina* leaf, twig and stem biomass; Feller and Mathis (1997); ATLSS; Ulanowicz et al. (1999); this study

Table 1 continued

Compartment no.	Compartment	Parameter	References
47–51	Herbivores and inquilines associated with *L. racemosa*—leaf miners (47), stem miners (48), stem girdlers (49), twig borers (50), inquilines (51)	Biomass, assimilation efficiency, *P*:*B*, *P*:*R*, C:N, N:P	Same as for *R. mangle*, adjusted for *L. racemosa* leaf, twig and stem biomass; Feller and Mathis (1997); ATLSS; Ulanowicz et al. (1999); this study
52–53	Ants (52) and other arthropods (53)	Biomass, *P*:*B*, *P*:*R*, C:N, N:P	This study; ATLSS
54–57	Reptiles—*Anolis* sp. (54), geckos (55), *Boa* sp. (56), crocodiles (57)	Density, wet weight, dry weight, %C, *P*:*B*, *P*:*R*, *R*:*C*, diet, C:N, %P	McKeon and Feller (2004); Jørgensen et al. (1991); ATLSS; Ulanowicz et al. (1999)
58–67	Birds—piscivores and scavengers (58), other carnivores (59), invertebrates and vegetation (60), aquatic invertebrate feeders and insectivores (61), nectarivores (62), raptors (63), frugivores (64), omnivores (65), insectivores (66), insectivores and frugivores (67)	Density, feeding guilds, wet weight, dry weight, %C, diet, C:N, %P	Mitten et al. (2004); http://www.birds.cornell.edu/programs/AllAboutBirds/BirdGuide/; Jørgensen et al. (1991); ATLSS; Ulanowicz et al. (1999)
68–73	Bacteria and fungi—sediment bacteria (68), sediment fungi (69), leaf litter bacteria and fungi (70), dead wood bacteria and fungi (71), live wood bacteria and fungi (72), green leaf bacteria and fungi (73)	Biomass, C content, *P*:*B*, *P*:*R*, *E*:*B*, N biomass, P biomass, C:N, N:P, leaf area of leaf litter, area wood, area green leaves	This study; Jørgensen et al. (1991); Carter and Suberkropp (2004), ATLSS; Ulanowicz et al. (1999)
74–76	Dead root—*R. mangle* (74), *A. marina* (75), *L. racemosa* (76)	Biomass, degradation rate, C:N, N:P, live:dead root biomass	Middleton and McKee (2001); this study
77–80	Leaf litter—*R. mangle* (77), *A. marina* (78), *L. racemosa* (79), *Thalassia* sp. (80)	Biomass, C content, litterfall, degradation, macrofaunal consumption, C:N, %P	This study; Middleton and McKee (2001)
81–85	Dead wood—*R. mangle* (81), *A. marina* (82), *L. racemosa* (83), imported dead wood (84), dead *Batis* sp. (85)	Biomass, C content, litterfall, degradation, C:N, N:P.	This study; CARICOMP data; Feller and Mathis (1997); Feller (2002); Middleton and McKee (2001)
86–87	Detritus [mud overlaying peat (86)], POC ([0–30 cm (87)]	Biomass, C content, degradation, C:N, N:P.	This study
88	DOC, DON, DOP (0–30 cm)	Biomass, DOC leaching from leaves, degradation, standing stock	This study; Alongi et al. (2001); Machiwa and Hallberg (2002); Lee et al. (2008)
89	DIC, NH_4^+, NO_3^-, NO_2^-, PO_4^-	Standing stock	This study; Lee et al. (2008)

P Production, *B* biomass, *R* respiration, *E* egestion, *POC* particulate organic C, *DOC* dissolved organic C, *DON* dissolved organic N, *DOP* dissolved organic P, *DIC* dissolved inorganic C, *C* consumption, *CARICOMP* Caribbean Coastal Marine Productivity Program, *ATLSS* across trophic levels system simulation

Avicennia germinans (L.) Stearn. (black mangrove) and *Laguncularia racemosa* (L.) C.F. Gaertn. (white mangrove). The transition zone was populated by a mixture of the three tree species, and the interior dwarf zone by monospecific stands of *R. mangle*.

Field data

Representative species of various functional groups (see Table 1) were sampled in each of the three forest zones and their dry weight per area was determined as described below.

Primary producers

Leaf, wood and root biomass (grams per square metre) was calculated for the mangrove tree species *R. mangle*, *L. racemosa* and *A. germinans*. Leaf biomass of *R. mangle* was estimated from the leaf area index assessed using hemispherical photography analysed with the Hemiview software package (Delta T Devices, UK) and wood and prop-root biomass from allometric relationships based on tree height and diameter (Cintrón and Schaeffer Novelli 1984) measured on nine replicate trees in each forest zone. Wood biomass of *A. germinans* and *L. racemosa* was obtained from Caribbean Coastal Marine Productivity Program (CARICOMP) data (CARICOMP—UNESCO; see also Koltes et al. 1998). To determine belowground root biomass, 50-cm deep cores were taken with a Russian peat corer (cross-sectional area 5 cm^2) in the transition zone, which contained primarily *A. germinans* and *L. racemosa*. Live and dead roots were separated from the background material, washed, dried at 80 °C, and weighed. Leaf production was measured from litterfall (CARICOMP data). Belowground accumulation rates of mangrove roots were determined using an implanted mass technique (McKee et al. 2007; McKee 2011).

Total lichen cover on the bark of trees was estimated for each tree species in the three different zones from percent cover estimations and an estimate of tree surface area, based on main stem height and diameter. Macroalgae were divided into two groups including submerged macroalgae and the most conspicuous intertidal macroalgae, *Bostrychia sp*., *Bostrychia sp*. biomass was measured in nine replicate 25 × 25-cm plots in each vegetation zone, whereas data on submerged macroalgae were taken from the literature (Table 1). Microbial mats were abundant on Twin Cays, especially in the dwarf zone, often building thick layers of floc (unconsolidated microbial layers). Coverage, biomass, productivity, respiration, N fixation, denitrification and P content of microbial mats were assessed (Joye and Lee 2004; Lee and Joye 2006; Lee et al. 2008). These mats were dominated by cyanobacteria and exhibited high rates of primary production, respiration, and N fixation. Microbial mats exhibited unique stable isotopic signatures (Lee 2006) and contributed to ecosystem productivity, especially in the dwarf forest zone.

Heterotrophic compartments

The heterotrophic compartments of the habitats on Twin Cays consisted of several crab species, molluscs, fauna inhabiting leaf litter and detritus (micro-, meio- and macrofauna), arthropods utilising the mangrove trees as a food source or for shelter, reptiles, birds, bacteria and fungi, and in the fringe forest zone root-fouling organisms on submerged *R. mangle* roots. Mammals were not part of the Twin Cays food web due to a lack of land-based mammals. Fish were excluded from the network due to a lack of quantitative data.

