



Plant–frugivore networks are robust to species loss even in highly built-up urban ecosystems

Saidy Mubamba¹ · Norman Nduna¹ · Stanford Siachoono¹ · Moses Chibesa¹ · Darius Phiri² · Lackson Chama¹

Received: 19 February 2022 / Accepted: 14 June 2022 / Published online: 3 July 2022
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2022

Abstract

Animal seed dispersal processes are an important aspect of ecosystem services, as they shape the survival of seed dispersers and the balanced distribution of propagules for many plant communities. Several studies within tropical wild ecosystems have generally shown that seed dispersal processes are highly generalised and robust to extinction. Studies examining seed dispersal networks in highly built-up urban ecosystems and their robustness to species loss or extinction are rare. We examined avian seed dispersal networks across an urban ecosystem characterised by a high human settlement and infrastructure of the built environment in Zambia to determine their network specialisation, interaction evenness and interaction diversity, as these three parameters are critical in driving the resilience of these mutualisms' interactions against extinction. A total of 405 individuals representing 11 species of birds were observed and recorded feeding on a total of 11 focal fleshy-fruited plant species. Network specialisation was generally low and remained similar across study areas. Interaction evenness and interaction diversity were not only high but also remained similar across study areas. Low specialisation and high interaction evenness and diversity show that mutualistic interactions in these networks are equally highly generalised, suggesting a stable and robust coexistence of species in plant–frugivore communities within urban ecosystems. Generally, our results seem to broadly suggest that opportunities for conservation still exist in these ecosystems provided urbanisation is accompanied by promoting either the management of remnant fruiting plants or the cultivation of new ones to support the avian communities existing in these areas.

Keywords Plants · Birds · Seed dispersal · Mutualism · Urbanisation

Introduction

Urbanisation is a pervasively growing global threat to biodiversity (Elmqvist et al. 2016; Kondratyeva et al. 2020). Research has shown that urbanisation is increasingly contributing towards extensive modification of biological communities at both local and landscape scales by reducing and fragmenting their natural habitats (Mckinney 2002; Emer et al. 2018). Recent forecasts suggest that the amount of

natural habitats likely to be transformed by urbanisation is expected to increase, on average, by more than three times between 2000 and 2030 (from 450,000 km² c. 2000) around the world (Elmqvist et al. 2016). And with 68% of the global human population predicted to live in urban areas by the year 2050 (United Nations 2019), this will most likely result in land use and land cover modifications, and environmental disturbances. Consequently, this will increase the pressure on local diversity of remnant species (Gaston 2010) and will induce the assembly of novel ecological communities (Swan et al. 2011; Kondratyeva et al. 2020). Already, over 80% of most urban areas across the globe are covered by pavement and buildings, of which only less than 20% remain vegetated (Mckinney 2008).

Generally, urbanisation impacts biodiversity and ecosystem services (e.g. soil formation and nutrient cycling, food and fresh water provision, etc.) both directly and indirectly (Elmqvist et al. 2016). Direct impacts consist of degradation, habitat loss, modified soils and other physical

Communicated by Francisco E. Fonturbel.

✉ Lackson Chama
lackson.chama@cbu.ac.zm

¹ Department of Zoology, Copperbelt University, Jambo Drive, Riverside, P.O. Box 21692, Kitwe, Zambia

² Department of Plant and Environmental Sciences, Copperbelt University, Jambo Drive, Riverside, P.O. Box 21692, Kitwe, Zambia

transformations caused by urban expansion (Escribano-Avila et al. 2018), whereas indirect impacts include changes in nutrient and water availability as well as an increase in abiotic stressors, like air pollution and changes in herbivory (Pickett and Cadenasso 2009). Arguably, land cover change is the most direct impact of urbanisation on biodiversity globally due to the growth of urban areas and associated activities, such as favouring the growth of non-native and native species that are frequently ecological generalists (Strohbach et al. 2009; Muller et al. 2013). Ultimately, this has been shown to severely affect the structure of ecosystems and can influence species diversity, ecological interactions and key ecological functions, such as animal-driven seed dispersal processes (Cruz et al. 2013; Silva et al. 2015; Valiente-Banuet et al. 2015; Yuan and Lu 2016). In fact, ecological interactions have been shown to be even more vulnerable to human propelled extinction than the species that drive these interactions (Valiente-Banuet et al. 2015). The ecological importance of interactions, such as the animal-mediated mutualistic seed dispersal processes, especially in the context of maintaining biodiversity and ecosystem dynamics are well documented (Howe and Smallwood 1982; Bascompte and Jordano 2007; Shikang et al. 2015; Timoteo et al. 2016). Therefore, altering or causing changes in disperser movement patterns that can affect seed removal and plant recruitment rates across ecosystems could result in several unforeseen consequences on biodiversity as a whole (Ciuti et al. 2012).

In recent years, the study of seed dispersal processes has shifted from examining one-on-one interactions between plants and frugivorous animals (Herrera 2002; Cordeiro and Howe 2003; Farwig et al. 2006), to the use of a community-wide approach involving the mechanistic understanding of seed dispersal network analysis (e.g. Carlo and Yang 2011; Chama et al. 2013; Dugger et al. 2018). This is because seed dispersal is mainly used as a mechanism to predict the consequences of species extinction and environmental perturbation to the entire community, especially in disturbed ecosystems (Guimarães Jr et al. 2006), such as urban environments. In fact, several factors have been shown to affect avian seed dispersers at a community level in disturbed environments, among which include predation pressure, habitat fragmentation size, edge heterogeneity, vegetation structure, human disturbances, food availability and landscape characteristics (e.g. surrounding matrix and patch connectivity; Yuan and Lu 2016; Cote et al. 2017; Gaynor et al. 2018). Many of these ecosystem disturbances affect the biological composition of communities whereby they alter their capacity to sustain key ecological functions, such as seed dispersal (Cruz et al. 2013). Further, most urban areas have also been shown to contain vegetation patches that are poorly connected to a certain degree (Francis and Chadwick 2013), largely driven by an increase in impervious surfaces and

promoting the management of landscapes that structurally simplifies vegetation within these areas (Baker and Harris 2007; McKinney 2008; Warren et al. 2015). Such attributes of habitat disturbance can undeniably impinge dispersal processes. Surprisingly, however, recent research shows that many avian frugivores seem to have developed adaptations in these environments irrespective of the various ecological disturbances they are subjected to (Murgui and Hedblom 2017). Whether these adaptations by avian frugivores translate into stable and thus robust seed dispersal networks in these ecosystems remains unclear.

Fruit-eating birds in wild tropical ecosystems have been shown to have access to a variety of fruits, largely attributed to the presence of a variety of fleshy-fruited plants, almost all year round, in those regions (Howe and Smallwood 1982; Chama et al. 2013). Several studies seem to generally suggest that such plant–frugivore interactions are robust to extinction in tropical wild ecosystems (Gonzalez-Castro et al. 2012; Dugger et al. 2018). However, studies examining how the community interactions between frugivores and their plant mutualists respond to ecological disturbances, such as urbanisation, are still rare (but see Cruz et al. 2013). Yet, seed dispersal processes play an important role in shaping plant recruitment and forest regeneration (D'Avila et al. 2010), albeit the benefits generated from the seed dispersal relationship between frugivorous animals and fleshy-fruited plants are reciprocal or mutual. Thus, any declines in plant population may affect the population of seed dispersers since fleshy fruits are important food resources for many frugivorous animals (Carlo and Yang 2011). Similarly, if seed dispersers decrease in numbers, it will affect the regeneration and restoration process of plant communities (Guimarães Jr et al. 2006). Unless we increase our understanding of the response of these ecologically critical mutualistic interactions to environmental disturbance, we are at risk of facing a total collapse in biological communities in the face of increased threats resulting from urbanisation. Although research has shown that dispersal networks in the tropical and subtropical ecosystems are generally resilient and thus robust to species extinction (e.g. Schleuning et al. 2011; Dugger et al. 2018), it remains unclear whether this also applies to those (seed dispersal networks) in highly built-up tropical urban areas, especially given the ecological disturbances that they are regularly subjected to.

