Complementary seed dispersal by three avian frugivores in a fragmented Afrotropical forest

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Abstract

Questions: To what extent does species-specific variation in gut passage time (GPT), habitat use and mobility of three key avian frugivores synergistically affect the distribution of Xymalos monospora seeds within and among isolated forest fragments?

Location: Three fragments of a severely fragmented cloud forest, Taita Hills, southeast Kenya.

Methods: We experimentally determined GPTs of X. monospora seeds and recorded movements and habitat use by Turdus helleri, Andropadus milanjensis and Tauraco hartlaubi through radiotelemetry, and combined these data to generate species-specific seed dispersal patterns.

Results: Differences in mobility and habitat use among the three frugivores caused significant complementarity in seed dispersal, despite the fact that gut transit times were highly comparable. While the most sedentary and forest-dependent species mainly led to short-distance dispersal away from parent trees, two more mobile species dispersed seeds further away from the source trees, both within indigenous forest patches and towards exotic plantations and isolated fruiting trees in the landscape matrix. A. milanjensis inhabiting a very small forest fragment spent significantly more time in the landscape matrix than conspecifics residing in the two larger fragments.

Conclusions: By varying distances over which seeds are carried away from parent trees and the habitat types in which they are ultimately deposited, avian frugivores affect the spatial distribution of seeds and early plant recruits in a distinct and complementary manner. Because landscape properties are expected to lead to different constraints on avian mobility for habitat specialists and for generalists, ecosystem processes such as avian seed dispersal are shaped by complex interactions between disperser behaviour and the environment.

Keywords: Africa; Birds; Cupressus; Eucalyptus; Exotic plantation; Fragmentation; Frugivores; Pinus; Taita Hills.

Nomenclature: Gill et al. (2009), International Plant Names Index (2008).

Introduction

Fleshy fruits are typically consumed by a wide array of frugivorous species that vary in the number of seeds that they disperse and in their putative effects on seed germination, and seedling growth and survival through handling, dispersal and deposition of seeds (Schupp 1993; Jordano & Schupp 2000). The cumulative seed dispersal pattern, i.e. the spatial distribution of seeds resulting from dispersal by frugivorous species that differ in feeding habits, mobility or physiology, may affect the colonization potential of fleshy-fruited plants and shape their population dynamics, genetic structure, community composition and diversity (Nathan & Muller-Landau 2000; Wang & Smith 2002; Levin et al. 2003). Frugivores are therefore regarded as key drivers of vegetation structure and dynamics (Herrera et al. 1994; Nathan & Muller-Landau 2000; Levin et al. 2003), especially in tropical rain forests that are dominated by fleshy-fruited trees (Fleming et al. 1987; Estrada et al. 1993) and are characterized by pervasive seed limitation (Clark et al. 1999; Hubbell et al. 1999).

Dispersal of animal-dispersed seeds is typically influenced by multiple biotic and abiotic factors that may either act separately or in concert, and can therefore be expected to be context-dependent. For instance, gut passage or regurgitation rates depend
on the behaviour, morphology and physiology of the frugivores, as well as on properties of seeds, such as size, pulp-to-seed ratio and the presence of secondary compounds (Murray et al. 1994; Traveset 1998). Mobility and habitat use of frugivores, in turn, not only depend on their behaviour and morphology (e.g. Jordano et al. 2007; Martínez et al. 2008), but may also vary with season (e.g. Gehring & Swihart 2004; Bowen et al. 2007), time of the day (Westcott et al. 2005), landscape structure (Bélisle et al. 2001; Revilla et al. 2004; Castellon & Sieving 2006; Levey et al. 2008) and/or the spatiotemporal distribution of critical resources such as food and water (e.g. Morales & Carlo 2006; Thies et al. 2006; Lehouck et al. 2009c). Species-specific gut passage or regurgitation times of swallowed seeds, in combination with the movement behaviour of frugivores while seeds are carried, determine the primary dispersal distance of animal-dispersed seeds (e.g. Murray 1988; Schupp 1993). This, in turn, may shape patterns of plant recruitment at multiple spatial scales (Jordano et al. 2007; Spiegel & Nathan 2007). At a local scale, seed dispersal may reduce density- or distance-dependent mortality as a result of decreased host-specific pathogen loading, seed predation, herbivory or sibling competition away from the parent tree (Janzen 1970; Connell 1971; Augspurger & Kelly 1984). At a larger (landscape-wide) scale, long-distance dispersal of seeds facilitates the colonization of new habitats by plants, which may affect their (meta)population survival and reproduction under directional habitat or climate change (Johst et al. 2002; Pearson & Dawson 2005; Trakhtenbrot et al. 2005; Nathan 2006).

