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The impact of introduced animals and plants on São Tomé seed-dispersal network

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The impact of introduced animals and plants on São Tomé seed-dispersal network

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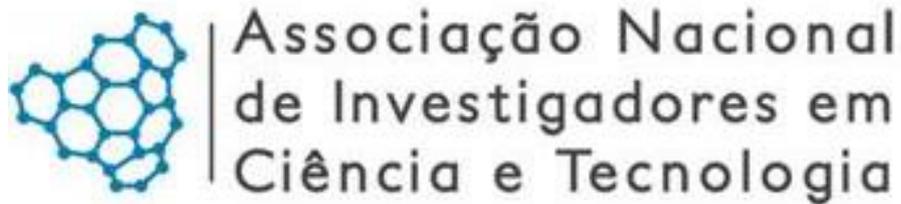
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Resumo

As invasões biológicas constituem uma das principais ameaças à biodiversidade a nível global, e os seus efeitos são especialmente preocupantes em ilhas oceânicas. O mar constitui um importante filtro à colonização, pelo que as comunidades insulares são tipicamente pobres em grandes vertebrados. A introdução destes em ilhas, tem portanto um elevado potencial para alterar a estrutura e funcionamento das comunidades nativas. Uma das funções ecológicas em maior risco de perturbação é a dispersão de sementes por animais, a qual é fundamental para a regeneração das comunidades vegetais.

Neste trabalho, avaliámos o efeito dos dispersores introduzidos na rede de dispersão de sementes da ilha de São Tomé, uma ilha vulcânica no golfo da Guiné com uma das mais altas densidades de espécies endémicas de todo o Mundo. O trabalho tem três objetivos específicos: (i) caracterizar a rede de dispersão de sementes em São Tomé, incluindo todos os principais grupos dispersores; (ii) avaliar as vantagens e desvantagens de combinar vários métodos de amostragem na caracterização de interações biológicas; e (iii) avaliar o papel funcional dos dispersores introduzidos e o seu potencial para perturbar as redes de dispersão de sementes nativas, nomeadamente testando se dispersores nativos e introduzidos diferem consistentemente na sua posição topológica nas redes ou no tamanho das sementes dispersadas.

Durante um ano, compilámos interações entre plantas e os dispersores das suas sementes, através de cinco métodos complementares de amostragem: observações diretas, revisão literária, questionários, análise de excrementos e conteúdos estomacais. Após a reconstrução da rede de dispersão, avaliámos se a origem dos dispersores (nativos vs. introduzidos) ou a largura da sua garganta afeta o seu papel enquanto dispersores de sementes, nomeadamente: número de plantas dispersadas, grau de seletividade (d'), "species strenght" e tamanho das sementes dispersadas.

A rede de São Tomé revelou 419 interações entre 22 espécies de dispersores (12 aves, 2 morcegos, 1 cobra e 7 mamíferos não voadores) e 150 espécies de plantas. Duas das plantas mais frequentemente dispersadas, *Cecropia peltata* e *Rubus rosifolius* são espécies altamente invasoras. Cada método de amostragem revelou-se principalmente útil para um pequeno grupo de dispersores, fornecendo por isso informação altamente complementar. Os questionários provaram ser o método de amostragem que contribuiu com mais interações, seguido da análise de excrementos e de conteúdos estomacais. Os dispersores nativos e introduzidos não diferiram significativamente em nenhum dos três descritores topológicos analisados, no entanto os

dispersores introduzidos tenderam a dispersar espécies com sementes maiores. Esta diferença deve-se especificamente à maior largura da garganta dos dispersores introduzidos.

No seu conjunto, estes resultados apontam para um importante potencial perturbador dos dispersores introduzidos, ao alterarem a pressão seletiva em favor de espécies com sementes grandes. Estas diferenças no tamanho das sementes dispersadas não se refletiu contudo em diferenças na topologia das interações estabelecidas, alertando para a necessidade de considerar simultaneamente características biológicas na interpretação das redes de interações.

Palavras-chave: Descritores topológicos, Dispersão de sementes, Espécies introduzidas, Interações biológicas, Invasões biológicas, Redes ecológicas, Tamanho dos dispersores, Tamanho das sementes.

Abstract

Biological invasions are a major threat to global biodiversity, and their effects are particularly serious on oceanic islands. Due to the barrier posed by the sea to colonization, oceanic islands are typically poor on large vertebrates. Therefore, their introduction on islands, has a high disruptive potential over the structure and function of native communities. One of the ecological functions at greatest risk is that of animal seed dispersal, which is fundamental for the regeneration of plant communities.

