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Abstract

The ecological role and significance of “African wild bananas” *Ensete ventricosum* (Welw.) Cheesman (Musaceae) are unknown. We considered if *E. ventricosum*, with its sustained flowering and fruiting, might act in some ways like a keystone species by supporting animal populations during periods of resource scarcity. We deployed camera traps facing flowers or fruits of *E. ventricosum* for a total of 40 camera months in the Bwindi Impenetrable National Park, Uganda. We recorded 1,691 visitor events by 11 vertebrate species to flowers and fruits (1,129 events by five species to flowers and 562 events by eight species to fruits); these visitors included potential pollinators and seed dispersers. Frequent visitors to flowers were the African dormouse *Graphiurus murinus* (53.3%), Nectar bat *Megaloglossus woermanni* (43.8%), and sunbirds (family Nectariniidae) (2.4%) while those to fruits were Carruther’s mountain squirrel *Funisciurus carruthersi* (54.1%), L’hoest’s monkey *Allochrocebus lhoesti* (18.7%), and Forest giant pouched rat *Cricetomys emini* (18.6%). Flower visitors were mainly nocturnal (with birds favoring dusk), while fruit visitors exhibited both diurnal and nocturnal activity patterns. The data indicate that by producing flowers and fruits continuously, *E. ventricosum* should support animal populations when other flower and fruit resources are scarce. We speculate that establishing these plants in degraded areas may facilitate forest resilience and recovery while providing fallback resources to many species. Such plant species are prime contenders for protection and restoration.

Keywords

Bwindi, *Ensete ventricosum*, fallback species, flowering phenology, fruiting phenology, pollination, seed dispersal

Introduction

African wild bananas, sometimes called “false bananas,” *Ensete ventricosum* (Welw.) Cheesman (Musaceae), are monocarpic single-stemmed herbaceous plants (Cheesman, 1947; Neumann & Hildebrand, 2009; Simmonds, 1962). These plants occur where there is sufficient moisture and light, including forest gaps and clearings, shrublands, and riverine areas (Baker & Simmonds, 1953; Birmeta, 2004). Of the seven *Ensete* species, only *E. ventricosum* occurs in Uganda (Baker & Simmonds, 1953; Fuller & Madella, 2009; Lejju, Robertshaw, & Taylor, 2006). *E. ventricosum* has been domesticated in Ethiopia where it is widely cultivated and the processed stem, root, and flowers (but not the fruits) are eaten (Bizuayehu, 2008; Garedew, Ayiza, Haile, & Kasaye, 2017). We know little about the ecology of wild *E. ventricosum*.

Little is known about the ecology of most tropical species (Ghazoul & Sheil, 2010)—so in that sense

E. ventricosum is typical. The challenge for anyone confronting such a vast scale of unknowns and seeking to inform management and conservation is to know where to focus and what to assess (Meijaard & Sheil, 2012). One suggestion is to identify those taxa and characteristics which influence, or may determine, the persistence of others. Such taxa are often labeled as ecological keystone species (hereafter “keystone species”; see

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Diaz-Martin, Swamy, Terborgh, Alvarez-Loayza, & Cornejo, 2014; Kattan & Valenzuela, 2013; Peres, 2000). Identifying such taxa and characterizing the nature and significance of their ecological contribution remain challenging. The aim is not to simply classify species into two classes (i.e., keystone and nonkeystone species) but to better recognize their role and contribution. Camera traps offer a simple option.

E. ventricosum is uncommon in the East African mountain forests but can be locally common in disturbed and open sites and at forest edges. It produces a persistent inflorescence with large amounts of nectar and protein-rich pollen and numerous fleshy fruits (Katende, Birnie, & Tengnäs, 1995; Nayar, 2010; F. S. and D. S., personal observation). We postulated that *E. ventricosum* is a potential keystone species based on our informal observations over 2 years that it produces flowers and fruits all year-round thus potentially supporting nectivores and frugivores when other food resources are scarce. Unfortunately, we cannot readily assess whether a species has such attributes. We propose a three-step process: (a) identify a promising species (i.e., *E. ventricosum*), (b) make an initial assessment, and (c) address more specific questions if justified. The second step is what we present in this article.