Frugivores may vary in their effectiveness as seed dispersers both in terms of quantity, i.e. in the number of seeds dispersed, and quality, i.e. in survival and recruitment rates of seeds after dispersal (Schupp 1993). Whereas quantitative variation in seed dispersal has been well documented in temperate and tropical ecosystems, qualitative variation in dispersal effectiveness has long been ignored. Nevertheless, frugivores may strongly vary in their impact on plant recruitment, e.g. through differential ability to move among isolated habitat patches during gut passage of swallowed seeds or use of (micro)habitats that are favourable for seed germination and growth. When habitat patches are heterogeneously distributed across landscapes, movements of some seed dispersers, but not others, may become spatially constrained (e.g. Kremen et al. 2007). For example, in an Israeli desert ecosystem, yellow-vented bulbuls (Pyconotus barbatus) distributed seeds within natural forest patches around wadis, while larger-sized, sympatric Tristan’s starlings (Onychognathus tristramii) did so among isolated wadis (Spiegel & Nathan 2007). Similarly, in a temperate secondary forest in northwest Spain, rates of seed removal, dispersal and deposition by five related Turdus species of comparable size and physiology varied significantly with their level of gregariousness (Martínez et al. 2008). Based on such evidence, Jordano et al. (2007) and Spiegel & Nathan (2007) proposed to expand the concept of ‘seed disperser effectiveness’ by implicitly incorporating effects of dispersal distance and habitat use. Complementary seed dispersal by frugivores, here defined as their differential contribution to the spatial distribution of seeds and seedlings, may hence arise from interspecific variation in number of seeds dispersed, seed handling behaviour, movement patterns and habitat use. In heterogenous landscapes, effectiveness of seed dispersal likely varies among habitat patches, both directly through variation in the composition of frugivore guilds, and indirectly through environmental effects on frugivore behaviour and performance. This, in turn, may affect the level of complementarity of seed dispersal and, hence, plant population dynamics, genetic structure, community composition and diversity (Nathan & Muller-Landau 2000; Wang & Smith 2002; Levin et al. 2003).

Despite the potential implications for population ecology and conservation biology of fleshy-fruited plants, especially in heterogeneous landscapes, variation in complementary seed dispersal and its effects on the spatial distributions of seeds dispersed from single plants (seed shadows sensu Nathan & Muller-Landau 2000) remain poorly understood. To fill this gap, we studied variation in seed dispersal of Xyonalos monospora (Harv.) Warb. (Monimiaceae) by three sympatric avian frugivores inhabiting a severely fragmented cloud forest in southeast Kenya. Together, the three species disperse over 80% of all X. monospora seeds in the study area (Lehouck et al. 2009b), and 7 years of capture-recapture data (Lens et al. 2002) in combination with 3 years of visual observations (V. Lehouck, unpubl. data) suggest interspecific variation in mobility and tolerance to forest disturbance. To understand the behavioural and ecological drivers of dispersal of X. monospora seeds within a fragmented forest ecosystem, we quantified species-specific gut passage times (GPTs) and movement characteristics of the three key avian frugivores, and studied if, and to what extent, variation in these...
traits affect dispersal of X. monospora seeds in three isolated forest fragments.

