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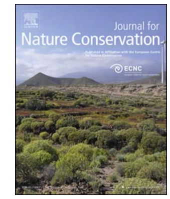

Disproportionately large ecological role of a recently mass-culled flying fox in native forests of an oceanic island

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ABSTRACT

Human-wildlife conflicts pose a growing threat to many species worldwide and require increasingly innovative and multi-disciplinary resolutions. Because of their apparent simplicity and political appeal, lethal approaches like culling are often favoured, decisions to cull are typically poorly supported by scientific evidence and the limitations and drawbacks of culls minimised. As natural habitats decline and fruit crop production expands, fruit-eating bats in the Old World (family Pteropodidae) are increasingly in conflict with fruit farmers. This conflict is exemplified on Mauritius where the government has implemented two mass culls of a threatened flying fox (*Pteropus niger*) since 2015 in response to fruit-grower concerns. The culls and illegal hunting reduced the bat population by > 50%. In this context, we sought to investigate the ecological role and service provided by the targeted flying fox through seed dissemination to gauge what may be lost as the species becomes rarer or extinct. We randomly sampled the woody native community in six of the best-preserved moist-to-wet native forests of Mauritius using 90 plots of 100 m^2 each and identified and measured the stem size of all woody plants ≥1 cm in diameter. Species were classified by whether their fruits occur in the diet of the flying fox in an exclusive, confirmed or likely manner and we assumed that fruit consumption is equivalent to potential seed dissemination. The relative importance of these three categories to the total woody plant community was then quantified as the proportion of species richness, stem density and basal area (as a surrogate of biomass) that they represent. We also investigated whether the main traits of species (seed size, fruit size, and maximum stem diameter) vary among bat-dispersal categories and differ from those of species whose fruits are not currently known to be eaten by the flying fox. On average, although about a quarter of the native woody species (24.6%) have fruits confirmed as eaten and seeds dispersed by the flying fox, these species comprise about half (53.1%) of the stems sampled and the majority (63.1%) of the basal area of native woody plant in the island's native forests. About half of that latter biomass figure comprises species for which the flying fox is the exclusive native vertebrate frugivore and seed disperser. Plants disseminated by the flying fox are typically large trees with large fruit and seeds. These trees are often key components of the canopy, therefore fulfilling structural engineer roles that provide resources and conditions for the survival of many forest species. The flying fox plays a disproportionally large ecological role in maintaining forest structure and biodiversity in the long-term. Consequently, lethal approaches to the conflict with fruit-farmers threaten not only an endangered species, but ecological processes central to the viability of native forests. Our findings highlight the importance of including the ecological costs of culling in decision-making processes intended to resolve human-wildlife conflicts.

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1. Introduction

As human populations increase and encroach on natural habitats, the needs of wildlife are increasingly in conflict with those of people. Consequently, human-wildlife conflicts are a growing threat to species worldwide (Madden, 2004), and resolutions require increasingly innovative and multi-disciplinary approaches to be resolved (Dickman, 2010; White & Ward, 2011). However, lethal approaches, including mass culling, are still commonly employed in attempts to resolve such conflicts (Donnelly & Woodroffe, 2015; Florens, 2016; Gibbs & Warren, 2015; Immonen & Husby, 2016). If culls are to form part of a resolution, it is critical that they not only alleviate the conflict, but avoid creating new and larger problems. New problems arise when species targeted for culls play critical ecological (e.g. Vincenot, Florens, & Kingston, 2017) and even economic (Scanlon, Petit, Tuiwawa, & Naikatini, 2014) roles in the broader landscape or ecosystem context within which the conflict is embedded. These ecological roles, and services provided through them, are directly threatened by culls and should consequently be more accurately described and taken into consideration when developing conflict-resolution strategies. This quantification of ecological roles would promote the resolution of human-wildlife conflicts which itself rests on processes that are rational, balanced and transparent (Hamman, Woolaston, & Lewis, 2016).

Old World fruit bats (Chiroptera, family − Pteropodidae) occur throughout much of the palaeotropics and subtropics where they often fulfil ecological keystone roles as pollinators and seed disseminators (Cox, Elmqvist, Pierson, & Rainey, 1991; Fujita & Tuttle, 1991). Many trees that they pollinate or disseminate are themselves keystone species like figs, or are canopy trees (Muscarella & Fleming, 2007; Shanahan, So, Compton, & Corlett, 2001) that fulfil physical ecosystem engineer roles, providing conditions and resources essential to myriad species (Jones, Lawton, & Shachak, 1997). Flying foxes, pteropodids in the genera *Pteropus* and *Acerodon,* are the largest of the Pteropodidae, and are capable of long-distance flight (Roberts, Catterall, Eby, & Kanowski, 2012) and dispersal of large seeds (McConkey & Drake 2015), itself an ecological function increasingly weakening as frugivores capable of disseminating larger seeds go extinct (Hansen & Galetti 2009) or ecologically extinct (Redford, 1992). Consequently, they can play pivotal roles in seed dispersal on remote islands that are hard to access by other vertebrate frugivores. Moreover, within human-fragmented landscapes, the ecological roles of flying foxes may be enhanced relative to other pollinators and seed disseminators because of their high mobility (Oleksy, Racey, & Jones, 2015; Roberts et al., 2012). Furthermore, flying foxes often occur on oceanic islands (Vincenot et al., 2017) which themselves have often sustained high rates of extinction of birds or other seed-disseminating vertebrates (Blackburn, Cassey, Duncan, Evans, & Gaston 2004; Cheke & Hume 2008). These extinctions serve to elevate the flying foxes' relative importance in seed dissemination and pollination.

