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The upsizing of the São Tomé seed dispersal network by introduced animals

Ruben H. Heleno[1#], Filipa Mendes[1], Ana P. Coelho[2,3], Jaime A. Ramos[4], Jorge M. Palmeirim[2], Ana Rainho[2], Ricardo F. de Lima[2]

[1] Centre for Functional Ecology (CFE-UC), Department of Life Sciences, University of Coimbra, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal; [2] Centre for Ecology, Evolution and Environmental Changes (cE3c) and Department of Animal Biology, Faculty of Sciences, University of Lisbon, 1749-016 Lisboa, Portugal; [3] Department of Biology & CESAM, University of Aveiro, Campus de Santiago, 3810-193 Aveiro, Portugal; [4] Marine and Environmental Sciences Centre (MARE), Department of Life Sciences, University of Coimbra, 3004-517 Coimbra, Portugal; # corresponding author: rheleno@uc.pt

Abstract

Biological invasions are a major threat to global biodiversity with particularly deleterious consequences on oceanic islands. The introduction of large terrestrial animals – generally absent on islands – can disrupt important ecosystem functions, such as the dispersal of native seeds. However, while the consequences of plant invasions received much attention, the potential of introduced animals to change insular seed dispersal networks remains largely unknown. Here, we collated evidence from five sampling methods to assemble qualitative and quantitative, multi-guild seed dispersal network for the island of São Tomé (Gulf of Guinea) and explore whether native and introduced seed dispersers consistently differ in their topological roles, in their gape width, and in the size of the dispersed seeds. Our network included 428 interactions between 23 dispersers (14 birds, 2 bats, 1 snake and 6 non-flying mammals) and 133 plant species. Each method (direct observations, identification of seeds in droppings and stomachs, questionnaires, and literature review) was particularly informative for a small group of dispersers, thus rendering largely complementary information. Native and introduced dispersers did not differ in their topological position in the either qualitative or

quantitative networks (linkage level, specialization d', and species strength). However, introduced dispersers tend to have much larger gape widths and to disperse significantly larger seeds. Our results point to a general upsizing of the seed dispersal network in the island of São Tomé driven by the recent arrival of large, introduced animals. We argue that this pattern is likely common on other oceanic islands where introduced dispersers might counteract the general pattern of seed dispersal downsizing resulting from the selective extinction of larger animals.

Keywords: Biological Invasions, Biological Change, Dispersers Size, Ecological Networks, Gulf of Guinea Islands, São Tomé and Príncipe, Seed Dispersal

Introduction

Biodiversity is rapidly declining as a result from different anthropogenic pressures, threatening key ecosystem functions and human well-being (Díaz et al 2019, Brauman et al 2020). Biological invasions are one of such key pressures, often driving native species to the verge of extinction and altering the complex network of mutualistic and antagonistic interactions that supports rich biological communities (Chapin et al. 2000, Heleno et al. 2009). While no area on Earth is safe from biological invasions, oceanic islands – i.e. those that have never been connected to a continent – are particularly vulnerable to the introduction of new species by virtue of their relatively simple and naïve biota (Whittaker and Fernández-Palacios 2007, Bellard et al. 2017). Oceanic islands are particularly rich in endemic taxa, and due to the strong filter imposed to the colonization by large animals, their floras have typically evolved in the absence from large terrestrial vertebrates (Paulay 1994, Bowen and VanVuren 1997), which play important ecological roles in continental ecosystems, including as seed dispersers (Galetti et al. 2001, Jordano et al. 2007, Timóteo et al. 2018).

Seed dispersal is a critical process in the life cycle of most seed plants, allowing seedlings to recruit away from the parent plant, and thus maintaining regional diversity by facilitating the recolonization of disturbed grounds and the colonization of new areas (Janzen 1971, Traveset et al. 2014). Due to the scarcity of large terrestrial vertebrates, seed dispersal services on islands, are largely secured by birds, bats and lizards (Lord 2004, Traveset et al. 2014), which are naturally limited in the size of the seeds they can disperse by their gape width (Wheelwright 1985). Furthermore, human-induced extinctions have been particularly detrimental for the larger frugivores both on continents and on islands (Pérez-Méndez et al.

2014, Heinen et al. 2018, Hansen and Galetti 2009), leading to a generalized downsizing of the frugivores assemblages and to a shift of seed dispersal services towards smaller seeds (Dirzo et al. 2014, Bello et al. 2015, Galetti et al. 2015). On the other hand, oceanic islands have also received countless introductions of large terrestrial vertebrates during their recent history of human colonization (Elton 1958, Vitousek et al. 1996, Hofman and Rick 2018). Although the direct negative effects of such introductions on native species have been widely documented (Bellard et al. 2017), we still know relatively little about how large animals might affect key ecosystem functions, including seed dispersal (Fricke and Svenning 2020).

Changes on the assemblage of insular seed dispersers, particularly in a context of biological invasions, have a strong potential to change native seed dispersal services. Surprisingly, the impacts of plant invasions (Traveset and Riera 2005, Heleno et al. 2009, Heleno et al. 2013) and disperser's extinctions (Rumeu et al. 2017, Vizentin-Bugoni et al. 2019) concentrated most attention, and the effects of introduced animals remain largely unexplored (but see Traveset et al. 2019). Species-interaction networks are a most valuable tool to evaluate such effects by simultaneously considering the species (nodes) and the interactions (links) that bind them together into functional and self-persistent communities (Bascompte and Jordano 2013, Heleno et al. 2014). Nevertheless, the diffuse nature of seed dispersal interactions (often involving very different groups of dispersers), represents a challenge for ecologists aiming to quantify changes on seed dispersal networks at the community level, with very few studies considering more than one guild of dispersers (e.g. Donatti et al. 2011, Escribano-Avila et al. 2018). One way to consider the contribution of multiple dispersal guilds and correctly evaluate changes on seed dispersal services is to combine the results of several sampling methods, such as direct observation of frugivory and the identification of seeds recovered from animal faeces. Beehler (1983) was probably the first to combine data from these two sampling methods to jointly quantify frugivorous interactions at the community level. Similar approaches were more recently implemented by Ruggera et al. (2015), Ramos-Robles et al. (2016), and further expanded by Timóteo et al. (2018) for the construction of quantitative interaction matrices based on cumulative frequencies of occurrence. While no method is free from its own bias, either used in isolation or in combination, a growing number of studies advocates for the combination of data from different sources reduce biases when assembling community-level frugivory networks (e.g. Jordano 2016, Escribano-Avila et al. 2018, Schlautmann et al. 2021). We expect that each method will be particularly effective for documenting the seeds dispersed by a restricted group of dispersers, thereby contributing with complementary information.

