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Ecosystem services provided by a large endangered primate in a forest-savanna mosaic landscape

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ABSTRACT

Forested landscapes are increasingly affected by human activities, but little is known about the role of large endangered frugivores as seed dispersers in such ecosystems. We investigated the role played by the bonobo (*Pan paniscus*) in a human-altered forest-savanna mosaic in Democratic Republic of the Congo. The studied groups are part of a community-based conservation programme but live at the interface with human activities. We identified dispersed species via faecal analysis, classified them into a regeneration guild and a seed size category, determined the effect of gut transit on seed germination, and the habitat use of bonobos. Bonobos dispersed intact seeds of 77 species, 80.8% of which were large-seeded (≥10 mm long), of which few can be dispersed by sympatric frugivores. They dispersed a majority (49%) of shade-bearers that thrive in forest understory with limited amount of light, all of which were large-seeded. Transit had an overall positive effect on seed germination. Bonobos used various habitat types, showing preferences for understory with intermediate light availability and dominated by woody or herbaceous vegetation. This dispersal pattern probably enhances recruitment of shade-bearers, and we thus hypothesized that those species benefited from directed dispersal by bonobos. This threatened frugivore provides unique dispersal services and likely plays a paramount functional role in the regeneration of late successional forests in this mosaic landscape. Management plans should pay particular attention to the role of large and rare frugivores in human-dominated regions as their disappearance could disrupt forest succession to a climax state.

1. Introduction

Forest communities are threatened by habitat loss and degradation, and increasing human population growth around the world (Haddad et al., 2015). Agricultural expansion (e.g. shifting slash-and-burn agriculture) and wood extraction create patches of secondary vegetation within primary forests, alter forest structure, and increase fragmentation (Mayaux et al., 2013; Norris et al., 2010). Forested landscapes have thus become dominated by forest–agriculture mosaics and percolated landscapes composed of vegetation at contrasting successional stages, including open and secondary habitats (Norris et al., 2010). In addition, bush-meat hunting depletes forests of their larger fauna, including ecologically important taxa such as frugivores (Fa et al., 2002; Vidal et al., 2013). Defaunation disrupts animal-mediated seed-dispersal, a crucial process for the regeneration of a large proportion of plant species (Kurten, 2013; Markl et al., 2012), and can have long lasting effects by modifying the composition of forest communities (Effiom et al., 2014; Kurten, 2013; Vanthomme et al., 2010).

Frugivores, especially large-bodied, are a key element of these mutualistic interactions with plants and thus play an invaluable role for forest resilience and conservation in the face of all the emerging threats (Vidal et al., 2013). Numerous populations of these large species inhabit non-optimal ecosystems with modified vegetation and spatio-temporal distributions of fruit resources (Arroyo-Rodríguez et al., 2015; Bregman et al., 2014; Hockings et al., 2015; Lenz et al., 2011; Lindsell et al., 2015), which can largely affect their degree of frugivory, habitat use, and the subsequent seed rain they generate. In addition, abiotic characteristics such as canopy openness can strongly limit the survival of seedling species with particular light requirements (Montgomery, 2004). Ultimately, changes in these traits can have cascading effects on the seed-dispersal effectiveness of frugivores. Therefore, the level of resilience of forest communities increasingly depends on the ability of

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frugivores to maintain their ecosystem services in such changing environmental conditions (Albert et al., 2014; Lenz et al., 2011; Lindsell et al., 2015). Because seed-dispersal effectiveness is context-dependent (Schupp, 2007), a thorough exploration of seed-dispersal services in degraded habitats is strongly needed for the implementation of effective landscape-scale conservation plans. Despite evidence that habitat alteration affects various components of seed dispersal of specific plant species, (Cf. Markl et al., 2012) few studies have evaluated seed-dispersal services from the perspective of dispersal agents in human-altered landscapes (but see Abedi-Lartey et al., 2016; Albert et al., 2014; Arroyo-Rodríguez et al., 2015; Lenz et al., 2011; Zhou et al., 2008). Many large-bodied frugivore populations are closely dependent on primary forests and rapidly disappear in human-dominated environments (Urquiza-Haas et al., 2009), whereas others show considerable ecological flexibility and maintain their seed-dispersal services in degraded areas (e.g., Albert et al., 2014; Arroyo-Rodríguez et al., 2015; Lenz et al., 2011). These disturbance-tolerant species that contribute effectively to the restoration of degraded forests are usually common and widespread such as cercopithecines and howler monkeys (Albert et al., 2014; Arroyo-Rodríguez et al., 2015), and hornbills (Lenz et al., 2011).