Densities of the largest and most conspicuous gastropods that were not part of the smaller litter fauna, namely *Cerithidea* sp., *Littorina angulifera* and *Melampus coffeus*, were sampled in three transects across all three zones at the CARICOMP site where leaf litter was taken. Snails were dried at 60 °C, weighed, and stored for stable isotope analysis. Leaf litter fauna was sampled at eight transects in April and November 2001. Three replicates were taken in the fringe, transition and dwarf zones. An area of 25 × 25 cm of leaf litter and underlying detritus (soft mud on peat surface) was sampled, and detritus and leaves were rinsed above a fine-mesh sieve (63 μM). The organisms were grouped into Harpacticoidea, Copepoda, Amphipoda, Isopoda, Tanaidacea, Ostracoda, Nematoda, Oligochaeta, Polychaeta, Gastropoda, Turbellaria and Acari. An initial examination on invertebrate infauna in mangrove peat revealed extremely low numbers. As extraction of fauna from mangrove peat is highly time consuming, the fauna in mangrove peat was not included in this study.

Information on arthropods utilising the mangrove trees was collated from the literature (Feller and Mathis 1997; Feller 2002) and data generated during the present study. The density of leaf miners and stem miners on *R. mangle* was measured according to methods in Feller and Chamberlain (2007). Tree density measurements obtained from CARICOMP (Koltes et al. 1998) were used to estimate arboreal arthropod density in each forest zone.

Biomass of sediment bacteria from peat samples was estimated by epifluorescent counting and biovolume estimation after staining with 4′,6-diamidino-2-phenylindole (Alongi 1988; see Online Resource 1). Bacteria associated with decaying leaf litter and fresh leaves were extracted similarly to peat samples, except that ten hole punches (0.625 cm diameter) from each leaf were formalin fixed.

Biomass of fungi was estimated by determining the activity of chitinase in the peat, following Miller et al. (1998). Estimation was a two-part process. First, enzyme activity in peat was measured in the field. Secondly, fungi from peat samples were cultivated, their enzyme activity measured, standard curves were developed, and fungal biomass was calculated from enzyme activity (see Online Resource 1).

Abiotic components

Dead root biomass for *A. germinans* and *L. racemosa* was measured from cores taken in the transition zone as described above. Leaf litter sampled during the leaf litter invertebrate sampling was separated into *R. mangle*, *A. germinans and L. racemosa* trees and *Thalassia* sp., rinsed, dried at 60 °C and weighed. To measure dead wood biomass, dead wood on the ground and in the canopy was collected in three replicate 4 × 4-m plots in the three forest zones. The coarse woody debris was sorted by species, fresh and dry weight measured, and nutrient content determined. Plots were resampled after 2 years in order to determine input rate into each forest zone.

A thin layer termed 'detritus' sometimes overlaid the mangrove peat. The mass of this detrital layer was determined by measuring the thickness of this layer, which ranged from 0 to 2 cm, and dry weight from a known volume. The mangrove peat below the thin detrital layer was termed 'particulate organic matter', and its dry mass was determined by drying a known volume of peat.

Dissolved organic nutrients were measured using a high temperature catalytic oxidation system [for dissolved organic C (DOC), and dissolved organic N] and ash hydrolysis-spectrophotometry for dissolved organic P (Lee et al. 2008). DOC leaching from leaves was determined from two decomposition experiments starting in April and November 2001, respectively (see Online Resource 1). Dissolved inorganic N [nitrate (NO_3^-), nitrite (NO_2^-), ammonia and phosphate (PO_4^{3-})] were measured using the phenol hypochlorite method for ammonium, the cadmium reduction method for $NO_3^- + NO_2^-$, spectrophotometry for NO_2^-, and PO_4^{3-} was analysed colorimetrically using the molybdate blue method (see Lee et al. 2008 for methodological details).

Determination of C, N, and P contents

Samples for total C, N and P analysis were dried at the Carrie Bow Cay field station laboratory at 50–80 °C in air, brought back to the Carnegie Institution of Washington, where they were completely dried at 50 °C under N_2. Samples were weighed (0.2–2 mg) into tin boats for further analysis (Wooller et al. 2003). The C and N contents of primary producers, heterotrophs, and detrital components were measured using an elemental analyser (Carlo Erba 2500) attached to a Thermo Finnigan Delta Plus XL isotope ratio mass spectrometer (Fogel et al. 2008) (see Table 1 for exceptions). P content was analysed using methods modified from Aspila et al. (1976) for the various ecosystem components by comparing digestion of weighed, dried and combusted samples which were subsequently measured spectrophotometrically for total P concentration normalized for dry weight (see Table 1 for exceptions). Organic PO_4^{3-} was determined by subtraction.

The C, N and P contents (as % of dry weight) were used to express the stoichiometry of individual compartments by weight, and to calculate C, N and P standing stock per area for each compartment in each forest zone.

Network building

We calculated biomass in C, N and P and quantified trophic and respiratory flows for all identified compartments (see Table 1). With these, balanced C, N and P budgets for all compartments and for all three forest zones were produced as described below.

Species abundance and biomass were measured for the components included in the networks. Productivity (P) and/or respiration (R) for certain species were measured during this project and metabolic parameters not measured were estimated using P:biomass (P:B), P:R, and consumption (C):B ratios from the literature. Where C, N or P contents were not available for a certain compartment, that of a compartment similar in feeding guild, taxonomic group and size was used. All biomass was expressed as grams of C or N or P per square metre and all flows as grams of C or N or P/square metre per year. Sources for data, ratios, and equations used to calculate flows are listed in Table 1. In addition to the trophic and respiratory flows, boundary flows were included as imports and/or exports to and from the systems (Online Resource 1).

Using this information, quantities were assigned to feeding links among and between biotic and abiotic compartments following the method of Ulanowicz and Scharler (2008) (see Online Resource 1). This resulted in nine networks, i.e. a C, N and P network for each of the three mangrove forest zones. Networks were mass balanced so that the nutrient balance for autotrophic nodes becomes—gross primary production (GPP) = net primary production (NPP) + R; and for all heterotrophic nodes—consumption (C) = $P + R + E$. R is included only for the C networks; N networks feature gaseous exchange only for microbial mats (denitrification); and there is no gaseous exchange for P.

Calculation of nutrient limitations and limiting sources

To identify the element limiting a given recipient compartment, the criterion of Liebig (1840) is usually invoked. In the network context, this translates into finding the element with the longest residence, or turnover time, in the given compartment. Furthermore, the limiting flow originating from a particular source compartment was calculated. The Liebig procedure normally cannot be applied to identify which particular source of that limiting nutrient is most crucial to the given compartment. Ulanowicz and Abarca-Arenas (1997), however, generalised the Liebig procedure by showing that both limiting elements and limiting flows are those to which the overall biomass inclusive system ascendency is most sensitive (see Online Resource 1).