In this work, we evaluated the potential effect of introduced dispersers into the seed dispersal network of São Tomé, a volcanic island in the Gulf of Guinea with one of the highest densities of endemic species in the World. There are three specific objectives to this work: (i) characterize the São Tomé seed dispersal network, including all the main dispersal guilds; (ii) evaluate the advantages and disadvantages of combining several sampling methods in the reconstruction of biological interactions; and (iii) assess the functional role of introduced dispersers and their potential to disrupt native seed dispersal networks, namely by testing if native and introduced dispersers consistently differ in their topological position in the networks or in the size of the dispersed seeds.

During one year, we compiled interactions between plants and their seed dispersers through five complementary sampling methods: direct observations, literature review, questionnaires, fecal samples and stomach content analysis. After rebuilding the seed dispersal network, we evaluated if the dispersers origin (natives vs. introduced) or their gape width affects their role as seed dispersers, namely their linkage level, specialization (d'), species strength and size of the dispersed seed.

The São Tomé network revealed 419 interactions between 22 dispersers species (12 birds, 2 bats, 1 snake and 7 non-flying mammals) and 150 plant species. Two of the most frequently dispersed plants, *Cecropia peltata* and *Rubus rosifolius* are highly invasive species. Each sampling method proved to be particularly informative for a small group of dispersers, and therefore their results are largely complementary. The questionnaires proved to be the sampling method that contributed with more interactions, followed by fecal and stomach content analysis. Native and introduced dispersers did not differ significantly in any of the three topological descriptors analyzed, however introduced dispersers tended to disperse species with larger seeds. This difference is largely explained by the larger gape width of the introduced dispersers.

Altogether, these results point to an important disruptive potential of introduced dispersers, by altering the selective pressure in favor of species with larger seeds. However, these differences

in the size of the dispersed seeds were not reflected in differences in the topological patterns of the interactions, highlighting the need to simultaneously consider biological traits while interpreting interactions networks.

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1. Introduction

Over the last decades there has been a growing consensus that biodiversity is crucial for ecosystem functioning and for the resulting ecosystem services that benefit human well-being (Hooper *et al*., 2005; Cardinale *et al*., 2012). However, human activities are causing a major extinction event, with extinctions estimated to be occurring 100-1000 times faster than the natural extinction rate (Pimm *et al*., 1995; Lawton *et al*., 1995). Such accelerating biodiversity loss is driven chiefly by global land use changes associated with agriculture and urban areas, and secondly by biological invasions (Chapin Iii *et al*., 2000). The advent of global commerce led to an increase of many plant and animal species in ecosystems where they did not occur naturally (Blakey, 1989). These anthropogenic introductions are increasing the homogenization of the earth's biota (Lodge, 1993), which reduces spatial diversity, as many restricted species are replaced by a few widespread species (McKinney and Lockwood, 1999).

While no area in the World is safe from biological invasions, islands are known to be particularly vulnerable to the introduction of new species by virtue of their relatively simple biota, evolved in the absence of strong competition from natural enemies (Assessment Millennium Ecosystem, 2005; Whittaker and Fernández-Palacios, 2007; González-Castro *et al*., 2012). This is particularly worryingly, given that islands are critical reservoirs of global biodiversity. Despite forming only 5% of the Worlds surface, they constitute 29% of the world's conservation hotspots (Myers *et al*., 2000) and host more than 600 globally threatened bird species (Ricketts *et al*., 2005). There are two main types of islands, continental islands, which result from the fragmentation and posterior isolation of the continental shelf to which they were once connected; and oceanic islands, which emerged directly from sea floor and were never connected to continental landmasses (Whittaker and Fernández-Palacios, 2007).

The extreme isolation of oceanic islands has particular consequences for the evolution of their biota, since their formation, islands biota is the consequence of biogeographical, ecological and evolutionary processes (Whittaker and Fernández-Palacios, 2007). Due to the differential colonization, islands communities are characterized as disharmonic regarding species composition (Gulick, 1932), supporting low fauna and flora diversity, and high proportion of unique species (Carlquist, 1974). Islands communities have evolved under low selective pressure from large vertebrates, filtered by the oceanic barrier to dispersal (Bowen and Vuren, 1997) (Woolfit and Bromham, 2005) and in addition to their small populations with low genetic diversity (Vitousek *et al*., 2013), often lack some of the main elements of the continent's biota (Vitousek, 1988) and island species have reduced defenses against external threats (Simberloff,

2000). As a result most documented species extinctions have occurred on islands (Manne *et al.*, 1999), including 97 of the 108 bird extinctions documented in the last 400 years (Clark *et al.*, 1998). Given their well-defined borders, the relative simplicity of their biological communities, and their replicated nature, oceanic islands have been often regarded has ideal natural laboratories for ecology and evolution (e.g. Whittaker and Fernández-Palacios, 2007). As such, islands allow us to build model systems to understand, predict and manage the impact of biodiversity losses (Paulay, 1994; Whittaker and Fernández-Palacios, 2007).