The bonobo, *Pan paniscus*, is a large endangered species that is endemic to the Democratic Republic of the Congo (D.R.C.) and preferentially uses primary mixed mature forests away from human presence in the Cuvette Centrale of the Congo Basin (Reinartz et al., 2006; White, 1992), where they have been shown to be effective seed dispersers (Beaune et al., 2013a; Idani, 1986; Tsuji et al., 2010). However, their behaviour in forest–savanna mosaics has only recently received more attention (Serckx et al., 2014; Thompson, 1997). Those habitats are characterized by high food resource variation which is thought to drive bonobos to display a certain level of behavioral plasticity and to feed regularly on fallback species that grow in forest edges and disturbed areas (Serckx et al., 2014). Moreover, such ecosystems are very patchy and facilitate access to forest interior to subsistence hunters, which substantially threaten the large frugivore community (Fa et al., 2002). As a consequence, the locally protected bonobos remain the largest species in a vast area of this ecosystem, suggesting that dispersal of numerous large-seeded plants falls to this endangered animal. Such large-seeded species are the main representatives of late successional tropical forests (Foster, 1986). Bonobos may thus provide unique seed-dispersal services and play a critical functional role in the forest-savanna mosaic, particularly for the maintenance of mature forests. However, the ecological role such endangered animal fulfil in impoverished and disturbed landscapes remain unexplored. In this study, we explored and compared seed dispersal services in bonobos and other sympatric frugivores discussing their respective role for forest regeneration. Additionally, we investigated functional traits (seed size, germination, regeneration guild, life form) of the dispersed plant species, and bonobo movement behaviour (i.e., seed-deposition sites) with regards to habitat preferences. Although this study focuses on a primate in a tropical region, the components that we discuss are relevant to other systems and human-modified regions.

2. Methods

2.1. Study area

The study took place in Democratic Republic of the Congo, close to the WWF-Malebo research station, in Bandundu province, (2°29′ 3.87S, 16°30′4.16E). The annual rainfall is between 1500 and 1600 mm, and mean daily temperature is approximately 25 °C (Vancutsem et al., 2006). Two dry seasons occur from June to August and February to March, and two wet seasons occur from September to January and April to May. The site is situated in the western Congolian forest–savanna mosaic, a landscape composed of a mixture of tropical semi-evergreen lowland rain forests and savanna matrix, representing respectively, approximately 60 and 40% of the total area. The landscape is characterized by a system of forest patches and corridors of variable sizes and shapes (Fig. 1) mainly associated with the hydrographic network of small rivers. As a transitional ecosystem, or ecotone, its fragmented spatial structure is natural, yet maintained by anthropogenic activities. Shifting slash-and-burn agriculture encroaches on forest patches, and cattle ranching, with its associated yearly fire regimes, restricts colonization of forests. This landscape thus has a large ratio of forest-edge area to forest interior area, and a relatively high proportion of forests at early successional stages. A striking feature is the diversity of forest types, canopy openness and understory vegetation encountered within relatively limited distances. We conducted field work in a section of 200 km^2 (Fig. 1) where two groups of bonobos are part of a community-based conservation programme led by the WWF-DRC and Mbou-Mon-Tour NGOs. Since 2001, those NGOs have reinforced the application of an ancestral taboo that proscribes killing or eating bonobos. The local ethnic group therefore does not hunt them (Inogwabini et al., 2008).

2.2. Frugivory and seed dispersal

Between May 2011 and June 2013, trackers of the WWF bonobo habituation programme regularly geolocated fresh nesting sites where they collected all fresh bonobo faeces found ($N = 2252$). Each faecal sample (individual faeces) was gathered in a separate plastic bag and washed through a 1-mm mesh sieve to retrieve the seeds prior to their identification. We identified intact seeds (with no obvious sign of damage) with the aid of a reference collection established from fruiting plants identified by specialists. We kept seed samples to perform germination trials. To compare the frequencies of seed dispersal, we computed the percentage of faecal samples that contained at least one seed of each species. We sorted the seeds according to the two categories defined by Serckx et al. (2015). First, 'important species' were present in >50% of faecal samples for at least 1 month, and occurred in >10% of sampled days (McLennan, 2013). Second, 'preferred species' were consumed disproportionately relative to their availability in the habitat (Marshall and Wrangham, 2007). We evaluated species availability with the aid of a bimonthly monitoring of trees ($N = 2585$) from species known to be consumed by bonobos or producing fleshy fruits. Further details can be found in Serckx et al. (2015). We also measured seed size (length and width) with a calliper. For the species that we did not measure, we gathered data from Amshoff et al. (1961) and Vivien and Faure (1985). We sorted seeds by length according to the following classes: small: <5 mm; medium: ≥5 to <10 mm; and large: ≥10 mm. In addition, we searched the literature for food species consumed and dispersed by other large frugivores species living in the area, i.e., primates (Lambert, 1999), and hornbills (Clark et al., 2001; Poulsen et al., 2002; Whitney et al., 1998), to assess the extent of seed dispersal redundancy.

2.3. Germination capacity

To test the effect of ingestion by bonobos on seed germination capacity, we conducted germination trials using dispersed and control seeds. We sowed dispersed seeds within two days after collection, and collected control seeds from several ripe fruits (as evaluated by humans) from several trees, avoiding fruits that showed signs of rot. We sowed a total of 1986 seeds (963 control; 1023 dispersed) of 16 species in a sterile cotton compress in individually labelled 9-cm diameter Petri dishes. The dishes were placed on a closed, predator-proof shelf in a shaded environment to prevent exposure to direct sunlight and seed desiccation. We checked each dish twice-weekly to record and remove