

Base metal fluxes from fig trees to soil on Barro Colorado Island, Panama: potential contribution of the common frugivorous bat *Artibeus jamaicensis*

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Abstract The contribution of animals to element fluxes in ecosystems is little known. We therefore estimated the contribution of a common frugivorous bat species (Phyllostomidae: *Artibeus jamaicensis*) to the base metal fluxes (Ca, Mg, and K) from fig trees to soil in a tropical lowland forest on Barro Colorado Island (BCI) because figs provide large parts of the Ca required by these mammals. We chose three individual old-growth fig trees on each of four geological units of BCI varying in soil exchangeable base metal concentrations. To assess element fluxes, we determined internal base metal cycling via canopy exchange and litterfall, external input through bulk and dry deposition, and contributions of bats through pellets and bat faeces as well as element absorption in bats. Assuming a consumption of 20 % of the total fig production by *A.*

jamaicensis, total mean fluxes from fig trees to soil were $24 \pm 7 \text{ g m}^{-2} \text{ year}^{-1}$ for Ca, 4.6 ± 1.6 for Mg, and 21 ± 4 for K, respectively. The largest part of Ca and Mg was cycled as bulk litterfall (79 ± 9 and 62 ± 15 %, respectively) and of K as canopy leaching (56 ± 12 %). *A. jamaicensis* contributed 1.7 ± 0.5 , 2.3 ± 0.6 , and 6.1 ± 1.8 % to the total fluxes of Ca, Mg and K under fig trees, respectively. The contribution of *A. jamaicensis* to the base metal fluxes below the fig canopy was similar to that of bulk deposition. Our results demonstrate that the contribution of a single frugivorous mammal species to internal base metal cycling in a tropical ecosystem may be similarly important as bulk deposition and can have measurable effects on local soil fertility.

Keywords *Artibeus jamaicensis* · Canopy budget · *Ficus insipida* · Keystone species · Litterfall · Panama · Species-specific nutrient cycling · Tropical lowland forest

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We dedicate this manuscript to the late Elisabeth K.V. Kalko who inspired our work.

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Introduction

Studies of mineral cycles in tropical ecosystems traditionally analyze transport of matter and elements via litterfall (e.g., McDonald and Healey 2000; Yavitt et al. 2004), and element fluxes in ecosystem solutions such as throughfall and stemflow (e.g., Cavelier et al. 1997; Hölscher et al. 2003; Hofhansl et al. 2011; Macinnis-Ng et al. 2012; McDowell 1998) or both (e.g. Golley et al. 1976; Tanner 1980). Fluxes of elements are usually separated in internal cycling including litterfall and canopy exchange processes, and external inputs through wet (usually measured as bulk deposition including the soluble part of coarse particulate dry deposition collected with open-top collectors) and dry deposition from the atmosphere (Hofhansl et al. 2011; Staelens et al. 2008; Ulrich 1983). However, the influence of herbivorous and frugivorous mammals, which may play an important role as seed dispersers (e.g., Terborgh and Wright 1994) is seldom considered in quantifying ecosystem-internal element fluxes although considerable parts of the aboveground biomass of trees can be consumed by animals (Coley and Barone 1996). In temperate forests, a number of studies have demonstrated that insect herbivores influence mineral and nutrient cycling (Hollinger 1986; Hunter et al. 2003; McDowell and Likens 1988; Stadler et al. 1998, 2001; Michalzik and Stadler 2005; Reynolds and Hunter 2001) by transport of minerals and nutrients in seeds, plant debris, faeces, excretes like honeydew, and as cadavers. Besides direct animal-induced fluxes, there are possible indirect animal-induced fluxes including mineral and nutrient leaching from damaged plant cells or plant responses to herbivory (Tukey 1970). Few studies addressed the influence of mammalian herbivores on mineral and nutrient transport in tropical forests (Feeley and Terborgh 2005; Fonte and Schowalter 2005; Stevenson and Guzmán-Caro 2010; Wolf et al. 2013) but none of them quantified the contribution of mammalian herbivores to total aboveground element fluxes.

Calcium plays a crucial role in vertebrates, particularly in reproduction, because Ca is essential for growth and skeletal development of the offspring (Barclay 1994; Kwiecinski et al. 2003; Stern et al. 1997; Studier et al. 1994; Studier and Kunz 1995). Among vertebrates, bats and birds particularly rely in their reproduction on Ca availability, because the parents have to provide all

the Ca necessary for the development of their offspring until the young are almost fully grown (Barclay 1994; O'Brien et al. 1998). In plants, Ca forms an important part of many proteins, as it controls stomata opening and thus respiration, contributes to the stabilization of cell membranes, and affects the synthesis of secondary walls and lignifications. Hence, Ca availability strongly influences forest and ecosystem development and functioning (Marschner 1995; McLaughlin and Wimmer 1999). All base metals (Ca, Mg, K) are delivered to plants via uptake through fine roots in the organic-rich forest floor and mineral soils. In soil, Ca is mainly delivered via cation exchange to the plants. In the internal element cycling of forest ecosystems, Ca is mostly cycled via litterfall while K fluxes are greatest in throughfall because of leaching from plant tissues. Magnesium is cycled by litterfall and throughfall to a similar extent (Chapin 1980; Parker 1983; Vitousek and Sanford 1986). Cycling of minerals via litterfall and throughfall is influenced by crown area and leaf area, particular events such as insect outbreaks, canopy structure and leaf roughness (Levia and Frost 2006), and the soil mineral status (Parker 1983; Vitousek and Sanford 1986). In turn, availability of exchangeable base metals in soils determines concentrations of base minerals in plant tissues such as fruits and leaves (Vitousek 1984), which subsequently drive mineral availability and thus the ability of animals to satisfy their nutritional needs.

On Barro Colorado Island (BCI), the fig tree *Ficus insipida* Willd. (Moraceae) is a keystone species for frugivores because of its abundance, asynchrony in fruiting, production of large crops and high nutritional value (Janzen 1979; Terborgh 1986; Wendelin et al. 2000). Particularly, fig fruits contain a high Ca concentration compared to other fruits (Albrecht 2012; O'Brien et al. 1998). *Ficus insipida* is a pioneer tree mainly found in the secondary forest on the north-eastern half of the island and along the shoreline of BCI (Albrecht 2012). The fig species occurs on all four geologic units of BCI (Albrecht 2012) representing a gradient of fertile to moderately fertile soils (Barthold et al. 2008; Dieter et al. 2010; Johnsson and Stallard 1989; Messmer et al. 2014; Wright et al. 2011). Density of *F. insipida* decreased in the last decades from >5 trees per hectare (Morrison 1978) to <1 tree per hectare (Albrecht 2012). Most *F. insipida* trees on BCI have established about 90–150 years ago when

agriculture on BCI was abandoned. The pioneer trees can no longer propagate under the canopy of the current dense old-growth forest (Albrecht 2012). Following this on-going decline in density of *F. insipida*, fruit production will strongly decline, affecting a wide range of frugivores feeding on *F. insipida*, such as *Artibeus jamaicensis* (Chiroptera: Phyllostomidae) (Handley and Leigh 1991; Morrison 1978). Bats are the main dispersers of fig trees and move minerals laterally because they carry fruits away to a temporary feeding roost, mostly within 25–200 m of the source tree, where the minerals are partly deposited (Handley and Morrison 1991; Morrison 1978). Generally, several dozens to several hundreds of bats usually feed on one fruiting fig tree (Kalko et al. 1996; Korine et al. 2000), carrying several thousands of fruits away. Thus, fruit bats are distributing large quantities of plant material containing Ca and other base minerals to different sites in the vicinity of a fruiting fig tree.

In this study, we determined Ca, Mg and K fluxes from *F. insipida* to soil through litterfall, throughfall and stemflow. Furthermore, we estimated the contribution of the bat species *A. jamaicensis* to Ca, Mg and K fluxes via dropped pellets and faeces based on Ca, Mg and K concentration data in fig fruits, pellets and faeces taken from Albrecht (2012). Retention in the animals was estimated based on mineral uptake data collected in feeding experiments of *A. jamaicensis* (Albrecht 2012). We tested two future scenarios, first assuming that the consumption of bats declines to 5 % of the fruits of *F. insipida* because population density of *A. jamaicensis* decreases as the abundance of figs decreases, and alternatively, that the fruit consumption increases to 20 % because of an increase of non-resident bats searching for food resources. Furthermore, we expected that Ca concentrations in fruit tissues varied according to soil chemical properties although likely in a less pronounced way because plants tend to maintain a genetically determined mineral concentration in their tissues with comparatively small variation. We further expected that fluxes of base metals in litterfall and throughfall are lower on mineral-poor soils compared to mineral-rich soils, which should enhance the contribution of bats to mineral cycling on mineral-poor soils. Consequently, the contribution of bats to the element fluxes from trees to soil should increase with decreasing soil Ca concentrations.

