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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 faibles. 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

riveraines de *Ficus* dans le parc national de Gonarezhou, au Zimbabwe. Peu d'arbres de deux espèces monoïques, *F. sycomorus* et *F. abutilifolia*, avaient des figues et la plupart des fruit du *F. sycomorus* étaient beaucoup plus petits que ceux que les arbres étaient capables de produire. D'importants peuplements de *F. capreifolia* dioïque étaient présents, mais les densités de figues étaient faibles et aucune figue femelle mature (contenant des graines) n'a été enregistrée. Même si les figuiers étaient peut-être la seule espèce à produire des fruits, les conséquences du faible investissement dans la reproduction par les trois espèces de Ficus étaient claires - il y avait trop peu de figues pour qu'elles jouent un rôle clé à l'échelle du paysage.

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; Terborgh, 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, Terborgh, & Wright, 1993; Tweheyo & Lye, 2003; Walther, 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 frees 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-Aréchiga, 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

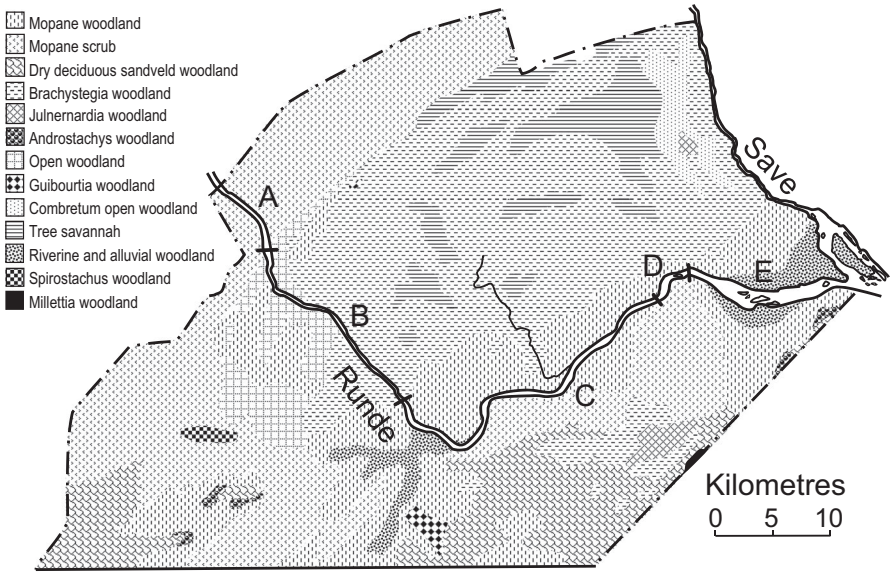

FIGURE 1 The Runde River in the northern part of Gonarezhou National Park based on an unpublished 1994 vegetation map produced by the Zimbabwe Parks Board. The four lines across the river delineate sections where different *Ficus* species predominated. From west to east, these sections were (a) Bridge 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

fig crops during seasons that are unfavourable for seedling establishment. As a result, fig trees may be less likely to fruit abundantly at this time, and less likely to merit keystone status than trees in more aseasonal environments.

Views on what constitutes a keystone species vary, but definitions often include having a high ecological significance at large spatial scales and interacting with numerous other species (Jordán, 2009; Mills, Soulé, & Doak, 1993). Furthermore, whether fig trees are keystone mutualists in Africa is unclear. Kissling, Rahbek, and Böhning-Gaese (2007) showed a continent-wide association between fig tree distributions and avian biodiversity, but Gautier-Hion and Michaloud (1989) doubted that fig trees could be of great significance for frugivores in tropical West Africa because densities of the trees were too low. In the more seasonal temperate forests of South Africa, Bleher, Potgeiter, Potgeiter, Johnson, and Böhning-Gaese (2003) emphasised the importance to birds of a coastal fig tree species that continued to fruit throughout the year, including times when few alternative fruits were available, whereas Hart, Grieve, and Downs (2013) found that fig trees were rare or absent in higher altitude forest fragments and so were unlikely to be significant for frugivores.

Worldwide, fig trees are often particularly diverse and abundant in riparian habitats (Pothasin, Compton, & Wangpakapattanawong, 2014). Here, we describe the dry season fruiting patterns of the three riparian fig tree species present along the major river system in a region of tropical southern Africa with a highly seasonal climate. Because fig trees in the area are largely or entirely confined to riverbanks, it was possible to record most of the figs being produced across an area of several hundred square kilometres. This allowed us to determine the extent of their reproductive investment and the quantity of resources they were providing for frugivorous vertebrates at a scale that covered their likely foraging ranges (Bonaccorso, Winkelmann, Todd, & Miles, 2014). To assess the extent of reproductive investment and the likely value of the trees to frugivores, we recorded the densities of trees, the numbers of figs present, if any, and their developmental stages.

2 | MATERIALS AND METHODS

2.1 | Study sites

Gonarezhou National Park is situated in the Lowveld of south-east Zimbabwe, approximately 21° south of the Equator. The climate of the region is strongly seasonal, with a long dry season punctuated by summer rains (Torrance, 1981). The Runde (Lundi) River is the only major river in the northern section of the park, where it runs for about 74 km from the western park boundary through to the junction with the Save (Sabi) River, close to the border with Mozambique. The Runde is ephemeral, with above-ground water restricted to isolated pools for several months during the dry season. Major vegetation types adjacent to the river include Mopane woodland/scrub, *Brachystegia glaucescens* woodland and some areas of riverine and alluvial woodland (Figure 1; Cunliffe, Muller, & Mapaura, 2012; Zisadza-Gandiwa et al., 2013). The stretch of the river inside the park runs through a generally sandy, undulating landscape, interrupted by two rocky areas to the east of Chipinda Pools and near Chitove Camp where low cliffs border the river. These changes in substrate divide the river into five discrete areas, which (from west to east) we refer to as the Bridge, Chipinda, Central, Chitove and Junction sections.