As most oceanic islands around the Word, the island of São Tomé (Gulf of Guinea, central Africa; see Supplementary material Appendix 1, Fig. A1) has seen early settlers deliberately or accidently introducing a large number of terrestrial vertebrates such as feral pig *Sus scrofa*, Mona monkey *Cercopitecus mona*, African civet *Civettictis civetta*, least weasel *Mustela nivalis*, as well as cats *Felis silvestris*, dogs *Canis lupus* and rats *Rattus rattus* (Dutton 1994). In line with what happened in many other islands, most of these species have readily integrated into native communities. Many of these introduced animals are known to regularly consume fruits and their large body size is unmatched by the native frugivores of São Tomé, which holds one of the highest densities of endemic species in the World (Jones 1994, Valente et al. 2020) and no documented species extinctions (IUCN 2021). We therefore expect that introduced animals will tend to have a larger gape width than native animals, readily integrating into the local seed dispersal networks and dispersing more species and larger seeds than native dispersers (Moran and Catterall 2010, Donatti et al. 2011).

Here, we characterize the seed dispersal network of São Tomé Island to evaluate if and how introduced dispersers are affecting native seed dispersal networks. We first evaluate the importance of collating multiple data sources when assembling community-level seed dispersal networks. We then explore whether native and introduced dispersers systematically differ in their topological roles within the seed dispersal network, namely in the number of species dispersed, their selectiveness, and their overall importance as dispersers. Finally, we test if native and introduced dispersers differ in their gape width and in the size of the dispersed seeds and we end discussing the potential implications of a seed dispersal upsizing on islands.

Methods

The island of São Tomé

Right at the equator, São Tomé (Republic of São Tomé e Principe) is one of the four volcanic islands in the Gulf of Guinea, 238 km west of the coast of Gabon (Appendix 1, Fig. A1), with the oldest exposed rocks dated between 1 and 8 MY (Caldeira and Munhá 2002). The islands' high relief (2024 m a.s.l.) intercepts the predominant south-west moist wind currents, causing yearly precipitations of up to 7000 mm, mostly concentrated between September and May. The mean monthly temperature is relatively constant around 26.2 ºC (Min.= 20.6 ºC; Max. 30.5 ºC) (UNFCCC 2019). Despite its small size, the island holds a large diversity of ecosystems, including mangroves and coastal sand dunes, extensive lowland forests, and montane and cloud forests on the highest altitudes (Jones et al. 1991). Large portions of the island are still covered by lush high-canopy rainforests, but most of it has now been altered by human influence, notably in the drier north and in coastal lowlands (Soares et al. 2020). Being sufficiently isolated from the mainland to allow allopatric speciation, and close enough to receive many colonizers from the Congo and the Niger basins, the island stands out globally due to the high concentration of endemic species (Measey et al. 2007, Valente et al. 2020). There are currently no recorded extinctions in the island of São Tomé (IUCN 2021). Some historical accounts refer the existence of very large lizards that eat the cattle, probably crocodiles, but their presence could not be confirmed by archaeological evidence (Ceríaco et al 2018). Similarly, some plants are probably very rare but none has yet been confirmed extinct on the island (Figueiredo et al. 2011).

Data collection

Here, we combined information on frugivory and potential seed dispersal interactions from various sources to build the seed dispersal network for São Tomé, excluding seed predation. Data was collected over the course of 18 months (from October 2015 to March 2017), across the entire island, including all main habitats and altitudinal range, and trying to avoid any geographical biases (Appendix 1, Fig. A1). Following Heleno et al. (2011), all interactions were classified into four categories according to the level of information available on seed fate, namely: (i) "confirmed seed dispersal" if the viability of the dispersed seeds is experimentally confirmed; (ii) "potential seed dispersal" if entire seeds are identified in stomach contents or faeces but there is no confirmation of seed viability; (iii) "frugivory" if fruit consumption is reported without clear information on seed fate; and (iv) "seed predation" if there is evidence of the physical or chemical destruction of seeds, including destroyed seeds found in droppings or stomachs. The subsequent analyses include interactions of frugivory, potential and confirmed seed dispersal and exclude cases of seed predation. Therefore this dataset should be considered as a network of potential seed dispersal, including disperser species that range along a continuum from poor to highly efficient dispersers (Schupp et al. 2010, Heleno et al. 2011b). Data was obtained by combining independent evidence from five complementary approaches: 1) identification of undamaged seeds in bird and mammal faeces; 2) direct observation of frugivorous interactions in the field; 3) identification of undamaged seeds in the stomach of dead animals; 4) oral questionnaires to local hunters and farmers; and 5) a literature review of frugivory records. The spatial origin of the data obtained, the temporal window sampled by each method, and the number of samples analysed are described in Appendix 1, Fig. A1 and in Table A1. Bird droppings were collected during 91 mist-netting sessions in 9 sites (1077 birds captured). All birds were placed in paper bags for up to one hour to produce a dropping and released on site. Mammal faeces were collected during standardized observation transects (see below) and along additional free searches for latrines, shelters, caves, roosting trees, and abandoned houses in 10 sites across the island (Fig. A1, Table A1). Droppings were air-dried and all undamaged seeds were later extracted and identified by comparison with a reference collection assembled for this study from fresh field samples and from herbarium specimens. Direct observations of frugivorous interactions were recorded along 23 standardized transects where one observer with binoculars registered all frugivorous interactions detected along 500 m forest trails walked in approximately 1 hour, frequently stopping to observe fruiting trees from a hidden position. Transects were performed in 13 sites encompassing the main habitats and altitudinal range of the island. Stomachs of hunted animals were collected with the help of a network of hunters from 13 sites, whose hunting activities spread across the entire island. The hunters recorded the species, site and date of shooting, and kept the stomach contents in alcohol, from where seeds were latter extracted and identified as described above. Questionnaires were performed orally to 15 local hunters, nature guides, scientists, and farmers, from 6 villages, asking them to report their own direct observations of fruit consumption by animals where they could confidently recognize both species involved (i.e. the plant and the animal species). Finally, an exhaustive literature search was performed to retrieve all published frugivorous interactions reported for São Tomé on scientific papers, grey literature, unpublished data, and natural history books. There was an effort to collect data with the different methods across the entire island (Fig. A1) and during the entire duration of the project (Table A1). For most methods, sampling covered the 18 months of the study but was particularly intense between August and October 2016. However, data collected from questionnaires, literature searches, and the analyses of bird and mammal droppings include interactions from the entire year, and therefore we believe that any temporal sampling biases should have a small effect in the overall dataset. Plant taxonomy and origin follows the most updated checklist of flowering plants for the island (Figueiredo et al. 2011).