Ascendency is a system-level index that quantifies jointly the degree of trophic-flow organisation inherent in the network and its total system throughput (TST) (Hirata and Ulanowicz 1984). The theory of the ascendency index and associated calculations are outlined in Online Resource 1, whereas the specific equations (1, 2) used for the sensitivity calculations are presented here to demonstrate which changes in biomass and flows impact the ascendency value. Applying the ascendency calculations to identify (1) limiting nutrients and (2) limiting flows, the activities on the compartmental level are put into context of the ecosystem level. For each forest zone, the turnover time for each nutrient in each recipient compartment was calculated to identify the limiting nutrient (1). In the ascendency calculation, an increased biomass of an element (k), and a slower turnover time of k in the node (p) compared to the turnover time of the entire system, contribute to a higher value of ascendency (Eq. 1; Online resource 1):

$$\frac{\partial A_B}{\partial B_{pk}} = 2\left(\frac{T_{...}}{B_{..}} - \frac{1}{2}\frac{T_{pk}+T_{pk}}{B_{pk}}\right), \quad (1)$$

where A_B is the biomass inclusive ascendency, B_{pk} the biomass of node p in terms of element k, T the total throughput and B the total biomass.

Nutrients with a faster turnover time compared to that of the system contribute negatively to the system's ascendency, and nutrients with an equal turnover time in a compartment to that of a system contribute a very small amount to the system's ascendency. The system is therefore most sensitive to the slowest compartmental turnover times in relation to the system's turnover time for the same element.

As the ascendency calculations in the identification of limiting nutrients have not yet been widely applied, we also calculated the turnover time for each compartment for comparison.

Then, the limiting flows (2) were calculated from the rate of depletion of a specific nutrient in a source node relative to its standing stock, where the nutrient flow with the highest relative depletion rate constitutes the limiting flow (Ulanowicz and Abarca-Arenas 1997). This limiting flow results in a high ascendency value (Eq. 2; Online Resource 1).

$$\frac{\partial A_B}{\partial T_{rp}} = \log\left(\frac{T_{rp}B^2}{T_{..}B_rB_p}\right) \quad (2)$$

The highest sensitivity value from the above equation is calculated for the limiting flow that depletes its source at the fastest rate compared to its availability.

The limiting nutrient, and the limiting flow are not necessarily the same, since Eq. 1 is calculated for recipient nodes, and Eq. 2 is calculated for source nodes (see details in Online Resource 1).

To investigate the stoichiometry of and transfer efficiencies between trophic levels, the individual compartments were then apportioned over the various trophic levels according to their feeding activity (Ulanowicz 1986; Ulanowicz and Kay 1991). Investigations on the elements C, N and P per trophic level, their transfer efficiencies and recycling rates were conducted by analysing all networks using the software WAND (Allesina and Bondavalli 2004).

Results

C:N:P stoichiometry of biota and trophic levels

General biotic and abiotic groups

The C:N:P stoichiometry differed strongly between living and non-living compartments in all three mangrove forest zones (Fig. 1). High SDs of mean C:N, C:P and N:P resulted from considerable variability of C:N:P within groups (as in Fig. 1). Therefore, results of a two-way ANOVA (on log-transformed data) showed statistically significant differences only between the three major groups including primary producers, heterotrophic compartments and abiotic compartments (C:N, $F = 346.7$, $p < 0.001$; C:P, $F = 309.47$, $p < 0.001$; N:P, $F = 20.64$, $p < 0.001$), but not between zones ($p > 0.05$) nor for a compartment groups × zone interaction ($p > 0.05$). Heterotrophs showed lower C:N and C:P and had less variable ratios than primary producers or abiotic compartments (Fig. 1).

Functional groups and compartments

R. mangle green and senescent leaves and microbial mats are two of the most important primary producer groups in terms of biomass and occur in all three forest zones (Table 2). The C:N for *R. mangle* green leaves was similar from one zone to another, whereas the C:N for microbial

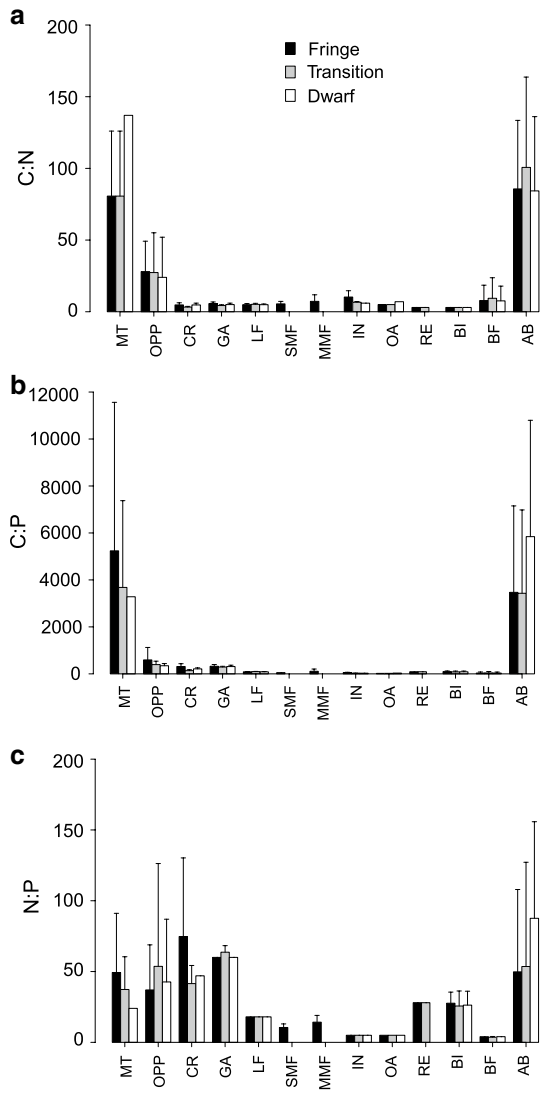

Fig. 1 Mean (±SD) of C:N (**a**), C:P (**b**) and N:P (**c**), by weight, for major abiotic and biotic groups in the fringe, transition and dwarf zone. *MT* Mangrove trees, *OPP* other primary producers, *CR* crabs, *GA* gastropods, *LF* litter fauna, *SMF* sessile macrofauna, *MMF* mobile macrofauna, *IN* insects, *OA* other arthropods, *RE* reptiles, *BI* birds, *BF* bacteria and fungi, *AB* abiotic

mats was halved in the dwarf zone compared to the fringe and transition zones. The C:P and N:P increased from the fringe to the dwarf zone for *R. mangle* green leaves, illustrating the relative decrease of P in the dwarf zone. Microbial mats, however, showed a decreasing C:P and an increasing N:P from the fringe to the dwarf zone (Table 2), which is due to the greater presence of N and P relative to C. *R. mangle* leaf litter had higher C:N and C:P compared to those of green leaves in all three zones. Primary tree consumers (Fig. 1) had, in general, a higher C:N ratio, but a lower C:P and N:P ratio compared to organisms feeding primarily on leaf litter (Fig. 1) in all three zones. These ratios may reflect the lower P content in source material such as leaf litter compared to e.g. *R. mangle* green leaves (Table 2). The higher C:P and N:P of leaf litter in the dwarf zone compared to the fringe and transition zone support the assertion that there was a lower amount of available P in this zone. However, overall differences between C, N and P biomass (in grams per square metre; Online Resource 2) of all compartments were not statistically different between the three forest zones ($p > 0.05$), but there were significant differences (for C, $F = 81.38$, $p < 0.001$; for N, $F = 47.79$, $p < 0.001$; for P, $F = 39.88$, $p < 0.001$) between functional groups (trees, other primary producers, heterotrophs, abiotic compartments). Across trophic levels, both N and P were incorporated in higher relative proportions compared to C in organisms feeding on trophic levels ≥II (Fig. 2). In addition, P is accumulated at a higher rate relative to N in heterotrophs in comparison to trophic level I (Fig. 2).