Materials and methods

Study site

The study sites are located in Panama on BCI in the Gatún Lake at latitude 9°08'–9°11'N and longitude 79°49'–79°52'W (Fig. 1). The climate is classified as Tropical Monsoon [Am] in the Koeppen Climate Classification with a mean annual precipitation (MAP) of 2600 mm and a pronounced dry season between January and April with an average rainfall of around 90 mm (Windsor 1990). Mean annual temperature is ca. 27 °C (Leigh 1999). Vegetation is classified as a Tropical Moist Forest in the Holdridge system (Holdridge and Budowski 1956) with old-growth forest in the southern part of the island and a ~100 year old secondary forest in the northern and eastern part (Foster and Brokaw 1996).

Barro Colorado Island consists of four geological units (Fig. 1). Bohio is deeply dissected and is made up of basaltic conglomerates, Caimito marine (in the following C. marine) on the small north-eastern outcrop is composed of limestone and tuffaceous sand and siltstone, and the flat Caimito volcanic (C. volcanic) of basaltic agglomerates in a sandy matrix. The island is capped by a flat lying andesitic lava flow building a plateau (Andesite) (Johnsson and Stallard 1989; Woodring 1958). Soils on BCI are fertile with respect to pH, Ca and Mg concentrations, but poor in K compared to other lowland tropical forests (Barthold et al. 2008; Dieter et al. 2010; Messmer et al. 2014; Wright et al. 2011).

Fig tree *Ficus insipida*

We selected three individuals of *F. insipida* on each of the four geological units in the secondary forest (Fig. 1). We measured stemflow, throughfall and litterfall in the years 2011 and 2012 and sampled soils at a distance of <3 m from the stem in the 0–10 cm depth interval during the dry season 2011. The canopy area of each fig tree was determined by considering the canopy as a polygon with 12 edges with an angle of 30° between each side and averaged $238 \pm 100 \text{ m}^2$ (SD; $n = 11$) (Table 1).

In the year 2011, the tree F11 died after losing a big branch during a heavy storm in 2010. Until this tree died, we sampled throughfall and stemflow, while litterfall almost ceased in 2011. Density of *F. insipida* was ~1 canopy tree per hectare in the secondary forest in 2011 (Albrecht 2012). Total amounts of fruits

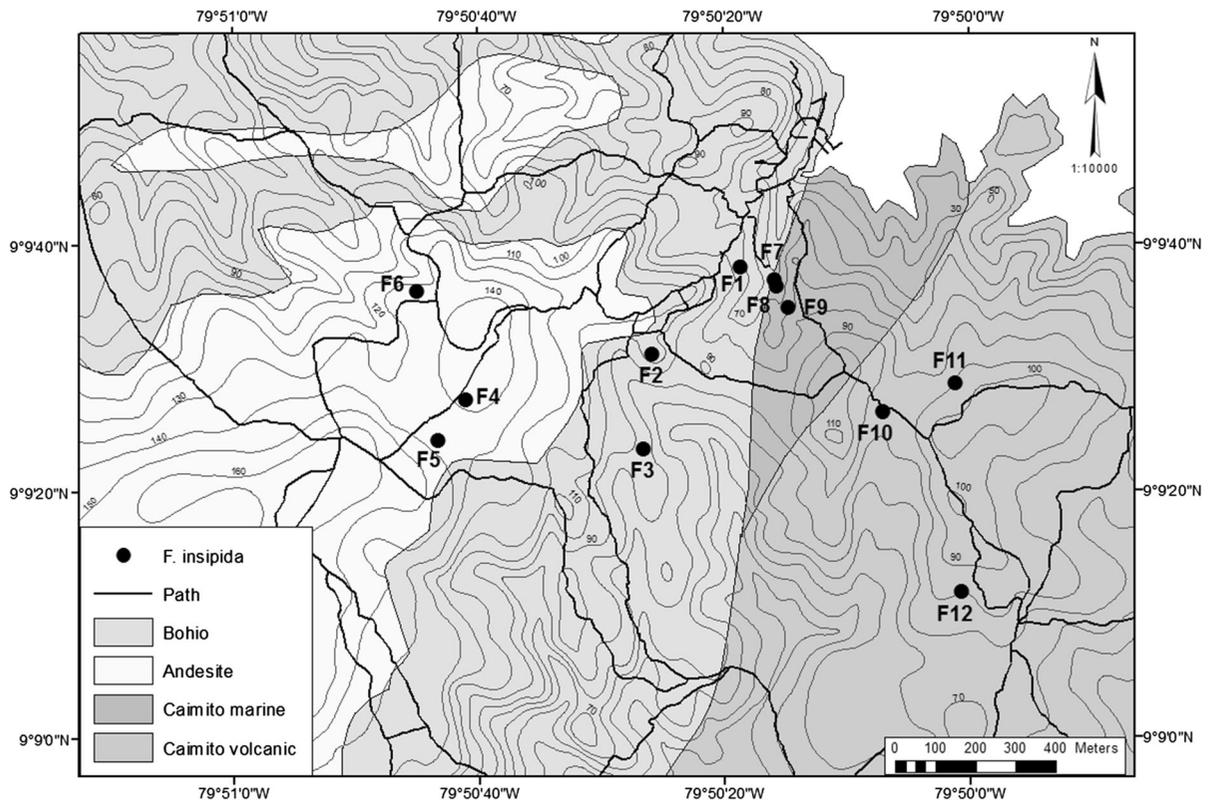


Fig. 1 Study sites on Barro Colorado Island, F1–F3 on Bohio, F4–F6 on Andesite, F7–F9 on C. marine, F10–F12 on C. volcanic. All sites are located in the mature secondary forest on the north-eastern half of the island

Table 1 Crown area and base metal concentrations in fig fruits used for the calculation of the bat contribution to aboveground fluxes

	Crown area (m ²)	Ca (mg g ⁻¹)	Mg (mg g ⁻¹)	K (mg g ⁻¹)
Bohio	301 ± 183	10.8 ± 3.7	2.6 ± 0.4	29.1 ± 7.5
Andesite	217 ± 69	8.2 ± 2.5	3.1 ± 0.2	38.5 ± 8.1
C. marine	230 ± 10	15.2 ± 2.5	2.2 ± 0.5	35.0 ± 3.6
C. volcanic	188 ± 68	8.5 ± 1.4	3.1 ± 0.4	29.9 ± 1.1

Crown areas ($n = 3$ on Bohio, Andesite and C. marine; $n = 2$ on C. volcanic because tree F11 died in 2011) and base metal concentrations of fruits (Bohio, $n = 8$; Andesite, $n = 6$; C. marine, $n = 5$; C. volcanic, $n = 3$). Each individual sample included at least 10 dried fruits). Base metal concentrations of figs were taken from Albrecht (2012)

per tree were estimated by using the data of Morrison (1978) who reported 113 fruits per square meter crown area and the respective crown area of the individual trees (see below in Eq. 1).

Bats *Artibeus jamaicensis*

The estimated population of *A. jamaicensis* is around 3000 individuals on the 15.6-km² island which results

in a density of around 2 individuals per hectare (Handley and Leigh 1991). The diet of *A. jamaicensis* consists to 75 % of fruits of *F. insipida*. Each single *A. jamaicensis* consumes 7–9 fig fruits daily which sums up to around 2300 fruits yearly (10–15 % of the totally available fig fruits per hectare). Based on this range we set our lower scenario to a consumption of 5 % and the higher one to a consumption of 20 % of the total fruit stock. A single fig fruit weighs on average about 9 g

with a water content of about 80 % (Morrison 1978; Albrecht 2012). This proportion results in an annual consumption per bat and hectare of 2100–2700 fruits. *Artibeus jamaicensis* exhibits a particular fruit handling behavior: The bat carries the whole fruit to a feeding roost 25–200 m away from the fruiting tree, where the juice is extracted by pressing a bole of pulp with their strong tongue to their ridged palate. The juice is swallowed and dry, squeezed-out pellets are spat out (Handley and Morrison 1991). Dropped pellets then may be found in small piles, distinct clusters or are broadly dispersed, depending on the height of the feeding roosts. The area covered by pellets of feeding bats can be up to 100 m² (Handley and Morrison 1991).