Here, we clarify which animals feed on *E. ventricosum* and when this occurs. We used camera traps to record animals that visited flowers and fruits and show that these simple and relatively low-cost methods offer novel insights that can inform conservation practice.

Methods

Site: The study was conducted in the Bwindi Impenetrable National Park (“Bwindi”) in Uganda (0°53′–1°08′ S, 29°35′–29°50′ E), a UNESCO World Heritage site since 1994 (Howard, 1991; International Union for Conservation of Nature, 1994). Bwindi’s climate is equatorial with two dry seasons from December to January and June to August (Kasangaki, Bitariho, Shaw, Robbins, & McNeilage, 2012). Annual rainfall ranges from 1,130 to 2,390 mm and the mean temperature ranges between 7°C and 29°C depending on elevation (ITFC unpublished). Bwindi has rugged topography and is relatively rich in plant and animal species, including several large mammals of international conservation interest such as the Mountain gorillas (*Gorilla beringei beringei* Matschie), Eastern chimpanzees (*Pan troglodytes schweinfurthii* Giglioli), and African bush elephant (*Loxodonta africana* Blumenbach). The forest has been influenced by prolonged human activity and much of the area has persistent herbaceous and secondary vegetation—which is known to be decades old and believed to result primarily from human activities including fires, timber extraction,

and cultivation as well as from natural processes including landslides and feeding by elephants (Babaasa et al., 2004; Butynski, 1984; Ssali, Moe, & Sheil, 2017).

Camera-trap observations were conducted between November 2011 and February 2013 spanning rainy and dry seasons. We selected 40 *E. ventricosum* plants located in a valley containing secondary vegetation near the Institute of Tropical Forest Conservation (ITFC)—a research station at Ruhija (2,355 m asl). We deployed between five and six cameras at any one time and moved them after 30 to 40 days for seven trapping periods, facing different plants each time (see Supplemental Material for details).

Results

From a total of 892 camera-trap days over 13 months, 3,480 out of 55,850 flower visitor images and 7,704 out of 55,587 fruit visitor images were useable. The total number of verified vertebrate camera-trap “events” (i.e., an animal seen in one or more of the event images) was 1,129 and 562 for flower and fruit visitors, respectively (Tables 1 and 2). All animal images were of single individuals except for 24 events which included groups of two or three L’hoest’s monkeys *Allochrocebus l’hoesti* P. Sclater feeding on fruit, and one event with one image of a Servaline genet *Genetta servalina* Pucheran photographed with an African dormouse *Graphiurus murinus* Desmarest in its mouth (Figure 1).

