Few figs for frugivores: Riparian fig trees in Zimbabwe may not be a dry season keystone resource

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Abstract
Most plants flower and fruit at times of year when probabilities of pollination and seedling establishment are high. Fig trees (Ficus spp.) are often considered as keystone resources for vertebrate frugivores, in part because of year-round fig production. This unusual fruiting phenology results in the maintenance of fig wasp populations, but in seasonal environments this means fruiting occurs during periods when the chances of seedling establishment are low. Under these circumstances, selection is expected to favour any individuals that reduce or eliminate fruiting at these times. Here, we describe a large-scale survey of the extent of dry season fruiting by three riparian Ficus species in Gonarezhou National Park, Zimbabwe. Few trees of two monoecious species, F. sycomorus and F. abutilifolia, had figs, and most crops of F. sycomorus were far smaller than the trees were capable of producing. Large stands of the dioecious F. capreifolia were present, but fig densities were low and no mature female (seed containing) figs were recorded. Even though fig trees may have been the only species bearing fruit, the consequences of the low investment in reproduction by the three Ficus species were clear—there were too few figs for a landscape-scale keystone role.

KEYWORDS
Agaonidae, dioecy, Ficus, phenology, seed dispersal

Résumé
La plupart des plantes fleurissent et fructifient à des moments de l’année où les probabilités de pollinisation et d’établissement des semis sont élevées. Les figuiers (Ficus spp.) sont souvent considérés comme des ressources clés pour les frugivores vertébrés, en partie grâce à la production de figues toute l’année. Cette phénologie de fructification inhabituelle entraîne le maintien des populations de guêpes des figuiers, mais dans les environnements saisonniers, cela signifie que la fructification se produit pendant les périodes où les chances d’établissement des semis sont faibless. Dans ces circonstances, la sélection devrait favoriser tous les individus qui réduisent ou éliminent la fructification à ces moments. Nous décrivons ici une étude à grande échelle portant sur l’étendue de la fructification en saison sèche par trois espèces
**1 | INTRODUCTION**

Fig trees (Ficus spp., Moraceae) are a group of mainly tropical and subtropical plants that are often regarded as keystone mutualists (Dev, Kjellberg, Hossaert-McKey, & Borges, 2011; Lambert & Marshall, 1991; Terbohrg, 1986). The genus is characterised by its unusual enclosed inflorescences (figs, also called syconia) which after pollination develop into compound accessory fruits. Their keystone status reflects the importance of figs in the diets of many tropical mammals and birds, with more vertebrates recorded as eating figs than any other fleshy fruits (Shanahan, So, Compton, & Corlett, 2001) and an increasing realisation that the insects associated with the figs are themselves important in the diet of birds (Mackay, Gross, & Rossetto, 2018; Matthews, Cottee-Jones, Bregman, & Whittaker, 2017). The importance of figs for vertebrates is a result of several biological features: fig trees can be abundant, they can produce large crops, figs are easy to eat and have a high calcium content, different species of fig trees produce figs that vary in size and location, thereby favouring different groups of vertebrates, and figs are often produced at times of the year when few other fruits are available (Foster, 2014; Lambert & Marshall, 1991; O’Brien et al., 1998; Shanahan & Compton, 2001; Shanahan et al., 2001).

Many tropical and subtropical trees display a sub-annual, synchronised flowering pattern (Kinnaird, 1992, Chapman, Wrangham, & Chapman, 1994, but see Kattan & Valenzuela, 2013). This contrasts with the year-round fruiting displayed by many fig trees, which is seen as being a particularly significant trait because it means that they can support frugivore populations through periods of shortage when little other food is available (van Schaik, Terbohrg, & Wright, 1993; Twehoyo & Lye, 2003; Wathler, Geier, Lien-Siang Chou, & Bain, 2018). Fig trees are pollinated exclusively by small host-specific pollinating wasps (Hymenoptera, Agaonidae), and their year-round fruiting is linked to their protogynous inflorescences and dependence on these short-lived insects for pollination (Janzen, 1979).