Characterization of seed size and dispersers' gape width

To explore the relationship between dispersers' gape width and the size of dispersed seeds, the width (i.e. the second longest axis, which is the one limiting ingestion) of up to five seeds per species was measured with a digital calliper (precision 0.01mm). For plant species absent from the reference collection (chiefly those reported during questionnaires), seed width was gathered from the literature (see Supplementary material Appendix 2, Table A2). The gape width of birds was measured on live animals during mist netting sessions. The gape width of mammals and reptiles was preferably measured on animals recently killed by local hunters and complemented by measuring specimens from the Science Museum of the University of Coimbra and from the collections of the Instituto de Investigação Científica Tropical of the University of Lisbon. Sample size for gape width measurements on each species is shown in Table A1.

Data analysis

All interactions were merged into a qualitative (binary) and a quantitative (weighted) seed dispersal matrix quantifying the frequency of frugivory and seed dispersal records between each fruiting plant species and their animal dispersers. For the quantitative matrix, interaction frequency was estimated by combining the number of records obtained from each sampling method between plant species *i* and disperser species *j*, considering each sample as an independent evidence of interaction *ij* using the rule: 1 record = 1 dropping or 1 stomach of seed disperser *j* with the presence of undamaged seeds of plant *i*, 1 transect where seed disperser *j* was observed ingesting fruits of plant *i*, 1 questionnaire where seed disperser *j* was reported to consume the fruits of plant *i*, or 1 published reference with evidence of seed dispersal of plant *i* by the seed disperser *j* (see a similar approach in Timóteo et al. 2018). This measure is therefore equivalent to the pooled frequency of occurrence of interactions *ij* among all samples, thus providing a coarse estimate of the quantitative component of seed dispersal effectiveness of interaction ij.

We described the topological role of native and introduced dispersers in the network using three key species-level descriptors, calculated for the qualitative and quantitative version of the São Tomé network: linkage level, specialization (d') and species strength. Linkage level is a simple measure of trophic generalism reflecting the number of plant species dispersed by each animal species. Disperser specialization (d') expresses the animals' selectiveness for particular plants as the departure from the random use of resources based on the number of interaction events recorded for each plant species (Blüthgen et al. 2006). Finally, animal species strength reflects their cumulative importance as seed dispersers for the entire plant community, based on the sum of all plant dependencies on each disperser (see Bascompte et al. 2006). Both versions of the seed dispersal network were visualized and described with package *bipartite* (Dormann et al. 2008) in R (R Development Core Team 2020).

First, we evaluated if the origin (native or introduced) of the dispersers (predictor) influenced their topological roles within the qualitative and quantitative seed dispersal network, namely on: linkage level, specialization (d') and species strength (responses), using univariate Generalized Linear Models with package *lme4* in R (R Development Core Team 2020). Error distributions were adjusted to a Gamma distribution with an inverse link function (Grafen and Hails 2002) to achieve normality. We then used a similar procedure to evaluate if native and introduced dispersers differed on the size of the dispersed seeds using three complementary response variables: mean seed size of their dispersed species (i.e. mean seed size); size of the largest seed species dispersed (i.e. maximum seed size); and mean size of their dispersed seeds standardized by the frequency of interaction of each species (i.e. weighted seed size). Differences on the mean gape width of native and introduced dispersers were evaluated with a General Linear Model. The residuals of all models have been visually inspected for violations of normality and homoscedasticity.

Results

The seed dispersal network of São Tomé described 428 interactions between 23 seed disperser species and 133 dispersed plant morphotypes (Fig. 1a – quantitative network; Appendix 3 Fig. A2 – qualitative network). The seed dispersers' assemblage includes 14 bird species, two bats, one snake and six non-flying mammals (Table 1). Most animals were endemic to the Gulf of Guinea, except for three non-endemic native species (1 bird and 2 bats), and the six non-flying mammals, all introduced (Table 1).

