Fruit bats can disperse figs over different land-use types on Mount Kilimanjaro, Tanzania

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Introduction
The past centuries have seen agricultural land and human settlement increase from 5% to 39% globally (Ellis et al., 2010). The influence of land-use intensification on key-stone taxa, such as bats, has been studied mainly in Europe and the New World (e.g. Harvey & González Villalobos, 2007; Flynn et al., 2009; Williams-Guillén & Perfecto, 2010), neglecting the Old World tropics. This is worrisome, as human population growth and land-use intensification in African are among the most profound worldwide (Cincotta, Wisnewski & Engelman, 2000; Ellis et al., 2010). In particular, Mt. Kilimanjaro belongs to the 25% most densely populated areas in Africa (Balmford et al., 2001) and is therefore highly threatened to further land-use intensification.

In fragmented and intensively used habitats, seed dispersal by animals plays an important role for plant species persistence and reforestation (Muscarella & Fleming, 2007). Fruit bats can function as dispersal agents (Kunz et al., 2011), as they can cover long distances and may pass over suboptimal landscapes. Hereby, they might connect fragmentated habitats which might be more difficult for other dispersal agents, for example rodents (Shilton et al., 1999). Through dispersal away from the parent, seeds can escape natural enemies accumulated around the parent (Janzen, 1970; Connell, 1971). Fruit bats disperse a wide variety of fruits approximately 20% of all tree species in the East Usambaras, Tanzania (Seltzer, Ndangalasi & Cordeiro, 2013). Often depending on the seed size, bats can carry away the whole fruit, spit out seeds elsewhere or swallow seeds and deposit them elsewhere. In Neo-tropical bats, gut passage has been shown to increase germination success of fig seeds in Panama (Heer, Albrecht & Kalko, 2010). However, effects of bat gut passage on fig germination in Africa remains widely unknown.

Ficus (Family Moraceae) is a globally distributed tree genus which has 105 species in the Afrotropics (Shanahan et al., 2001). They are important pioneer plants in early succession stages (Corner, 1967; Harrison, 2005), hence for reforestation. Figs serve as an important food source for fruit bats (Monadjem et al., 2010); hereby, bats might disperse the seeds. An important fig species in the Kilimanjaro region is Ficus sur Forskk 1775, it occurs in natural forests and traditional gardens (Hemp, 2006), and fruit bats are known to feed on it. We studied if bats can function as dispersers of F. sur, in the landscape mosaic of Kilimanjaro’s southern slopes. We tested if fruit bats occur with similar diversities in different land-use types and how bat gut passage affects the germination of fig seeds.

Materials and methods
Our study was conducted on the southern slope of Mount Kilimanjaro, Tanzania, at nineteen sites with four land-use types (1300–2000 m a.s.l.): natural forests (4), traditional home gardens (5), intensive coffee plantations (5) and grasslands used to feed the cattle (5). The most common land-use type is traditional home garden (Hemp, 2006). The local Chagga people grow different crops and keep animals in these gardens. This results in a mosaic of small garden patches with layered highly diverse vegetation (Hemp, 2006).

We sampled fruit bats twice at each site, between December 2010 and March 2011 and between June 2011 and September 2011, using ten to fifteen ground-based mist-nets (6 × 2.5 m), following a common bat capturing protocol (Kunz & Parsons, 2009). Netting started at sunset and ended at 01.00 hours. Bats were identified (Hayman &
Hill, 1971; Taylor, 2000) and nonpermanently marked with haircuts. Recaptures were excluded from further analysis. Abundance or capture success was measured as the number of bats per mist-net hour (mnh – one mnh equals using one 2.5-m net for 1 h).

For the germination experiments, we caught four individuals of the most abundant bat *Epomophorus wahlbergi* and fed them with fig fruit parts of six individual *F. sur* trees in total for eight nights. Later, we collected seeds of three distinct treatments: seeds from the faeces (‘defecated’), seeds spit out by the bat after juice extraction (‘spit’) and ‘control’ seeds from fruits parts not handled by bats.