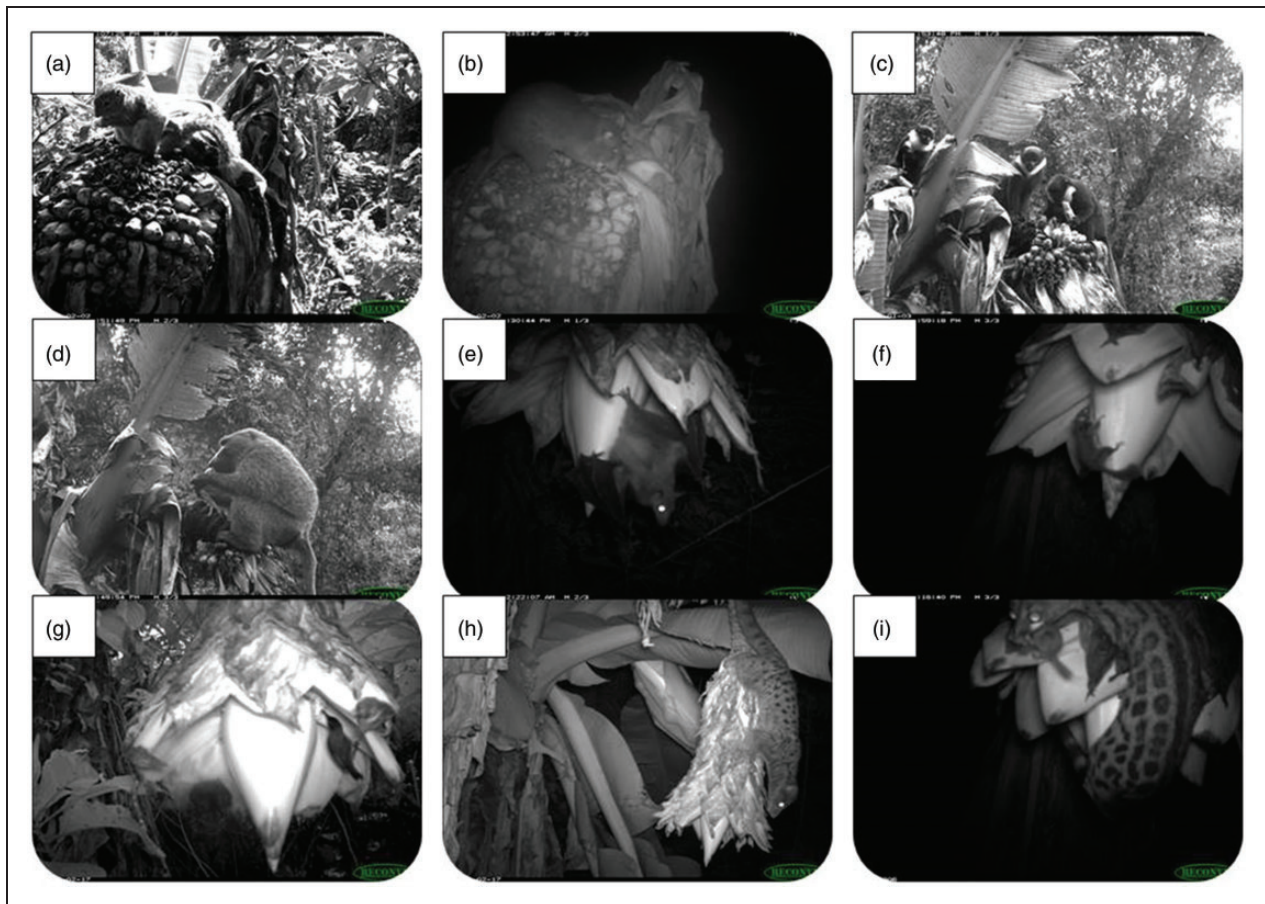
The most common flower visitors were the African dormouse (53.3%), Nectar bat *M. woermanni* Pagenstecher (43.8%), and sunbirds (family Nectariniidae; 2.4%) (Table 1 and Figure 1). Fruits were visited by Carruther’s mountain squirrel *F. carruthersi* Thomas (54.1%), L’hoest’s monkey (18.7%), and Forest giant pouched rat *C. emini* Wroughton (18.6%) (Table 2 and Figure 1). The plants were also visited by predators including *Servaline genet* (0.1%), African wood

Table 1. Number of Flower Visitor “Events” During a Total of 475 Camera Days ($n = 3,480$ Useable Images Out of a Total of 55,850 Images).

Common name	Scientific name	Camera events
African dormouse	<i>Graphiurus murinus</i> Desmarest, 1822	597
Nectar bat	<i>Megaloglossus woermanni</i> Pagenstecher, 1885	491
Sunbirds	Nectariniidae	27
African palm civet	<i>Nandinia binotata</i> Gray, 1830	4
Servaline genet	<i>Genetta servalina</i> Pucheran	1
Total		1,120

Table 2. Number of Fruit Visitor “Events” During a Total of 417 Camera Days ($n = 7,704$ Clear Images Out of a Total of 55,587 Images).