Most African fig trees have a monoecious breeding system, where the figs on each tree can both produce seeds and support the development of the fig wasps that can transport pollen between trees. The year-round fruiting pattern of many monoecious Ficus species is often associated with between-tree fruiting asynchrony, but within-tree synchrony (Bronstein, Gouyon, Gliddon, Kjellberg, & Michaloud, 1990). Within-tree fruiting synchrony forces outcrossing and may aid pollinator attraction (Janzen, 1979) and asynchrony at the population level ensures that there are always some trees available for the short-lived adult fig wasps to colonise. A smaller number of African Ficus have a dioecious breeding system, where figs on female trees exclusively produce seeds, whereas figs on male trees only support fig wasp development and do not become attractive to vertebrates. In dioecious species, it is only the male trees that support pollinator populations and so are required to have at least some individuals fruiting throughout the year. This difference between sexes trees female trees to concentrate their fruiting efforts during those parts of the year when seeds are more likely to establish successfully (Kjellberg & Maurice, 1989; Patel, 1996). Their more seasonal fruiting may reduce the value of some dioecious fig trees to vertebrates, because only mature figs on female trees provide frugivores with food.

Some African fig wasps achieve huge dispersal distances between trees (Ahmed, Compton, Butlin, & Gilmartin, 2009), but the year-round presence of figs at different developmental stages is nonetheless important for monoecious fig trees, because it helps to maintain local sources of pollinators. Although populations of monoecious fig trees benefit from this year-round fruiting, there is a cost for those individuals living in highly seasonal environments. This is because fig seed longevity is poor (Garcia, Hong, & Ellis, 2005; Vázquez-Yanes, Rojas-Aráchiga, Sánchez-Coronado, & Orozco-Segovia, 1996) and the trees are likely to be investing resources into reproduction at times of the year when opportunities for seeds to survive and seedlings to successfully establish are minimal. Species inhabiting arid environments that produce seeds during the dry season are therefore less likely to generate new plants than at other times of year. Fig production during the dry season can also contribute to water stress on the trees (Patiño, Herre, & Tyree, 1994). These factors suggest that natural selection should favour individuals that reduce their reproductive investment at such times (Kjellberg & Maurice, 1989), because individuals which only fruit during optimum periods (or release fig wasps which pollinate such individuals) should be at an advantage. Such a selective pressure can be manifested in trees not fruiting at suboptimal times, or in trees producing smaller...
FIGURE 1 The Runde River in the northern part of Gonarezhou National Park based on an unpublished 1994 vegetation map produced by the Zimbabwe Parks Board. The four lines across the river delineate sections where different *Ficus* species predominated. From west to east, these sections were (a) Bridge section with *F. sycomorus* and *F. capreifolia*; (b) Chipinda section with *F. abutilifolia*; (c) Central section with *F. sycomorus*; (d) Chitove section with *F. abutilifolia*; and (e) Junction section with *F. sycomorus* and *F. capreifolia*. Dash–dot lines indicate the park’s boundaries.
unsuitable for fig trees, and all three species were restricted to riversides in the area with the exception of some *F. sycomorus* at the sides of the Tambahata Pan near the junction with the Save River. Consequently, our riverside censuses, which took place in July and August 1994, will have covered almost all the fig trees in the area.

*Ficus sycomorus* is a medium-sized monoecious tree that has a preference for riverine environments in drier areas (Burrows & Burrows, 2003). Its large figs (40 mm diameter) are produced on leafless branches from the trunk and major branches. The figs are pollinated by *Ceratosolen arabicus* Mayr and fed on by a wide range of birds, fruit bats and primates when ripe (Brain, 1988; Shanahan et al., 2001). *Ficus abutilifolia* is a monoecious shrub or small tree. It is a ‘rock-splitter’, restricted to rocky areas. Its pollinator is *Elisabethiella comptoni* Wiebes (Berg & Wiebes, 1992), and its figs are located in the leaf axils. They reach 20 mm in diameter and are eaten by birds and mammals (Shanahan et al., 2001; http://pza.sanbi.org/ficus-abutilifolia). *Ficus capreifolia* is a small dioecious shrub pollinated by *Kradibia gestroi afrum* (Wiebes). Only the figs on female trees ripen to become attractive to frugivores. Birds are likely to be the main seed dispersers of the 30 mm mature diameter figs. *Ficus capreifolia* is exclusively associated with riparian habitats (Burrows & Burrows, 2003).