Methods

Study area

The study was conducted in the Taita Hills forest of southeast Kenya (03°20’S, 38°15’E, alt 1200-2208 m), a severely fragmented cloud forest located at the northernmost edge of the Eastern Arc Mountains biodiversity hotspot (Burgess et al. 2007). The regional climate is dominated by heavy rains during the cold season (March-May/June) and short rains during the warm season (October-December). Soils are composed of a high-humic A-horizon overlaying a pinkish, acid sandy loam (Beentje 1988). Major loss and fragmentation of the Taita forest started ca. 200 years ago, and currently only 2% of the original cloud forest cover is retained in three larger fragments (90, 133 and 179 ha), nine small ones (2-8 ha) and several tiny patches (<2 ha) (Beentje 1988; Appendix S1). Indigenous forest vegetation is classified as moist montane forest and comprises tree species such as Strombosia scheffleri, Newtonia buchananii, Chrysophyllum sp., Albizia gummifera, Cola greenwayi, Macaranga conglomerata, Syzygium stipiflorum, X. monospora, Tabernaemontana staaffiana and Phoenix reclinata (Beentje 1988). Most indigenous forest fragments are bordered by exotic stands of Eucalyptus saligna, Cupressus lusitanica and Pinus spp. planted for timber during the 1950-1980s (Beentje 1988; Mbuthia 2003), and are on average 5497 (±654) m apart from neighbouring forest fragments, embedded within a mosaic of human settlements and smallholder cultivation plots (Beentje 1988). Despite significant loss, fragmentation and deterioration of indigenous forest over the last decades, the Taita forest continues to harbour a highly diverse flora and fauna, including several endemic bird, amphibian, reptile and plant species (Beentje 1988; Burgess et al. 2007).

Tree and bird species

X. monospora (Harv.) Warb. (Monimiaceae) is a 6-20-m tall, dioecious tree, with small, cream-greenish flowers that are arranged in unisexual panicles or racemes and fleshy, ovoid, yellow to reddish, single-seeded fruits (Verdcourt 1968). Average dimensions of 120 fruits/seeds collected from 12 trees were: fruit length (11.8 ± 0.4 mm), fruit width (9.4 ± 0.3 mm), seed length (9.6 ± 0.2 mm), seed width (7.3 ± 0.4 mm). In the Taita Hills, trees produce fruit during April-November (peaking in June to August), and fruits are mainly dispersed by birds (Lehouck et al. 2009b), with no evidence of secondary seed dispersal over long distances (J. Decoene and V. Lehouck, unpubl. data).

Within the study area, three forest specialist birds, i.e. occurring almost exclusively in undisturbed forest where they exclusively breed (Bennun et al. 1996), are responsible for dispersing over 80% of all X. monospora fruits (Lehouck et al. 2009b). These are (i) Andropadus milanjensis (stripe-checked greenbul), a medium-sized passerine (36-54 g, gape width ca. 10 mm) that lives in pairs or small groups and mainly forages on fruits in the middle stratum and canopy, but occasionally attends ant swarms to feed on insects. In the Taita Hills, this species is abundant in the larger forest fragments and occurs at lower densities in most of the smaller fragments; (ii) Turdus helleri (Taita thrush), a medium-sized passerine (47-85 g, gape width ca. 12 mm) that feeds on fruits and arthropods. It is endemic to the Taita Hills, where it only survives in the three largest fragments and in one medium-sized fragment; (iii) Tauraco hartlaubi (Hartlaub’s turaco), a larger species (195-275 g, gape width ca. 12.5 mm) that lives in pairs or small groups and is nearly strictly frugivorous (Fry et al. 1988). In the Taita Hills, it occurs in low densities in larger forest fragments and only rarely visits the smallest ones. Ingestion of X. monospora seeds by each of the three frugivorous species significantly increased their probability and rate of germination as compared to non-ingested control seeds, and similar results were obtained for seeds of sympatric plant species (V. Lehouck et al., unpubl. data).

Bird movements

Movement behaviour of the three study species was examined in one small forest fragment (MAC, 3 ha indigenous forest/25 ha including exotic stands), one intermediate-size fragment (CHA, 90/95 ha) and one large fragment (NGA, 133/161 ha) (see Appendix S1 for the landscape configuration around these fragments). Individuals were captured with standard mist-nets between July-September 2005 and July-September 2006, i.e. during the fruiting season of X. monospora. Upon capture, each individual was weighed, measured and banded with a steel numbered band and a unique combination of colour bands. A total of 30 adult A. milanjensis (four in CHA, 12 in MAC, 14 in NGA) and nine adult T. helleri (one in CHA, eight in NGA) were fitted
with lightweight Pip radio transmitters (Biotrack Ltd, Dorset, UK) glued to their interscapulars. Two T. hartlaubi (one in MAC, one in NGA) were provided with a tail-mounted TW-4 transmitter (Biotrack Ltd.) sewn to their rectrices (methodological details in Sykes et al. 1990; Kenward 2001). Each transmitter weighed <2.5% of the species’ mean body mass, which is less than half the threshold value proposed by Kenward (2001). Apart from a temporary increase in preening behaviour immediately after release, tagged individuals behaved, flew and fed normally, and recaptured individuals were in normal body condition. Following a 24-h habituation period, individuals were tracked with portable TR-4 receivers (Telonics, Mesa, AZ, USA) and three-element flexible Yaggi antennas (Biotrack Ltd.). To increase accuracy of mapping and to enhance behavioural observations, individuals were approached up to 10 m without interfering with their natural behaviour (homing-method sensu Millsbaugh & Marzluff 2000), and GPS location (Garmin 60CSX; accuracy 5-15 m), habitat type (indigenous forest, exotic plantation, farmland) and behaviour (resting, preening, feeding, moving) were recorded every fifth minute. Both in 2005 and 2006, individual birds were tracked for an average of 30 h over 20 days (06:30 to 18:30), with tracking sessions randomized according to forest fragment and time of day.