Ninety-six seed morphotypes (72%) could be fully identified to the species level, of which 70% were native to São Tomé and 30% were introduced. Four morphotypes could only be identified to the genus level, and 33 could not be identified and therefore could not be classified as either native or introduced (Fig. 1a, Fig. A2). The Black-capped Speirops (*Zosterops lugubris*) was the most generalist frugivore, dispersing the seeds of 66 plant species, followed by the introduced mona monkey (46 species), the São Tomé thrush (*Turdus olivaceofuscus*, 44 species) and the Straw-coloured fruit bat (*Eidolon helvum*, 27 species)(see Supplementary material Appendix 4, table A4). The most frequently dispersed plants were the natives *Ficus kamerunensis* (Moraceae), *Harungana madagascariensis* (Hypericaceae) and *Psydrax subcordata* (Rubiaceae), and the introduced and highly invasive *Rubus rosifolius* (Rosaceae) and *Cecropia peltata* (Urticaceae) (Global Invasive Species Database 2017). Questionnaires was the sampling method contributing with more information (51.6% of all interactions), followed by the identification of undamaged seeds in faeces (36.0%), records retrieved from the literature (13.3%), and finally by the direct observation of interactions along transects (4.0%), and the identification of seeds in the stomach of hunted animals (2.8%) (Fig. 1b). Only 7% of the interactions have been identified by two or more sampling methods, and nine out of the

23 species of seed dispersers had all their interactions reported by a single sampling method (Fig.1b; Appendix 4).

We found no differences between the topological role of native and introduced dispersers, either in terms of linkage level (Mean±SD Natives= 14.8±17; Introduced= 29.3±11; $t_{1,21}$=1.53; p=0.141), quantitative species strength (Natives= 5.6±13; Introduced= 3.2±5; $t_{1,21}$=0.111; p=0.912), or quantitative specialization d' (Natives= 0.46±0.2; Introduced= 0.44±0.1; $t_{1,21}$=-0.23; p=0.820) (Fig. 2a-c, Table 1). These results were not altered when comparing species roles derived from qualitative networks (Appendix 3, Table A3).

As expected, the gape width of introduced dispersers was considerably greater than that of the native seed dispersers (Natives= 10.9±4mm; Introduced= 40.6±27mm; $t_{1,21}$= -4.54; p<0.001). Accordingly, introduced seed dispersers tended to disperse significantly larger seeds than the native dispersers, either in terms of mean seed size ($t_{1,21}$= 2.52; p=0.019), maximum seed size ($t_{1,21}$=2.77; p=0.011), and weighed mean seed size ($t_{1,21}$=3.27; p=0.004) (Fig. 2d-f).

Discussion

Here we reconstruct the multi-guild seed dispersal network of São Tomé island, revealing the shared importance of birds (chiefly the Black-capped Speirops), bats (chiefly the Straw-colored fruit bat) and several introduced terrestrial mammals for the dispersal of 133 plant species (Fig. 1a). We show that introduced seed dispersers have, on average, a much greater gape width than the native seed dispersers of São Tomé, tending to disperse larger seeds, and thus shifting seed dispersal services in the direction of large-seeded species. We argue that this might be a common pattern in other oceanic islands across the globe, where the introduction of large dispersers can invert the general downsizing of the seed dispersal services resulting from the selective defaunation of larger dispersers (Hansen and Galetti 2009, Galetti et al. 2015).

In addition to the extremely high proportion of endemic species that characterizes São Tomé fauna and flora, this seed dispersal network also stands out due to the presence of two unusual frugivores: a snake *Naja peroescobari* (sub order: Serpentes), and humans *Homo sapiens*. As far as we are aware, this is the first time that a snake is reported as consuming fruits and acting as a potential seed disperser. These records came from 5 questionnaires performed to hunters from different villages who reported to have seen the endemic *N. peroescobari* (until recently considered introduced; Ceríaco et al. 2017) directly consuming the fruits of the invasive *R. rosifolius*, and the native *Sterculia tragacantha*. Although the information retrieved from questionnaires should be taken with care, as neither fruit consumption or seed viability can be unequivocally confirmed, fruit consumption by snakes has also been suggested in the Galapagos (Olesen et al. 2018) and probably deserves further scrutiny in future seed dispersal assessments. Secondly, the direct dependence from a large proportion of the rural population from small scale farming and livestock farming, often with fuzzy borders with secondary forest (Jones et al. 1991) creates many opportunities for effective endozoochorous seed dispersal by humans into natural areas. In this study we directly asked hunters what fruits they ingested while in the forest, and we report 18 species for which humans may act as effective seed dispersers (Appendix 4, Table A4). São Tomé was uninhabited when first discovered by Portuguese sailors in c.1470, and therefore we considered *H. sapiens* as a recently introduced seed disperser in this ecosystem.

Complementarity across sampling methods

Most seed dispersal studies to date have focused on the services provided by a single guild of dispersers, such as frugivorous birds (García and Martínez 2012, Heleno et al. 2013), and few have evaluated the services provided by several guilds of dispersers (see Almeida and Mikich 2018, Escribano-Avila et al. 2018). This compartmentalization on the focus of seed dispersal studies steams chiefly on the inadequacy of a single method to sample seed dispersal by strikingly different functional groups, such as small birds, bats, lizards, ants, arboreal primates or terrestrial carnivores. However, multi-guild studies are critical to provide a complete overview of the seed dispersal services available to plants.

The island of São Tomé offers several challenges for seed dispersal studies, including the steep terrain with limited access to some parts of the island and the very high canopy of most forests. To assemble the most complete vertebrate seed dispersal network possible, we collated evidence of frugivory and seed dispersal interactions from five sampling methods. As expected, each method revealed particularly informative for a specific group of dispersers, and nine dispersers were recorded by only one sampling method. Questionnaires were the most informative source of information for the seeds dispersed by bats, non-flying mammals, and snake. Seed dispersal by birds was often captured by different sampling methods, and particularly by the analysis of droppings collected from mist netted birds. Combining information from multiple sources is thus highly beneficial for assembling more complete seed dispersal networks, as these sources are largely complementary. On the other hand, it is important to note that not all sources of information have the same degree of accuracy or are subject to the same biases (Escribano-Avila et al. 2018). For example, methods based on animal captures or observations are naturally vulnerable to biases in species catchability and detectability, respectively. Questionnaires, in turn, are biased towards conspicuous animals of economic importance (e.g. hunted species) and are also more vulnerable to taxonomic errors during the interpretation of species common names. While the interactions obtained from the application of questionnaires should be considered with particular care, ignoring this source of information would result in missing approximately half of all interactions reported here, many of which likely representing cases of legitimate seed dispersal. Therefore, the systematic use of questionaries is at least a valuable source of preliminary information from poorly studied ecosystems with a strong presence of rural communities, and disregarding such empirical knowledge seems imprudent. Finally, not all methods are equally informative in relation to the fate of ingested seeds and consequently towards estimating seed dispersal effectiveness (Schupp et al. 2010). In this respect, intact seeds retrieved from animal droppings are clearly the most informative method to infer legitimate seed dispersal, particularly if the viability of dispersed seeds can be experimentally confirmed, while most other methods can only provide information of frugivory and potential seed dispersal (Carlo and Yang 2011).