The arrival of introduced species affects native species, namely through increased competition, reduced reproductive success and changes in the density and distribution (Traveset and Riera, 2005). These processes may eventually lead to local or global extinctions, which likely to trigger disturbances in ecosystem functions, and potentially causing further extinction cascades (Rumeu *et al.*, 2017). The effects of introduced species might not always be direct (for example when competing for trophic resources and space), but can also be indirect, when introduced species affect the fitness of native counterparts by diverting ecological services and processes provided by indirect species interactions, such as pollination, seed dispersal, root-mycorrhizal associations or top-down control from natural enemies (Traveset and Riera, 2005; Hansen *et al.*, 2002; Meehan *et al.*, 2002). The often diffuse nature of these processes, represent a challenge for ecologists aiming to quantify such impacts at the community level (Christian, 2001; Heleno *et al.*, 2013).

In recent decades, species-interactions networks have emerged has a most valuable tool, allowing scientists to observe how species interact with each other in natural communities, to assess the mechanisms that hold those communities together and therefore prevent future species losses (Heleno *et al.*, 2014). Furthermore, ecological networks are important to evaluate changes in mutualistic-interactions ensuring the introduction of alien plants and animals (Bartomeus *et al.*, 2008; Memmott and Waser, 2002), being highly informative for conservation and ecosystem restoration efforts (Forup *et al.*, 2008).

Plants form the base of most terrestrial ecosystems and in order to overcome their reduced mobility, many plants rely on animal for dispersing their seeds (Howe and Smallwood, 1982). In the tropics, most plant species are dispersed by animals and about 50-75% of the trees produce fleshy fruits adapted for endozoochory (Howe and Smallwood, 1982). Seed dispersal is a critical process on plants life history, that allows them to escape resource competition and high

mortality under the mother plant and to increase their range and colonize new areas (Nathan and Muller-Landau 2000; Traveset, *et al.*, 2014).

Native seed dispersal networks can be disrupted by the introduction of exotic plants and animals (Moragues and Traveset, 2005; Morales and Aizen, 2006), but such impacts rarely have been evaluated, and even less so in the particular context of oceanic islands (Christian, 2001). Furthermore, when they have been studied, most attention has been dedicated to the disruptive effects of introduced plants (Morales and Traveset, 2009). One such study documented the massive integration of alien plants into the dispersal networks of the island of São Miguel-Azores, where they form an astonishing 59% of the seeds dispersed in one of the last remnants of the native laurel forest (Heleno, *et al.*, 2013). Only two studies have shown the disruptive effects of introduced dispersers on the fitness of native plants. One took place in South Africa, where the invasion of the Argentine ant (non-disperser) lead two main disperser ant species to the verge of extinction, strongly conditioning the dispersal and recruitment of large seeded plants (Christian, 2001). The other one was conducted in the Balearic Islands where, the local extinction of a frugivorous lizard after the introduction of carnivorous mammals and snakes, led to a detrimental effect on the reproduction of an endemic shrub of which the lizard was the only disperser (Traveset and Riera, 2005). Nevertheless, both studies still take a species-centered approach and the joint disruptive effects of introduced dispersers on the overall structure of insular seed dispersal networks remains unexplored.

Not all species have the same potential to become invasive, but it has been shown that invasive species tend to have several common attributes, including their tendency to be trophic and habitat generalists (Sakai *et al.*, 2001; Lee, 2002). Therefore, we can expect that the interactions established by introduced dispersers and their impacts will not be random, but synergistic. One trait known to be critical for seed dispersal is body size (Lord, 2004). The body size of a disperser is strongly associated with its gape width and therefore with the size of the fruits and seeds that it can ingest. For example, large animals can disperse both small and large seeds, while small animals can only disperse small seeds (Levey, 1987) (Fenner, 2000). Furthermore, animal size is also related with their spatial mobility, making large animals more likely to disperse seeds over long distances (Fragoso *et al.*, 2003; Holbrook and Loiselle, 2009).

To date, most seed dispersal studies have been based on a single sampling method, usually the identification of intact seeds in the droppings (Heleno *et al.*, 2013), or direct frugivorous observations (Olesen *et al.*, 2010). More recently, a few studies tried to collate information from

more than one sampling strategy, in order to improve the characterization of seed dispersal interactions (Correia, *et al*. 2017; Donatti *et al*., 2011), nevertheless, the consequences of such data aggregation on the interpretation of the results has not been fully evaluated.