Albrecht (2012) estimated in feeding experiments the fractions of the mineral content in fruits (Table 2) which were taken up by bats (considered in this study as output of the system) or are released to the soil of the feeding roosts as faeces and dropped pellets (considered as inputs to the system of which the faeces are separate additional fluxes to the soil while the pellets represent a fraction included in total litterfall which, however, could not be separated from our litterfall samples). Concentrations of Ca, Mg and K in whole fruits were taken from Albrecht (2012) for each of the geological units and used for our flux estimations (Table 1). It was not possible to collect fruits of each single tree equipped for this study because of the irregular fruiting phenology. Therefore, partly fruits of adjacent fruiting trees on the same geological unit were sampled and used for calculations.

The fractional contribution of *A. jamaicensis* to transport of element *i* per fig tree ($AJT_{F,i}$) was calculated with Eq. 1:

$$AJT_{F,i} = (113 \times CA_F \times w_d \times (c_i/1000)) \times bat_{prop} \quad (1)$$

Table 2 Distribution of base metals among pellets, faeces and uptake by *A. jamaicensis*

	Ca (%)	Mg (%)	K (%)	Na (%)
Pellets	80	42	34	56
Faeces	16	45	31	34
Uptake	4	13	35	10

Data compiled from Albrecht (2012)

where CA is the crown area of the single tree, w_d is the dry mass of figs averaging 1.65 g, c_i is the concentration of Ca, Mg and K in mg g⁻¹ in the fig fruit, respectively, and bat_{prop} is the proportion of a crop these bats are estimated to consume, i.e. 0.05 and 0.2, respectively (corresponding to 5 or 20 %). Afterwards, the contribution of pellets, faeces and uptake by *A. jamaicensis* to mineral fluxes was calculated according to the element distribution among these three fractions of the bat-processed fruit (Table 2).

Bulk precipitation and throughfall

Bulk precipitation and throughfall were collected in 2-L sampling bottles on which a funnel with a diameter of 115 mm was placed. The whole sampler was made of polyethylene. To reduce contamination with plant debris and soil particles, we used a polyethylene net with a mesh-width of 1 mm placed between the funnel and the sampling bottle. Evaporation was reduced by using a table-tennis ball placed at the bottom of the funnel. Each collector was wrapped with aluminum foil to reduce the impacts of radiation on the collected solution. The sampling bottles and funnels were cleaned prior to installation with deionized water. The sampling bottles were regularly cleaned after each sampling with deionized water and entirely replaced by clean bottles after 1 year. The five sampling bottles of bulk precipitation were located near the research station in the lab clearing at a height of 1 m. Throughfall was collected with nine samplers at a height of 30 cm above ground. We placed the samplers beneath the canopy in a way that only the throughfall below the fig trees was collected. However, an influence of understory on throughfall chemistry cannot be excluded.

Weekly sampling lasted from May to December 2011 and from May to December 2012, corresponding with the onset and the end of the wet season. During the weekly sampling, the volume of each sampler was recorded and bulk precipitation and throughfall solution were bulked proportionally per fig tree and collected for chemical analysis.

Stemflow

Stemflow was measured on each of the 12 selected fig trees. Due to high buttress roots of *F. insipida*, we

constructed a spiral of polyurethane foam around the tree trunk at a height between 1.5 m and 3 m above ground (modified after Likens and Eaton 1970). The gap between the spiral and the stem was closed with silicone sealing. The spiral was connected with a funnel protected with a mesh against input of larger particles, and a blackened hose to a 150-L barrel. The height and the diameter of the water table were measured and weekly stemflow volume was calculated for each single fig tree. Each week, 100 mL of the stemflow water were sampled for chemical analyses. After sampling and measurements the barrel was cleaned.

Litterfall

Litterfall was collected below each fig tree with three litterfall traps, respectively. The litterfall traps were constructed using a square of PVC tubes with a length of 50 cm representing a surface area of 0.25 m². Traps were screened with nylon-mesh with a mesh-width of 1 mm positioned 0.5 m above ground. Litterfall was collected weekly from January 2011 to the end of December 2012. Litterfall traps were bulked and litterfall was separated into fig leaves (FFP), leaves of other species (LFP), and woody and reproductive parts (RFP). The samples were dried to constant weight at 60 °C and stored in sealed bags until transport to Bern, Switzerland, for further chemical analysis.

Chemical analysis

On the day of sampling, samples of bulk precipitation, throughfall and stemflow were filtered (pore-size 4–7 µm, Grade 392, Munktell) and 100-mL aliquots of each sample were frozen until water and air-dried. Litterfall samples were transported to Berne, Switzerland for further chemical measurements.

Soil samples were air-dried, sieved to particle size <2 mm, and exchangeable cations (Ca, Mg and K) were extracted using an unbuffered 1M NH₄NO₃ solution (soil to solution ratio 1:20) by shaking for 2 h at room temperature on an orbital shaker (modified DIN 19730 2008).

The separated samples of litterfall (FFP, LFP, and RFP) of each fig plot were weighed and pooled for the dry and wet seasons of 2011 and 2012, respectively. Samples were ground and a 250 mg sub-sample was digested using HNO₃ and H₂O₂ (ratio 4:1, v/v) in a microwave (MLS Ethos, Germany).

Concentrations of Ca, Mg, K and Na in bulk precipitation, throughfall, stemflow, digests of litterfall samples and soil extracts were measured with flame atomic absorption spectroscopy (AAS, Zeenit 700P, Analytik Jena).

Calculations and statistical analyses

Fluxes of Ca, Mg, K and Na in bulk precipitation and throughfall were calculated as the product of the volume-weighted mean (VWM) concentrations of each rainy season and the total water volume. The unmeasured dry season precipitation (<5% of annual precipitation) was neglected. Data gaps of throughfall samples (<3 %) were filled by the mean VWM concentration of the remaining trees on the respective geological unit on the day of sampling. All our flux estimates refer to the area covered by fig canopies. The fluxes caused by *A. jamaicensis* were additionally scaled from the size of the canopy to the smaller size of the feeding roosts of about 100 m² to estimate the real local soil input.

Stemflow fluxes of each fig tree are based on the VWM concentrations and the total water volumes and were divided by the canopy area of the corresponding fig tree. Data gaps of stemflow volume (25 %) were filled by regression of stemflow on throughfall ($R^2 = 0.34$).

Annual fluxes of Ca, Mg and K in litterfall were calculated by multiplying the concentration in the digested samples with the corresponding litterfall mass per square meter and combining the fluxes of dry and wet season fluxes per year.

Throughfall is the amount of open bulk precipitation that is not retained by the vegetation but passes the canopy layer and is altered chemically through the interaction with the canopy (canopy exchange, CE) and dry deposition (DD). Canopy exchange represents internal fluxes and dry deposition represents external inputs from sea spray or atmospheric particles such as volcanic exudates or dust. To determine the contribution of bulk deposition (i.e. wet deposition + soluble part of the gravitationally settled coarse particulate deposition), dry deposition, and canopy exchange (i.e. retention or leaching of a mineral by the canopy) to throughfall, the canopy budget model of Ulrich (1983) was applied. In most studies, Na⁺ is assumed to have negligible interactions in the canopy because fluxes of these ions are usually large relative to concentrations

in plants (e.g., Lilienfein and Wilcke 2004; Parker 1983; Staelens et al. 2008). To calculate dry deposition, a deposition ratio (DR) was calculated according to Eq. 2:

$$DR = (TF_{Na} + SF_{Na}) / BD_{Na} \quad (2)$$

where TF and SF are the calculated Na fluxes in throughfall and stemflow, respectively, and BD are the Na fluxes in bulk precipitation. Dry deposition was calculated according to Eq. 3:

$$DD_i = DR \times BD_i - BD_i \quad (3)$$

The subscript *i* represents the elements Ca, Mg, and K. Canopy exchange (CE) was calculated with Eq. 4:

$$CE_i = TF_i + SF_i - BD_i - DD_i \quad (4)$$

A positive result for CE indicates net canopy leaching, while a negative result means net canopy uptake of the respective element.

Standard deviations of aboveground fluxes (litterfall, throughfall, stemflow, canopy exchange, bulk precipitation and dry deposition) were calculated using the mean of the variances of the years 2011 and 2012, respectively.

One-way analysis of variance (ANOVA) followed by Tukey's honest significant differences (HSD) post hoc test (with the Spjotvoll/Stoline modification for uneven *n* if necessary) was used to test for significant differences in the water and element fluxes with throughfall and mass, element concentrations and fluxes in the separated litterfall fractions among the geological units. All ANOVAs were performed after testing whether the underlying assumptions were met by Levene's Test and test for normality of the residuals (with/without log-transformation of data). Tukey HSD multiple range tests at the 95 % level were used to test for differences between sites. Statistical analyses were computed with STATISTICA for Windows (STATSOFT, Tulsa, OK, USA).