While attenuating method-specific sampling biases, combining information provided by different methods might also introduce a new sort of bias, potentially overestimating the importance of species that are primarily sampled by methods providing a high number of samples. To explore such effect, we assessed whether species roles systematically increase with the proportion of samples obtained by each method (Appendix 5, Fig. A3). The lack of significant correlations shows that the source of information does not systematically inflate species functional roles. Although the interpretation of networks assembled from multiple methods must be done with caution, we advocate that this combination is particularly valuable for assessing multi-guild seed dispersal services (Jordano 2016, Acevedo-Quintero et al. 2020).

Disruptive potential of introduced dispersers

Overall, native and introduced animals dispersed a similar number of species (linkage level), they did not differ in their selectiveness for resources (specialization d') and they appear to be equally important as seed dispersers for the plants of São Tomé (species strength). Therefore, topologically - i.e. considering the position of nodes and links in the network, regardless of their biological identity - both native and introduced dispersers exhibited very similar functional roles (Fig. 2a-c). However, introduced dispersers have consistently larger (on average four times larger) gape widths than their native counterparts. As a result, introduced dispersers, and chiefly large terrestrial mammals, are less constrained on the diversity of fruits that they can consume and disperse than the relatively small-gaped native dispersers. Indeed, we found that introduced dispersers tend to disperse species with larger seeds (Fig. 2d-f), likely favouring their recruitment when compared to small-seeded species. In addition to their greater gape width, large, introduced animals might systematically differ from native dispersers (chiefly birds and bats) on other functional traits, such as having longer gut-passage times, average dispersal distances, or specific feeding preferences (Godínez-Alvarez et al. 2020, Levey et al. 2006, Messeder et al. 2020), which can further affect the quality of the provided seed dispersal services.

Although the conclusions of this study are naturally limited to the island of São Tomé, we argue that this result might reflect a more general pattern found on other highly invaded islands across the globe. There are three main lines of evidence supporting the generality of these proposition: **1**) Large terrestrial mammals are generally absent from oceanic islands, as they are less likely to colonize remote territories due to the filter effect imposed by the ocean (Paulay 1994, Whittaker and Fernández-Palacios 2007), which results in the absence of large native terrestrial dispersers in many oceanic archipelagos (e.g. Culliney et al. 2012, Heleno et al. 2013). **2**) The introduction of many large terrestrial mammals by early human colonizers has been a very common practice on islands across the globe for thousands of years (Hofman and Rick 2018, Longman et al. 2018, Lugo et al. 2012). **3**) The positive relationship between dispersers' body size and the size of dispersers seeds seems to be a robust generalization that has received sufficient confirmation from multiple studies focusing on different biological and biogeographic realms (e.g. Wheelwright 1985, Moran and Catterall 2010, Donatti et al. 2011, Traveset et al. 2019).

Seed dispersal downsizing and upsizing

The upsizing of the São Tomé seed dispersal network due to biological invasions contrasts with the most commonly documented cases of seed dispersal downsizing resulting from selective defaunation of the larger frugivores (Hansen and Galetti 2009, Galetti et al. 2015). Larger dispersers have been declining and continue to decline due to an increased extinction risk, chiefly associated with over-exploitation and more stringent ecological requirements (Vidal et al. 2014, Galetti et al. 2015, Naniwadekar et al. 2019). Indeed, the absence of large dispersers is a signature of anthropogenic impacts on many ecosystems worldwide (Vidal et al. 2013, Dirzo et al. 2014, Pérez-Méndez et al. 2016, Emer et al. 2018, Heleno et al 2020), linked to the "empty forest syndrome" (Redford 1992, Wilkie et al. 2011). Body-size also positively associated with increased extinction risks of native insular species (Heinen et al. 2018), and in relative terms, the defaunation of the larger dispersers is likely particularly serious on oceanic islands (Hansen and Galetti 2009). However, the widespread anthropogenic introduction of large terrestrial dispersers on oceanic islands, where they are naturally scarce or absent, can invert the general pattern of downsizing to an overall seed dispersal upsizing, as observed in São Tomé.

It has been shown that the truncation on the size of seed dispersers and consequently on the size of dispersed seeds, alters the selective pressures for plant recruitment, eventually leading to rapid evolutionary changes on fruit and seed size (Galetti et al. 2013, Traveset et al. 2019), and eventually to long-term vegetation shifts (Christian 2001, Vidal et al. 2013). Here, we show that the arrival of large bodied introduced species to oceanic islands, will tend to shift the selective pressures on the opposite direction, contributing towards un upsizing of the seed dispersal services (Fig. 3). The relative weight of these two drivers (i.e. the extinction and introduction of large dispersers) seems to vary substantially across islands (e.g. Hansen and Galetti 2009, Heinen et al. 2018, Moser et al. 2018). In some cases, the species introductions (including for conservation purposes; Hansen et al. 2010) might offset the functional loss associated with the extinction of large native dispersers (Hansen and Galetti 2009, Kaiser-Bunbury et al. 2010). The functional consequences of such replacement has been documented in the Balearic islands were the introduction of pine marten *Martes martes* accelerated the local extinction of native lizards, shiftingd the selection regime for the seeds of a native shrub (Traveset et al. 2019). Such changes in the assembly of seed dispersers can directly affect plant community composition by altering the selective pressures acting upon the size of dispersed seeds (Christian 2001). However, the magnitude and direction of these effects will naturally depend on the treatment conferred to the seeds (i.e. the ratio between legitimately dispersed vs destroyed seeds), on the patterns of seed deposition at multiple spatial scales (Celedón-Neghme et al. 2013), and on the identity and origin of the dispersed plants, many of which could not be ascertained in this study (n=33). Given such levels of uncertainly, it is currently difficult to infer about the long-term effects of the incorporation of large-bodied frugivores on the future of São Tomé forests.