Seed dispersal

To assess species-specific time windows during which X. monospora seeds can be dispersed by the study species, we captured 90 adult A. milanjensis and 27 adult T. hartlaubi and fed each individual with bananas to clear their guts (Denslow et al. 1987). If during two subsequent defecations, no seeds were present in the faeces, each individual was force-fed three to five X. monospora fruits during a single feeding session, and time intervals between swallowing and defecating were recorded as a measure of GPT. To minimize stress during GPT experiments, birds were individually held in clean cotton bags in situ and were checked every 5 min until all seeds were defecated (in rare cases, birds were released earlier). Birds were released at their site of capture within 3 h. Since we failed to catch a representative number of T. hartlaubi in the field, we performed 31 feeding experiments on five captive individuals belonging to four Tauraco species (similar in size and weight to T. hartlaubi; Appendix S2) in Antwerp Zoo (Belgium). As GPT is mainly a function of body mass (Traveset & Verdú 2002) and is generally comparable among congeners (Izhaki & Safriel 1990; Charalambidou et al. 2003), these individuals were considered valid proxies for T. hartlaubi. After a seedless diet mainly consisting of bananas and pellets (see also Denslow et al. 1987), each Tauraco was fed five ripe, intact X. monospora fruits that had been collected in the Taita Hills and were stored at 5°C. On average 96% (A. milanjensis), 94% (T. helleri) and 99% (Tauraco spp.) of all seeds fed were subsequently retrieved in faeces. As <5% of seeds were regurgitated, these data were not used in further analysis.

Throughout this paper, we assume that the average distance flown by a frugivore within a time interval equal to its median GPT, reflects the average distance over which seeds are dispersed by the species. To obtain species-specific GPT, movements of tagged individuals were recorded for at least 1 h and for up to 12 h in a single tracking session, either immediately following the observed intake of a X. monospora fruit, or starting at a random point in time. For each tracking session, bird movements recorded during time intervals that coincided with median seed retention times were used for analysis of seed movement. Because presumed dispersal distances following the intake of a X. monospora fruit did not statistically differ from those covered during random sessions (A. milanjensis: F1,554 = 3.51, P = 0.06; T. hartlaubi and T. helleri P > 0.20), nor among tracking sessions before 11.00, between 11.00 and 15.00 or after 15.00 (A. milanjensis: F2,574 = 1.40, P = 0.25; T. hartlaubi: F2,134 = 1.97, P = 0.14; T. helleri: F2,332 = 1.31, P = 0.27), data were pooled in all analyses.

Statistical analysis

Differences in mean GPT values among species were tested with non-parametric Mann-Whitney U-tests, averaging values per feeding session to account for individual variance (Charalambidou et al. 2003). Differences in movement distances among species were tested with linear mixed models (PROC Mixed) after log-transformation of the data. Differences in proportion of time spent in different habitat types (insufficient data available for T. helleri and T. hartlaubi) were tested with a binomial distribution model (PROC Glimmix). To account for individual variation in movement behaviour, factor ‘individual’ was included as a random effect in all of the statistical tests. As among-individual variation in movement distances during median GPTs was low (<10% of the total variation), tracking sessions

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of all individuals were pooled. All analyses were performed with SAS v. 9.1.3 (SAS Inc. 2004).