Using community ecological parameters, such as network specialisation, interaction evenness and diversity, this study examined the effects of urbanisation on avian seed dispersal networks especially in the context of their robustness to species extinction. We predicted that avian seed dispersal networks in the urban ecosystem are highly specialised and therefore weakly structured. Effectively, this means that avian seed dispersal networks in urban ecosystems are not robust to species extinction as compared to those reported in

the wild tropical and subtropical ecosystems (Albrecht et al. 2012; Dugger et al. 2018).

Materials and methods

Study area

This study was conducted in Kitwe district ($-12^{\circ} 48' 8.75''$ S/ $28^{\circ} 12' 47.63''$ E; elevation of 1213 m asl, Fig. 1),

within the Copperbelt Province of Zambia, from 30th Oct. 2018 to 31st Mar. 2019. Located in the central part of the province and covering approx. 777 km², Kitwe is the second largest city in terms of population size (517,543) in Zambia (after the capital, Lusaka). The city was founded in 1936 and obtained its status as a city in 1966 (Mwitwa et al. 2016). The city whose mean annual rainfall and temperature are roughly 1288 mm and 20 °C, respectively, is one of the fairly developed commercial and industrial areas in the nation, hosting a complex of mining activities on its North-western

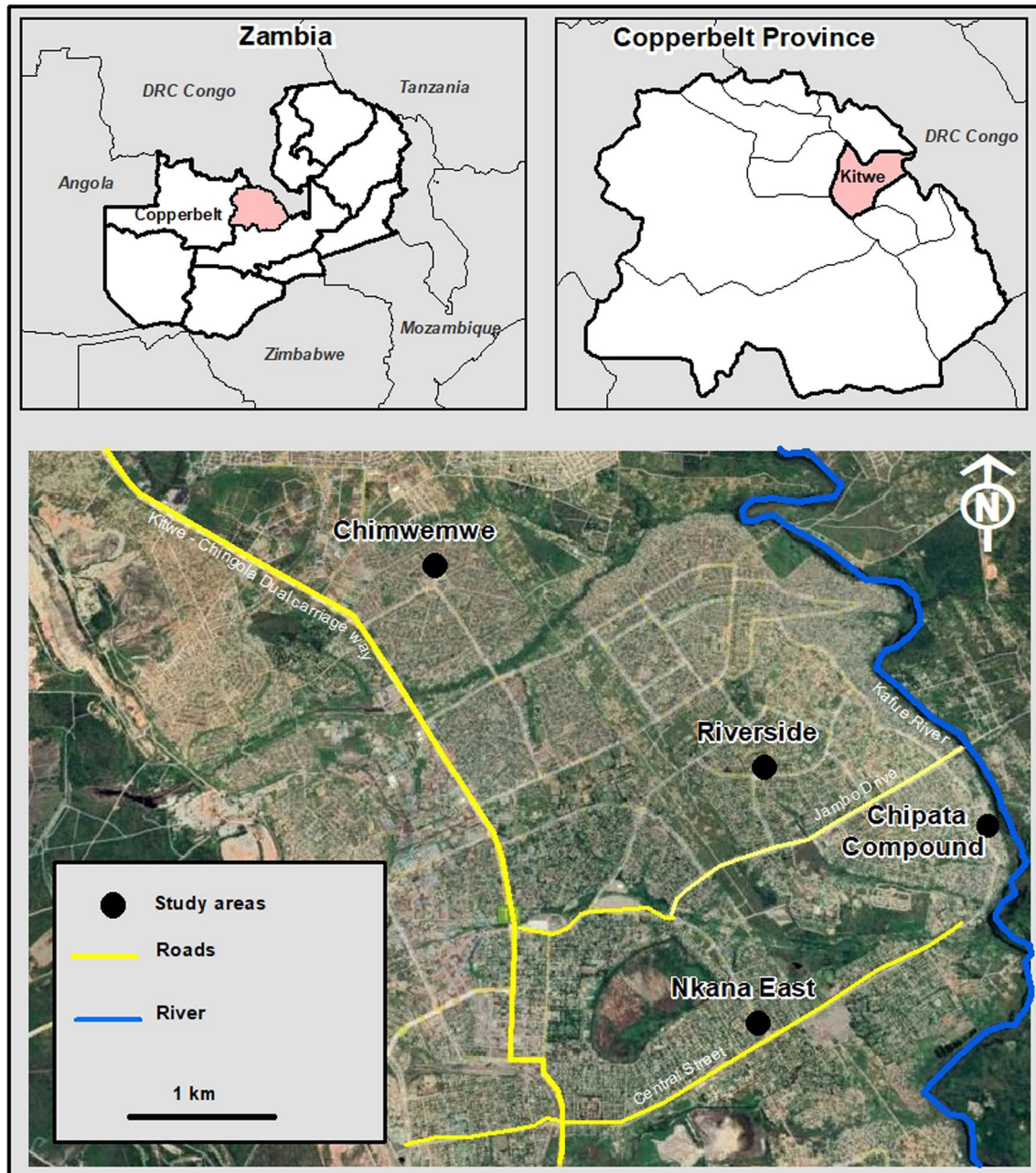


Fig. 1 Kitwe District map, showing the study sites

and Western edges (Mwakikagile 2010). Further, the city is composed of several townships and suburbs, some of which were selected in the context of undertaking this research (Fig. 1).

Research design

Within Kitwe's urban environment, we selected four townships, namely, *Riverside*, *Nkana west*, *Chimwemwe* and *Chipata Compound*, based on their socio-economic designations (henceforth referred to as *high-cost*, *medium-cost*, *mixed-cost* and *low-cost* residential areas, respectively; Fig. 1). Here, *high cost* represents areas of high-household income, *medium cost* represents areas of moderate or medium income; *low cost* represents areas of low income, while *mixed cost* denotes residential areas that have both medium- and low-cost attributes. We used these criteria because it has the potential to influence the richness of fleshy-fruited plants found across designations. For example, a pattern of higher biodiversity has been observed in affluent residential areas, than in low-income and predominantly minority populated neighbourhoods (Hope et al. 2003; Leong et al. 2018). Therefore, our assumption was that the richness of fruiting plant species could increase with increasing socio-economic status of a residential area. This is because highly affluent communities are likely to have the capacity to not only plant but also pay for the costs (e.g. water bills, outsourcing labour, etc.) of managing fruiting plant species in their backyard gardens. Consequently, such areas are likely to attract more avian frugivores than those of lower socio-economic status.

In each of the study areas, we first conducted extensive random reconnaissance walks to identify the fruiting plants with a view to establishing sampling plots and observation points. Thus, three replicates of 50 m by 100 m plots were established in each study area. A distance of at least 700 m apart from each plot was employed, in order to reduce the potential for counting the same birds more than once (Chama et al. 2013).

Assessment of plant–frugivore interactions

Field observations were undertaken to assess the interactions between frugivorous birds and all fleshy-fruited plant species in each study area. All fleshy-fruited plants in each plot were identified to species level (Forest Dept. 1979; Palgrave 2002) and observed for feeding activities by visiting avian frugivores. Where several individuals of a single plant species occurred, only one individual was randomly selected as a focal plant for undertaking the observations. Observations were conducted during the main fruiting season from November, 2018 to March, 2019 when most plant species were at their peak of ripening (Forest Dept. 1979; Palgrave

2002). We split the observation surveys in two sessions, i.e. early morning (07:30–10:30 a.m.) and late afternoon (3:00–5:00 p.m.), as these are times when most birds are active (Menke et al. 2012; Chama et al. 2013). On each focal plant in a study plot, observations were conducted on three different days per week with the aid of a pair of binoculars (Bushnell Legend E-Series—10×42), from a hidden position and at a distance of 10–15 m.