Conclusions

Here, we assembled a multi-guild quantitative seed dispersal network for the island of São Tomé and showed that the incorporation of large-gaped introduced terrestrial mammals is favouring the dispersal of large-seeded plant species. We argue that this upsizing of the seed dispersal network might be common on other highly invaded oceanic islands across the globe, where native seed dispersers tend to be relatively small and the introduction of large terrestrial animals is common.

Data availability statement

Species interaction data is available in the Supplementary material Appendix 3, Table A2.

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Conflict of interest

The authors declare no conflict of interest.

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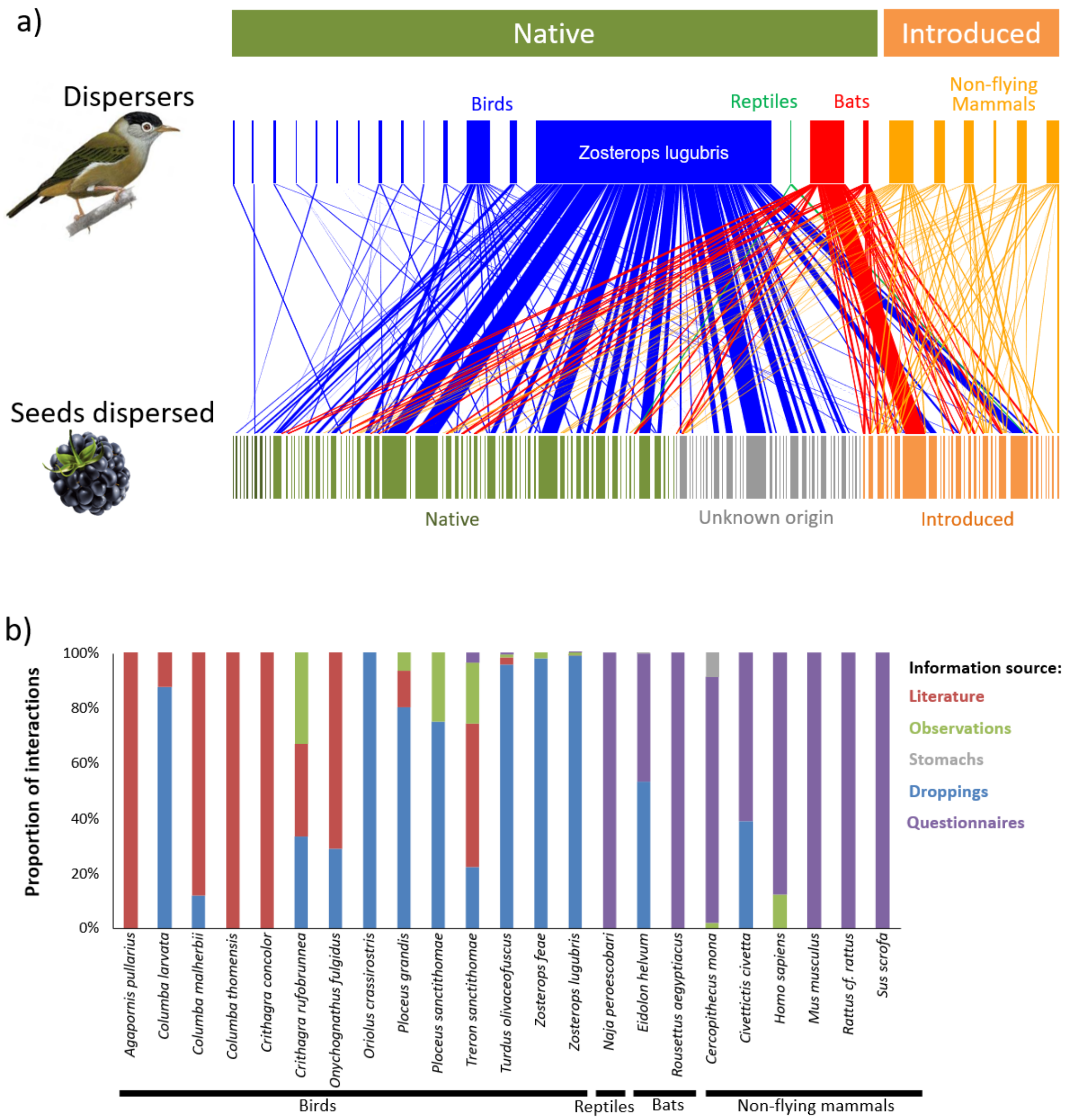

Figure 1. (a) Visualization of the quantitative seed dispersal network of São Tomé Island (see also the qualitative (unweighted) interaction network in Appendix 3, Fig. A2). Higher boxes represent seed dispersers whereas lower boxes represent plant species. The width of each interaction is proportional to its frequency of occurrence; **(b)** Proportion of the interactions of each disperser species that was retrieved from each of the five sampling methods. The full interaction list, including species names, is available in the Supplementary material Appendix 4, Table A4.