Nutrient limitations

Limiting nutrient of recipient compartment: ascendency calculations

The nutrient limitation of individual compartments was calculated by the system ascendency's sensitivity to changes in turnover rates of a particular nutrient in a particular compartment, and also by calculating compartmental turnover rates for each nutrient and compartment as a reference. From the ascendency analysis it was apparent that in all zones mangrove trees were primarily P limited. Sensitivity values for N were in most cases slightly lower, in contrast to those for C, which diverged considerably more, indicating a possible co-limitation by N (Online Resource 2). Similarly, microbial mats were P limited, and their co-limitation by N was less pronounced compared to that of mangrove trees. Sensitivity values for N and P were more similar at higher trophic levels

Table 2 C:N:P (by weight) of two primary producer groups (*R. mangle* leaves and microbial mats) and *R. mangle* leaf litter in the three mangrove forest zones on Twin Cays, Belize

Mangrove forest zones	*R. mangle* green leaves			*R. mangle* leaf litter			Microbial mats		
	C:N	C:P	N:P	C:N	C:P	N:P	C:N	C:P	N:P
Fringe	46.7	1570.2	33.6	58.4	4018.5	68.8	21.7	479.9	22.1
Transition	45.2	1537.6	34.0	76.4	4697.4	61.5	19.9	390.9	19.6
Dwarf	45.4	2136.5	47.1	63.8	6037.0	94.6	11.6	391.8	33.1

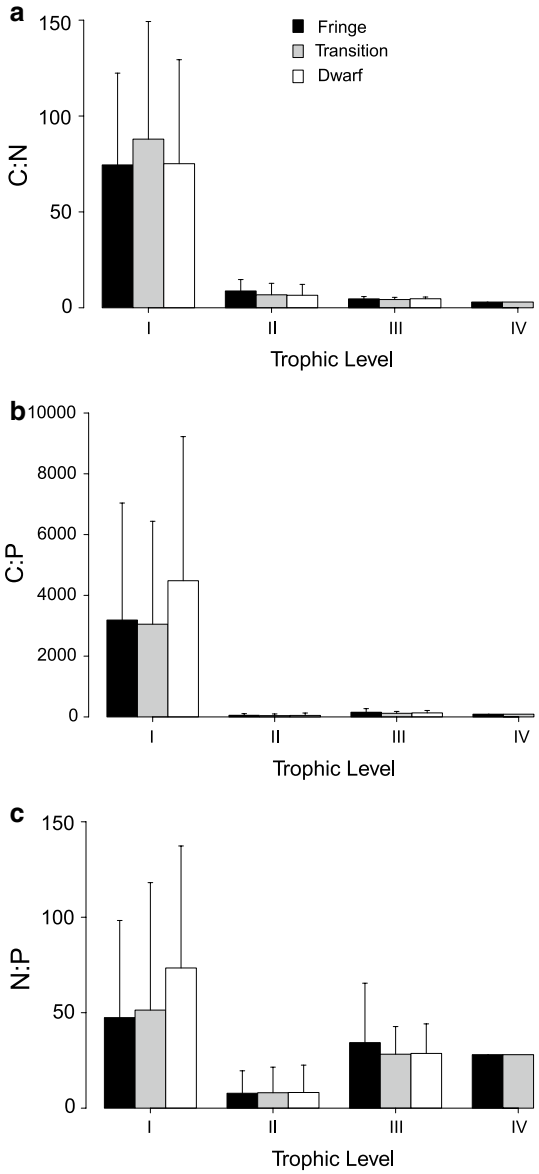

Fig. 2 Mean (±SD) of C:N (**a**), C:P (**b**) and N:P (**c**), by weight, across trophic levels for the fringe, transition and dwarf zone

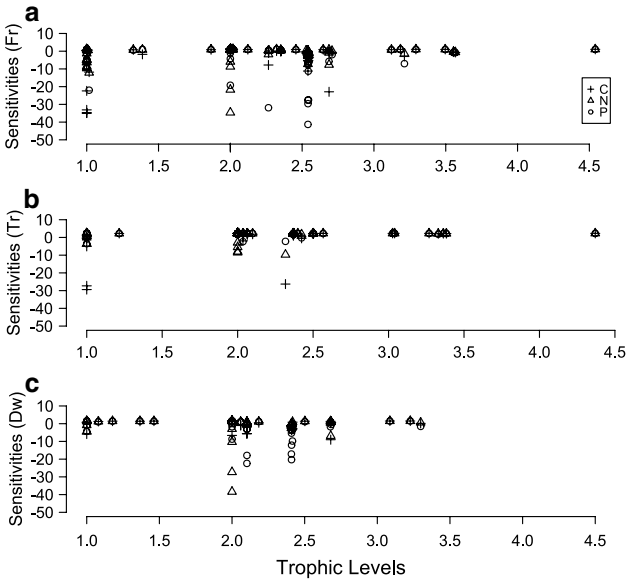

Fig. 3 Sensitivity values for C (**a**), N (**b**) and P (**c**) for all compartments. Compartments have been plotted according to the trophic level they belong to. Sensitivity values are given in Online Resource 2. *Fr* Fringe, *Tr* transition, *Dw* dwarf

(indicating a higher degree of co-limitation by P and N) and were most similar at the highest trophic levels (reptiles, selected compartments of birds, crabs, leaf litter fauna, insects; Fig. 3). Bacteria and fungi (compartments 68–73) were P limited throughout all zones, as were the first-order consumers of trees (insects consuming green leaves, twigs and wood, compartments 37–51). Crabs, larger gastropods and leaf litter fauna (compartments 9–28) were limited by N. More than 50 % of reptile and bird compartments (compartments 54–67) were limited by N, followed by C and P. The fauna associated with submerged *R. mangle* prop roots in the fringe zone (compartments 29–36) were limited by P.

Limiting nutrient of recipient compartment: turnover/biomass calculations

There was nearly a 100 % overlap in the compartmental nutrient limitations derived from ascendency analysis and those calculated by individually comparing supply (total input stoichiometry) to requirement (biomass stoichiometry) for comparison (Online Resource 2). Only one of 174 compartmental nutrient limitations of all three forest zones differed and showed C limitation from the sensitivity value, and P limitation from the calculation of turnover rates. The latter were very similar for the two elements, differing by only 0.3 %. In summary, both P and N showed slower turnover rates in individual compartments in relation to the system from the ascendency analysis, causing nutrient limitation. Nutrient limitations apparent from the stoichiometry calculation of supply and requirement (the check to the sensitivity values) arise when the stoichiometry of the flow entering a compartment is dissimilar to the stoichiometry of the node.