Results

Median GPT values of *X. monospora* seeds were of the same order of magnitude in the three study species (*A. milanjensis* 33 min, 24-54 min; *T. hartlaubi* 40 min, 30-47 min; *T. helleri* 34 min, 26-57 min; median and 25th and 75th percentiles, respectively) and did not significantly differ among species ($\chi^2 = 0.62, P = 0.73$; Fig. 1a-c). Presumed dispersal distances of *X. monospora* seeds varied between 5 and 194 m and significantly differed among bird species (Table 1; $F_{2, 26.7} = 5.19, P = 0.01$). In pairwise post hoc comparisons, values significantly differed between *T. hartlaubi* and *T. helleri* only (Tukey-Kramer $t_{23.6} = 3.07, P = 0.01$; other comparisons $P > 0.05$), with the largest average distances and the longest distribution tails recorded in *T. hartlaubi*, followed by *A. milanjensis* and *T. helleri* (Table 1, Fig. 1d-f). The percentage of movements beyond 150 m during median GPTs was particularly low in *T. helleri* (3%) but higher in *A. milanjensis* (12%) and *T. hartlaubi* (16% and 38% in each of the two individuals, respectively; Fig. 1d-i). Distances moved by *A. milanjensis* during median GPTs did not significantly differ among fragments ($F_{2, 22.7} = 1.05, P = 0.37$; no comparison for other species).

More than half of the 30 tagged *A. milanjensis* visited plantations or scattered trees in farmland at least once during tracking, thereby moving up to 600 m away from indigenous forest edges. Individuals inhabiting the smallest fragment (MAC) spent significantly more of their time outside indigenous forest compared to individuals inhabiting the two larger fragments ($F_{2, 290} = 5.41, P = 0.005$; Figure 1).
Table 1. Distances moved by three avian frugivores during median and maximum gut passage times (GPT) of *X. monospora* seeds (mean ± SE and highest value).

<table>
<thead>
<tr>
<th>Species</th>
<th>Displacement during median GPT (m)</th>
<th>Displacement during maximum GPT (m)</th>
<th>Highest displacement value during maximum GPT (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. milanjensis</em></td>
<td>61.0 ± 5.2</td>
<td>127.3 ± 30.6</td>
<td>419.8</td>
</tr>
<tr>
<td><em>T. hartlaubi</em></td>
<td>114.9 ± 51.5</td>
<td>255.2 ± 48.6</td>
<td>653.0</td>
</tr>
<tr>
<td><em>T. helleri</em></td>
<td>44.7 ± 3.7</td>
<td>86.5 ± 17.7</td>
<td>373.0</td>
</tr>
</tbody>
</table>

CHA-MAC: $t_{290} = -2.72$, $P = 0.02$; NGA-MAC: $t_{290} = 2.53$, $P = 0.03$; CHA-NGA: $t_{290} = -1.29$, $P = 0.4$; Table 2). One *A. milanjensis* individual inhabiting fragment MAC spent 96.8% of its time in plantations and farmland. During tracking, both *T. hartlaubi* spent nearly half of their time in exotic plantations bordering indigenous forest fragments or in isolated trees in farmland (% time spent ± SE: exotic plantation 15.37 ± 8.29; trees in farmland 30.39 ± 0.94; indigenous fragment 54.24 ± 7.35) and wandered up to 460 m away from indigenous forest boundaries. In contrast to *A. milanjensis* and *T. hartlaubi*, all nine tagged *T. helleri* consistently restricted foraging and movements to within the indigenous boundaries of a single forest fragment.

Discussion

While transit times of ingested *X. monospora* seeds were comparable among the three frugivorous birds of a severely fragmented African cloud forest, species-specific differences in mobility and degree of forest dependency caused strong complementarity in seed dispersal. The highly sedentary and strictly forest-dependent *T. helleri* mainly caused short-distance dispersal away from parent trees, i.e. more than 85% of the seeds were dispersed over 10 m or more. Such short-distance movements are widely assumed to reduce density- or distance-dependent seed mortality through a decrease in sibling competition or local pathogen infestation (Augspurger 1983; Augspurger & Kelly 1984), which is supported by a significant increase in seed germination and seedling survival of *X. monospora* with distance from the parental tree (Lehouck et al. 2009a). *A. milanjensis* and *T. hartlaubi*, in contrast, dispersed seeds over longer distances, both within indigenous forest patches and across forest boundaries to exotic plantations and small patches of fruiting trees within the landscape matrix. These mobile species may therefore facilitate the colonization of new habitat patches by *X. monospora* trees and other fleshy-fruited species with similar transit times (Higgins et al. 2003; Levin et al. 2003). Fitness advantages for plants of the observed complementarity in dispersal of their seeds are mainly related to risk spreading: seeds that are deposited at short distances from the parent tree have a high probability of ending up in (micro)habitats that are suitable for germination and growth, while seeds dispersed over longer distances have a high probability of colonizing new habitats, however, at the potential cost of facing less favourable environmental conditions (Harper 1977). Due to the more frequent use of the landscape matrix by *A. milanjensis* that reside in small forest fragments, seeds from trees growing in such fragments may have a higher probability of moving through the landscape than those from conspecific trees in larger fragments. Whether, and to what extent, such asymmetrical seed dispersal additionally affects the genetic signature of forest fragmentation, requires further study.