We sowed 929 seeds (292 defecated, 318 spit and 319 controls) in petri dishes under standardized conditions (21°C). Each of the 24 (eight captivity nights × three treatments) petri dishes contained ~40 seeds on filter paper (except at the fifth capture night where the bat had only defecated nineteen seeds). We recorded number of germinated seeds daily for thirteen consecutive days. If no seeds of a particular night germinated in any of the treatments, they were excluded from analysis.

**Results and discussion**

Overall, bat abundance was significantly higher in the traditional home gardens than in other land-use types ($F_{3,34} = 7.486, P < 0.001$; generalized linear mixed effects model, fixed: habitat, random: site nested in season, Fig. 1). We caught five bat species in our sites (*Epomophorus wahlbergi, E. gambianus, Lissonycteris angolensis, Rousettus aegyptiacus, R. lanosus*). With 55.5% of all captures, *E. wahlbergi* was the most abundant species (Table 1), being dominant in grasslands (83%) and in coffee plantations (80%). *Epomophorus wahlbergi* was not only most abundant, but also the only species occurring in all land-use types. The species composition did not differ among the four land-use types (analysis of similarity Clarke (1993): $R = 0.1796; P = 0.066$). Four of five species were caught in at least two land-use types (Table 1).

Our overall germination percentage of 49.3% after 13 days was similar to former studies with figs in the tropics, for example, Heer, Albrecht & Kalko (2010) found 50% of the seeds germinated after 6–12 days using different fig species. The germination rate did not differ between the treatments as only 0.3% of the variation in germination was explained by treatment (Analysis of deviance with a quasi-binomial error distribution: $F = 2.632, P = 0.138$).

![Figure 1](https://example.com/fig1.png)

**Fig 1** Abundance (median, quartiles and outliers) for all five fruit bat species was higher in home gardens (Chagga) than in other land-use types at Mount Kilimanjaro. Significant differences are indicated by different letters (post hoc Tukey’s test)

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Relative abundance of five fruit bat species caught in four land-use types as percentage of the total number of individuals. The overall species richness and the amount of mist-net hours (mnh) are also given for each of the four land-use types</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Authority</td>
</tr>
<tr>
<td>Epomophorus gambianus</td>
<td>Ogilby 1953</td>
</tr>
<tr>
<td>Epomophorus wahlbergi</td>
<td>Sundevall 1846</td>
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<tr>
<td>Lissonycteris angolensis</td>
<td>Bocage 1898</td>
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<tr>
<td>Rousettus aegyptiacus</td>
<td>Geoffroy 1810</td>
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<tr>
<td>Rousettus lanosus</td>
<td>Thomas 1906</td>
</tr>
<tr>
<td>Total number of individuals</td>
<td></td>
</tr>
<tr>
<td>Species richness</td>
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<td>Total mnh</td>
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$F_{2,12} = 0.023, P = 0.98$. This suggests that seeds ingested survived the gut passage and germinated similar to control seeds. Bats are known to feed on other fig species and other small-seeded species (Seltzer, Ndangalasi & Cordeiro, 2013). Our results suggest that small seeds can survive gut passage, indicating an important role for fruit bats as dispersers of small-seeded species. Handled seeds might have an advantage as they are probably dispersed further than not handled seeds (Shilton et al., 1999), and the risk of pathogen attack reduces farther away from the parent (Peters, 2003). Furthermore, bats occurred in several land-use types suggesting that they can disperse seeds between land-use types and hereby connect natural and human used areas.

Overall, bat species richness did not differ between land-use types, but the abundance was highest in the home gardens. This suggests that no land-use type completely excluded fruit bats, but home gardens seem to provide a more suitable habitat. The current mosaic of land-use types on Kilimanjaro’s southern slopes is increasingly subjected to ongoing human population growth and land-use intensification. Therefore, future studies should focus on roosting location, dispersal distance and feeding behaviour of fruit bats to further assess the importance of the land-use types and their connectivity. The suitable habitats for fruit bats further reduce due to human impacts; seed dispersal services of fruits bats might become an uncertainty in the future.

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