Limiting flows emanating from source compartment: ascendency calculations

The limiting flows in the systems, which convey the highest depletion rate of a nutrient from a source compartment in relation to depletion of other sources (Ulanowicz and Abarca-Arenas 1997), were almost exclusively those for P transport (P, 97 %; N, 2 %; C, 0 %). The proportionally

highest depletion rate, and therefore possible bottlenecks in P transport in all three zones predominantly originated from the sediment bacteria and fungi compartments (68–73), followed by non-living compartments (74–89) and insect compartments (37–52). Overall, of the three nutrients investigated, P was depleted at the fastest rate from the various source compartments, highlighting P transfers between compartments as bottlenecks in the Twin Cays ecosystem.

Ecosystem-level characteristics

The material exchange of internal flows (excluding flows across system boundary) between trophic levels in general decreased from trophic level I to trophic level IV for C and N flows resembling a exponential decline, whereas that of P flows was more akin to a linear decrease (Fig. 4). The largest differences between C, N and P flows were apparent especially for the first two trophic levels. The networks from the dwarf zone showed the smallest C flows, and from the transition zone they were lowest for N and P flows over all trophic levels. The relatively high N and P flows in the dwarf zone resulted from the extensive microbial mats that were relatively enriched in N and P compared to the mangrove trees.

Mean transfer efficiencies (the proportion of flow into one trophic level that is passed on to the next) for the first four trophic levels (I–IV) were in general highest for P, followed by N and C (Fig. 5; Table 3). Transfer efficiencies for N were twice as high compared to those for C for the fringe and transition zones, and about three times as high in the dwarf zone. Transfer efficiencies for P were four times that of C in the fringe and transition zones, and ca. nine times in the dwarf zone (Fig. 5; Table 3). The highest transfer efficiencies were apparent at trophic level I, where they ranged from ca. 21 to 27 % for C, 38—48 % for N and 30–81 % for P, and the lowest at trophic level IV (Fig. 5). Although transfer efficiencies were generally higher for P and N compared to C, especially at trophic level I, they were similar to each other at trophic level IV. The largest difference between trophic levels for C, N and P was apparent in the dwarf zone (Fig. 5). Overall, these results reflect the biomass dominance of proportionally C-rich mangrove trees (lower C transfer efficiency) and rates of recycling of the three nutrients. The percentage of the TST recycled, which was calculated as Finn's cycling index (FCI) (Finn 1980), was highest for P overall, and highest in the dwarf zone at 84.3 % (fringe, 51.0 %; transition, 15.4 %; Table 3). Recycling rates were fairly similar between the zones for N and decreased slightly from the dwarf (16.8 %) to the fringe zone (12.4 %). Recycling of C was highest in the fringe forest zone (10.6 %) and decreased to 6.5 % in the dwarf (Table 3).

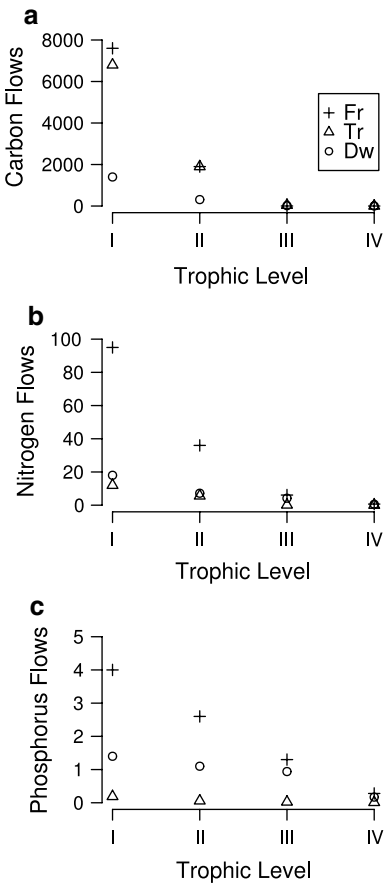

Fig. 4 Total flows of C (**a**), N (**b**) and P (**c**) (g m^{-2} $year^{-1}$) across trophic levels for the fringe, transition and dwarf zone; for abbreviations, see Fig. 3

Discussion

Although the concept of ecological stoichiometry has its beginnings in marine ecosystems through the Redfield ratio (Redfield 1934), most subsequent stoichiometric analyses, especially those of consumers, have been conducted in freshwater lakes or river ecosystems. Wide ranges of nutrient ratios are reported in the literature for invertebrates, comprising the largest number of heterotrophs in this and other studies, both on a molar and percent weight basis (e.g. Cross et al. 2003, 2005; Evans-White et al. 2005; Zhang et al. 2013). Comparisons to literature values are not exceptionally informative due to the ranges reported being generally large; still, our values for invertebrates fell within those from the literature (e.g. Cross et al. 2003; Evans-White et al. 2005). To further elucidate the stoichiometry within the invertebrate group on Twin Cays, we looked at feeding guilds, especially at herbivores (mangrove tree consumers) and detritus feeders (on abiotic sources). Heterotrophs on Twin Cays incorporated proportionally

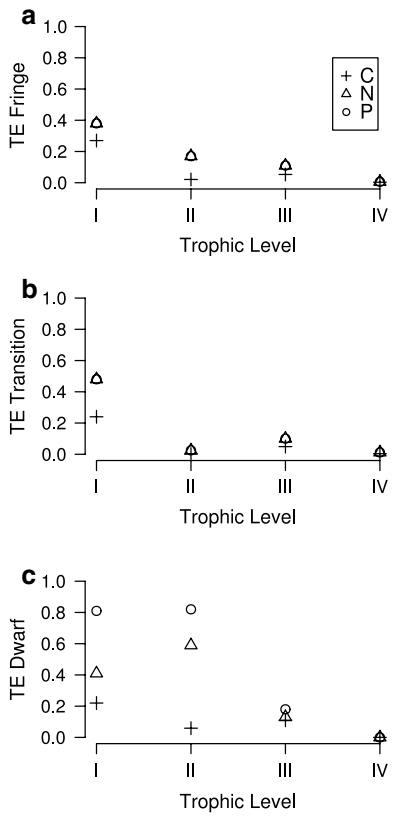

Fig. 5 Transfer efficiencies (*TE*) of C (**a**), N (**b**) and P (**c**) across trophic levels for the fringe, transition and dwarf zone on a scale from 0 to 1

Table 3 Finn cycling index (*FCI*; proportion of total system throughput recycled), transfer efficiency (*TE*) at trophic level (*TL*) I and over the first four TL (*I–IV*) for the three mangrove forest zones and nutrients (C, N, P)

		FCI (%)	TE (%) at TL I	TE (%, mean) over TL I–IV
Fringe	C	10.6	27.1	7.8
Transition	C	9.3	24.3	7.4
Dwarf	C	6.5	21.5	9.5
Fringe	N	12.4	38.4	14.5
Transition	N	15.0	48.3	15.6
Dwarf	N	16.8	40.8	28.2
Fringe	P	51.0	64.8	34.1
Transition	P	15.4	30.0	29.3
Dwarf	P	84.3	80.9	45.3

more N and P into their biomass relative to their diets and showed stoichiometric homeostasis in their nutrient ratios (i.e. lower variability) when compared to primary producers. Organisms utilising mangrove trees or their litter as a primary food source, such as leaf, wood and twig borers, stem girdlers as well as crabs and larger gastropod species, achieved the highest degree of homeostasis in the system. These groups may supplement their herbivorous diet through nutrient richer microbial cells attached to sediment or leaf litter, or employ an omnivorous strategy when needed to supplement a herbivorous diet [e.g. the tree crab *Aratus pisonii* (Diaz and Conde 1998)]. This strategy and the presence of nutrient-rich primary producers (e.g. microbial mats), as well as bacteria and fungi, may alleviate N and P shortage in the food web as a whole and contribute to a biomagnification of N and P at higher trophic levels, as described e.g. for the Baltic Sea ecosystem by Bradshaw et al. (2012). Mangrove trees on Twin Cays also showed some degree of compensation for the different availability of nutrients through reabsorption of nutrients before leaf abscission (Feller et al. 2002).