All fruit-eating birds on each focal fruiting plant were observed for a period of 30 min, before moving to the next plant within the 5 h' time per day (Albrecht et al. 2012). Thus, each plant was observed for a total of 1.5 h (i.e. 30 min/day×3 observation days). We identified (i.e. using Sinclair and Ryan 2010) and recorded all visiting birds that were seen consuming fruit on each focal fleshy-fruited plant under observation. The number of visitations that the bird made within the time (30 min) of observation per day were also recorded. The number of individual birds and the time they spent feeding was equally recorded. In cases where a group of conspecific birds visited a plant and individual observations could not be done simultaneously, only one individual that was best visible was randomly chosen and observed with regard to its fruit consumption (Menke et al. 2012). The total number of observation hours for all the focal plants was 67.5.

Statistical analysis

To test the effects of urbanisation on the robustness of seed dispersal networks, we analysed the response of key indices at network level, namely, *specialisation* ($H2'$), *interaction evenness* and *interaction diversity*. Network specialisation ($H2'$) defines the link complementarity across all species in a community (Kaiser-Bunbury and Blüthgen 2015). It is quantified with the values ranging from 0 to 1, where 0 denotes complete generalization and vice versa. Thus, a higher specialisation denotes a high dependency of each species on few limited partners. Effectively, this implies a narrow niche breadth and a highly specialised seed dispersal process (Blüthgen et al. 2006). On the other hand, low specialisation indicates a higher functional redundancy among partners (Blüthgen 2010), which implies that there is high niche breadth of both plants and frugivores, and reveals that plants benefit from seed dispersal of generalised frugivores. Unlike network specialisation, interaction evenness defines the uniformity in interaction frequencies across all links in the networks, with high values (closer to 1) reflecting more uniform spread of interaction among species (Blüthgen et al. 2008; Kaiser-Bunbury and Blüthgen 2015), while interaction diversity is the quantitative similarity to the total number of links across species in the network (Kaiser-Bunbury and Blüthgen 2015; Landi et al. 2018). Higher interaction

diversity (greater than 1) implies a higher community stability and robustness.

Thus, at the onset of our analysis, we computed the plant–frugivore interaction data to plot seed dispersal networks by means of the bipartite package. The bipartite package uses the R environment to provide statistical functions for visualising food webs and calculating a series of indices commonly used to describe two-trophic-level ecological webs, e.g. seed–disperser, plant–pollinator and predator–prey systems (Dormann et al. 2008). Thus, we compiled the interaction frequencies of each fleshy-fruited plant species (*p*) with each frugivore species (*f*) for each study site in the quantitative interaction matrix. Here, the interaction frequencies (between plants and frugivores) were calculated using the number of feeding visits that each identified bird made on each fruiting plant species (Vazquez et al. 2012). From these data, we calculated, analysed and compared the specialisation ($H2'$), interaction evenness and interaction diversity across networks from each study area using mixed-effects models with maximum likelihood. Further, we undertook a post hoc test with Tukey Honest Significant Difference (HSD) to compare the variance in the mean network specialisation, interaction evenness and interaction diversity across study areas. We then used the mean network indices in our seed dispersal networks to compare with what has already been documented in the wild ecosystems (e.g. Schleuning et al. 2011; Menke et al. 2012). Finally, we used repeated-measures analysis to test if the richness of both fleshy-fruited plants and avian frugivores differed across study areas. We then performed linear regression models to test if our network parameters (specialisation ($H2'$), interaction evenness and interaction diversity) correlated with the richness of both the fleshy-fruited plants and avian frugivores following Chama et al. (2013). All statistical analyses

were performed in R statistical software version 4.1.3 (The R Development Core Team 2022).

Results

Plant species composition

We observed a total of 11 species of focal fleshy-fruited plants (including both native and exotic plants, i.e. representing a total of 45 individuals across all four study areas; Table 1). Of these, nine were in the high-cost, seven in the mixed-cost and four each in both the medium- and low-cost residential areas. Plant species richness remained similar across study areas ($F_{3,8} = 3.66$; $p > 0.05$). Plant species that recorded the most interactions or fruit-eating visits by frugivores included the Pawpaw (*Carica papaya*; $n = 108$), followed by Woodland water berry (*Syzygium guineense*; $n = 78$), Guava (*Psidium guajava*; $n = 74$) and the Sycamore fig (*Ficus sycomorus*; $n = 53$). In contrast, the Avocado (*Persea americana*) and Mango (*Mangifera indica*) had the least number of visitors with a total count of 1 and 2 birds, respectively (Fig. 4; Table 2).

Bird species composition

A total of 11 avian frugivore species, representing a total of 405 individuals, were recorded feeding on focal fleshy-fruited plant species (Table 3). Of these, 11 were in the high-cost, 8 in the medium-cost and 6 each in the mixed- and low-cost residential areas. Frugivores species richness remained similar across study areas ($F_{3,8} = 3.68$; $p > 0.05$). Avian frugivores species with the most fruit-eating interactions across study areas were the Common Bulbul (*Pycnonotus*

Table 1 List of fleshy-fruited plant species, their origin, area where they were present and corresponding total number of individuals observed across an urban ecosystem in Zambia (Forest Dept. 1979; Palgrave 2002)

Plant spp. code	Common name	Scientific name	Origin	Area where present				Total no. of individuals
				High	Medium	Mixed	Low	
<i>T</i> ₁	Sycamore fig	<i>Ficus sycomorus</i>	Native	✓				2
<i>T</i> ₂	Common wild fig	<i>Ficus burkei</i>	Native	✓				1
<i>T</i> ₃	Shepherds tree	<i>Boscia angustifolia</i>	Native	✓				1
<i>T</i> ₄	Guava	<i>Psidium guajava</i>	Exotic	✓	✓	✓	✓	12
<i>T</i> ₅	Nill	<i>Phyllanthus muellerianus</i>	Native	✓				2
<i>T</i> ₆	Woodland water berry	<i>Syzygium guineense</i>	Native	✓	✓	✓	✓	5
<i>T</i> ₇	Alexandra palm	<i>Archontophoenix alexandrae</i>	Exotic	✓	✓	✓		4
<i>T</i> ₈	Pawpaw	<i>Carica papaya</i>	Exotic	✓	✓	✓	✓	11
<i>T</i> ₉	Mango	<i>Mangifera indica</i>	Exotic	✓		✓		2
<i>T</i> ₁₀	Manna	<i>Alhagi maurorum</i>	Exotic			✓	✓	4
<i>T</i> ₁₁	Avocado	<i>Persea americana</i>	Exotic			✓		1
Total								45

Table 2 List of fruiting plant species and their total number of feeding interactions with avian frugivores (see Fig. 4 for details about the species of avian frugivores that interacted with each fruiting plant species)

Plant spp. code	Common name	Scientific name	Origin	No. of frugivores-feeding interactions				Total interactions
				High	Medium	Mixed	Low	
T_1	Sycamore fig	<i>Ficus sycomorus</i>	Native	53	0	0	0	53
T_2	Common wild fig	<i>Ficus burkei</i>	Native	18	0	0	0	18
T_3	Shepherds tree	<i>Boscia angustifolia</i>	Native	12	0	0	0	12
T_4	Guava	<i>Psidium guajava</i>	Exotic	17	24	15	18	74
T_5	Nill	<i>Phyllanthus muellerianus</i>	Native	11	0	0	0	11
T_6	Woodland water berry	<i>Syzygium guineense</i>	Native	39	15	13	11	78
T_7	Alexandra palm	<i>Archontophoenix alexandrae</i>	Native	07	08	07	0	22
T_8	Pawpaw	<i>Carica papaya</i>	Exotic	21	37	30	20	108
T_9	Mango	<i>Mangifera indica</i>	Exotic	07	0	03	0	10
T_{10}	Manna	<i>Alhagi maurorum</i>	Exotic	0	0	10	08	18
T_{11}	Avocado	<i>Persea americana</i>	Exotic	0	0	01	0	01
Total								405