Island endemic bats are particularly understudied and are also more threatened than other bat species (Conenna, Rocha, Russo, & Cabeza, 2017). Island flying-foxes are no exception, being among the most threatened bats in the world (Vincenot et al., 2017). Twenty-eight of the 31 species of *Pteropus* assessed as threatened (IUCN SSC, 2015) are island species, with population declines driven primarily by hunting (Mildenstein, Tanshi & Racey, 2016) and widespread habitat transformation (Caujapé-Castells et al., 2010; Strasberg et al., 2005). Remaining native food resources are further eroded by the effects of invasive alien plants (Florens, Baider, Seegoolam, Zmanay, & Strasberg, 2017; Monty, Florens, & Baider, 2013; Welch & Leppanen, 2017) and animals (Krivek 2017; Baider & Florens, 2006; Welch & Leppanen, 2017). As natural habitats decline and fruit crop production expands, fruit-eating bats are increasingly incorporating non-native fruit crops into their diet, bringing them into conflict with fruit farmers (Aziz, Olival, Bumrungsri, Richards, & Racey, 2016). Lethal solutions to this conflict are on the rise (Vincenot et al., 2017), for instance, it is legal to kill the threatened *Pteropus rufus* on Madagascar from May to August and whenever it is found on crop fields (O'Brien, 2011), and Mauritius recently weakened its biodiversity protection law to legalize mass culling campaigns of the threatened *Pteropus niger* (Florens, 2016).

The ecological importance of flying foxes as pollinators and seed disseminators is well established (Fujita & and Tuttle, 1991; Nyhagen et al., 2005; Shanahan et al., 2001; Aziz et al.,2017), and declines of their populations can disrupt these mutualisms (McConkey & Drake, 2006) resulting in negative consequences for plant reproduction, recruitment and ultimately the sustainability on plant populations and communities (McConkey et al., 2012; Beckman & Rogers, 2013). However, the importance of flying foxes is typically defined through the number or composition of plant species found in their diet, and whose reproduction and dissemination therefore depend in part or solely on them (e.g. Nyhagen et al., 2005). We consequently set out to explore the ecological importance of flying foxes using more detailed information about the plant community, such as the proportion of the biomass that bat-serviced species comprise in their habitats. We investigated this aspect on an island where government culls recently reduced the population of the sole surviving flying fox species, *Pteropus niger,* by over 50% (Vincenot et al., 2017). In particular, we investigate the proportion of the species, stem density and biomass (using basal area as surrogate) of native woody plants of the island's forests that are 1. likely serviced, 2. confirmed to be serviced and 3. exclusively serviced (through frugivory) by flying foxes, and investigate the main traits that distinguish these three categories from other native woody plants of the community and between themselves. We discuss the findings within its ecological and conservation context and in the light of threats besetting the flying fox species.

2. Methods

2.1. Study area

Mauritius, centred on 20° 20′ S; 57° 34′ E, is a 7.8 M years old volcanic island of 1865 km^2, with a maximum elevation of 828 m and located some 900 km east of Madagascar (Fig. 1a). It is found in the Mascarene archipelago (also comprising Rodrigues and La Réunion), a biodiversity hotspot (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). Mean annual rainfall varies from 800 mm on the west coast to 4000 mm in the central uplands, and mean annual temperature is 22 °C (Staub, Stevens, & Waylen, 2014). The native biota is typical of oceanic islands; relatively depauperate but with high endemism (Baider et al., 2010; Cheke & Hume, 2008). Prior to human colonization in the early 17th century, three main zonal communities occurred on the island: a small dry palm-rich woodland in the driest, leeward side of the south-east trade winds (annual rainfall < 1000 mm), a semi-dry evergreen forest more inland, and a moist-to-wet forest covering the wettest half of the island including the uplands and much of the south and east slopes (annual rainfall ≥ 2000 mm). A fourth zonal community, the mossy forest, occurred on some of the highest mountain tops but occupied a few km^2 only. There were distinct fringing coastal communities and patches of azonal communities (e.g. heath on shallow soils, marshes on poorly drained soils) occurred within the wet forest zone (Cheke & Hume, 2008; Vaughan & Wiehe, 1941). The main community (the moist-to-wet forest) is typically dense and species rich for an oceanic island setting and not exceeding 20 m high (Florens, Baider, Martin, & Strasberg, 2012; Lorence & Sussman, 1986; Vaughan & Wiehe, 1941).

Habitat destruction since human colonization in 1638 spared only about 5% of native vegetation, which survives in a highly fragmented state (Florens, 2013). Native forest remnants are among the most invaded by alien plants worldwide (Florens et al., 2016) and this invasion is causing major forest degradation (Florens et al., 2017). Overall, extinction rates are high (e.g. 9% in flowering plants, 57% in land birds) and endangerment rates higher (Baider et al., 2010; Cheke & Hume,