Results

Precipitation and throughfall fluxes

Water fluxes with precipitation in the wet seasons 2011 and 2012 were 2931 and 2466 mm, respectively. Mean throughfall of the 12 study sites was 2610 and

2133 mm, respectively, without significant differences among the geological units. Mean interception loss was 9 % in 2011 and 12 % in 2012 of precipitation. Mean annual stemflow was 3.8 mm in 2011 and 3.2 mm in 2012, representing <0.2 % of precipitation (Table 3).

Base metal fluxes with throughfall were significantly higher than those with bulk precipitation, particularly for K. The throughfall/bulk deposition ratios ranged from 5 to 20 for Ca, 10 to 45 for Mg, and from 27 to 63 for K, with the highest ratio for all elements on C. volcanic. Ca, Mg and K fluxes with throughfall differed significantly among the geological units. On Andesite, the base metal fluxes were the lowest and on C. volcanic the highest (Table 3).

Base metal fluxes with stemflow were low compared with total throughfall fluxes (throughfall + stemflow). Stemflow accounted for 0.4 % of the Ca fluxes to soil, 0.5 % of Mg fluxes, and 0.8 % of K fluxes and was not significantly different among geological units (Table 3).

Dry deposition and canopy exchange

Average dry deposition of the 12 fig trees in the wet seasons 2011 and 2012 was $6.3 \pm 2.8 \text{ kg ha}^{-1} \text{ year}^{-1}$ of Ca, 2.2 ± 0.7 of Mg, and 4.2 ± 1.9 of K, respectively. The significantly highest dry deposition of Ca and K occurred on C. volcanic and the lowest on Bohio (Table 3). All base metals were net leached from the canopy (i.e. canopy exchange was positive) and the leaching fluxes were consistently higher than dry and bulk deposition together. Average canopy exchange of all 12 fig trees in the years 2011 and 2012 was $33 \pm 25 \text{ kg Ca ha}^{-1} \text{ year}^{-1}$, $12 \pm 11 \text{ kg Mg}$ and $123 \pm 43 \text{ K}$. Canopy leaching of Ca, Mg and K was greatest on C. volcanic and smallest on Andesite (Table 3).

Litterfall

Average litterfall mass of all 12 fig trees in 2011 and 2012 was $13.1 \pm 2.9 \text{ Mg ha}^{-1} \text{ year}^{-1}$. Litterfall mass was not significantly different among the four geological units. Litterfall was higher in 2012 than in 2011 although the difference was only significant for Bohio

Table 3 Water and base metal fluxes with bulk deposition (BD), throughfall (TF), stemflow (SF), dry deposition (DD), and canopy exchange (CE) on four different geological units in the rainy seasons of 2011 and 2012

	Volume (mm year ⁻¹)	Ca (kg ha ⁻¹ year ⁻¹)	Mg (kg ha ⁻¹ year ⁻¹)	K (kg ha ⁻¹ year ⁻¹)
BD ^a	2698 ± 127	4.5 ± 0.2	1.55 ± 0.1	3.0 ± 0.1
TF ^a				
Bohio	2413 ± 44	36 ± 5B	13 ± 2B	137 ± 30AB
Andesite	2419 ± 131	23 ± 6B	10 ± 2B	88 ± 20B
C. marine	2463 ± 112	47 ± 17AB	11 ± 3B	125 ± 24AB
C. volcanic	2388 ± 138	71 ± 27A	31 ± 11A	171 ± 39A
SF ^a				
Bohio	3.9 ± 2.5	0.12 ± 0.07	0.05 ± 0.04	1.05 ± 1.18
Andesite	3.9 ± 0.7	0.14 ± 0.03	0.08 ± 0.04	0.98 ± 0.61
C. marine	3.5 ± 0.7	0.17 ± 0.09	0.05 ± 0.03	0.60 ± 0.26
C. volcanic	4.3 ± 0.8	0.18 ± 0.06	0.09 ± 0.03	0.90 ± 0.24
DD ^a				
Bohio	–	4.2 ± 0.7B	1.6 ± 0.2	2.7 ± 0.5B
Andesite	–	6.7 ± 1.4AB	2.5 ± 0.7	4.4 ± 0.9AB
C. marine	–	5.2 ± 0.7B	1.8 ± 0.2	3.4 ± 0.5AB
C. volcanic	–	9.5 ± 1.9A	2.9 ± 0.5	6.4 ± 1.3A
CE ^a				
Bohio	–	28 ± 5B	10 ± 2B	132 ± 29AB
Andesite	–	12 ± 5C	6 ± 2B	82 ± 19B
C. marine	–	37 ± 17B	7 ± 3B	119 ± 24AB
C. volcanic	–	57 ± 25A	27 ± 10A	162 ± 39A
BD				
Panama ^b		28	4	14
Costa Rica ^c		20	5.4	6.2
Costa Rica ^d		5.2	0.7	5.9
Puerto Rico ^e		13	8.5	4.7
TF				
Panama ^b		35	8	63
Panama ^f		37	10	50
Panama ^g		29.4	7.7	56
Costa Rica ^c		22.3	7.6	58.8
Costa Rica ^d		12.4	3.4	41.1
Puerto Rico ^e		22.7	13.4	51.6
Puerto Rico ^h		21.6	–	67.6
SF				
Costa Rica ^d		6.0	1.7	14.5
Amazonia ⁱ		–	0.3	2.2
Malaysia ^j		–	0.18	0.7
DD				
Costa Rica ^c		5.7	1.5	1.8
CE				
Costa Rica ^c		–3.5	0.7	50.8

Means of the 2 years and standard deviations (for $n = 2$ years from the three replicate measurements for TF, SF, DD, and CE per geological unit considered) are shown. Upper case letters indicate significant differences among the geological units calculated with Tukey HSD post hoc tests ($p < 0.05$)

^a Present study

^b Cavelier et al. (1997)

^c Hofhansl et al. (2011)

^d Hölscher et al. (2003)

^e McDowell (1998)

^f Golley et al. (1976)

^g Macinnis-Ng et al. (2012)

^h McDonald and Healey (2000)

ⁱ Jordan (1978)

^j Radzi Abas et al. (1992)

and *C. marine*. The three considered litterfall fractions contributed similar masses to total litterfall (Table 4).

Average annual base metal flux with litterfall of all 12 fig trees was $265 \pm 78 \text{ kg ha}^{-1} \text{ year}^{-1}$ for Ca, $42 \pm 12 \text{ kg ha}^{-1} \text{ year}^{-1}$ for Mg, and $94 \pm 26 \text{ kg ha}^{-1} \text{ year}^{-1}$ for K. Calcium fluxes with litterfall were significantly lowest on Andesite and Mg fluxes were lowest on *C. marine*, while there were no significant differences in K fluxes among the four geological units. Fluxes of base metals in the litterfall fractions and in total litterfall did not differ significantly between the years 2011 and 2012. On Bohio, significantly higher Ca fluxes occurred with the litterfall of fig leaves (FFP) compared to leave litterfall fractions from non-figs (LFP) and woody and non-reproductive parts (RFP), while there were no significant differences among litterfall fractions concerning Mg fluxes (Table 4). Potassium fluxes were significantly higher in the RFP than in FFP and LFP on *C. marine* and Andesite compared to *C. volcanic* (Table 4).

Fluxes through *A. jamaicensis*

Total mass of fruits averaged $44 \pm 9 \text{ kg}$ per tree with the highest mass on Bohio and the lowest on *C. volcanic* (Table 5). However, differences were not significant either because of similar crown areas (Table 2) and therefore a similar amount of fruits or an overall high variability in the mass of fruits between trees of the same species (Albrecht, 2012). Average base metal yield of the fruits of all 12 trees was $471 \pm 184 \text{ g}$ of Ca, $119 \pm 22 \text{ g}$ of Mg, and $1433 \pm 264 \text{ g}$ of K per tree. Calcium concentrations in fruits differed significantly among the four geological units (Table 5). A removal of only 5 % of the total annual fruit production of a single fig tree by *A. jamaicensis* would correspond to an average mass of $2.2 \pm 0.4 \text{ kg year}^{-1}$, and a consumption of 20 % to $8.7 \pm 1.8 \text{ kg year}^{-1}$, respectively (Table 6).