Table 3 List of bird species and their total number of individuals observed feeding on fleshy-fruiting plant species across an urban ecosystem in Zambia (Sinclair and Ryan 2010)

Bird species code	Common name	Scientific name	Feeding individuals per study area				Total no. of individuals
			High	Medium	Mixed	Low	
B_1	Yellow-Fronted Canary	<i>Crithagra mozambica</i>	4	0	0	0	04
B_2	Black-Faced Canary	<i>Crithagra capistrata</i>	4	0	0	0	04
B_3	African Yellow White-Eye	<i>Zosterops senegalensis</i>	39	20	15	14	88
B_4	Common Bulbul	<i>Pycnonotus barbatus</i>	47	21	22	16	106
B_5	Black-collared Barbet	<i>Lybius torquatus</i>	11	2	1	1	15
B_6	Spectacled Weaver	<i>Ploceus ocularis</i>	5	0	0	0	05
B_7	Red-Faced Mousebird	<i>Urocolius indicus</i>	24	11	14	10	59
B_8	Golden Weaver	<i>Ploceus ocularis</i>	9	2	0	2	13
B_9	Speckled Mousebird	<i>Colius striatus</i>	28	26	21	17	92
B_{10}	Tropical Boubou	<i>Laniarius major</i>	6	1	3	0	10
B_{11}	Black-backed Barbet	<i>Lybius minor</i>	8	1	0	0	09
Total							405

barbatus; $n = 106$), followed by the Speckled Mousebird (*Colius striatus*; $n = 92$), African Yellow White-eye (*Zosterops senegalensis*; $n = 88$), and the Red-faced Mousebird (*Urocolius indicus*; $n = 59$; Table 3; Fig. 4).

Network specialisation across study sites

The mean network specialisation ($H2'$) ranged from 0.177 ± 0.039 (SD, if not otherwise stated; high cost) to 0.179 ± 0.075 (mixed cost), 0.421 ± 0.164 (medium cost) and 0.257 ± 0.214 (low cost). Network specialisation remained similarly low across study areas ($F_{3,8} = 0.258$; $p = 0.854$; Fig. 2a). Moreover, it was unaffected by the increase in the richness of both fleshy-fruiting plants ($F_{1,10} = 1.65$; $p > 0.05$) and avian frugivores ($F_{1,10} = 1.44$; $p > 0.05$).

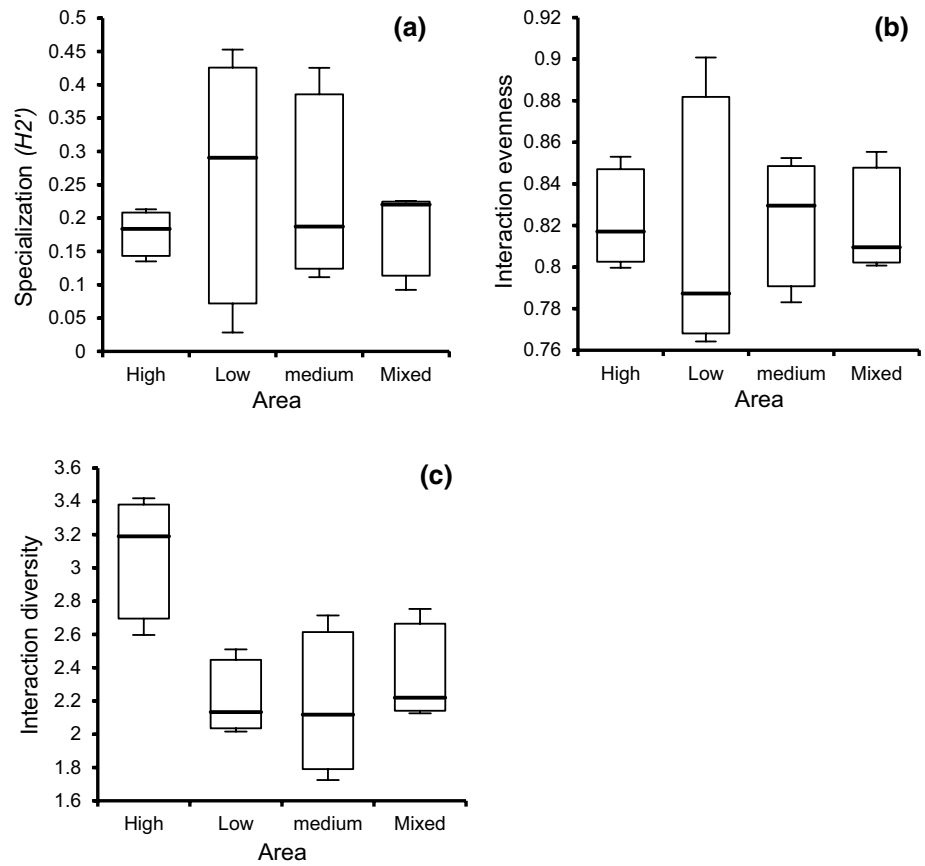
Network interaction evenness across study sites

The mean network interaction evenness ranged from 0.817 ± 0.07 (low cost) to 0.822 ± 0.035 (medium cost), 0.822 ± 0.029 (mixed cost) and 0.823 ± 0.027 (high cost). It remained similarly high across study areas ($F_{3,8} = 0.01$; $p > 0.05$; Figs. 2b and 4). Like network specialisation, interaction evenness was unaffected by the richness of both the fleshy-fruiting plants ($F_{1,10} = 1.65$; $p > 0.05$) and avian frugivores ($F_{1,10} = 0.329$; $p > 0.05$).

Interaction diversity across study sites

The mean interaction diversity across networks ranged from 2.186 ± 0.498 (medium cost) to 2.220 ± 0.258 (low

Fig. 2 The mean network specialisation ($H2'$) (a), interaction evenness (b) and interaction diversity (c) of seed dispersal mutualistic networks across an urban ecosystem in Zambia

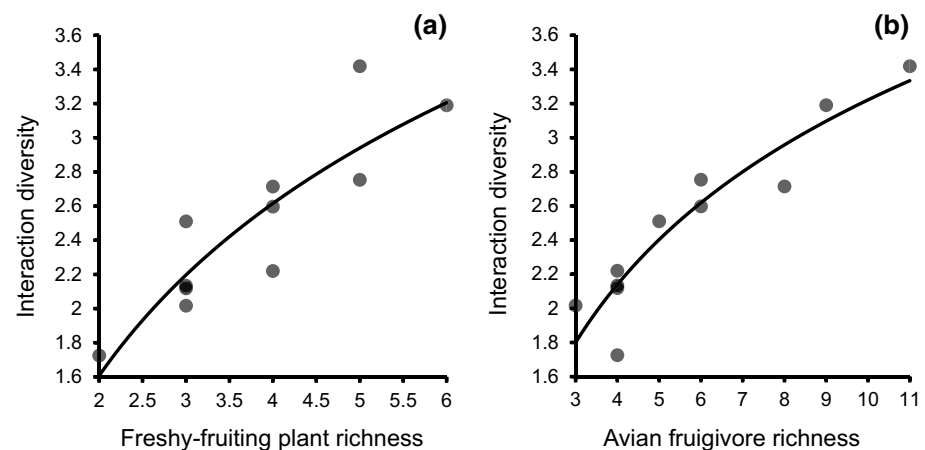


cost), 2.366 ± 0.339 (mixed cost) and 3.068 ± 0.424 (high cost). Species interaction diversity remained similar across study areas ($F_{3,8} = 3.361$; $p = 0.076$; Fig. 2c and Figs. 4). However, it increased significantly with increasing richness in both the fruiting plants ($F_{1:10} = 38.34$; $p < 0.001$; Fig. 3a) and avian frugivores ($F_{1:10} = 86.04$; $p < 0.001$; Fig. 3b).