### Sampling

The Runde River and adjacent sections of major tributaries were surveyed for fig trees from the western park boundary, near the bridge at Chipinda Pools, to the junction with the Save River (Figure 1), a distance of about 74 km. Two teams surveyed the two banks independently, using binoculars. The locations of the trees were recorded using 1:50,000 maps (Government Printer, Zimbabwe) and GPS. The presence of figs was recorded, together with crop sizes, and their

| Sub-populations | Trees | Trees fruiting | Trees with mature fruit | Mean crop size |
|-----------------|-------|----------------|-------------------------|---------------|
| *Ficus sycomorus* |       |                |                         |               |
| Bridge          | 32    | 13 (40.6%)     | 2 (6.2%)                | 970.5         |
| Central         | 149   | 59 (39.6%)     | 14 (9.4%)               | 71.3          |
| Junction        | 74    | 31 (41.9%)     | 5 (6.8%)                | 53.1          |
| *Ficus abutilifolia* |       |                |                         |               |
| Chipinda        | 756   | 168 (22.2%)    | 12 (1.6%)               | 155.3         |
| Chitove         | 52    | 11 (21.1%)     | 0                       | 10.8          |
| *Ficus capreifolia* |       |                |                         |               |
| Bridge          | 532   | 124 (23.3%)    | 6 (1.1%)                | 61.8          |
| Junction        | 517   | 84 (16.2%)     | 2 (0.4%)                | 166.1         |

**FIGURE 2** The frequency of *F. sycomorus* along the Runde River in the Gonarezhou National Park. The breaks in its distribution are where the river passes through the rocky Chipinda and Chitove sections of the river

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**TABLE 1** Estimates of tree densities, fruiting frequencies and crop sizes in *Ficus* populations along the Rundi River, Gonarezhou National Park, Zimbabwe. Sub-populations are listed from west to east.
stage(s) of development (prepollination, pollinated and developing, or ripe and suitable for frugivores). Where necessary, pruning poles were used to remove fruits to confirm their stage of development.

Some *F. sycomorus* had the remnants of old crops of dried figs still attached to their branches. These were not included in the counts. Only individuals of *F. abutilifolia* estimated by eye to have a volume of foliage greater than 2 m$^{3}$ were scored as this was the minimum volume at which fig production by this species was observed. *Ficus capreifolia* spreads vegetatively, sometimes forming continuous thickets. Where individuals could not be distinguished, 10-m lengths were arbitrarily taken as representing a single individual. The very large numbers of this species precluded a census of the populations, and counts were taken for 100 m sections each 500 m to provide estimates of totals based on approximately 20% of the plants. In the absence of ripe figs, the sexes of the mature plants were determined later, based on samples of a single fig from each individual. These were stored in 70% ethanol prior to dissection and microscopic examination. Figs on female trees lacked male flowers and their female flowers had far longer styles than those from male trees.

### RESULTS

Our census recorded a total of 255 large *F. sycomorus* (Table 1). The trees were present at relatively low densities along most of the length of the river and for short distances up the major tributaries, but were absent from the two areas with rocky substrates (Figure 2). They averaged about five trees per kilometre along the nonrocky stretches of river, with the highest concentrations around junctions with the tributaries and at the sides of some of the larger persistent pools. Mature individuals were readily identified by the presence of active or old fruit-bearing branches. There was little evidence of recent recruitment, although five small trees were present and groups of around 20 small saplings were present beneath two of the mature trees. These saplings were unlikely to survive for long as they were situated in the bed of the river, in contrast to all the mature trees, which were on the riverbanks or on stabilised sand bars.