Common name	Scientific name	Camera events
Carruther’s mountain squirrel	<i>Funisciurus carruthersi</i> Thomas, 1906	300
L’hoest’s monkey	<i>Allochrocebus l’hoesti</i> P. Sclater	104
Forest giant pouched rat	<i>Cricetomys emini</i> Wroughton, 1910	103
Olive baboon	<i>Papio anubis</i> Lesson	29
African dormouse	<i>Graphiurus murinus</i> Desmarest, 1822	14
African soft-furred mice	<i>Praomys</i> sp Thomas, 1955	3
African wood owl	<i>Strix woodfordii</i> A. Smith, 1834	1
African palm civet	<i>Nandinia binotata</i> Gray, 1830	1
Total		555

**Figure 1.** Selected images of animals visiting and utilizing *E. ventricosum* fruits and flowers. The animals are (a) Carruther’s mountain squirrel *Funisciurus carruthersi* Thomas, (b) Forest giant pouched rat *Cricetomys emini* Wroughton, (c) L’hoest’s monkey *A. l’hoesti* P. Sclater, (d) Olive baboon *Papio anubis* Lesson, (e) Nectar bat *Megaloglossus woermanni* Pagenstecher, (f) African dormouse *G. murinus* Desmarest, (g) Sunbird (Nectariniidae), (h) African palm civet *Nandinia binotata* Gray, and (i) Servaline genet *G. servalina* Pucheran.

owl *Strix woodfordii* A. Smith (0.2%), and the African palm civet *N. binotata* Gray (0.2%) (Tables 1 and 2).

Flower visitor events were mainly recorded during the night with bird visits peaking at dusk (Figure 2). We saw clear indications of animals feeding on floral resources, possibly nectar, and searching for prey in the inflorescences. The Nectar bat and sunbirds were often recorded

with their snouts and bills inserted into the perianths, while the African dormouse, African palm civet, and Servaline genet were commonly seen moving in and out of flowers.

Fruit visitors exhibited both diurnal and nocturnal activity patterns with Carruther’s mountain squirrel, L’hoest’s monkey, and Olive baboon *P. anubis* Lesson

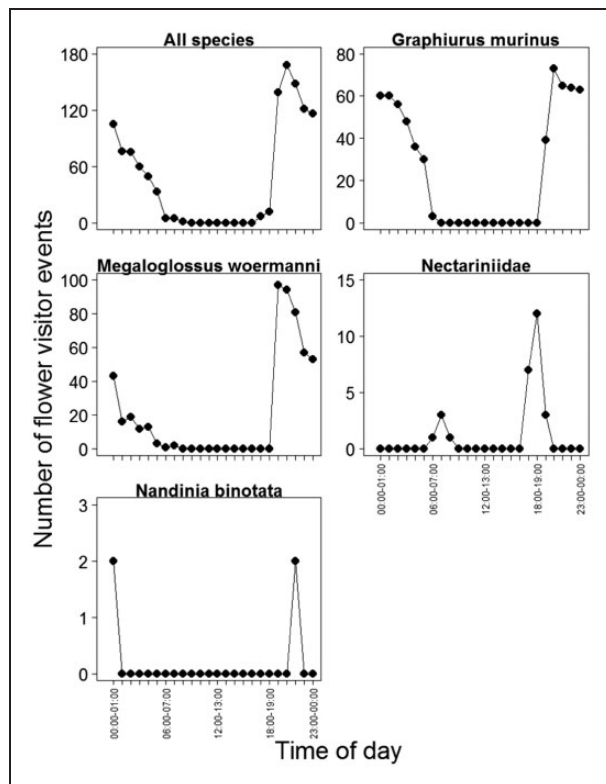


Figure 2. Number of flower visitor “events” with four or more observations (range = 1–597; see Table 1) versus time of day during a total of 11,241 camera hours. *G. servalina* ($n < 4$ “events”) was observed between 19:00 and 20:00 hours.

observed during daytime, while the African dormouse, Forest giant pouched rat, and African soft-furred mice *Praomys sp* were observed at night (Figure 3). Several animals were recorded holding and eating fruits (see Figure 1). Monkeys and baboons also appeared to be touching and smelling fruits to gauge if they were ripe. They often plucked the fruits (sometimes more than one finger at a time), placed them in the mouth, and used their teeth to remove the skins. The larger rodents (i.e., Carruther’s mountain squirrel and Forest giant pouched rat) appeared to first nip off the tip of the fruits and then fill their often distended cheeks with pulp and seeds. The African wood owl and the African palm civet may have been seeking prey (Figure 1 and Table 2).