The mangrove trees had the highest C:N and C:P of all primary producers and this may make this food source less desirable as a large gap to consumer stoichiometry must be bridged. Nevertheless all parts of the trees were not only highly important food sources to the invertebrates consuming trees, but also featured prominently in the quantity consumed. However, in mangrove systems such as Twin Cays, the fraction of the nutrient-poor primary production consumed may largely depend on the specialisation of feeding guilds present in the ecosystem rather than on stoichiometry. Previous studies showed that on Twin Cays, xylem- and phloem-feeding wood borers remove over 50 % of the *R. mangle* canopy, and leaf-feeding herbivores about 6 % (Feller 2002), which constitutes a significant percentage of primary production removed from the system. In addition, wood borers may supplement their diets with e.g. nutrient richer fungi, but we lack specific information on this feeding link in the Twin Cays forest.

In nutrient-poor systems such as mangroves, the recycling of nutrients is especially important to sustain suitable stoichiometric requirements of organisms. Speculations that small-sized organisms are highly important to allow efficient consumer-driven nutrient recycling (e.g. Vanni 2002) can, for mangrove systems, be extended to include larger organisms that can efficiently utilise the abundant mangrove litter. Here, consumers of different sizes are necessary to break down leaf litter into a series of progressively smaller fragments to allow further digestibility and a larger surface area to be colonised by fungi and bacteria (Scharler 2012). The high degree of nutrient cycling of the limiting nutrient corroborates the notion that both the larger (crabs, gastropods) and smaller (leaf litter fauna) invertebrate communities are of utmost importance in the recycling process along with the microbial organisms.

Few whole ecosystem studies have been reported in the literature that include the three macronutrients, and we compare indices pertinent to our work to those calculated in one such study of a temperate shallow coastal ecosystem

of the Sylt-Rømø Bight, Germany (Baird et al. 2008). We calculated a higher TST for C (from two to ten times), highest contributors to which were the mangrove trees and throughputs through the dissolved organic and inorganic nutrient compartments. On the contrary, the TST of N and P were considerably lower on Twin Cays (0.1–0.5 times for N and 0.01–0.2 times for P) compared to the Sylt-Rømø Bight. Recycling of nutrients (as FCI) was lower on Twin Cays for C and N as compared to the Sylt-Rømø Bight, and recycling of P was comparable only for the Twin Cays dwarf zone (ca. 80 %), but lower in the fringe and transition zones. Mangrove trees, which contribute a considerable amount to throughput, have overall lower recycling rates compared to the prominent primary producers in the Sylt-Rømø Bight. When comparing the FCI normalised by P, we obtained a C:N:P_{FCI} of 0.2:0.5:1 for the Bight, and 0.2:0.3:1 for Twin Cays (mean of zones). N recycling was thus proportionally lower on Twin Cays, perhaps as a result of the microbial mat activities. The recycling of N was, however, lower only in the fringe and dwarf zones (0.2:0.2:1 and 0.1:0.2:1, respectively), whereas it was highest in the transition zone (0.6:1:1). In the fringe, there was probably some N supplied by the sea, whereas in the dwarf zone it was supplied by the extensive microbial mats.

A comparison of the nutrient limitations between the oligotrophic Twin Cays system to one such other study of the meso- to eutrophic Chesapeake Bay system (Ulanowicz and Baird 1999) revealed both similarities and differences. In both ecosystems, about 50 % of recipient compartments were limited by P. However, a large proportion of these comprised fish species in the Chesapeake system, which were absent from the Twin Cays model. Only 3 % of compartments were C limited in the former, whereas 12 % were C limited on Twin Cays. The limiting flows from the source compartments revealed further differences. Where 98 % of flows from source compartments were P limited on Twin Cays, this amounted to 52 % for P, and 43 % for N in Chesapeake Bay (Ulanowicz and Baird 1999). Although the two studies used the same algorithms to calculate nutrient limitations, there are two major differences due to network construction which may influence this comparison. Firstly, the network structure is different, which is mainly due to the nature of the ecosystems (e.g. mangrove trees and associated insects, lack of water column on Twin Cays). Secondly, whereas for the Twin Cays networks, the integrity of the measured stoichiometry of compartments was carried through network building and the layered balancing procedure (Online Resource 1), the Chesapeake C, N and P networks were constructed and balanced separately (Ulanowicz, personal communication).

Recycling was an important mechanism on Twin Cays to provide adequate amounts of nutrients to the food web, aided by the relatively high transfer efficiencies of especially N and P between trophic levels, resulting in a substantial decrease of C:N and C:P at trophic levels ≥II. Calculations of the compartmental nutrient limitations have revealed the dominance of P limitation, followed by N, implying that both P and N demands are sometimes unmet. Efficiencies of transfer were of similar magnitude at all trophic levels, but higher for P in the dwarf forest zone compared to the fringe or transition forest zones. In a previous study, the severe P limitation of mangrove trees in the dwarf forest zone has been highlighted through fertilisation experiments and growth responses, and a N or N+P limitation in the fringe and transition zones (Feller et al. 2002). Although our study calculated P limitations for all trees in all forest zones, the sensitivity coefficients for N were very close to those of P. The analysis of limiting flows on the other hand showed that P was depleted proportionally the fastest from most compartments, revealing an overall shortage of P on Twin Cays. The microbial mats on the other hand may have contributed to the enrichment in N relative to P across the food web supporting various trophic levels. Overall, the P limitation of the primary producers was repeated in some, but not all compartments at higher trophic levels. Although the first-order tree consumers were similarly limited by P, the leaf litter consumers (crabs, larger gastropods, leaf litter fauna) were limited by N. This pattern was repeated in all forest zones.

In conclusion, we found high recycling rates for the nutrient that showed higher transfer efficiencies and was the limiting nutrient. The compartmental nutrient limitation of the primary producers was repeated for some, but not for all higher trophic level groups. Significant differences in C:N:P were found between primary producers, heterotrophs and abiotic compartments, however not between forest zones. C:N:P decreased with trophic level, where the largest differences between trophic levels were apparent for C:P. The analysis of flows revealed a comparatively faster source node depletion rate for P. P was thus the limiting flow constituting a bottleneck for nutrient transfers in the Twin Cays ecosystem which possibly influences food web structure (e.g. Sterner and Elser 2002), and population (Andersen et al. 2004) and system growth.