In contrast to *F. sycomorus*, *F. abutilifolia* was only found in the rocky Chipinda and Chitove stretches of the river. The Chipinda (more westerly) rocky section was by far the longer of the two areas and supported most of the 808 *F. abutilifolia* trees considered sufficiently large to have potentially borne figs (Table 1). This species averaged about 35 plants per kilometre along these rocky sections. The third species, *Ficus capreifolia*, was absent from most of the length of the river but formed two large populations of approximately equal size on stabilised sand bars at the eastern and western boundaries of the reserve. In these areas, *F. capreifolia* tended to form dense, largely monospecific stands, often covering hundreds of square metres each. A total

### TABLE 2

| Species          | Number of trees | Trees with mature figs | Mean fig number (mature crops only) | Sex ratio (% female) | Estimated mature figs present |
|------------------|-----------------|------------------------|------------------------------------|----------------------|-------------------------------|
| *F. sycomorus*   | 255             | 19                     | 137.6                              | N/A                  | 2,615                         |
| *F. abutilifolia*| 808             | 12                     | 115.0                              | N/A                  | 1,380                         |
| *F. capreifolia* | 5,245           | 40                     | 144.6                              | 1.9%                 | 145                           |

Note: Values for *F. capreifolia* are extrapolated from samples of 20% of the total population. Only female figs of this dioecious species are attractive to frugivores. *Ficus capreifolia* crop counts include both male and female trees.

### TABLE 3

Levels of asynchrony within fig crops on individual trees along the Rundi River, Zimbabwe

| Species          | Trees with figs | Trees with figs releasing wasps | Potentially self-pollinating trees |
|------------------|-----------------|---------------------------------|-----------------------------------|
| *F. sycomorus*   | 103             | 19 (18.4%)                      | 4 (3.9%)                          |
| *F. abutilifolia*| 179             | 12 (6.7%)                       | 2 (1.1%)                          |
| *F. capreifolia* | 208             | 8 (3.8%)                        | N/A                               |
of 1,049 F. capreifolia sample units were identified, giving an arbitrary population estimate based on area covered of 5,245 (Table 1).

Taken as a group, fig trees were present along the whole length of the river, but the numbers of potentially fruiting trees were concentrated along certain sections due to the clumped distributions of two of the three species. These localised relatively high densities of fig trees did not lead to large numbers of mature figs being available, however. Fruiting frequencies were higher in F. sycomorus, with figs present on about 40% of the trees, but only a proportion of these had mature figs available to be eaten. Furthermore, crop sizes were generally extremely small for such large trees, with most crops numbering <100 figs (Table 1 and Figure 3a). The small numbers of figs on the trees occupied only a fraction of the fig bearing branches on the trees, most of which were empty. The frequency of fruiting by F. abutilifolia individuals was only about half of that of F. sycomorus, and trees with mature fruit at the time we surveyed were either very scarce (Chipinda population) or entirely absent (Chitove population). Most of the crops were also small, with less than 100 figs (Figure 3b). Ficus capreifolia had a similarly low proportion of sample units with any figs and small average crop sizes. Furthermore, most of the figs were on male plants and would never become attractive to frugivores (Table 1 and Figure 3c). No mature female (seed containing) figs were present on any of the more than 1,000 sample units, showing that the functional sex ratio during our sampling period was heavily skewed towards male plants, which are not attractive to frugivores.

Based on the censuses of F. sycomorus and F. abutilifolia and sampling of the F. capreifolia populations, we estimate that for all three species combined there were less than 5,000 figs that were mature and waiting to be eaten on the 6,000 or so trees present along the 74 km of river (Table 2). Development of most of the crops of F. sycomorus and F. abutilifolia was sufficiently synchronised to prevent self-pollination, although a small number of trees did have unpollinated figs while simultaneously releasing pollinator fig wasps (Table 3).

4 | DISCUSSION

Fig trees are a regular component of riparian forests across much of southern Africa (Werger & van Bruggen, 1978). They were growing along the Runde River in Zimbabwe in sufficient numbers to potentially offer a major resource to fruit-eating birds, fruit bats and the wide range of other mammals which also feed on figs (Shanahan et al., 2001). However, during the dry season when figs would have been of particular value to these animals, this potential was not realised, with fig trees only capable of supporting small populations of frugivorous animals and very few birds were observed in the trees. Even in combination, the three species of fig tree were providing little dry season food for frugivores in Gonarezhou. To put this in perspective, a single individual of F. sycomorus can produce well in excess of 20,000 figs per crop (J. Greeff, unpublished), so one tree fully laden with mature figs could have offered more resources to frugivores than all the trees together were providing along the whole river. This dearth of figs resulted from a combination of factors.