Here, we evaluate the potential disruptive effects of introduced dispersers on the dispersal network of São Tomé Island in the Gulf of Guinea. Since its colonization in the 1470s, many alien species have been introduced to these islands either intentionally such as pigs *Sus scrofa* and the black cobra *Naja melanoleuca,* the mona monkey *Cercopitecus mona* (Bocage, 1904a,b; Frade, 1984; Feiler, 1993) african civet *Civettictis civetta*, and weasel *Mustela nivalis* (Bocage, 1904b; Dutton, 1994; Cobert, 1978), or accidently, such as rodents: *Rattus rattus, R. norvegicus,* and *Mus musculus* (Bocage, 1904a,b; Frade, 1984; Feiler, 1993). With the exception of the endemic shrew *Crocidura thomensis*v (De Balsac and Hutterer, 1982), all non-flying mammals on the island were introduced (Lever, 1985; Excell, 1944). Most of these animals have high mobility, large body size, and broad omnivorous diets and therefore, might disperse a considerable array of native and introduced plants, having a potential disruptive effect of the island seed dispersal networks and consequently on plant recruitment patterns.

Here we reconstructed the seed dispersal networks of the island of São Tomé with three specific objectives: 1) Provide a first all-inclusive characterization of seed dispersal in this unique island, including all main disperser guilds; 2) Evaluate the potential advantages and disadvantages of compiling seed-dispersal interactions from different sampling protocols; 3) Evaluate the functional role of introduced dispersers and their potential to disrupt native seed dispersal networks, namely by testing if native and introduced dispersers differ in key functional traits, in their topological position in the networks, or in the size of dispersed seeds.

2. Methods

2.1. Study site

The island of São Tomé is part of the Democratic Republic of São Tomé and Príncipe in the Gulf of Guinea (Figure 2.1). The island was formed approx. 13 million years ago, right at the equator and lies 255km off the west coast of Gabon, having a total area of 857 km^2 (Atkinson *et al.*, 1991).
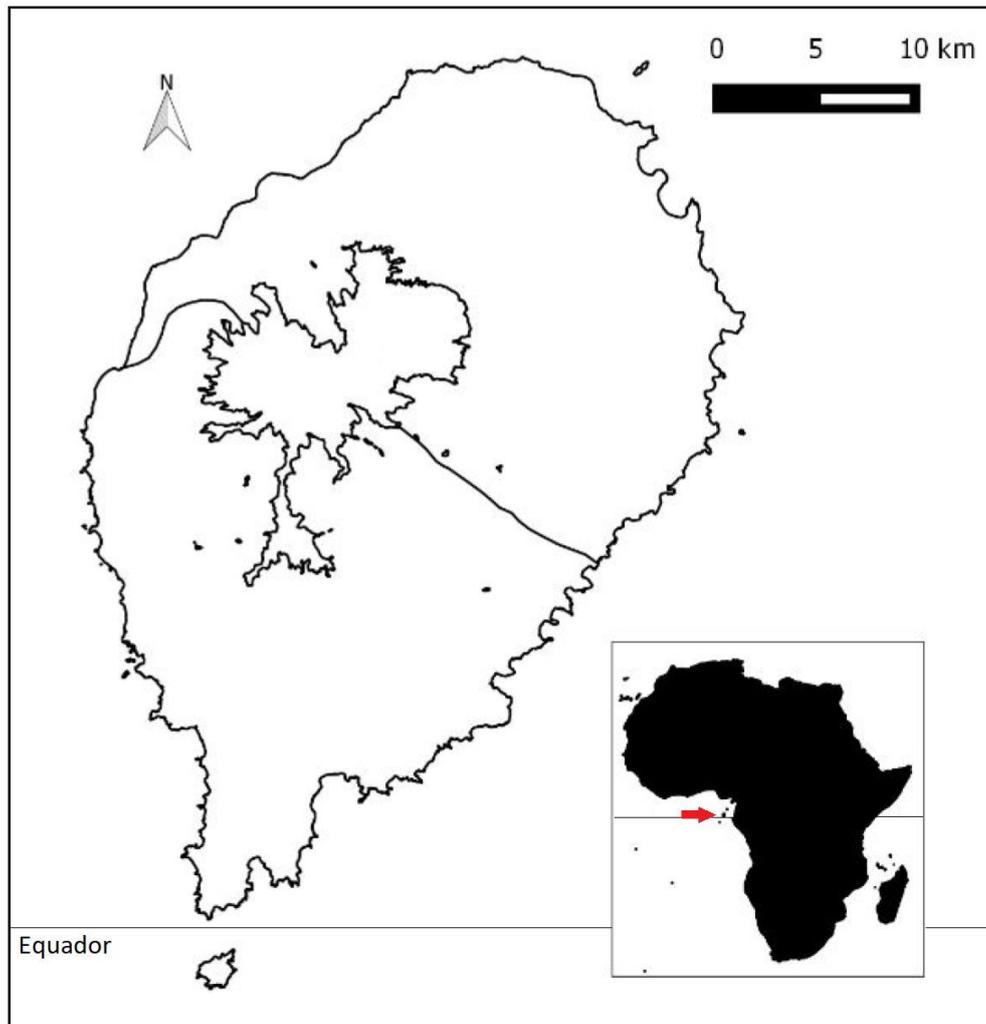