Fluxes of Ca, Mg and K through pellets, faeces, and absorption induced by *A. jamaicensis* were not significantly different among the geological units (Table 6). Assuming a consumption of 5 % of total fruit production, the average Ca flux of all 12 fig trees induced by *A. jamaicensis* through pellets would be $79 \pm 21 \text{ mg m}^{-2} \text{ year}^{-1}$, and in case of a consumption of 20 % of the fruit production, the average Ca flux would be $316 \pm 87 \text{ mg m}^{-2} \text{ year}^{-1}$. Fluxes of Ca through faeces averaged for all 12 fig trees 15.5 ± 4.6 and $62 \pm 17 \text{ mg m}^{-2} \text{ year}^{-1}$ for 5 and 20 % fruit

consumption, respectively (Table 6A). Average Ca absorption of the 12 fig trees was 3.7 ± 0.02 or $14.7 \pm 0.08 \text{ mg m}^{-2} \text{ year}^{-1}$ for the consumption of 5 and 20 % of the annual fruit production, respectively (Table 6A).

Magnesium fluxes through pellets averaged for all 12 fig trees 10.7 ± 1.5 or $43 \pm 6 \text{ mg m}^{-2} \text{ year}^{-1}$ for the consumption of 5 or 20 %, respectively. The fluxes of Mg by faeces were higher than those by pellets and averaged for all 12 fig trees 11.6 ± 1.6 or $46 \pm 4 \text{ mg m}^{-2} \text{ year}^{-1}$ for 5 and 20 % fruit consumption, respectively. Average Mg absorption was 2.7 ± 0.4 or $11 \pm 1.5 \text{ mg m}^{-2} \text{ year}^{-1}$ (Table 6B).

Of all base metals, *A. jamaicensis* influenced K cycling most strongly. This bat species cycled on average of all 12 fig trees 104 ± 12 or $417 \pm 50 \text{ mg m}^{-2} \text{ year}^{-1}$ K through pellets for 5 and 20 % fruit consumption, respectively. Average K fluxes with faeces were 96 ± 12 or $384 \pm 47 \text{ mg m}^{-2} \text{ year}^{-1}$ for 5 % and 20 % fruit consumption. Absorption of K averaged for all 12 fig trees 107 ± 13 or $426 \pm 52 \text{ mg m}^{-2} \text{ year}^{-1}$ (Table 6C). The three pathways of K flux through bats contributed similar amounts to total bat-induced K fluxes.

Proportional contribution of *A. jamaicensis* to aboveground fluxes

The proportional contributions of bats to fluxes of base metals were not correlated with the concentrations of individual exchangeable cations (Ca, Mg and K) nor with the sum of base metals in soils (Table 7).

If we assumed an average fruit consumption of 12.5 % by *A. jamaicensis*, the largest contribution to the Ca fluxes reaching the soil was consistently via litterfall and canopy leaching accounting together for around $94 \pm 2 \%$ of total Ca fluxes. Minor proportions were contributed by bulk and dry deposition which together accounted for $5 \pm 2 \%$ of total Ca fluxes reaching the soil. The average contribution of bats through pellets, faeces and absorption to Ca cycling was $1.1 \pm 0.3 \%$ (Fig. 2a).

The highest Ca flux caused by bats was the flux via pellets contributing around $0.4 \pm 0.1 \%$ to the Ca fluxes reaching the soil below the fig canopy when assuming 5 % fruit consumption and $1.4 \pm 0.4 \%$ when assuming a consumption of 20 % of fruits by bats. Input of Ca via faeces was 0.07 % (5 % consumption) and 0.3 % (20 % consumption), and was marginally significantly highest

Table 4 Mass of litterfall and base metal fluxes in three litterfall fractions

	Litterfall (Mg ha ⁻¹ year ⁻¹)	Ca (kg ha ⁻¹ year ⁻¹)	Mg (kg ha ⁻¹ year ⁻¹)	K (kg ha ⁻¹ year ⁻¹)
Bohio				
FFP	4.2 ± 1.2	138 ± 39a	16 ± 3	39 ± 18
LFP	4.7 ± 1.6	65 ± 12b	15 ± 6	24 ± 6
RFP	5.4 ± 0.4	84 ± 24ab	16 ± 2	44 ± 14
Σ	14.3 ± 1.3	287 ± 47A	47 ± 7A	108 ± 27
Andesite				
FFP	2.6 ± 0.8	65 ± 23	11 ± 4	23 ± 7b
LFP	4.4 ± 1.1	65 ± 11	15 ± 3	25 ± 3b
RFP	5.1 ± 1.4	64 ± 9	16 ± 8	49 ± 18a
Σ	12.1 ± 2.1	193 ± 24B	41 ± 8A	97 ± 20
C. marine				
FFP	2.6 ± 1.1	110 ± 66	7 ± 2	20 ± 5b
LFP	4.8 ± 0.8	93 ± 9	10 ± 1	33 ± 4ab
RFP	5.0 ± 1.0	104 ± 8	12 ± 4	40 ± 10a
Σ	12.4 ± 1.5	307 ± 58A	29 ± 2B	93 ± 15
C. volcanic				
FFP	3.5 ± 1.2	70 ± 26	17 ± 7	20 ± 12
LFP	5.3 ± 0.9	98 ± 27	19 ± 3	24 ± 3
RFP	6.0 ± 2.0	122 ± 73	18 ± 7	37 ± 15
Σ	13.6 ± 3.4	274 ± 79A	50 ± 13A	76 ± 29

Means of the 2 years and standard deviations (for the three replicates of litterfall fractions and total litterfall measurements per geological unit considered) are shown. Upper case letters indicate significant differences among the geological units, lower case letters among the litterfall fractions ($p < 0.05$)

FFP leaves of fig trees, LFP leaves of other species on the fig plots, RFP woody and reproductive parts on fig plots

Table 5 Total mass of fruits per tree and year, mass of fruits assumed to be consumed by *A. jamaicensis* (5 or 20 %, respectively) and amounts of Ca, Mg and K in the fruit crop

	Bohio	Andesite	C. marine	C. volcanic
Fruit (kg)	56 ± 34	40 ± 13	43 ± 2	35 ± 9
5 % (kg)	3 ± 2	2 ± 1	2 ± 0.1	2 ± 0.5
20 % (kg)	11.2 ± 6.8	8.1 ± 2.6	8.6 ± 0.4	7.0 ± 1.8
Ca (g)	606 ± 369AB	330 ± 106B	651 ± 30A	296 ± 76B
Mg (g)	147 ± 89	126 ± 40	96 ± 4	109 ± 28
K (g)	1629 ± 993	1557 ± 498	1501 ± 69	1045 ± 270

Deviations are standard deviations of three trees per geological unit. Upper case letters indicate significant differences among geological units ($p < 0.05$)

on C. marine and lowest on C. volcanic. Absorption of Ca by bats was significantly highest on Andesite with 0.025 or 0.1 % of total fluxes to the soil, respectively, assuming 5 or 20 % fruit consumption by bats (Fig. 2a). Contributions of absorption to total fluxes to the soil on Bohio, C. marine and C. volcanic were 0.014 ± 0.0003 or 0.057 ± 0.001 %, respectively.

Magnesium was mainly cycled via litterfall and canopy exchange that together accounted for 89 ± 3 % of the Mg fluxes to the soil below the fig

canopy. Contribution of bulk and dry deposition amounted to 9.1 ± 2.6 % of the Mg fluxes to the soil and average contribution of bats was 1.5 ± 0.4 % (Fig. 2b). Contribution of bat faeces to Mg fluxes reaching the soil was higher than the contribution of pellets. Proportional contribution of bats via pellets, faeces and absorption to Mg fluxes reaching the soil were significantly related to the geological units in the order, C. volcanic < Bohio < C. marine < Andesite (One-way ANOVA with Tukey's HSD: F (3,