2.2 | Study plants

Three taxonomically unrelated *Ficus* species were present along the river—*F. sycomorus* L. (Subgenus *Sycomorus*), *F. abutilifolia* (Miq.) Miq. (Subgenus *Urostigma*) and *F. capreifolia* Delile (Subgenus *Ficus*) (Berg & Wiebes, 1992). The savannah away from the rivers is largely

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

Sub-populations	Trees	Trees fruiting	Trees with mature fruit	Mean crop size	Functional sex ratio % Female (*n*)
Ficus capreifolia					
Bridge	532	124 (23.3%)	6 (1.1%)	61.8	0.74% (124)
Junction	517	84 (16.2%)	2 (0.4%)	166.1	4.22% (71)

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

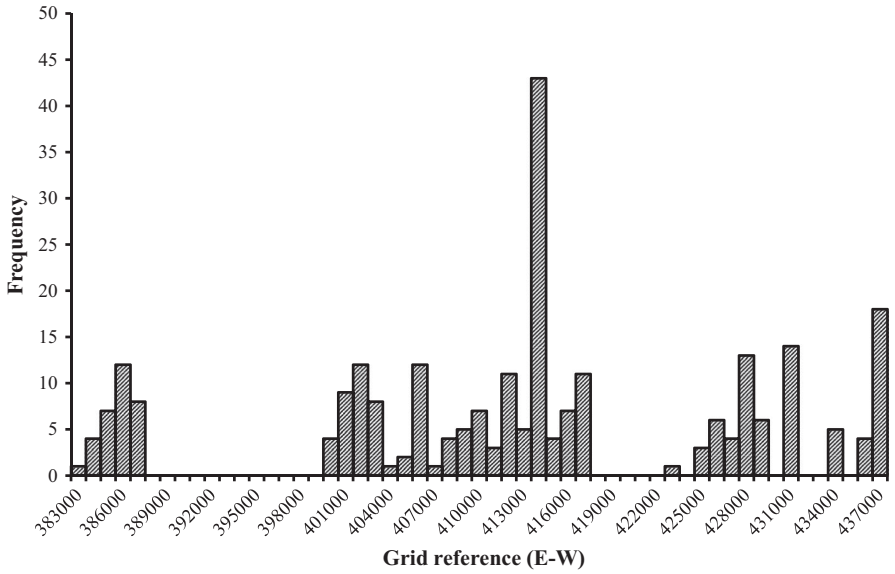

FIGURE 2 The frequency of *F. sycomorus* along the Runde River in the Gonarezhou National Park. The breaks in its distribution are where the river passes through the rocky Chipinda and Chitove sections of the river

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).

2.3 | 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

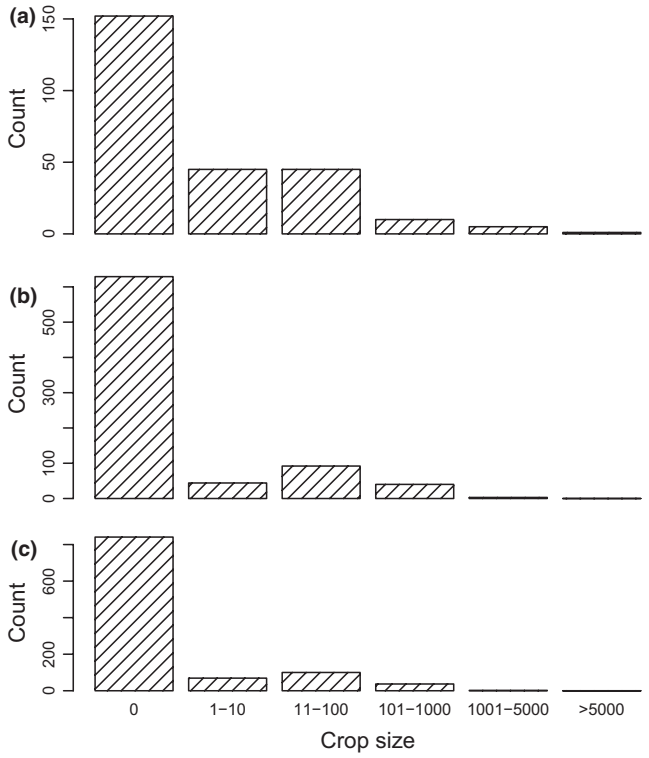

FIGURE 3 Fig tree crop size frequencies on trees along the Runde River in July and August 1994. (a) *Ficus sycomorus*, (b) *F. abutilifolia* and (c) *F. capreifolia*

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.

3 | 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 3 Levels of asynchrony within fig crops on individual trees along the Rundi River, Zimbabwe

	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

TABLE 2 *Ficus* as a resource for frugivorous vertebrates along the Rundi River, Zimbabwe

	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.

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. abutulifolia* 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 monoecious 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 (Damstra, 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 (Patiño 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 monocultures 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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