Figure 2.1 – Map of São Tomé and their location in relation to mainland Africa (red arrow; adapted from (de Lima *et al.*, 2013). The contour lines are showing the three main regions: Montane (between 800- and 1400-m a.s.l.), North (up to 800-m a.s.l. and less than 2000 mm of annual rainfall) and South (up to 800-m a.s.l. and more than 3000 mm of annual rainfall).

The São Tomé rainforest consists of three different ecological zones: 1) Lowland rainforest, up to 800m a.s.l., 2) montane forests, from 800m to 1400m a.s.l. and 3) mist forest, from 1400m to the highest peak at 2024m (Holdridge, 1947; Silva, 1958).

There are two main seasons in the island: the rainy season, between September and May, with a small dry season (gravanito) between December and January, and an extended dry season (gravana), between June and August (Melo and Jones, 2008). The island's high relief intercepts the south-west moist wind currents, which causes precipitation in the southwestern regions of over 7000 mm per year (Bredero *et al.*, 1977). In the northeastern part of the island annual rainfall is less than 2000 mm, while at the northern end it can be c. 600 mm. On the other hand, in the south-west and in the high interior areas rainfall is constant throughout the year. At sea level, the average temperature is 22 to 23°C, with the average relative humidity being 80%. At higher altitudes, the maximum temperature is on average 25°C, similar to that of the coast. However, the absolute minimum is much lower, of about 9°C (Burlison and Tye, 1991).

São Tomé is located near the Congo Basin, one of the world's richest centers of biodiversity. It is at the right distance to be colonized by a multitude of different taxa, and far enough to allow them to evolve in isolation, holding an extraordinary array of endemic species (Melo and Jones, 2008). The volcanic origin, rainy climate and high mountains, creates microclimates leading to the adaptation and colonization of different plants and animals (Melo and Ryan, 2012). The island is listed as an endemic bird area (EBA) by Birdlife International (Stattersfield *et al.*, 1998).

Discovered by the Portuguese in the 1470s, São Tomé has a long record of deforestation, habitat modification and biological invasions. The changes made since its human occupancy severely impacted the island's biodiversity (Dutton, 1994). During the 16th century the island was recognized as the world's primary producer of sugarcane. As a result much of the lowland forests were destroyed. In the course of the 17th century, the lowland and montane rainforest (Atkinson *et al.*, 1991) was replaced by coffee and cocoa plantations, and this small island became the largest producer of cocoa in the world (Melo and Ryan, 2012).