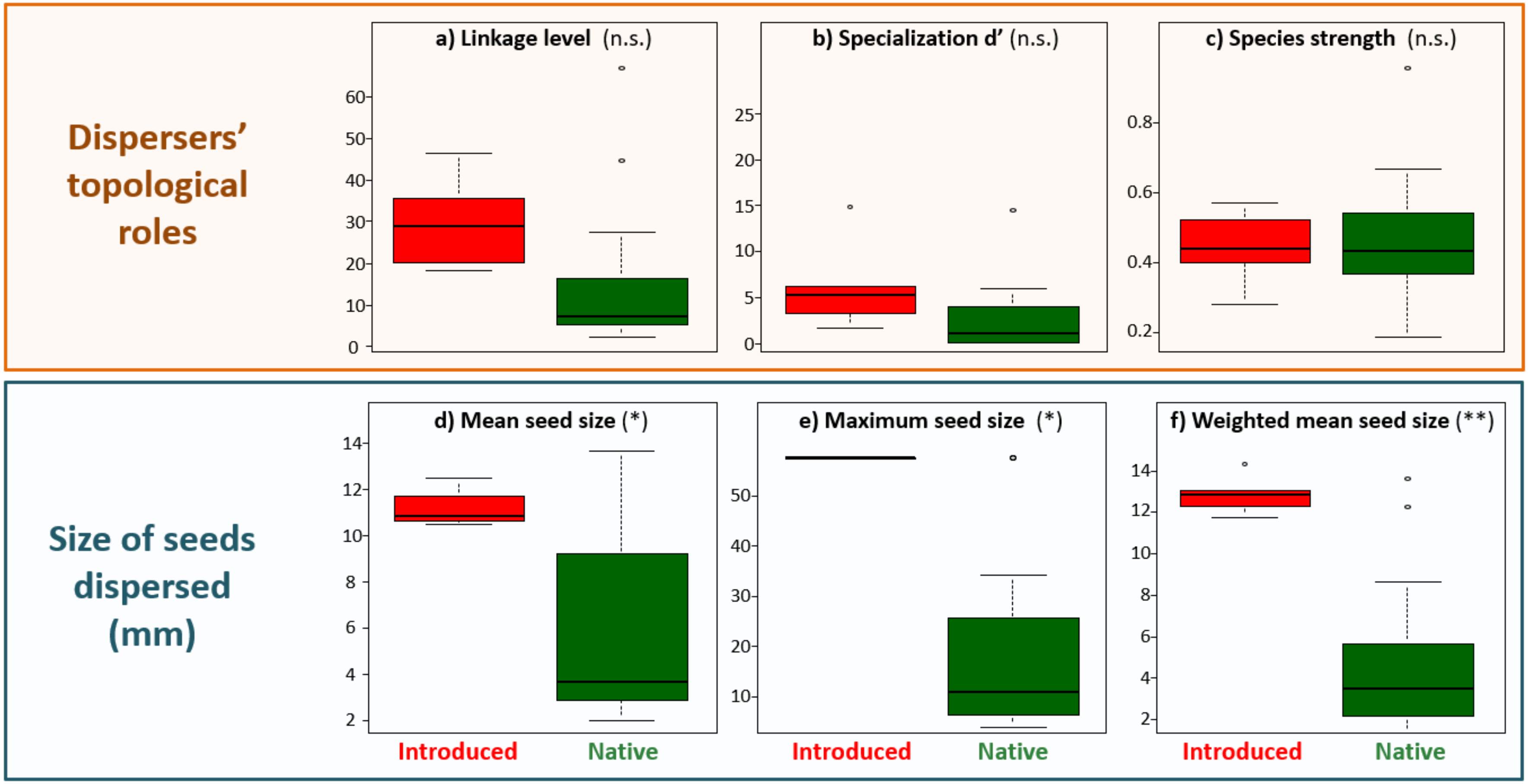

Figure 2. Differences between the roles of native and introduced seed dispersers in the island of São Tomé. The top panels show the lack of statistically significant differences on key topological roles describing different aspects of the interaction patterns established by native and introduced dispersers in the seed dispersal network, namely on a) linkage level, b) specialization, and c) species strength. The bottom panels show differences on the size of the seeds dispersed by introduced and native seed dispersers, namely on the d) mean seed size of the dispersed species, e) seed size of the largest dispersed species, and f) mean seed size of the dispersed seed species weighted by their respective interaction frequency. * $P<0.05$; ** $P<0.01$.