The results and conclusions from this study are based on networks that were partly constructed from system-specific data, and partly from data originating from the literature. As it is not possible to measure each flow in a network, supplements from the literature are in general necessary in ecological network analysis; however, these may introduce errors in model structure. In addition, another common drawback in network construction, applicable to the Twin Cays networks, is the lack of species-specific information for each single species and changes thereof over time, resulting in a temporal snapshot. The interpretations from our study arose from networks that were constructed

as best as possible within the framework of this study. To increase the level of confidence more system-specific data are needed, especially increased temporal resolution would assist in interpreting variability.

Author contribution statement U. M. S. collated data, built and analysed networks, and wrote the manuscript. R. E. U. developedthe network analysis methodology. All authors provided input data to the network analysis andto the manuscript.

Acknowledgments Funding for this study was provided by a US-National Science Foundation Biocomplexity grant (DEB-998 1483). Fieldwork was conducted on the Carrie Bow Cay field station of the Smithsonian Institute. M. Carpenter and A. Chamberlain, Q. Roberts, V. Brenneis, B. Smallwood and D. Thornton are gratefully acknowledged for assistance in the field. Q. Roberts, V. Brenneis and P. Zelanko helped with C and N elemental analysis at the Geophysical Laboratory, Carnegie institution of Washington. M. F. and M. J. W. gratefully acknowledge support from the Smithsonian Institution's Loeb Fellowship and the Carnegie Institution of Washington, M. E. J. M. gratefully acknowledges the laboratory of D. Capone for material and instrumental support. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US government.

References

Allen AP, Gillooly JF (2009) Towards an integration of ecological stoichiometry and the metabolic theory of ecology to better understand nutrient cycling. Ecol Lett 12:369–384

Allesina S, Bondavalli C (2004) WAND: an ecological network analysis user-friendly tool. Environ Model Softw 19:337–340

Alongi DM (1988) Bacterial productivity and microbial biomass in tropical mangrove sediments. Microb Ecol 15:59–79

Alongi DM, Wattayakorn G, Pfitzner J et al (2001) Organic carbon accumulation and metabolic pathways in sediments of mangrove forests in southern Thailand. Mar Geol 179:85–103

Andersen T, Elser JJ, Hessen DO (2004) Stoichiometry and population dynamics. Ecol Lett 7:884–900

Anderson DM, Glibert PM, Burkholder JM (2014) Nutrient sources, harmful algal blooms and eutrophication: composition, and consequences. Estuaries 25:704–726

Aspila K, Agemian H, Chau A (1976) A semi-automated method for the determination of inorganic, organic and total phosphatein sediments. Analyst 101:186–197

ATLSS (across trophic levels system simulation). http://www.cbl.umces.edu/~atlss/ATLSSdetail.html. Accessed July 2010

Baird D, Asmus H, Asmus R (2008) Nutrient dynamics in the Sylt-Rømø Bight ecosystem, German Wadden Sea: an ecological network analysis approach. Estuar Coast Shelf Sci 80:339–356

Bradshaw C, Kautsky U, Kumblad L (2012) Ecological stoichiometry and multi-element transfer in a coastal ecosystem. Ecosystems 15:591–603

Carter MD, Suberkropp K (2004) Respiration and annual fungal production associated with decomposing leaf litter in two streams. Freshwater Biol 49:1112–1122

Cintrón G, Schaeffer Novelli Y (1984) Methods for studying mangrove structure. In: Snedaker SC, Snedaker JG (eds) Mangrove ecosystem: research methods. UNESCO/SCOR, Paris, pp 91–113

Clark KB, DeFreese D (1987) Population ecology of Caribbean Ascoglossa (Mullusca: Opisthobranchia): a study of specialized algal herbivores. Am Malacol Bull 5:259–280

Coma R, Ribes M, Gili J-M, Zabala M (1998) An energectic approach tot he study of life-history traits of two modular colonial benthic invertebrates. Mar Ecol Prog Ser 162:89–103

Cross WF, Benstead JP, Rosemond AD, Bruce Wallace J (2003) Consumer-resource stoichiometry in detritus-based streams. Ecol Lett 6:721–732

Cross WF, Benstead JP, Frost PC, Thomas SA (2005) Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives. Freshwater Biol 50:1895–1912

Diaz H, Conde JE (1998) On the food sources for the mangrove tree crab *Aratus pisonii* (Brachyura: Grapsidae). Biotropica 20:348–350

Ellison AM, Farnsworth EJ (1992) The ecology of Belizean mangrove-root fouling communities: patterns of epibiont distribution and abundance, and effects on root growth. Hydrobiologia 247:87–98

Evans-White MA, Stelzer RS, Lamberti GA (2005) Taxonomic and regional patterns in benthic macroinvertebrate elemental composition in streams. Freshwater Biol 50:1786–1799

Feller IC (2002) The role of herbivory by wood-boring insects in mangrove ecosystems in Belize. Oikos 97:167–176

Feller IC, Chamberlain A (2007) Herbivore responses to nutrient enrichment and landscape heterogeneity in a mangrove ecosystem. Oecologia 153:607–616

Feller IC, Mathis WN (1997) Primary herbivory by wood-boring insects along an architectural gradient of *Rhizophora mangle*. Biotropica 29:440–451

Feller IC, McKee KL, Whigham DF, O'Neill JP (2002) Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. Biogeochemistry 62:145–175

Finn JT (1980) Flow analysis of models of the Hubbard Brook ecosystem. Ecology 61:562–571

Fogel ML, Wooller MJ, Cheeseman J et al (2008) Unusually negative nitrogen isotopic compositions ($\delta^{15}N$) of mangroves and lichens in an oligotrophic, microbially-influenced ecosystem. Biogeosciences 5:1693–1704

Gili J-M, Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol Evol 13:316–321

Hillebrand H, Borer ET, Bracken MES et al (2009) Herbivore metabolism and stoichiometry each constrain herbivory at different organizational scales across ecosystems. Ecol Lett 12:516–527

Hirata H, Ulanowicz RE (1984) Information theoretical analysis of ecological networks. Int J Syst Sci 3:261–270

Jin-Eong O, Khoon G, Clough B (1995) Structure and productivity of a 20-year-old stand of *Rhizophora apiculata* Bl. mangrove forest. J Biogeogr 22:417–424

Jørgensen LA, Jørgensen SE, Nielsen SN (1991) ECOTOX: ecological modelling and ecotoxicology. Elsevier

Joye SB, Lee RY (2004) Benthic microbial mats: Important sources of fixed nitrogen and carbon to the Twin Cays, Belize ecosystem. Atoll Res Bull 528:1–24. doi:10.5479/si.00775630.528.1

Kathiresan K, Bingham BL (2001) Biology of mangroves and mangrove ecosystems. Adv Mar Biol 40:81–251

Kensley B, Schotte M (1989) Guide to the marine isopod crustaceans of the Caribbean

Koch V, Wolff M (2002) Energy budget and ecological role of mangrove epibenthos in the Caeté estuary, North Brazil. Mar Ecol Prog Ser 228:119

Kohlmeyer J, Bebout B (1986) On the occurrence of marine fungi in the diet of *Littorina angulifera* and observations on the behavior of the periwinkle. Mar Ecol 7:333–343