Discussion

Our aim was to test the fitness of avian seed dispersal networks in the urban ecosystems and establish if they are as robust as those reported in tropical wild ecosystems. Overall, our results indicated a similarly low specialisation across all seed dispersal networks, whereas interaction evenness remained similarly high. In contrast, species interaction diversity varied marginally across networks. It was slightly

Fig. 3 The mean network interaction diversity correlation with a fresh-fruiting plant richness and b avian frugivore richness



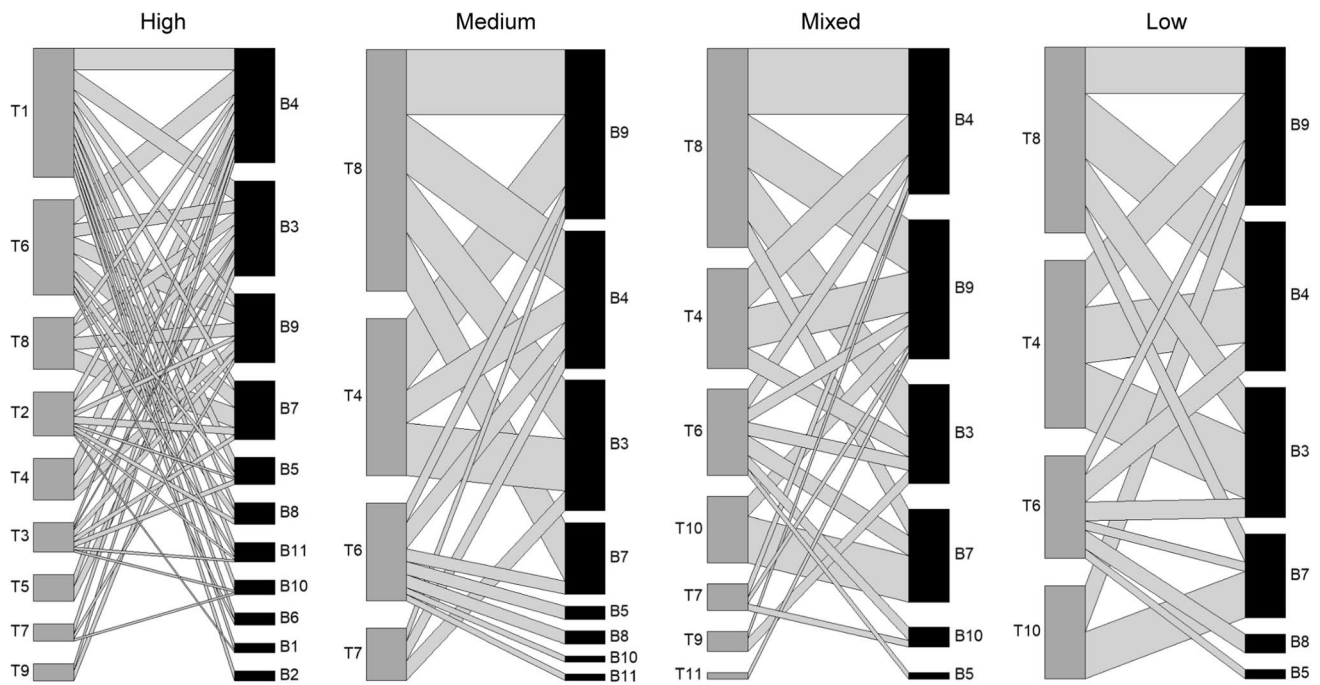


Fig. 4 Seed dispersal networks for high-, medium-, mixed- and low-cost residential study areas. In each of the networks, the grey bars (on the left) represent a node of different fleshy-fruited plant species (letter codes T1 to T11), while the black bars (on the right) represent a node of different bird species (B1 to B11). The light-grey lines between the two nodes highlights the partners that each species (of

plants and birds) interacts with in the network. The size of the line indicates the strength of the interaction, i.e. the thicker the line, the stronger the mutualistic interaction and vice versa. Full names of plants and birds represented by each letter code in the networks are shown in Tables 1 and 3, respectively

higher in the high-cost than in the rest of the residential areas studied, all of which remained similar. Generally, the results suggest that the avian seed dispersal networks in the studied urban ecosystems are stable and well organised. This is contrary to our earlier prediction that avian seed dispersal networks in highly built-up tropical urban ecosystems are not robust in the context of facing extinction. Although species interaction diversity differed slightly across networks, the difference was marginal, suggesting that these seed dispersal networks have either adapted or are broadly highly resilient to disturbance, and they also do not seem to be affected by the socio-economic status of human communities in which they exist.

Network specialisation across study areas

The mean network specialisation remained similarly low across study areas, suggesting a high redundancy threshold in the associations between plants and frugivores. A high redundancy in associations depicts a stable synchronicity of species in these plant–frugivore communities. Effectively, this could mean that these networks are highly generalised, which potentially increases their robustness to extinction. High functional redundancy has been shown to contribute to the persistence of networks such that even if some

interactions disappear, the plant–frugivore community will still remain robust towards land use and land cover changes (Bascompte and Jordano 2007).

The low specialisation depicted in these networks from a highly built-up human-dominated urban ecosystem is similar to those found in the wild or areas with less ecosystem disturbance (e.g. Schleuning et al. 2011; Chama et al. 2013). Generally, seed dispersal networks in the wild ecosystems of the tropics have been shown to be highly robust, as they exhibit very low mean community specialisation ($H2' < 0.5$; Dugger et al. 2018). Thus, the fact that the specialisation in the studied networks was comparably very low suggests that seed dispersal networks in the tropics will remain robust even in highly built-up environment, provided the opportunities that drives these interactions, such as the presence of fleshy-fruited plant species and avian frugivores, continue to exist. In this case, the preservation or growth of fleshy-fruited plant species should especially be strongly promoted, as this is crucial towards making urban ecosystems attractive for avian frugivores to thrive.

Network interaction evenness across study areas

Overall, the results from this study shows that the mean network interaction evenness remained similarly high across

study areas. Effectively, this suggests that the frequency of the interaction assembly among species of both plants and their avian frugivore mutualists was uniformly spread in the community, albeit in a highly heterogeneous pattern. The assemblages of mutualistic communities have been shown to be centred on highly asymmetric and coevolutionary interactions that have shaped their persistence to environmental change over time (Jordano et al. 2003). This means that while a bulk of species may have a few interactions, a few other species have many more interactions than expected by chance (e.g. if a plant species depends strongly on an animal species, the animal depends weakly on the plant) and this pattern is uniformly spread across the network (Bascompte et al. 2006; Fig. 4). Thus, even if some species may only depend on a few partners, the higher and uniform interaction evenness suggests that higher functional robustness occurs within these networks, as the risks of losing a link or entire species or even fluctuations of frequencies are spread evenly (Kaiser-Bunbury and Blüthgen 2015).

Asymmetric coevolutionary interactions have been shown to be often stable and less sensitive to habitat disturbance, and their capabilities to remain resilient are strengthened at community rather than one-on-one interaction basis (Pauw et al. 2009; Fontúrbel and Murúa 2014). This is because interacting parties in these relationships are more likely to persist in spite of changes in environmental conditions and the demographic changes of their interacting parties (Fontúrbel and Murúa 2014). Our results highlight the importance of asymmetrically even interactions in mutualistic networks, as this is critical in driving both the diversity and coexistence of species in these communities (Paine 1980; Schoener 1983; Bascompte et al. 2006), especially in the face of threats, such as those coming from urbanisation. Even in an extreme scenario, plant–animal interactions assembled on a higher interaction evenness (albeit asymmetrically) could coevolve to develop strategies that are suitable for them to survive in such conditions (Fontúrbel and Murúa 2014). In this case, it seems highly unlikely that the networks in our study area could easily collapse even if one or two individuals are eliminated from the community due to extinction (Yachi and Loreau 1999; Wang and Loreau 2014).