Habitat use by animals is often asymmetrical, and their preference for particular microhabitats may influence movement directions and/or dispersal distances depending on the spatial pattern of favoured microhabitats (e.g. Levey et al. 2005; Carlo & Morales 2008). In this study, the probability that seeds were deposited into the landscape matrix was context-dependent, in that it varied between different-sized forest fragments. Earlier studies compared variation in dispersal distances and habitat use during seed deposition at higher taxonomic levels (e.g. mammals versus birds; Galindo-Gonzalez et al. 2000; Jordano et al. 2007), or in relation to interspecific variation in body size (Jetz et al. 2004; Jordano et al. 2007; Spiegel & Nathan 2007) and social behaviour (Martínez et al. 2008). While our study was restricted to three avian frugivore species and three forest patches only, our results suggest that interspecific variation in body size, and in mobility and degree of forest dependency in particular, may cause complementarity of seed dispersal in a context-dependent way, i.e. depending on the inter-
action between the behaviour of seed dispersal vectors and the environment.

While complementary seed dispersal may be a common phenomenon in spatially structured populations, it may be absent when the landscape matrix hampers mobility of all dispersal vectors. Although our design did not allow us to replicate fragment size, results from our study suggest that species that are capable of exploring the landscape matrix do so more frequently when inhabiting smaller forest fragments, probably as a result of temporal food shortages. The hypothesis of asymmetrical use of the landscape matrix around different-sized forest fragments by forest birds may have important conservation implications, yet needs to be tested with more species, more different-sized forest fragments and in different landscape contexts.

Apart from direct positive or negative effects of gut passage on seed germination (Traveset 1998; Traveset & Verdu 2002), seed dispersal by frugivores may indirectly shape plant dynamics, e.g. by seed deposition at different distances from the parent trees (Jordano et al. 2007; Spiegel & Nathan 2007) or in different microhabitats that differ in suitability for seed germination and seedling establishment (Schupp 1993; Jordano & Schupp 2000). Despite the fact that retention times of X. monospora seeds did not vary among the three bird species, seed dispersal distance by the large-bodied and strictly frugivorous T. hartlaubi was estimated to be twice that of the smaller-bodied and partly frugivorous A. milanjensis and T. helleri. More than 60% of the dispersed X. monospora seeds were estimated to be deposited within 60 m of parental trees (see also Howe et al. 1985; Clark et al. 1999, 2005), while dispersal over 150 m (often referred to as ‘long distance dispersal’; see Levey et al. 2008) was rare. As GPTs for seeds of other Afromontane tree species were broadly similar to those of X. monospora (V. Lehouck et al., submitted), and dispersal distances tended to level-off within the gut retention range of Xymalos seeds (Fig. 1), dispersal distances estimated for X. monospora seeds likely apply to a wide range of species, including those with longer GPTs. Such a rapid levelling-off of distances moved by birds through time is commonly reported in the literature and results in broadly similar dispersal seeds of plant species dispersed by the same frugivore community (Westcott & Graham 2000; Weir & Corlett 2007). Even when disregarding the variation in distance over which seeds were carried by the frugivorous species (i.e. difference between T. helleri and T. hartlaubi only), interspecific variation in habitat use still caused strong complementarity in seed dispersal.