Koltes KH, Tschirky JJ, Feller IC (1998) Carrie bow Cay, Belize. In: Kjerfve B (ed) CARICOMP—Caribb. coral reef, Seagrass mangrove sites. UNESCO, Paris, pp 79–94

Lange OL, Büdel B, Meyer A et al (2000) Lichen carbon gain under tropical conditions: water relations and CO_2 exchange of three *Leptogium* species of a lower montane rainforest in Panama. Flora 195:172–190

Lapointe BE, Littler MM, Littler DS (1992) Nutrient availability to marine macroalgae in siliclastic versus carbonate-rich coastal waters. Estuaries 15:75–82

Lee RY (2006) Primary production, nitrogen cycling and the ecosystem role of mangrove microbial mats on Twin Cays, Belize

Lee R, Joye S (2006) Seasonal patterns of nitrogen fixation and denitrification in oceanic mangrove habitats. Mar Ecol Prog Ser 307:127–141

Lee RY, Porubsky WP, Feller IC et al (2008) Porewater biogeochemistry and soil metabolism in dwarf red mangrove habitats (Twin Cays, Belize). Biogeochemistry 87:181–198

Liebig JJ (1840) Chemistry and its application to agriculture and physiology. Taylor and Walton, London

Littler MM, Taylor PR, Littler DS et al (1985) The distribution, abundance and primary productivity of submerged macrophytes in a Belize barrier-reef mangrove system. Atoll Res Bull 289:1–22. doi:10.5479/si.00775630.289.1

Machiwa JF, Hallberg RO (2002) An empirical model of the fate of organic carbon in a mangrove forest partly affected by anthropogenic activity. Ecol Modell 147:69–83

MacIntyre IG, Toscano MA, Lighty RG, Bond GB (2004) Holocene history of the mangrove islands of Twin Cays, Belize, Central America. Atoll Res Bull 510:1–18

McClanahan TR (1998) Predation and the distribution and abundance of tropical sea urchin population. J Exp Mar Bio Ecol 221:231–255

McKee KL (1995) Mangrove species distribution and propagule predation in Belize: an exception to the dominance predation hypothesis. Biotropica 27:334–345

McKee KL (2011) Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. Estuar Coast Shelf Sci 91:475–483

McKee KL, Cahoon DR, Feller IC (2007) Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. Glob Ecol Biogeogr 16:545–556

McKeon CS, Feller IC (2004) The supratidal fauna of Twin Cays, Belize. Atoll Res Bull 526:1–22. doi:10.5479/si.00775630.526.1

Middleton BA, McKee KL (2001) Degradation of mangrove tissues and implications for peat formation in Belizean island forests. J Ecol 89:818–828

Miller M, Palojärvi A, Rangger A et al (1998) The use of fluorogenic substrates to measure fungal presence and activity in soil. Appl Environ Microbiol 64:613–617

Mitten S, McKeon CS, Feller IC (2004) Winter and summer bird communities of Twin Cays, Belize. Atoll Res Bull 527:1–20. doi:10.5479/si.00775630.527.1

Modlin RF (1996) Contributions to the ecology of Paranebalia belizensis from the waters off central Belize, Central America. J Crustac Biol 16:529–534

Nordhaus I (2004) Feeding ecology of the semi-terrestrial crab *Ucides cordatus cordatus* (Decapoda: Brachyura) in a mangrove forest in northern Brazil. Thesis, Zentrum für Tropenökologie, University of Bremen

Perry DM (1988) Effects of associated fauna on growth and productivity in the red mangrove. Ecology 69:1064–1075

Persson J, Fink P, Goto A et al (2010) To be or not to be what you eat: regulation of stoichiometric homeostasis among autotrophs and heterotrophs. Oikos 119:741–751

Redfield AC (1934) On the proportions of organic derivatives in sea water and their relation to the composition of plankton. In: Laboratory LS-F (ed) James Johnstone memorial volume. University Press, Liverpool, pp 176–192

Rodriguez W, Feller IC (2004) Mangrove landscape characterization and change in Twin Cays, Belize, using aerial photography and Ikonos satellite data. Atoll Res Bull 513:1–24. doi:10.5479/si.00775630.513.1

Scharler U (2012) Whole food-web studies: mangroves. In: Wolanski E, McLusky DS (eds) Treatise on estuarine coastal science. Academic Press, Waltham, pp 271–286

Schwinghamer P, Hargrave B, Peer D, Hawkins CM (1986) Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. Mar Ecol Prog Ser 31:131–142

Smith VH, Tilman GD, Nekola JC (1999) Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environ Pollut 100:179–196

Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton

Sterner RW, George NB (2000) Carbon, nitrogen, and phosphorus stoichiometry of cyprinid fishes. Ecology 81:127–140

Taylor PR, Littler MM, Littler DS (1986) Escapes from herbivory in relation to the structure of mangrove island macroalgal communities. Oecologia 69:481–490

Ulanowicz RE (1986) Growth and development

Ulanowicz RE, Abarca-Arenas LG (1997) An informational synthesis of ecosystem structure and function. Ecol Modell 95:1–10

Ulanowicz RE, Baird D (1999) Nutrient controls on ecosystem dynamics: the Chesapeake mesohaline community. J Mar Syst 19:159–172

Ulanowicz RE, Kay JJ (1991) A package for the analysis of ecosystem flow networks. Environ Softw 6:131–143

Ulanowicz RE, Scharler UM (2008) Least-inference methods for constructing networks of trophic flows. Ecol Model 210:278–286

Ulanowicz RE, Bondavalli C, Heymans JJ, Egnotovich MS (1999) Network analysis of trophic dynamics in South Florida Ecosystem, FY 98: the mangrove ecosystem. http://www.cbl.umces.edu/~atlss/mngrv701.html. Accessed Nov 2012

Vanni MJ (2002) Nutrient cycling by animals in freshwater ecosystems. Annu Rev Ecol Syst 33:341–370

Vanni MJ, Flecker S, Hood JM (2002) Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. Ecol Lett 5:285–293

Wooller M, Smallwood B, Jacobson M, Fogel M (2003) Carbon and nitrogen stable isotopic variation in *Laguncularia racemosa* (L.) (white mangrove) from Florida and Belize: implications for trophic level studies. Hydrobiologia 499:13–23

Zhang J, Liu SM, Ren JL et al (2007) Nutrient gradients from the eutrophic Changjiang (Yangtze River) Estuary to the oligotrophic Kuroshio waters and re-evaluation of budgets for the East China Sea Shelf. Prog Oceanogr 74:449–478

Zhang Z-S, Song X-L, Lu X-G, Xue Z-S (2013) Ecological stoichiometry of carbon, nitrogen, and phosphorus in estuarine wetland soils: influences of vegetation coverage, plant communities, geomorphology, and seawalls. J Soils Sediments 13:1043–1051

Zuccarello GC, Yeates PH, Wright JT, Bartlett J (2001) Population structure and physiological differentiation of haplotypes of *Caloglossa leprieurii* (Rhodophyta) in a mangrove intertidal zone. J Phycol 37:235–244