Network interaction diversity across study areas

As observed from our results, the mean interaction diversity was significantly high and broadly similar across seed dispersal networks. Ecologically, a higher interaction diversity signals a higher heterogeneity in the magnitude of interacting partners and their complementary response to environmental disturbance (Almqvist et al. 2003; Hooper et al. 2005). Generally, however, interaction diversity can sometimes suffer from interference between consumer species, which could impact negatively

on potential complementarity effects, and thus reduce ecosystem function even in the face of increasing consumer diversity (Montoya et al. 2003; Finke and Denno 2004; Tylianakis et al. 2010). Nonetheless, a higher interaction diversity has also been shown to not only increase network stability but also the functional performance in the context of enhancing the fitness of the community (Hector et al. 1999) to environmental threats.

Our findings agree with Cruz et al. (2013) suggesting that seed dispersal networks can be complex and variable even in a highly managed urban area and that a network approach remains an important monitoring tool to detect the status of crucial ecosystem functions in such rapidly changing and human-dominated environments. Therefore, any potential effects of interaction interference are likely to be temporal rather than long-term where interaction diversity is high, like in the case of the studied seed dispersal networks. Besides, a higher interaction diversity generally also suggests higher richness and evenness of species as well as generalization of interactions. This is further supported by the fact that interaction diversity in the studied networks was positively correlated with the richness of both fleshy-fruited plants (Fig. 3a) and avian frugivores (Fig. 3b). In fact, several species of fleshy-fruited plants (namely, *Carica papaya*, *Syzygium guineense*, *Psidium guajava* and *Ficus sycomorus*) and avian frugivores (namely, *Pycnonotus barbatus*, *Colius striatus*, *Zosterops senegalensis* and *Urocolius indicus*) had more interactions than others in our study area. Such species have a disproportionately greater contribution to the overall organization and cohesion of networks (Mello et al. 2011, 2015; Sebastián-González 2017; Bomfim et al. 2018). Obviously, by occupying central network positions, these plants benefit from the dispersal services provided by many species of frugivores, while the birds are able to consume fruits on multiple plant species (Jordano 2000; Chama et al. 2013). Nonetheless, the removal of such highly connected species could diminish crucial ecological interactions and consequently compromise the stability or integrity of these networks (Kaiser-Bunbury et al. 2010; Galetti et al. 2013; Correa et al. 2016). Therefore, such species of both plants and birds should especially be at the centre of conservation efforts if these interactions and their ecosystem functions are to be preserved.

Our findings are similar to those found in the study of pollination networks where species interaction diversity was shown to increase with increased abundance of beneficial resources, such as plant species diversity and pollinators that provide pollination services to crop plants (Albrecht et al. 2007). Although Albrecht et al. (2007) further showed that interaction diversity tends to somewhat decline more rapidly in disturbed environments, our results show that human-settled urban ecosystems have the potential to support stable and robust ecological processes if they can promote the

hosting of a diversity of plant and animal species that are especially critical in driving these ecological systems.

Conclusion

Our findings broadly suggest that avian seed dispersal networks in urban ecosystems are highly generalised. This means that there is a high redundancy in plant–frugivore associations (links), signifying stability of coexistence among species in these communities. Thus, even if some species may only have one species that they interact with, the chances that such species would go extinct are rare because the few partners that they interact with are potentially linked to several others, as highlighted by the high interaction evenness across networks. And collectively, such a combination of interactions shapes the fitness of both fleshy-fruited plant species and avian frugivores against the threats of extinction. For plants, this provides an assurance that their seeds or propagules will be dispersed, while for frugivores this ensures that there is adequate availability of fruits for them to feed on, and this is critical for their fitness. Our findings bring out some lessons of conservation importance about urban ecosystems, i.e. they have the potential to support key ecological processes, such as seed dispersal networks even in the face of heightened human disturbance. Therefore, there is a need for the creation of awareness about the conservation opportunities that exist in these areas. Activities, such as the planting of a diversity of fleshy-fruited plants and educating the human communities living in these areas about the ecological importance of birds, should especially be promoted. The planting of native rather than exotic fruiting plant species should especially be encouraged. For key conservation agencies, these results should propel them to widen their conservation efforts beyond the boundaries of protected areas, which are often wild and remote, by also considering resource preservation opportunities in urban ecosystems. Species of both plants and avian frugivores with higher interactions are especially critical not only in the maintenance of network stability but also ecosystem function and should be the focus of conservation efforts (Correa et al. 2016).

Acknowledgements The authors would like to thank the residents of Kitwe particularly in the four study areas for their cooperation during the period that we conducted this study within their premises. Special thanks to Stephen Syampungani for providing help during the data collection exercise.

Author contributions SM and LC originally conceived and formulated the research idea. SM, assisted by MC and NN, undertook the fieldwork. DP did the mapping of the study area. LC and SM analysed the data. SM, LC, NN, SS, DP and MC wrote the manuscript.

Funding This study was funded by the government loans board, administered through the Ministry of Higher Education in Zambia. The funders had no role to play in the study design, data collection, analysis, manuscript development and choice of journal to which this work was submitted.

Availability of data and material The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable to this study.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

Consent to participate Not applicable to this study.

Consent for publication Not applicable to this study.

References

- Albrecht M, Duelli P, Schmid B, Muller CB (2007) Interaction diversity within quantified insect food webs in restored and adjacent intensively managed meadows. *J Anim Ecol* 76(5):1015–1025. <https://doi.org/10.1111/j.1365-2656.2007.01264>
- Albrecht J, Neuschütz EL, Farwig N (2012) Impact of habitat structure and fruit abundance on avian seed dispersal and fruit predation. *Basic Appl Ecol* 13:347–354. <https://doi.org/10.1016/j.baae.2012.06.005>
- Almqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. *Front Ecol Environ* 1(9):488–494. [https://doi.org/10.1890/1540-9295\(2003\)001\[0488:RDECAR\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2)
- Baker PJ, Harris S (2007) Urban mammals: What does the future hold? An analysis of the factors affecting patterns of use of residential gardens in Great Britain. *Mamm Rev* 37(4):297–314. <https://doi.org/10.1111/j.1365-2907.2007.00102>
- Bascompte J, Jordano P (2007) Plant–animal mutualistic networks: the architecture of biodiversity. *Annu Rev Ecol Syst* 38:567–593. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095818>
- Bascompte J, Jordano P, Olesen JM (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312(5772):431–433. <https://doi.org/10.1126/science.1123412> (PMID: 16627742)
- Blüthgen N (2010) Why network analysis is often disconnected from community ecology: a critique and an ecologists guide. *Basic Appl Ecol* 11(3):185–195. <https://doi.org/10.1016/j.baae.2010.01.001>
- Blüthgen N, Menzel F, Blüthgen N (2006) Measuring Specialization in species interaction networks. *BMC Ecol* 6(9):1–12. <https://doi.org/10.1186/1472-6785-6-9>
- Blüthgen N, Frund J, Vazquez DP, Menzel F (2008) What do interaction network metric tell us about specialization and biological traits? *Ecol* 89(12):3387–3399. <https://doi.org/10.1890/07-2121.1>
- Bomfim JDS, Guimarães PR Jr, Peres CA, Carvalho G, Cazetta E (2018) Local extinctions of obligate frugivores and patch size reduction disrupt the structure of seed dispersal networks. *Ecography* 41(11):1899–1909. <https://doi.org/10.1111/ecog.03592>