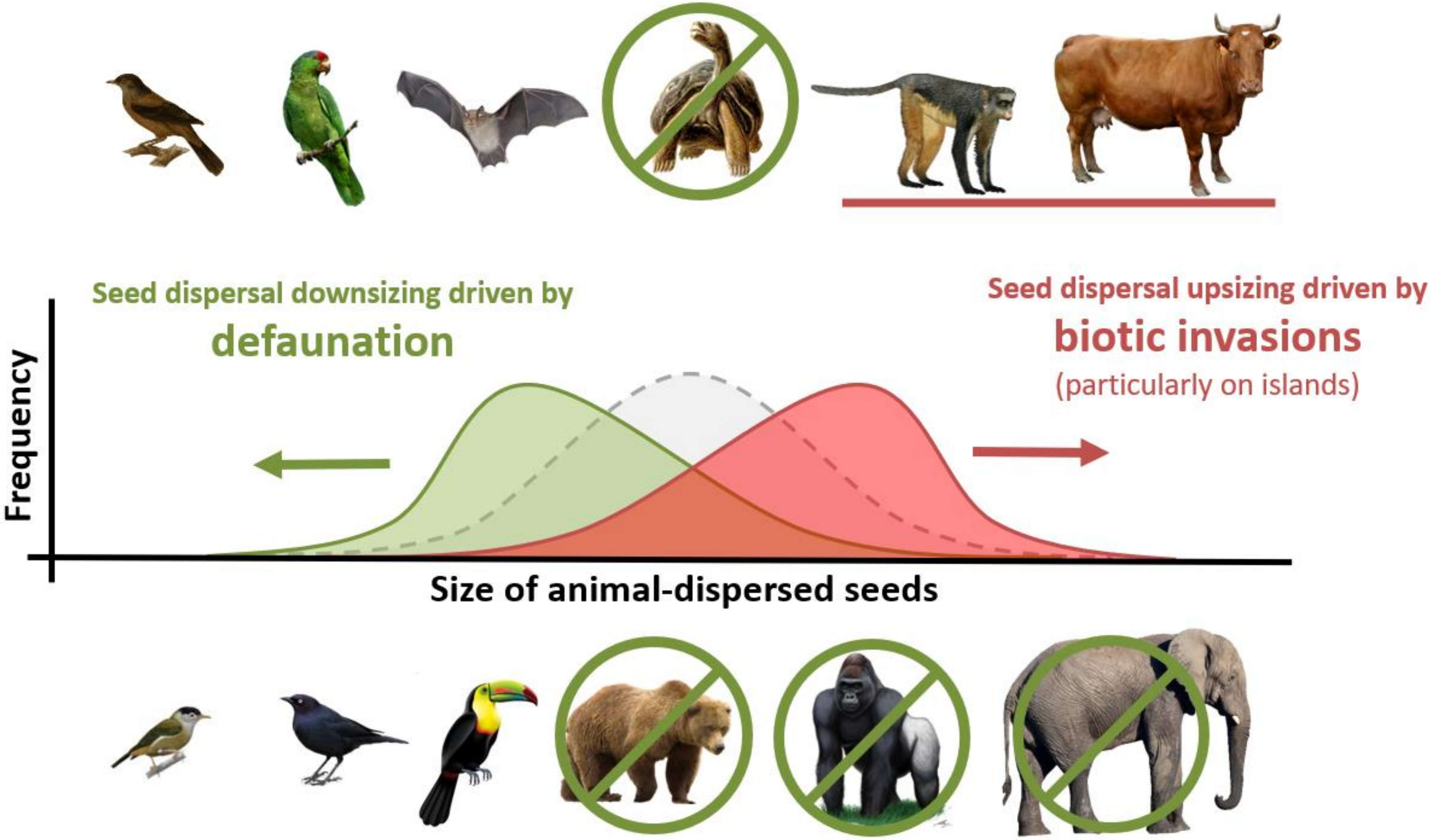

Figure 3. Opposing effects of the selective pressures caused by the selective defaunation of large terrestrial vertebrates (particularly on continents), and the effects of large species introductions (particularly on oceanic islands) on the size of the dispersed seeds.

Table 1.

Characterization of the seed dispersers of São Tomé, their topological roles within the seed dispersal network, and the size of dispersed seeds. CR-Critically Endangered, EN-Endangered, VU-Vulnerable, NT-Near Threatened, LC-Least Concern, DD- Data Deficient.

Disperser species	Origin	IUCN status	Gape width (mm)	Species-level descriptors					Size of dispersed seeds (mm)		
				Linkage level	Species strength		Specialization (d')		Maximum	Mean	Weighted mean
					Quantitative	Qualitative	Quantitative	Qualitative			
Birds											
Agapornis pullarius	Native (non-endemic)	LC	7.05	2	0.094	0.222	0.404	0.100	26.00	13.65	13.65
Columba larvata	Native (endemic spp.)	LC	6.50	7	0.328	2.008	0.306	0.402	5.80	2.86	2.58
Columba malherbii	Native (endemic)	NT	10.15	16	4.141	5.785	0.428	0.415	17.20	3.66	3.59
Columba thomensis	Native (endemic)	EN	13.61	7	1.072	1.936	0.434	0.383	11.10	3.74	5.38
Crithagra concolor	Native (endemic)	CR	12.66	4	3.200	3.200	0.947	0.834	9.37	3.99	4.22
Crithagra rufobrunnea	Native (endemic)	LC	10.26	6	0.125	0.751	0.186	0.093	57.83	11.55	8.73
Onychognathus fulgidus	Native (endemic)	LC	9.44	7	0.158	0.883	0.207	0.093	57.83	12.30	12.30
Oriolus crassirostris	Native (endemic)	VU	11.16	15	5.311	6.883	0.537	0.519	7.50	3.59	2.85
Ploceus grandis	Native (endemic)	NT	10.22	5	0.358	0.962	0.444	0.222	17.00	6.56	5.74
Ploceus sanctithomae	Native (endemic)	LC	10.39	4	0.088	0.754	0.247	0.273	4.26	2.02	2.02
Treron sanctithomae	Native (endemic)	EN	13.30	16	3.361	4.006	0.537	0.246	6.50	2.20	1.59
Turdus olivaceofuscus	Native (endemic)	LC	8.95	44	14.882	19.520	0.364	0.386	23.00	3.09	2.05
Zosterops feae	Native (endemic)	NT	4.04	6	1.008	1.421	0.661	0.341	4.26	2.21	2.42
Zosterops lugubris	Native (endemic)	LC	5.64	66	52.898	38.202	0.663	0.487	11.10	2.42	2.33
Reptiles											
Naja peroescobari	Native (endemic)	DD	20.00	2	0.139	0.291	0.387	0.179	6.10	3.33	1.49
Bats											
Eidolon helvum	Native (non-endemic)	NT	17.11	27	6.043	4.424	0.636	0.074	57.83	9.48	4.65
Rousettus aegyptiacus	Native (non-endemic)	LC	14.09	18	2.367	2.916	0.395	0.108	34.40	9.21	7.65
Non-flying mammals											
Cercopithecus mona	Introduced	LC	33.50	46	15.286	12.737	0.466	0.139	57.83	10.65	12.33
Civettictis civetta	Introduced	LC	50.00	20	3.352	3.365	0.566	0.114	57.83	11.70	12.88
Homo sapiens	Introduced	LC	54.38	18	6.336	6.199	0.517	0.299	57.83	12.45	14.37
Mus musculus	Introduced	LC	11.66	25	1.788	3.868	0.280	0.068	57.83	10.79	13.07
Rattus cf rattus	Introduced	LC	11.83	32	4.507	5.636	0.399	0.082	57.83	10.46	12.89
Sus scrofa	Introduced	LC	82.43	35	6.158	7.029	0.405	0.107	57.83	10.86	11.81