Discussion

Our study is the first to describe the animals visiting African wild bananas. Our data show that bats and sunbirds form the bulk of flower visitors, while primates and rodents are the most common fruit visitors. Flower visitors are likely involved in pollination, while fruit visitors likely help deposit seeds away from the parent crown thereby reducing seed mortality (Janzen, 1970; Liu, Li, Wang, & Kress, 2002; Nyiramana, Mendoza, Kaplin, &

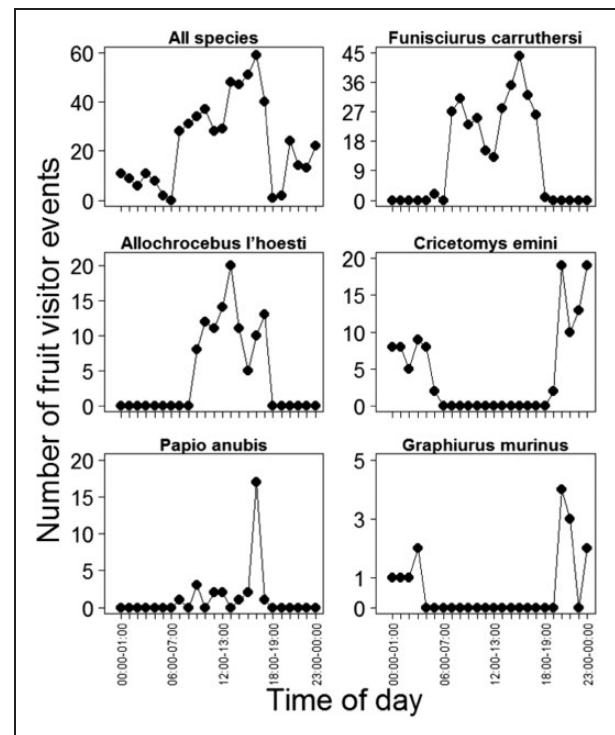


Figure 3. Number of fruit visitor “events” with four or more observations (range = 1–300; see Table 2) versus time of day during a total of 6,987 camera hours. *Praomys sp*, *S. woodfordii*, and *N. binotata* ($n < 4$ “events”) were observed between 21:00 and 01:00, 00:00 and 01:00, and 20:00 and 21:00, respectively.

Forget, 2011). We also found that flower visitors were mainly nocturnal, while fruit visitors exhibited both diurnal and nocturnal activity patterns. This indicates that *E. ventricosum* can sustain a diverse faunal community with some temporal segregation. Given our observations it seems reasonable to suppose that these species help maintain pollinators (especially bats and sunbirds) and seed dispersers that can themselves support other species. For example, the Nectar bat and sunbirds are recognized pollinators for a wide range of plants including *Kigelia africana*, *Nuxia congesta*, *Albizia gummifera*, *Musa sp.*, *Dalbergia sp.*, and *Anthocleista vogelii* (Fleming & Muchhala, 2008; Fujita & Tuttle, 1991; Nsor, 2015; Weber, Kalko, & Fahr, 2009). Few studies have determined what limits the abundance of these animals, but one multisite evaluation of banana (*Musa spp.*) pollinating bat species in tropical Brazil has shown that their abundance is positively correlated to local food resources (Luz, Costa, & Esbérard, 2015). We suspect that dormice too may play a role in pollen transfer and pollination—and noting that the role of such rodents in pollination has been widely overlooked (Ratto et al., 2018)—this indicates the need for further study (see e.g., Biccard & Midgley, 2009).