- Carlo TA, Yang AS (2011) Network models of frugivory and seed dispersal: challenges and opportunities. *Acta Oecol* 37(6):619–624. <https://doi.org/10.1016/j.actao.2011.08.001>
- Chama L, Berens DG, Downs CT, Farwig N (2013) Habitat characteristics of forest fragments determine specialization of plant-frugivore networks in a mosaic forest landscape. *PLoS One* 8(1):e54956. <https://doi.org/10.1371/journal.pone.0054956>
- Ciuti S, Muhly TB, Paton DG, McDevitt AD, Musiani M, Boyce MS (2012) Human selection of elk behavioural traits in a landscape of fear. *Proc R Soc B* 279:4407–4416. <https://doi.org/10.1098/rspb.2012.1483>
- Cordeiro NJ, Howe HF (2003) Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *PNAS* 100(24):14052–14056. <https://doi.org/10.1073/pnas.2331023100>
- Correa SB, Araujo JKM, Penha JMF, Nunes da Cunha C, Stevenson PR, Anderson JT (2015) Overfishing disrupts an ancient mutualism between frugivorous fishes and plants in Neotropical wetlands. *Biol Conserv* 191:159–167. <https://doi.org/10.1016/j.biocon.2015.06.019>
- Correa SB, Arujo JK, Penha J, Nunes da Cunha C, Bobier KE, Anderson JT (2016) Stability and generalization in seed dispersal networks: a case study of frugivorous fish in Neotropical wetlands. *Proc R Soc B* 283(1836):20161267. <https://doi.org/10.1098/rspb.2016.1267>
- Cote J, Bestion E, Jacob S, Travis J, Légrand D, Baguette M (2017) Evolution of dispersal strategies and dispersal syndromes in fragmented landscape. *Ecography* 40(1):56–73. <https://doi.org/10.1111/ecog.02538>
- Cruz JC, Ramos JA, Silva LP, Tenreiro PJ, Ruben H (2013) Seed dispersal networks in an urban novel ecosystem. *Eur J for Res* 132(5–6):887–897. <https://doi.org/10.1007/s10342-013-0722-1>
- D’Avila G, Gomes-Jr A, Canary AC, Bugoni AL (2010) The role of avian frugivores on germination and potential Seed dispersal of the Brazilian Pepper *Schinus terebinthifolius*. *Biota Neotrop* 10(3):47–51. <https://doi.org/10.1590/S1676-06032010000300004>
- Dormann CF, Gruber B, Fründ J (2008) The bipartite package. Version 0.73. R Project for Statistical Computing, Vienna
- Dugger PJ, Blendinger PG, Böhning-Gaese K, Chama L, Correia M, Dehling DM, Emer C, Farwig N, Fricke EC, Galetti M, García D, Grass I, Heleno R, Jacomassa FAF, Moraes S, Moran C, Muñoz MC, Neuschulz EL, Nowak L, Piratelli A, Pizo MA, Quitián M, Rogers HS, Ruggera RA, Saavedra F, Sánchez MS, Sánchez R, Santillán V, Schabo DG, da Silva FR, Timóteo S, Traveset A, Vollstädt MGR, Schleuning M (2018) Seed-dispersal networks are more specialized in the Neotropics than in the Afrotropics. *Glob Ecol Biogeogr* 28(2):1–14. <https://doi.org/10.1111/geb.12833>
- Elmqvist T, Zipperer W, Güneralp B (2016) Urbanization, habitat loss, biodiversity decline: solution pathways to break the cycle. In: Seto KC, Solecki WD, Griffith CA (eds) *The Routledge handbook of urbanization and global environmental change*. Routledge, Abingdon, pp 139–151
- Emer C, Galetti M, Pizo MA, Guimarães PR Jr, Moraes S, Piratelli A, Jordano P (2018) Seed-dispersal interactions in fragmented landscapes—a metanetwork approach. *Ecol Lett* 21(4):1–10. <https://doi.org/10.1111/ele.12909>
- Escribano-Avula G, Lara-Romero C, Heleno R, Traveset A (2018) Tropical seed dispersal networks: emerging patterns, biases and keystone species traits. In: Dattilo W, Rico-Gray V (eds) *Tropical Seed dispersal networks*. Springer International Publishing AG, Mallorca, pp 93–110
- Farwig N, Böhning-Gaese K, Bleher B (2006) Enhanced seed dispersal of *Prunus africana* in fragmented and disturbed forests? *Oecologia* 147(2):238–252. <https://doi.org/10.1007/s00442-005-0288-9>
- Finke DL, Denno RF (2004) Predator diversity dampens trophic cascades. *Nature* 429:407–410. <https://doi.org/10.1038/nature02554>
- Fontúrbel FE, Murúa MM (2014) Microevolutionary effects of habitat fragmentation on plant–animal interactions. *Adv Ecol Res*. <https://doi.org/10.1155/2014/379267>
- Forest Department (1979) *Know your trees: some of the common trees found in Zambia*. Forest Department, Lusaka
- Francis RA, Chadwick MA (2013) *Urban ecosystem: understanding the human environment*, 1st edn. Routledge, London
- Galetti M, Guevara R, Côrtes MC, Fadini R, Matter SV, Leite AB, Labecca F, Ribeiro T, Carvalho CS, Collevatti RG, Pires MM, Guimarães PR, Brancalion PH, Ribeiro MC, Jordano P (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* 340(6136):1086–1090. <https://doi.org/10.1126/science.1233774>
- Gaston K (2010) *Urban ecology*. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511778483>
- Gaynor J, Hojnowski C, Carter N, Brashares J (2018) The influence of human distance on wildlife nocturnality. *Science* 360(6394):1232–1235. <https://doi.org/10.1126/science.aar7121>
- Gonzalez-Castro A, Traveset A, Nogales M (2012) Seed dispersal interactions in the Mediterranean Region: contrasting patterns between Islands and Mainland. *J Biogeogr* 39(11):1938–1947. <https://doi.org/10.1111/j.1365-2699.2012.02693>
- Guimarães PR Jr, Gray VR, Dos Reis SF, Thompson JN (2006) Asymmetries in specialization in ant-plant mutualistic networks. *Proc R Soc B* 273(1597):2041–2047. <https://doi.org/10.1098/rspb.2006.3548>
- Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, HöGberg P, Huss-Danell K, Joshi J, Jumpponen A, Körner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O’donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze ED, Siamantziouras ASD, Spehna EM, Terry C, Troumbis AY, Woodward FI, Yachi S, Lawton JH (1999) Plant diversity and productivity experiments in European grassland. *Science* 286(5442):1123–1127. <https://doi.org/10.1126/science.286.5442.1123>
- Herrera CM (2002) Seed dispersal by vertebrates. In: Herrera CM, Pellmyr O (eds) *Plant–animal interactions: an evolutionary approach*. Blackwell Science, Oxford, pp 85–210
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75(1):3–35. <https://doi.org/10.1890/04-0922>
- Hope D, Gries C, Zhu W, Fagan WF, Redman CL, Grimm NB, Nelson AL, Martin C, Kinzig A (2003) Socioeconomics drive urban plant diversity. *PNAS* 100(15):8788–8792. <https://doi.org/10.1073/pnas.1537557100>
- Howe HF, Smallwood J (1982) Ecology of seed dispersal. *Annu Rev Ecol Evol Syst* 13(1):201–228. <https://doi.org/10.1146/annurev.es.13.110182.001221>
- Jordano P (2000) Fruits and frugivory. In: Fenner M (ed) *Seeds: the ecology of regeneration in natural plant communities*, 2nd edn. Commonwealth Agricultural Bureau International, Wallingford, pp 125–166. <https://doi.org/10.1079/9780851994321.0125>
- Jordano P, Bascompte J, Olesen JM (2003) Invariant properties in coevolutionary networks of plant–animal interactions. *Ecol Lett* 6(1):69–81. <https://doi.org/10.1046/j.1461-0248.2003.00403.x>
- Kaiser-Bunbury CN, Blüthgen N (2015) Integrating network ecology with applied conservation: a synthesis and guide to implementation. *Ann Bot* 7:plv076. <https://doi.org/10.1093/aobpla/plv076>
- Kaiser-Bunbury CN, Muff S, Memmott J, Müller CB, Calfisch A (2010) The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecol Lett* 13(4):442–452. <https://doi.org/10.1111/j.1461-0248.2009.01437.x>