Table 6 Ca, Mg and K fluxes below the fig canopy

	Bohio	Andesite	C. marine	C. volcanic
(A) Calcium				
	(g m ⁻² year ⁻¹)			
LT	22.2 ± 4.4a	12.8 ± 2.4a	21.4 ± 5.0a	17.6 ± 0.5a
FFP	13.8 ± 2.7ab	6.5 ± 2.0a	11.0 ± 5.5a	5.5 ± 3.9abc
RFP	8.4 ± 2.0b	8.4 ± 0.5a	10.4 ± 0.6a	12.2 ± 3.6a
CE	2.8 ± 0.5AB,c	1.2 ± 0.4B,b	3.7 ± 1.6AB,b	7.2 ± 3.8A,ab
BD	0.45 ± 0.003d	0.5 ± 0.001c	0.5 ± 0.01c	0.5 ± 0.01c
DD	0.42 ± 0.1d	0.7 ± 0.1bc	0.5 ± 0.1c	1.1 ± 0.3bc
	(mg m ⁻² year ⁻¹)			
P*	200	151	281	157
F*	39	30	55	31
A*	9	9	9	9
	(g m ⁻² year ⁻¹)			
Total	26.1 ± 4.8	15.3 ± 2.3	26.4 ± 6.6	26.6 ± 3.8
(B) Magnesium				
	(g m ⁻² year ⁻¹)			
LT	3.2 ± 0.1a	2.7 ± 0.4a	1.9 ± 0.2a	3.1 ± 1.0a
FFP	1.6 ± 0.1b	1.1 ± 0.4b	0.7 ± 0.2b	1.3 ± 1.0ab
RFP	1.6 ± 0.1b	1.6 ± 0.7b	1.2 ± 0.3ab	1.8 ± 0.3a
CE	1.0 ± 0.2AB,c	0.6 ± 0.1B,b	0.7 ± 0.3B,b	3.4 ± 1.7A,a
BD	0.2 ± 0.001d	0.15 ± 0.001c	0.16 ± 0.001c	0.13 ± 0.03b
DD	0.2 ± 0.021B,d	0.25 ± 0.05AB,c	0.18 ± 0.02B,c	0.29 ± 0.03A,ab
	(mg m ⁻² year ⁻¹)			
P*	25	30	22	30
F*	27	33	23	32
A*	6	8	5	8
	(g m ⁻² year ⁻¹)			
Total	4.5 ± 0.2	3.7 ± 0.3	3.0 ± 0.4	7.0 ± 0.7
(C) Potassium				
	(g m ⁻² year ⁻¹)			
LT	8.3 ± 1.8ab	7.2 ± 1.6ab	6.0 ± 1.1b	5.2 ± 2.6ab
FFP	3.9 ± 1.6b	2.3 ± 0.6c	2.0 ± 0.4c	1.6 ± 1.4b
RFP	4.4 ± 0.2b	4.9 ± 1.8bc	4.0 ± 0.9b	3.7 ± 1.3ab
CE	13.2 ± 2.8AB,a	8.2 ± 1.9B,a	11.9 ± 2.4AB,a	16.5 ± 2.8A,a
BD	0.3 ± 0.02c	0.3 ± 0.01d	0.3 ± 0.02d	0.3 ± 0.03b
DD	0.3 ± 0.0B,c	0.4 ± 0.1AB,d	0.3 ± 0.0B,d	0.7 ± 0.2A,ab
	(mg m ⁻² year ⁻¹)			
P*	229	303	275	235
F*	211	279	254	217
A*	234	310	281	241
	(g m ⁻² year ⁻¹)			
Total	22.8 ± 1.0	17.0 ± 1.9	19.3 ± 3.3	23.5 ± 4.1

Internal fluxes are *LT* fig-derived litterfall (excluding leaves of other plant species), *FFP* fig leaves, *RFP* woody and reproductive parts, *CE* canopy exchange, and bat induced fluxes *P* pellets, *F* faeces, and *A* absorption. External fluxes are *BD* bulk deposition and *DD* dry deposition. Total flux is the sum of internal and external fluxes (without *FFP* and *RFP* which are aggregated as *LT*). Bat-related values represent a consumption of 12.5 % (mean of 5 and 20 %) of total fruits. Lower case letters in columns indicate significant differences among the compartments on each of the geological units. Upper case letters in a row indicate significant differences among geological formation per compartment (both significance levels set at $p < 0.05$). Deviations are standard deviations for three replicates per geological unit, $n = 3$

* There are no deviations for the bat-related fluxes because we used the same concentrations and masses of fruits and the respective crown area for calculation of the total base metal flux per crown area. To get fluxes per square meter, the fluxes per crown area were divided by the crown area

Table 7 Exchangeable base metals (Ca, Mg, and K) concentrations in the 0–10 cm mineral soil depth interval of soils developed on four different parent materials

	Ca (mmol _c kg ⁻¹)	Mg (mmol _c kg ⁻¹)	K (mmol _c kg ⁻¹)
Bohio	404 ± 218AB	81 ± 11A	12 ± 3A
Andesite	159 ± 19B	62 ± 7AB	4 ± 3B
C. marine	573 ± 49A	50 ± 16BC	8 ± 1B
C. volcanic	136 ± 50B	26 ± 8C	4 ± 2B

Deviations are standard deviations for $n = 3$. Upper case letters indicate significant differences between geological units ($p < 0.05$)

8) = 15.4, $p > 0.0011$). Fluxes via pellets contributed 0.18 or 0.7 % to the total fluxes reaching the soil on C. volcanic, 0.23 or 0.9 % on Bohio, 0.29 or 1.14 % on C. marine and 0.33 or 1.3 % on Andesite, respectively. The contribution of faeces was 0.19 % or 0.75 % on C. volcanic, 0.23 % or 0.96 % on Bohio, 0.3 or 1.2 % on C. marine and 0.35 or 1.38 % on Andesite to total Mg fluxes to the soil assuming 5 or 20 % fruit consumption by *A. jamaicensis*, respectively. Absorption of Mg by bats was 0.04 or 0.17 % on C. volcanic, 0.06 or 0.22 % on Bohio, 0.7 or 0.29 % on C. marine and 0.8 or 0.32 % on Andesite for the consumption of 5 or 20 % of the fruits, respectively.

Potassium was mainly cycled via canopy exchange and litterfall, contributing 92 ± 2 % to the total K flux to the soil below the fig canopy. Bulk and dry deposition together contributed another 3.8 ± 1.4 % to the K fluxes reaching the soil (Fig. 2c). Bat-derived fluxes were significantly highest on Andesite and lowest on Bohio and C. volcanic. The formation C. marine did not significantly differ from any other geological unit (One-way ANOVA with Tukey's HSD: $F(18, 8.9706) = 10.076$, $p = 0.00065$). For an assumed consumption of 5 or 20 % of fruits by *A. jamaicensis*, bat-induced fluxes through pellets contributed 0.4 or 1.6 % to the K fluxes reaching the soil on Bohio and C. volcanic, 0.6 or 2.4 % on C. marine and 0.75 or 2.8 % on Andesite, respectively. Through faeces, bats contributed 0.4 or 1.5 % on Bohio and C. volcanic, 0.56 or 2.1 % on C. marine and 0.7 or 2.7 % on Andesite. Absorption of K ranged between 0.43 or 1.64 % of the K fluxes reaching the soil on Bohio and C. volcanic, 0.6 or 2.3 % on C. marine and 0.8 or

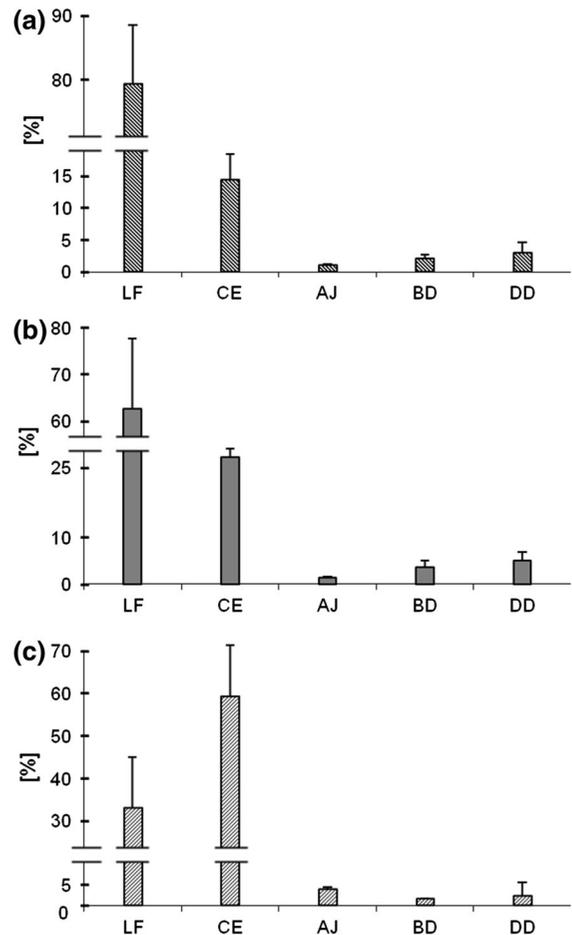


Fig. 2 Averaged proportional contribution (%) of litterfall (LF), canopy exchange (CE), bat *A. jamaicensis* (AJ), and the external fluxes bulk deposition (BD) and dry deposition (DD) to the total fluxes to the soil of **a** Ca, **b** Mg and **c** K on BCI. Proportions were calculated for a mean consumption of 12.5 % of figs by *A. jamaicensis* and were averaged over the years 2011 and 2012 (LF, CE, BD, DD). Error bars are standard deviations of 2011 and 2012 ($n = 3$ and on C. volcanic $n = 2$ in 2012)

2.9 % on Andesite for 5 or 20 % fruit consumption. This showed that bat-related K inputs via pellets and faeces may well contribute around 4 % to total K fluxes to the soil matching the contribution of dry and bulk deposition.