Quantitative knowledge of dispersal distances is particularly important in patchy environments where seeds may be distributed among isolated habitat blocks with different probabilities (Nathan & Muller-Landau 2000; Bohrer et al. 2005). Despite being considered a true forest specialist (Bennun et al. 1996), A. milanjensis regularly dwelled in exotic plantations and surrounding farmland, especially individuals that inhabited the smallest forest remnant. Such behaviour may explain why average seed dispersal distances were not significantly shorter in this fragment compared to the larger fragments, as would be expected if movements were constrained within indigenous forest boundaries (e.g. Serio-Silva & Rico-Gray 2002). T. hartlaubi also regularly ventured into farmland or mixed indigenous-exotic patches, independently of the size of the indigenous forest fragment. Excursions into the matrix were mainly directed towards isolated, fleshy-fruited trees or shrubs of indigenous (Ficus sp., Prunus africana, P. reclinata, Maesa lanceolata) as well as those of exotic (Maesopsis eminii, Cinnamom camphora, Lantana camara) origin, on which they foraged (Spanhove & Lehouck 2008; V. Lehouck et al., unpubl. data). Unless seeds consistently end up in unsuitable habitats for germination or seedling survival, such excursions may eventually lead to the colonization of new habitats by the trees. Results of this study further provide evidence that trees in small and isolated forest remnants or in pastures (so-called outlier assemblages) may comprise important sources of extraneous pollen and seeds, form nuclei for new populations and serve as interpopulation bridges for pathogens and herbivores (Levin 1995). Whereas the majority of X. monospora seeds from large forest fragments remained within the specific fragment boundaries, seeds from trees in small and isolated fragments had a higher chance of ending up in other forest patches (see above), some of which may be unoccupied by this species. As germination and survival rates of X. monospora seeds and seedlings in Eucalyptus, Pinus and Cupressus equalled those in indigenous forest (Lehouck et al. 2009a), exotic plantation plots may also act as recruitment nuclei (Guevara & Laborde 1993; Parrotta 1995; Zahn & Augspurger 2006). Because isolated trees were earlier shown to enrich and integrate population gene pools (Levin 1995; Albrich & Hamrick 1998), the importance of small, isolated habitat patches for maintaining metapopulation integrity cannot be overestimated.

Forest fragmentation may affect fruit-frugivore mutualisms in several ways. For example, reduced densities of quantitatively efficient dispersers (sensu
Schupp 1993) may result in reduced seed removal (Cordeiro & Howe 2003), while local extinction of long-distance dispersers (Kattan et al. 1994) and restriction of bird movements among isolated forest remnants (Castellon & Sieving 2006) may hamper colonization of new habitats by plants. Such seed dispersal limitation may affect (meta)population survival and reproduction under directional habitat or climate change (Johst et al. 2002; Pearson & Dawson 2005). At community level, variation in seed dispersal may affect species coexistence and species richness through altering competitive balances among plant species (Hurtt & Pacala 1995; Condit et al. 2002; but see Webb & Peart 2001). For instance, failure of seeds of dominant species to reach suitable microsites may facilitate local recruitment of less competitive species, hence increasing beta-diversity (‘winning-by-forfeit’, Hurtt & Pacala 1995). An earlier study in the Taita Hills revealed reduced removal rates of X. monospora seeds in small and disturbed forest fragments (Lehouck et al. 2009b), while over 700 h of radio-tracking (this study) only revealed two movement events between neighbouring forest fragments (ca. 760 m apart), albeit over a time-span of two consecutive days, and hence beyond the time window for dispersal of viable X. monospora seeds. While direct evidence for seed dispersal between isolated forest fragments in our study area is therefore lacking, other sympatric frugivores such as Ceratogyymna brevis (silvery-cheeked hornbill) and Onychognathus morio (eed-winged starling) are known to make uninterrupted movements beyond inter-fragment distances (Cordeiro et al. 2004; pers. obs.). Whether or not these rare and unpredictable long-distance dispersal events allow (meta)populations to persist in the long term, remains unclear (Johst et al. 2002; Trakhtenbrot et al. 2005). Action within forest fragments to maximize local survival of frugivores, and across landscapes to maximize their long-distance mobility, may be advisable to enhance such long-distance dispersal.

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**Supporting Information**

Additional supporting information may be found in the online version of this article:

**Appendix S1.** Map of the study area above 1200 m altitude (forest–shrubland boundary) with indication of the forest fragments CHA, MAC and NGA. Black polygons: indigenous forest fragments; grey polygons: plantations and isolated tree patches; white: settlements and smallholder cultivation plots (mainly bean, cabbage, maize, banana).

**Appendix S2.** Gut passage time of *X. monospora* seeds in five captive-held *Tauraco* species. \( N_{\text{individual}} \) = number of individuals; \( N_{\text{trial}} \) = number of feeding trials, each consisting of five *X. monospora* fruits.

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