For this study, we compiled information from all over the island, focusing on the surroundings of fifteen major localities, namely: Monte Café, Nova Moca, Lagoa Amélia, São Nicolau, Trindade, Cidade - São Tomé, Lembá, Bindá, São Miguel, Rio Quija, Cão Grande, Ribeira Peixe, Santa Jusefina, Cabumbé and Ribeira Afonso (Figure 2.2).
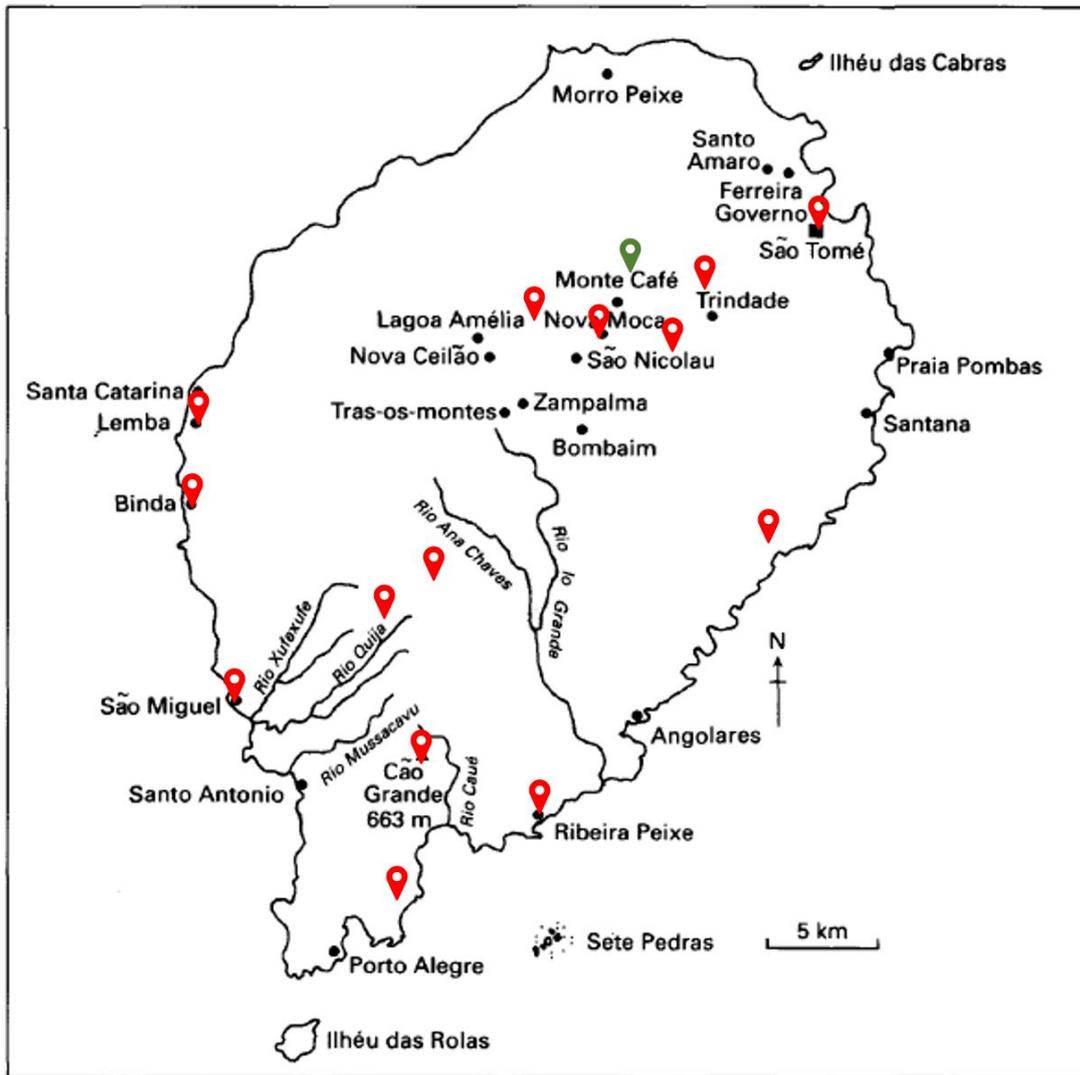
Figure 2.2 – Map of São Tomé Island, adapted from (Atkinson *et al*., 1991). Main sampling sites are shown in red, and the site were most data was collected (Monte Café) is shown in green.

2.2. Data collection

Several animal guilds in São Tomé are known to consume fruits and thus might act as seed dispersers, namely: birds, terrestrial mammals (including humans) bats, and some reptiles. In order to sample such a broad spectrum of interactions we implement five complementary sampling protocols between September 2015 and October 2016.

Fecal analyses – Bird seed dispersal was sampled by identifying undamaged seeds in the droppings of mist-netted birds. Captures occurred in Macambrará and Morro Claudina, near the Botanical Garden (half way between Nova Moca and Lagoa Amélia, see Figure 2.2), in October and November 2015, and in August and September 2016. A total of 24960 hours x meter of mist nets were operated in days of good weather. Birds were placed in paper bags for up to one hour or until they produce a dropping. All droppings were collected, air-dried, and stored. Later, all undamaged seeds were extracted and identified under a magnifying glass by comparison with a reference collection of seeds. Seed dispersal by mammals was sampled by identifying entire seeds on scats found in *Civettictis civetta* latrines, and on the floor of shelters, like caves, tree dwellings and abandoned houses in the case of bats. All feces detected were collected, placed in plastic bags, and the identity of the animal species that produced it was determined with the help of photography's and with the help of naturalist guides and local hunters. All entire seeds were extracted and identified as for the birds.

Stomach analyses – In São Tomé, hunting is an important activity (Carvalho *et al*., 2015). We've have established a large network of hunters in most villages across the island (Figure 2.2), which we used to obtain the stomach contents of their hunted animals. The hunters recorded the species, the site and date of the shooting, and collected stomach contents to plastic bags with alcohol. All seeds were latter extracted and identified, as described above.