Small numbers of individuals of both F. sycomorus and F. abutilifolia did have moderately large crops, but these were immature at the time they were surveyed. Even if figs were present, most individuals had only tiny crops. The often-extensive fruiting scars from previous F. sycomorus crops showed that most of the trees had produced far larger crops previously. Very few female trees of F. capreifolia were fruiting, and not one mature female fig was detected (Table 2).

Less than half of the F. sycomorus along the river had figs present, and most of the crops were tiny relative to the evident capacity of these large trees. A smaller proportion of F. abutilifolia were producing figs, and again, most crop sizes were small. Furthermore, most of the figs of both species that were present were immature and not of immediate value to frugivores. Finally, fruiting by the only dioecious fig tree species in the area, F. capreifolia, was almost entirely by male plants, which produce figs that are unattractive to vertebrates, but are required to maintain local pollinator populations. The very low frequency of dry season fruiting among the female trees of F. capreifolia is in line with predictions that dioecious fig tree species in seasonal environments should concentrate their seed production in those seasons where successful seedling establishment is most likely (Kjellberg & Maurice, 1989). The potential for cycling of pollinator populations on individual trees of F. sycomorus and F. abutilifolia was limited but could help maintain local populations during the dry season. Populations of the fig wasp associated with F. capreifolia could also potentially cycle on the male trees and the rarity of female figs meant that wasp populations would benefit because few dispersing females would be attracted to figs where they could not breed.

As with F. capreifolia, there are clear population level benefits of year-round fruiting for monocious species, because it maintains local pollinator populations, but natural selection does not operate routinely at this level and any seeds that individual trees produce during the dry season are likely to have to wait months for suitable conditions for germination, during which time mortalities must inevitably occur, as their seed longevity is poor (Garcia et al., 2005; Vázquez-Yanes et al., 1996). There are also few receptive figs on the trees at this time, so reproductive success via dispersal of their pollen will also be low. The low dry season fruiting frequencies we observed may therefore be adaptive, but some individuals nonetheless continued to fruit, rather than preserving their resources entirely by ceasing to produce figs. It may be that the costs involved in fruiting during one part of the year have minimal influence on the resources available to support fruiting at other times. Alternatively, there may be an element of local maladaptation in the trees’ dry season phenologies that reflects the long-distance gene flow exhibited by species such as F. sycomorus. Phenotypic plasticity is nonetheless present in the congeneric F. thonningii, which varies its fruiting in response to water availability in Zimbabwe (Damsra, Richardson, & Reeler, 1996). There will also be rewards for those individuals producing fig wasps towards the end of the dry season, because they have the potential to pollinate figs which subsequently produce seeds when conditions are more favourable. Alternatively, their low dry season fruiting investment may be a direct response to environmental conditions, particularly the availability of...
water, at least in F. sycomorus. Water stress can limit fruit production by fig trees (Patíno et al., 1994), and it was noticeable that the few individuals of this species that had larger crops were located next to the remaining major pools in the riverbed.

Elsewhere in Africa, riparian fig trees such as F. sycomorus can be much more abundant than in our study area (Makishima, 2005) and they even form virtual monocolonies along rivers in Kruger Park, South Africa (Adams & Snode, 2013; Bonaccorso et al., 2014). The abundance of riparian fig trees therefore varies greatly, but they can retain ecological significance in deserts even when at low densities (Ahmed et al., 2009; Brain, 1988; Wharton, Tilson, & Tilson, 1980). Irrespective of tree density, the dry season fruiting patterns among the fig trees along the Rundi River reduced their value to frugivores living in the reserve and the trees are unlikely to merit keystone status, at least at this time of year.

5 | CONCLUSION

Our results emphasise that a blanket assumption of keystone status for fig trees in Africa cannot be assumed, especially in more seasonal parts of the continent where even if all-season fruiting is maintained it is at reduced levels. The broader question is therefore not whether riparian fig trees are of ecological significance in Africa, but what are the environmental conditions that determine the extent of their significance.

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CONFLICT OF INTEREST
The authors declare no competing interests.