- Kondratyeva A, Knapp S, Durka W, Kühn I, Vallet J, Machon N, Martin G, Motard E, Grandcolas P, Pavoine S (2020) Urbanization effects on biodiversity revealed by a two-scale analysis of species functional uniqueness vs. redundancy. *Front Ecol Evol*. <https://doi.org/10.3389/fevo.2020.00073>
- Landi P, Minoarivelo HO, Brännström A, Hui C, Dieckmann U (2018) Complexity and stability of ecological networks: a review of the theory. *Popul Ecol* 60(4):1–28. <https://doi.org/10.1007/s10144-018-0628-3>
- Leong M, Dunn RR, Trautwein MD (2018) Biodiversity and socio-economics in the city: a review of the luxury effect. *Biol Lett* 14:20180082. <https://doi.org/10.1098/rsbl.2018.0082>
- Mckinney ML (2002) Urbanization, biodiversity, and conservation: the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *Bioscience* 52(10):883–890. [https://doi.org/10.1641/0006-3568\(2002\)052\[0883:UBAC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2)
- Mckinney ML (2008) Effects of urbanization on urban ecosystem: a review of plants and animals. *Urban Ecosyst* 11(2):161–176. <https://doi.org/10.1007/s11252-007-0045-4>
- Mello MAR, Marquitti FMD, Guimarães PR, Kalko EKV, Jordano P, de Aguiar MAM (2011) The missing part of seed dispersal networks: structure and robustness of bat-fruit interactions. *PLoS One* 6:e0017395. <https://doi.org/10.1371/journal.pone.0017395>
- Mello MAR, Rodrigues FA, Costa LDF, Kissling WD, Şekercioğlu ÇH, Marquitti FMD, Kalko EKV (2015) Keystone species in seed dispersal networks are mainly determined by dietary specialization. *Oikos* 124(8):1031–1039. <https://doi.org/10.1111/oik.01613>
- Menke S, Bohning-Gaese K, Schleuning M (2012) Plant-frugivore networks are less specialized and more robust at forest-farmland edges than in the interior of a tropical forest. *Oikos* 121(10):1553–1566. <https://doi.org/10.1111/j.1600-0706.2011.20210>
- Montoya JM, Rodriguez MA, Hawkins BA (2003) Food web complexity and higher-level ecosystem services. *Ecol Lett* 6(7):587–593. <https://doi.org/10.1046/j.1461-0248.2003.00469.x>
- Muller N, Ignatieva M, Nilon CH, Werner P, Zipper WC (2013) Patterns and trends in urban biodiversity and landscape design. *Urbanization, biodiversity and ecosystem services: challenges and opportunities*. Springer, Dordrecht, pp 123–174. https://doi.org/10.1007/978-94-007-7088-1_10
- Murgui E, Hedblom M (2017) Ecology and conservation of birds in urban environments. Springer, Cham. <https://doi.org/10.1007/978-3-319-43314-1>
- Mwakikagile G (2010) *The land and its people*, 1st edn. Continental Press, Pennsylvania
- Mwitwa J, Sibanjane M, Chipoya GC, Namiluko Y (2016) City region system situational analysis. RUFU Foundation, Kitwe
- Paine RT (1980) Food webs: linkage, interaction strength and community infrastructure. *J Anim Ecol* 49(3):666–685. <https://doi.org/10.2307/4220>
- Palgrave MC (2002) *Keith coates palgrave trees of southern Africa*. Struik Publishers, Cape Town
- Pauw A, Stoffberg J, Waterman RJ (2009) Flies and flowers in Darwin's race. *Evolution* 63(1):268–279. <https://doi.org/10.1111/j.1558-5646.2008.00547>
- Pickett S, Cadenasso M (2009) Altered resources, disturbances and heterogeneity: a frame work for comparing urban and non-urban soils. *Urban Ecosyst* 12:23–44. <https://doi.org/10.1007/s11252-008-0047>
- Schleuning M, Bluthgen N, Florchinger M, Braun J, Schaefer HM, Bohning-Gaese K (2011) Specialization and interaction strength in a tropical plant-frugivore network differ among forest strata. *Ecology* 92(1):26–36. <https://doi.org/10.1890/09-1842.1>
- Schoener TW (1983) Field experiments on interspecific competition. *Am Naturalist* 122(2): 240–285 <http://www.jstor.org/stable/2461233>
- Sebastián-González E (2017) Drivers of species' role in avian seed-dispersal mutualistic networks. *J Anim Ecol* 86(4):878–887. <https://doi.org/10.1111/1365-2656.12686>
- Shikang S, Fuqin W, Yuehua W (2015) Does the passage of seeds through frugivore gut affect their storage: a case study on the endangered plant *Euryodendron excelsum*. *Sci Rep* 5(1):11615. <https://doi.org/10.1038/srep11615>
- Silva FR, Montoya D, Furtado R, Memmott J, Pizo MA, Rodrigues RR (2015) The restoration of tropical seed dispersal networks. *Restor Ecol* 23(6):1–9. <https://doi.org/10.1111/rec.12244>
- Sinclair and Peter Ryan (2010) *Birds of Africa: south of the Sahara*. Struik Nature, Cape Town
- Strohbach MW, Haase D, Kabisch N (2009) Birds and City: Urban biodiversity, landuse and socioeconomic. *Ecol Soc* 14(2):31. <https://doi.org/10.5751/ES-03141-140231>
- Swan CM, Pickett STA, Szlavacz K, Waren P, Willey T (2011) Biodiversity and community composition in urban ecosystems: coupled human, spatial, and metacommunity processes. In: Niemela J (ed) *Urban ecology: patterns, processes, and application*. Oxford University Press, Oxford, pp 179–186. <https://doi.org/10.1093/acprof:oso/9780199563562.003.0021>
- The R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Timoteo S, Ramos JA, Vaughan IP, Memmott J (2016) High resilience of seed dispersal webs highlighted by the experimental removal of the dominant disperser. *Curr Biol* 26(7):910–915. <https://doi.org/10.1016/j.cub.2016.01.046>
- Tylianakis JM, Laliberté E, Nielsen A, Bascompte J (2010) Conservation of species interaction networks. *Biol Conserv* 143(10):2270–2279. <https://doi.org/10.1016/j.biocon.2009.12.004>
- United Nations, Department of Economic and Social Affairs, Population Division (2019) *World urbanization prospects: the 2018 revision (ST/ESA/SER.A/420)*. United Nations, New York
- Valiente-Banuet A, Aizen MA, Alcántara JM, Arroyo J, Cocucci A, Galetti M, García MB, García D, Gómez JM, Jordano P, Medel R, Navarro L, Obeso JR, Oviedo R, Ramírez N, Rey PJ, Traveset A, Verdú M, Zamora R (2015) Beyond species loss: the extinction of ecological interactions in a changing world. *Funct Ecol* 29(3):299–307. <https://doi.org/10.1111/1365-2435.12356>
- Vazquez DP, Morris WF, Jordano P (2012) Interaction frequency as a surrogate for the total effects of animal mutualist on plants. *Ecol Lett* 8(10):1088–1094. <https://doi.org/10.1111/j.1461-0248.2005.00810>
- Wang S, Loreau M (2014) Ecosystem stability in space: alpha, beta and gamma variability. *Ecol Lett* 17(8):891–901. <https://doi.org/10.1111/ele.12292>
- Warren JR, Pearson SM, Henry S, Rossouw K, Love JP, Olejniczak MJ, Elliott K, Bradford MA (2015) Cryptic indirect effects of exurban edges on a woodland community. *Ecosphere* 6(11):1–13. <https://doi.org/10.1890/ES15-00318.1>
- Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *PNAS* 96(4):1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>
- Yuan B, Lu C (2016) Effects of urbanization on bird diversity: a case study in Yizhou, Guangxi Province, China. *Asia Life Sci* 25(1):79–96