Direct observations – Direct observations of frugivorous interactions were recorded along transects and timed frugivory census to target fruiting plants. Each transect consisted of a 500m stretch of forest trails and paths available around Monte Café (Figure 2.2), and crossing a multitude of habitats. Each transect was walked in approximately 1 hour by one observer with binoculars. One random transect was sampled each day, five days per week, between July and October 2016. During the same period, timed observations were performed on focal trees, by recording all frugivores visiting and consuming fruits in selected fruiting tree. Tree species were selected according to plant phenology and at least 3 hours of observations were completed per

fruiting species per month. Trees were observed from the distance (c. 10m) by a hidden observer with binoculars.

Questionnaires – Questionnaires were orally performed to local hunters, nature guides, scientists and farmers, asking to report fruit consumption events that they have observed in the past and in which they could recognize both species involved (i.e. the plant and the animal).

Literature review – An exhaustive literature search was performed to document frugivorous interactions reported on scientific papers, grey literature, unpublished data, and São Tomé natural history books.

Characterization of seed size and dispersers gape width

We characterized the seed size of all plant species present in the reference collection by measuring the length (i.e. longest axis) and width (second longest axis), of at least five seeds have been measures per species, using a magnifying microscope. To characterize the dispersers gape, we measured the gape width of all dispersers with a digital caliper. Birds gape width was mostly measured on live animals during mist netting sessions. Mammals were essentially measures on animals recently killed by the local hunters. These measurements were complemented by measuring specimens from São Tomé, found in the Science Museum of the University of Coimbra and the Lisbon National Museum of Natural History and Science.

2.3. Data analysis

Interaction data was merged into a seed dispersal matrix quantifying all recorded interactions between fruiting plants and their animal dispersers in the island of São Tomé. Interactions frequency was quantified by means of frequency of occurrence of each interaction across all sampling methods using the rule: 1 sample (i.e. fecal sample, stomach sample, observation transect, questionnaire, or source reference) = 1 record. The seed dispersal network was visualized and described using selected species level descriptors calculated with package "bipartite" (Dormann *et al.*, 2008) in the statistical environment R (R Core Team, 2016).

The dispersers role in the network was described by three topological descriptors, namely: linkage level (or degree), specialization (d') and species strength. The species linkage level reflects the number of plant species dispersed by each animal species. Disperser specialization

(d') expresses the animals selectiveness for fruit which is estimated by comparing animals feeding choices with a proxy of resource availability based on plants marginal sums (Blüthgen *et al.*, 2006). Finally, animal species strength reflects their cumulative importance as a disperser for the whole plant community, being based on the sum of all plant dependencies on each animal (Bascompte *et al.*, 2006).

We evaluated if the origin (native or introduced) and the gape width of the dispersers (Predictors) influenced their interaction patterns within the seed dispersal network, namely on linkage level, specialization (d) and species strength (Dependent variables), using General Linear Models (GLM). Then, we evaluated if dispersers origin and gape width had an effect on the size of the dispersed seeds, using three complementary response variables: mean seed size of their dispersed species (i.e. mean size), size of the largest seed species dispersed (i.e. maximum size); and mean size of their dispersed seeds weighted/standardized by the frequency of interaction with each species (i.e. weighted size).

3. Results

The seed dispersal network of São Tomé described 364 unique interactions between 22 disperser species and 150 dispersed plant species (Figure 3.1). The dispersers assemblage is highly diverse and includes 12 bird species, two bats, one snake and seven non-flying mammal species (Table 7.1 – Supplementary information).