DATA AVAILABILITY STATEMENT
The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES
Adams, R. A., & Snode, E. R. (2013). Unique insights into dispersion distances among calling males of Wahlberg’s Epauletted fruit bat in Kruger National Park, South Africa. The Open Ecology Journal, 6, 54–60. https://doi.org/10.2174/1874213001306010054
Ahmed, S., Compton, S. G., Butlin, R. K., & Gilmartin, P. M. (2009). Wind borne insects mediate directional pollen transfer between desert fig trees 160 kilometers apart. Proceedings of the National Academy of Sciences, 106, 20342–20347.

Berg, C. C., & Wiebes, J. T. (1992). African fig trees and fig wasps. Koninklijke Nederlandse Akademie Van Wetenschappen Verhandelingen Afdeling Natuurkunde, 89, 1–298.
Bleher, B., Potgeiter, C., Potgeiter, C. J., Johnson, D., & Böhmig-Gaese, K. (2003). The importance of figs for frugivores in a South African coastal forest. Journal of Tropical Ecology, 19, 375–386.
Bonaccorso, F. J., Winkelmann, J. R., Todd, C. M., & Miles, A. C. (2014). Foraging movements of Epauletted fruit bats (Pteropodidae) in relation to the distribution of sycamore figs (Moraceae) in Kruger National Park, South Africa. Acta Chiropterologica, 16, 41–52. https://doi.org/10.3161/15081104X683255
Brain, C. (1988). Water gathering by baboons in the Namib desert. South African Journal of Science, 84, 590–591.
Bronstein, J. L., Gouyon, P.-H., Gliddon, C., Kjellberg, F., & Michaloud, G. (1990). The ecological consequences of flowering asynchrony in monoeious figs: A simulation study. Ecology, 71, 2145–2156. https://doi.org/10.2307/1938628
Burrows, J., & Burrows, S. (2003). Figs of Southern and South-Central Africa, (pp. 379). Hatfield, UK: South Africa. Umdaus Press.
Chapman, C. A., Wringham, R., & Chapman, L. J. (1994). Indices of habitat-wide fruit abundance in tropical forests. Biotropica, 26, 160–171.
Cunifltre, R., Muller, T., & Mapaura, A. (2012). Vegetation survey of Gonarezhou National Park. Zimbabwe: Unpublished final report on behalf of the Frankfurt Zoological Society.
Damstra, K. S. J., Richardson, S., & Reeler, B. (1996). Synchronized fruiting between tree species of Ficus thonnongii in seasonal dry habitats. Journal of Biogeography, 23, 495–500.
Dev. S. A., Kjellberg, F., Hossaert-McKey, M., & Borges, R. M. (2011). Fine-scale population genetic structure of two dioecious Indian keystone species, Ficus hispida and Ficus exasperata (Moraceae). Biotropica, 43, 309–316.
Foster, M. (2014). Can fruit pulp meet the calcium needs of tropical frugivorous passerines during reproduction? Journal of Tropical Ecology, 30, 79–88.
García, X., Hong, T. D., & Ellis, R. H. (2005). Seed dormancy and germination of Ficus lundellii (Moraceae) and tropical forest restoration. Tree Physiology, 26, 81–85.
Gautier-Hion, A., & Michaloud, P. (1989). Are figs always keystone resources in seasonal dry habitats? Journal of Biogeography, 23, 495–500.
Janzen, D. H. (1979). How to be a fig. Annual Review of Ecology and Systematics, 10, 13–51.
Jordan, F. (2009). Keystone species and food webs. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 364, 1733–1741. https://doi.org/10.1098/rstb.2008.0335
Kattan, G. H., & Valenzuela, L. A. (2013). Abundance and consumers of figs (Ficus spp.) in a tropical cloud forest: Evaluation of a potential keystone resource. Journal of Tropical Ecology, 29, 401–407.
Kinnaird, M. F. (1992). Phenology of flowering and fruiting of an East African riverine forest ecosystem. Biotropica, 24, 187–194.
Kjellberg, F., & Maurice, S. (1989). Seasonality in the reproductive phenology of Ficus - its evolution and consequences. Experientia, 45, 653–660.
Lambert, F. R., & Marshall, A. G. (1991). Keystone characteristics of bird-dispersed Ficus in a Malaysian lowland rain forest. Journal of Ecology, 79, 793–809.
Mackay, K. D., Gross, C. L., & Rossetto, M. (2018). Small populations of fig trees offer a keystone food resource and conservation benefits
for declining insectivorous birds. Global Ecology and Conservation, 14, e00403.