Aboveground fluxes as related to availability of base metals

In the 0–10 cm mineral soil layer, exchangeable Ca concentrations were significantly highest on C.

marine, and those of Mg and K were significantly highest on Bohio while concentrations of exchangeable Ca, Mg and K were lowest on C. volcanic (Table 7).

Exchangeable Ca concentrations in the 0–10 cm layer of the mineral soils correlated significantly positively with fluxes of Ca with pellets and faeces (Fig. 3). However, concentrations of exchangeable Ca did not show any correlation with the proportional contribution of bat-related fluxes of base metals in pellets and faeces (Fig. 3). Exchangeable Mg and K concentrations in soils were neither correlated with bat-derived fluxes nor aboveground fluxes with litterfall and canopy exchange of the respective base metals nor with the proportional contributions of bats to total Mg and K fluxes to the soil.

Discussion

Importance of the fluxes through bats

On BCI, base metal fluxes with bulk deposition were lower than in other tropical forests in Panama (Cavelier et al. 1997), Costa Rica (Hölscher et al. 2003; Hofhansl et al. 2011) or Puerto Rico (McDowell 1998). However, throughfall fluxes of Ca, Mg and K below fig canopies were higher than fluxes at other sites in Panama (Cavelier et al. 1997; Golley et al. 1976; Macinnis-Ng et al. 2012), Costa Rica (Hölscher et al. 2003; Hofhansl et al. 2011) and the Caribbean Islands (McDowell 1998; McDonald and Healey

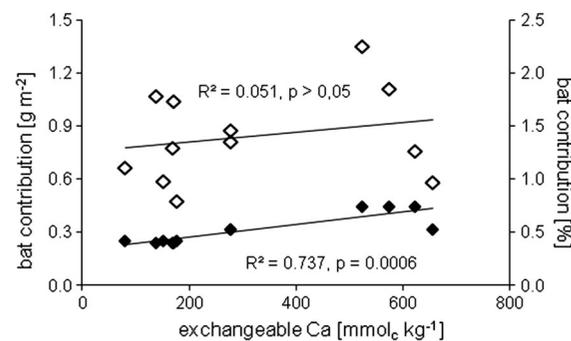


Fig. 3 Correlation between exchangeable Ca on the *x*-axis and bat-derived fluxes of Ca on the primary *y*-axis (black diamonds) and proportional contribution of bat-derived fluxes on the secondary *y*-axis (hollow diamonds) below canopies of *F. insipida* assuming a consumption of 20 % of total fruit crop by *A. jamaicensis*

2000) (Table 2). Fluxes of base metals with stemflow were lower than in Costa Rica (Hölscher et al. 2003), Amazonia (Jordan 1978) and Malaysia (Radzi Abas et al. 1992) (Table 2), which might be due to differences in canopy and/or bark structure or crown architecture (Levia and Frost 2003). In line with the low base metal fluxes with stemflow, Zimmermann et al. (2015) reported that stemflow only accounted for 1 % of rainfall on BCI, which is at the lower end of the values compiled by Levia and Frost (2003). Fluxes of Ca, Mg and K via canopy exchange processes (i.e. leaching of plant tissues) were higher, dry deposition of Ca and Mg was similar and of K higher than reported for Costa Rica (Hofhansl et al. 2011) (Table 2). Unexpectedly, the significantly greatest fluxes of Ca, Mg and K with throughfall, and consequently with dry deposition and canopy leaching, were measured on the C. volcanic formation (Table 2) which had the base metal-poorest soils on BCI (Messmer et al. 2014). This apparently contradicts the general notion that the more fertile soils are, the greater are nutrient fluxes with throughfall and litterfall because of increasingly inefficient mineral use (Parker 1983; Vitousek 1984). The great fluxes of Ca, Mg and K on C. volcanic were mainly related to the dying tree F11 showing an enhanced contribution of canopy exchange to the Ca, Mg and K fluxes reaching the soil by up to 40, 70 and 80 % compared to 14 ± 5 , 26 ± 9 and 59 ± 9 % (all trees except F11, $n = 11$) to fluxes of Ca, Mg and K, respectively. However, excluding tree F11 on C. volcanic from calculating the proportion of canopy leaching to total aboveground fluxes showed that on C. volcanic canopy exchange was still higher—although not significantly—than on the other geological units. This enhanced canopy leaching on C. volcanic could possibly be explained by more pronounced aging and stress effects or leaf damage by storms (Potter et al. 1991), insect invasion on weakened trees or frugivore activity of the fig trees on the poorest soils than on all other more fertile geological units resulting in enhanced mineral loss via throughfall (Ballestrini et al. 2007; Levia and Frost 2006; Stadler et al. 1998; Tukey 1970).

Total litterfall mass on BCI was in the upper range of reported litterfall masses in tropical forests on fertile to moderately fertile soils of 8 to 14 Mg ha⁻¹ year⁻¹ (McDonald and Healey 2000; Proctor 1983; Sayer and Tanner 2010; Vitousek and Sanford 1986;

Wieder and Wright 1995). Fig leaves persistently contributed least to total litterfall mass but most to Ca fluxes with litterfall because of the high concentrations of Ca in fig leaf tissues, except on *C. volcanic* (Table 3). Flux of Ca through litterfall was also higher than reported for another study site on BCI and the nearby Gigante Peninsula of 135–190 kg ha⁻¹ year⁻¹ (Sayer and Tanner 2010; Yavitt et al. 2004). Fluxes of K were highest in the fraction of woody and reproductive parts (Table 3), and were higher than previously reported on BCI or Costa Rica with fluxes between 40 and 60 kg ha⁻¹ year⁻¹ (Hofhansl et al. 2011; Yavitt et al. 2004). Fluxes of Mg, on the other hand, were higher than in Costa Rica (18 kg ha⁻¹ year⁻¹) (Hofhansl et al. 2011) but lower than the fluxes of 65 kg ha⁻¹ year⁻¹ previously reported by Yavitt et al. (2004) on *C. volcanic*. Magnesium fluxes with litterfall on *C. volcanic* were in the range as reported by Yavitt et al. (2004) confirming the elevated Mg flux with litterfall on this geological formation (Table 3).

The importance of litterfall for the Ca flux to soil (accounting for ~75 %) and canopy leaching for the K flux to soil (accounting for ~65 %) is in line with previous findings (Vitousek and Sanford 1986; Parker 1983). The contribution of the frugivorous bat *A. jamaicensis* to the base metal fluxes to soil accounted for 1 % of Ca, 1.3 % of Mg and 2.5 % of K in the form of dropped pellets and faeces below the canopy of fig trees with an average canopy area of 230 ± 100 m² (Fig. 2c; Table 1). Assuming that *A. jamaicensis* consumed 20 % of a crop, which is likely if the decline of the *F. insipida* abundance continues and food resources are getting scarce, then its contribution to the fluxes reaching the soil would account for 1.7 % of Ca, 2.1 % of Mg and 4 % of K below fig trees (Fig. 2). Thus, fluxes of Ca via pellets and faeces of *A. jamaicensis* were almost as high and higher as BD contributing 2 % to the Ca fluxes to soil. Fluxes of Mg are the least influenced by bats (Fig. 2b) because of the comparatively low Mg concentration in fig fruits (Tables 1, 5). The contribution of bats to K fluxes to the soil even exceeded the external input of K through bulk and dry deposition. If we assumed a decline of fruit consumption of *A. jamaicensis* to 5 % of total fruits, because the population of *A. jamaicensis* declines as a consequence of the reduced abundance of *F. insipida* in the long run, the contributions of *A. jamaicensis* to the Ca, Mg and K fluxes reaching the

soil below the fig canopy would drop to 0.4, 0.5, and 1 %, respectively, below the contributions of the external fluxes bulk and dry deposition.