Since *E. ventricosum* produce flowers and fruits year-round (like most true bananas), and are visited when other flowers and fruits are scarce, we infer that these plants can support species dependent on sustained access to such resources. Our observations suggest that more animals tend to visit the plants during the dry season compared with the wet season—which likely reflects the lower abundance of other similar food resources in this period. Trees bearing fleshy fruits tend to be scarce during or at the beginning of the dry season—a trend observed for selected fruiting species in both Bwindi and the nearby Nyungwe National Park (Adamescu et al., 2018; Polansky & Robbins 2013; Sun et al., 1996). Like fig trees (*Ficus* spp.) in many lowland forests, *E. ventricosum* has passed the initial evaluation given its use by a number of other species and thus has the potential to be viewed as a “keystone species” (see Diaz-Martin et al., 2014; Gautier-Hion & Michaloud, 1989; Lambert & Marshall, 1991; Mills, Soulé, & Doak, 1993; Peres, 2000; Terborgh, 1986). In Bwindi, there are some other tree species, including *Ficus densistipulata* De Wild., *Psychotria mahonii* C. H. Wright, and *Myrianthus holstii* Engl. that exhibit low seasonal fluctuation in fruit availability (none are common, e.g., *M. holstii* occurs at a density of just a few stems ha⁻¹, see Kissa & Sheil, 2012) and may together with *E. ventricosum* support frugivores during periods of scarcity (see the online supplementary material of Polansky & Robbins, 2013). *E. ventricosum* has thus passed our initial screening that aimed to assess if it might have some properties expected for a keystone species. Further more comprehensive evaluations would be needed to formalize this result and demonstrate that other species would be reduced or lost if *E. ventricosum* were absent (see e.g., Peres, 2000). Managers, however, may be more interested in simply using these plants to bolster food for valued pollinators and frugivores and to perhaps support forest recovery (see later and Supplemental Material).

E. ventricosum plants may benefit a broader range of species than we observed—for example, observations elsewhere have shown that primates will often avoid some food species for long periods but still rely on them when other preferred foods are unavailable (Marshall & Wrangham, 2007). While neither gorillas nor chimpanzees nor elephants visited our selected plants during the study, we believe all three would find them attractive food resources as all these animals occasionally seek out and damage banana plants (*Musa* spp.) in neighboring fields (various local people’s personal communication and F. S. and D. S., personal observation).

Implications for Conservation

Our study and others in tropical and temperate regions (e.g., Burton et al., 2015; Krauss, Roberts, Phillips, &

Edwards, 2018; Steen, 2017) show how camera traps can help characterize ecological processes and species. While such data are insufficient to rigorously determine “keystone functions,” they provide useful indications. Indeed, given the improving affordability, reliability, and accessibility of camera traps along with our profoundly limited knowledge of most species and interactions, it is important to examine the opportunities that are now possible through the simple application of such tools (Burton et al., 2015; Sheil, Mugerwa, & Fegraus, 2013). We encourage efforts to explore these opportunities.

Our observations indicate that *E. ventricosum* benefits a range of species, even when flowers and fruits are otherwise scarce. We believe that establishing *E. ventricosum* in disturbed landscapes through field-grown suckers or seedlings (see e.g., Katende et al., 1995; Tripathi, Matheka, Merga, Gebre, & Tripathi, 2017) would bolster ecological activity and conservation value and may facilitate forest recovery. Furthermore, other herbaceous species that sustain flower and fruit resources in other sites (e.g., many Musaceae and other Zingiberales) are prime contenders for providing similar valuable ecological roles and thus for protection and restoration (see e.g., Liu et al., 2002; Marod, Pinyo, Duengkae, & Hiroshi, 2010).

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The author(s) declare no potential conflict of interest with respect to the research, authorship and/or publication of this article.

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Supplementary Material

Supplementary material for this article is available online.

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