Makishima, H. (2005). *Ficus sycomorus* fruit production in a semi-arid land in northern Kenya: Implications for understanding a possible food resource of early hominids. *African Study Monographs*, Suppl., 32, 79–86.

Matthews, T. J., Cottee-Jones, H. E. W., Bregman, T. P., & Whittaker, R. J. (2017). Assessing the relative importance of isolated *Ficus* trees to insectivorous birds in an Indian human-modified tropical landscape. *Biodiversity and Conservation*, 26, 2803–2819.

Mills, L. S., Soulé, M. E., & Doak, D. F. (1993). The Keystone-species concept in ecology and conservation: Management and policy must explicitly consider the complexity of interactions in natural systems. *BioScience*, 43, 219–224.

O’Brien, T. G., Kinnaird, M. F., Dierenfeld, E. S., Conklin-Brittain, N. L., Wrangham, R. W., & Silver, S. C. (1998). What’s so special about figs? *Nature*, 392, 668.

Patel, A. (1996). Variation in a mutualism - phenology and the maintenance of gynodioecy in two Indian fig species. *Journal of Ecology*, 84, 667–680.

Patino, S., Herre, E. A., & Tyree, M. T. (1994). Physiological determinants of *Ficus* fruit temperature and implications for survival of pollinator wasp species - comparative physiology through an energy budget approach. *Oecologia*, 100, 13–20. https://doi.org/10.1007/BF00317125

Pothasin, P., Compton, S. G., & Wangpakapattanawong, P. (2014). Riparian *Ficus* tree communities: The distribution and abundance of riparian fig trees in Northern Thailand. *PLoS One*, 9, e108945. https://doi.org/10.1371/journal.pone.0108945

Shanahan, M., & Compton, S. G. (2001). Vertical stratification of figs and fig-eaters in a Bornean lowland rainforest: How is the canopy different? *Plant Ecology*, 153, 121-132.

Shanahan, M., So, S., Compton, S. G., & Corlett, R. (2001). Fig-eating by vertebrate frugivores: A global review. *Biological Reviews*, 76, 529–572.

Torrance, J. D. (1981). *Climate handbook of Zimbabwe*. Harare: Zimbabwe Meteorological Services.

Tweheyo, M., & Lye, K. A. (2003). Phenology of figs in Budongo Forest Uganda and its importance for the chimpanzee diet. *African Journal of Ecology*, 41, 306–316.

van Schaik, C. P., Terborgh, J. W., & Wright, S. J. (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, 24, 353–377.

Vázquez-Yanes, C., Rojas-Aréchiga, M., Sánchez-Coronado, M. E., & Orozco-Segovia, V. A. (1996). Comparison of light-regulated seed germination in *Ficus* spp. and *Cecropia obtusifolia*: Ecological implications. *Tree Physiology*, 16, 871–875.

Walther, B. A., Geier, J., Lien-Siang Chou, L. S., & Bain, A. (2018). The figs of winter: Seasonal importance of fruiting fig trees (*Ficus*: Moraceae) for urban birds. *Acta Oecologia*, 90, 28–34. https://doi.org/10.1016/j.actao.2017.11.015

Werger, M. J. A., & van Bruggen, A. C. (Eds.) (1978). *Biogeography and ecology of Southern Africa*. (pp. 1444). The Hague, Netherlands: Junk.

Wharton, R. A., Tilson, J. W., & Tilson, R. L. (1980). Asynchrony in a wild population of *Ficus sycomorus* L. *South African Journal of Science*, 76, 478–480.

Zisadza-Gandiwa, P., Mango, L., Gandiwa, E., Goza, D., Parakasingwa, C., Chinoitezvi, E., ... Muvengwi, J. (2013). Variation in woody vegetation structure and composition in a semi-arid savanna of Southern Zimbabwe. *International Journal of Biodiversity and Conservation*, 5, 71–77.