The bat-induced mineral fluxes are usually not homogeneously distributed over the fig canopy-covered area but concentrated on small local patches below feeding roosts covering around 100 m² either in the understory below fig trees or below adjacent canopy trees providing suitable feeding roosts (Handley and Morrison 1991). Scaled to this smaller area, bat-derived fluxes amount to 0.9 ± 0.4, 0.2 ± 0.1, and 1.9 ± 0.7 g m⁻² representing 3.7 ± 1.3, 4.7 ± 2 and 8.4 ± 3.4 % of total soil input of Ca, Mg and K, respectively, assuming 20 % fruit consumption and that the other fluxes do not change (Fig. 4). Therefore, frugivorous bats such as *A. jamaicensis* may considerably influence the spatial distribution of Ca, Mg and K by concentrating the input of these elements to small patches below feeding roosts. Furthermore, it can be speculated that the processing of the fruits through the intestinal tract of the bats might change the bioavailability of nutrients, because the faeces are likely more easily decomposed than the original fig fruit. Several studies showed that around one third of tree species are non-randomly distributed but in response to the spatial distribution of water and soil minerals (Condit et al. 2013; Dent et al. 2006; Harms et al. 2001; John et al. 2006). Therefore, even small frugivore-induced mineral inputs to soil may contribute to shaping the spatial distribution of tree species.

Taking additionally into account other animals feeding on figs on BCI, such as the other 13 canopy frugivorous bat species (Bonaccorso 1979) and howler monkeys (*Alouatta palliata*) (Nagy and Milton 1979), overall consuming roughly two thirds of dry mass of figs per hectare (Handley and Leigh 1991), clearly increases the proportion of mineral fluxes caused by animals. All of these frugivorous mammals together may account for contributions of 7.0 ± 2.3, 9.4 ± 3.7, and 20.9 ± 7.6 % of the Ca, Mg and K fluxes to soil, respectively, thus exceeding the contributions of BD and DD of Ca, Mg and K and getting close to the contribution of litterfall to K fluxes. However, these estimates of the contributions of both the howler monkeys and the other frugivorous bats are only approximations, mainly because the feeding behavior such as food handling, lateral movement of minerals by transport of fruit parts and seeds in faeces as well as absorption coefficients are unknown.

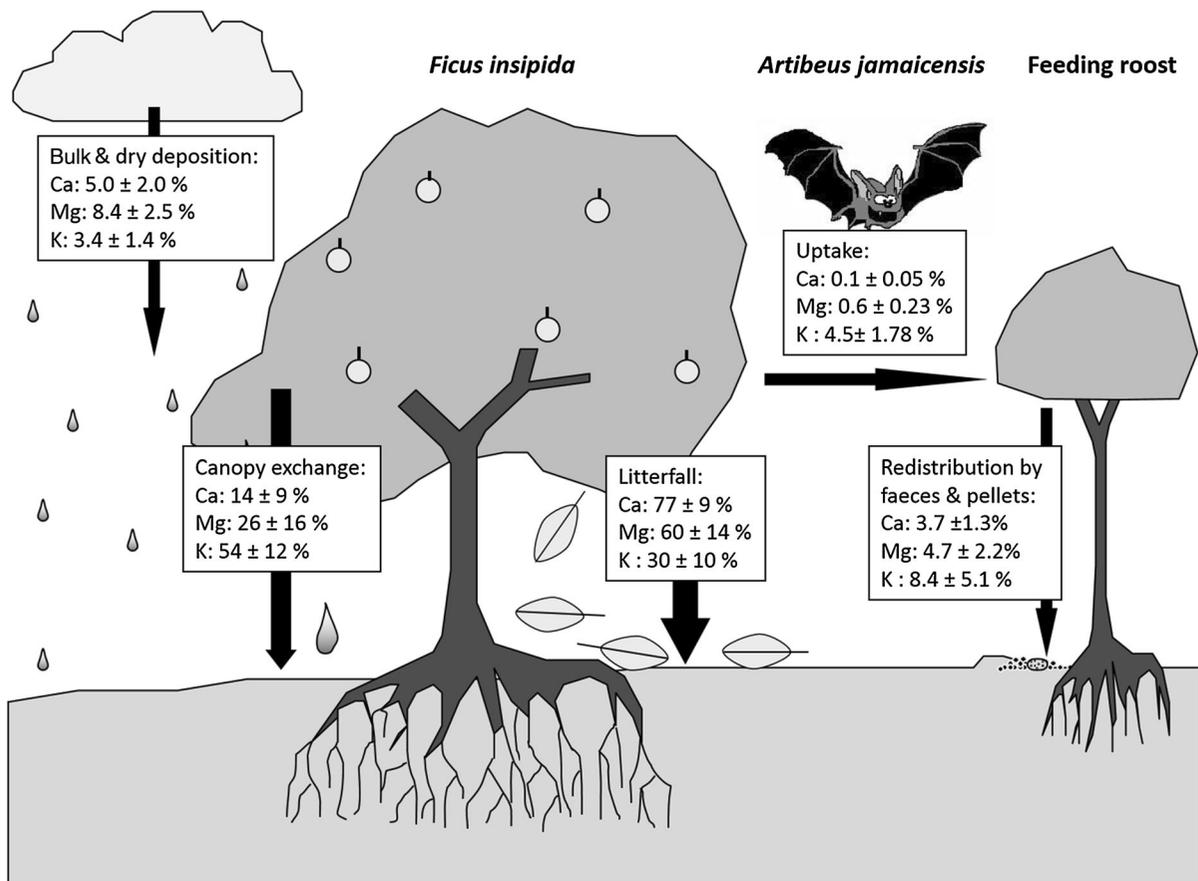


Fig. 4 Conceptual representation of the contribution of a common frugivorous bat (*Artibeus jamaicensis*) on the base metal fluxes in a tropical lowland forest in Panama. The proportional contributions of bulk deposition, canopy exchange (see Eq. 4 for its calculation, positive values indicate net leaching), litterfall and uptake and redistribution by *A. jamaicensis* have been calculated as if they all reached the same surface area to enable direct comparison assuming the high

fruit consumption scenario (20 % of the whole fruit stock is consumed by *A. jamaicensis*). However, canopy exchange and litterfall reach the area below the canopy of the studied fig trees (on average $238 \pm 100 \text{ m}^2$, $n = 12$) while the bat-related fluxes reach an estimated 100-m^2 feeding roost usually away from the fig crown and the base metals taken up by the bats remain in the bat biomass until they finally reach a local spot where the bat corpse is decomposed

Relationship between bat-related fluxes and soil properties

The contribution of bat-induced fluxes of Ca, Mg and K to the total soil input of these elements was, in contrast to our expectations, not correlated with the local availability of Ca, Mg, K or the sum of base metals in soil, although base metal fluxes with throughfall were related to exchangeable base metal concentrations in soil except for *C. volcanic* in line with Parker (1983). On *C. volcanic*, the high base metal leaching from the canopy might be attributable to the advanced aging,

stress and/or damaged leaves. The assumed reduced vitality of the *F. insipida* trees on *C. volcanic* might be reflected by the fact that we measured the smallest canopy areas on *C. volcanic* (Table 1). Excluding the *C. volcanic* formation from our analysis of the relationship between exchangeable base metal concentrations in soils revealed a marginally significant ($p < 0.1$) influence of exchangeable K on the contribution of bat-induced fluxes of K to the total soil input of this element but no relationship between exchangeable concentrations in soil and bat-related fluxes of Ca and Mg.

Conclusions

The frugivorous bat *A. jamaicensis* could contribute up to 1.7, 2.1 and 4 % to the total fluxes of Ca, Mg and K reaching the soil below the fig canopy, respectively, if it is assumed that bats consume 20 % of total fruits. Because the bat-related base metal fluxes with fruit pellets and faeces are usually concentrated on a ca. 100 m² area below feeding roosts, the contribution to total soil inputs of the feeding roost area would amount to 3.7, 4.7 and 8.4 % in this scenario of 20 % fruit consumption by *A. jamaicensis* which is similar in size to the bulk and dry deposition of Ca, Mg and K, respectively. Considering also other fig-eating mammals may further increase the proportional animal-related contribution to aboveground base metal fluxes. In the latter case, the contribution of the animal-related K fluxes to total K fluxes would exceed the contribution of bulk and dry deposition and possibly almost reach that of litterfall. Therefore, the contribution of animals to base metal fluxes should not be neglected in ecosystem studies focussing on mineral cycling. Furthermore, the animal-related part of ecosystem-internal base metal cycles may play a role in shaping the tree composition of tropical forests, because the small-scale spatial variability in distribution of base metals created by frugivorous animals may be a determining factor for local tree establishment and recruitment. Further studies are necessary to measure the fig consumption by the various frugivorous animal groups to substantiate our scenarios.

The contribution of *A. jamaicensis* and likely also of other frugivorous mammals does not seem to be correlated with exchangeable base metal concentrations in soils. Therefore, other factors such as canopy area and the related fruit production seem to be more important drivers of the proportional distribution of mineral fluxes. However, it has to be considered that the soils of our study were comparatively rich in base metals and further studies on base metal-poor soils as found in large parts of the tropics are necessary to confirm this conclusion.

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