Only one third (32%) of the plant species could be classified as native or introduced with certainty, as the majority of the seeds either could not be identified to the species level (44%) or the origin of the species is still not well established in the archipelago (24%). Of the species with known origin, 56% (n=27) were introduced and 44% (n=21) are native to the island. Overall, 9101 seeds were identified, of which 40% were from introduced species, 18% from native plants and 42% of plants with unknown origin. The most frequently dispersed plants are *Cecropia peltata*, *Rubus rosifolius*, *Ficus kamerunensis*, *Harungana madagascariensis* and two unidentified morphotypes "Seed 29" and "Seed 54". Two of these, *Cecropia peltata* and *Rubus rosifolius* are introduced in São Tomé, and considered highly invasive elsewhere (Global Invasive Species Database, 2017). *Cecropia peltata* is dispersed by the Straw-colored fruit bat *Eidolon helvum* (the main disperser) and by several birds (mainly the Green pigeon *(Treron sanctithomae)* and the Bronze-naped pigeon (*Columba malherbii*)). *Rubus rosifolius* was confirmed as being dispersed mostly by the São Tomé Speirops (*Speirops lugubris*).
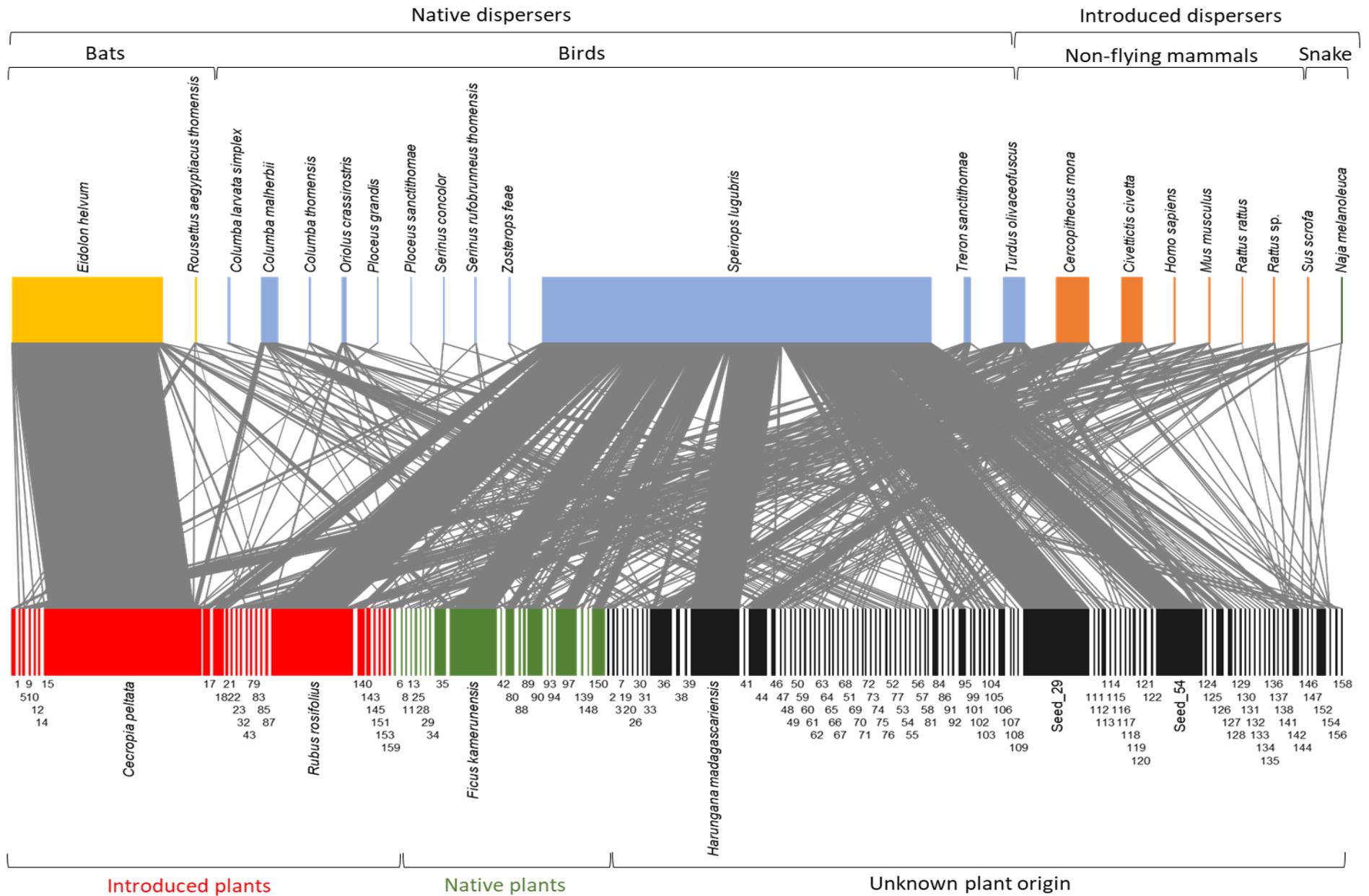
Figure 3.1 – Visualization of the seed dispersal network of the São Tomé Island. Higher boxes represent seed dispersers whereas lower boxes represent plant species. The width of each interactions is proportional to its frequency of occurrence. Plant species are labeled with a numeric code and species identity is available in Table S3.

The questionnaires were the sampling method that contributed with more interactions to the overall network (48% of the total), followed by the analysis of droppings and stomachs (28% and 18%, respectively). The direct frugivory observations and the literature review were not so informative, contributing each with less than 5% of the recorded interactions (Figure 3.2). Surprisingly, most interactions (87%) were detected only by one of the sampling methods, only 11% of the interactions were recorded by two different sampling methods and less than 2 by three sampling methods. The total number of interactions recorded by each sampling method was largely correlated with the number of unique interactions retrieved by that method (i.e. those not detected by any source) identified (rho=0.975; p=0.005; R^2=0.506).
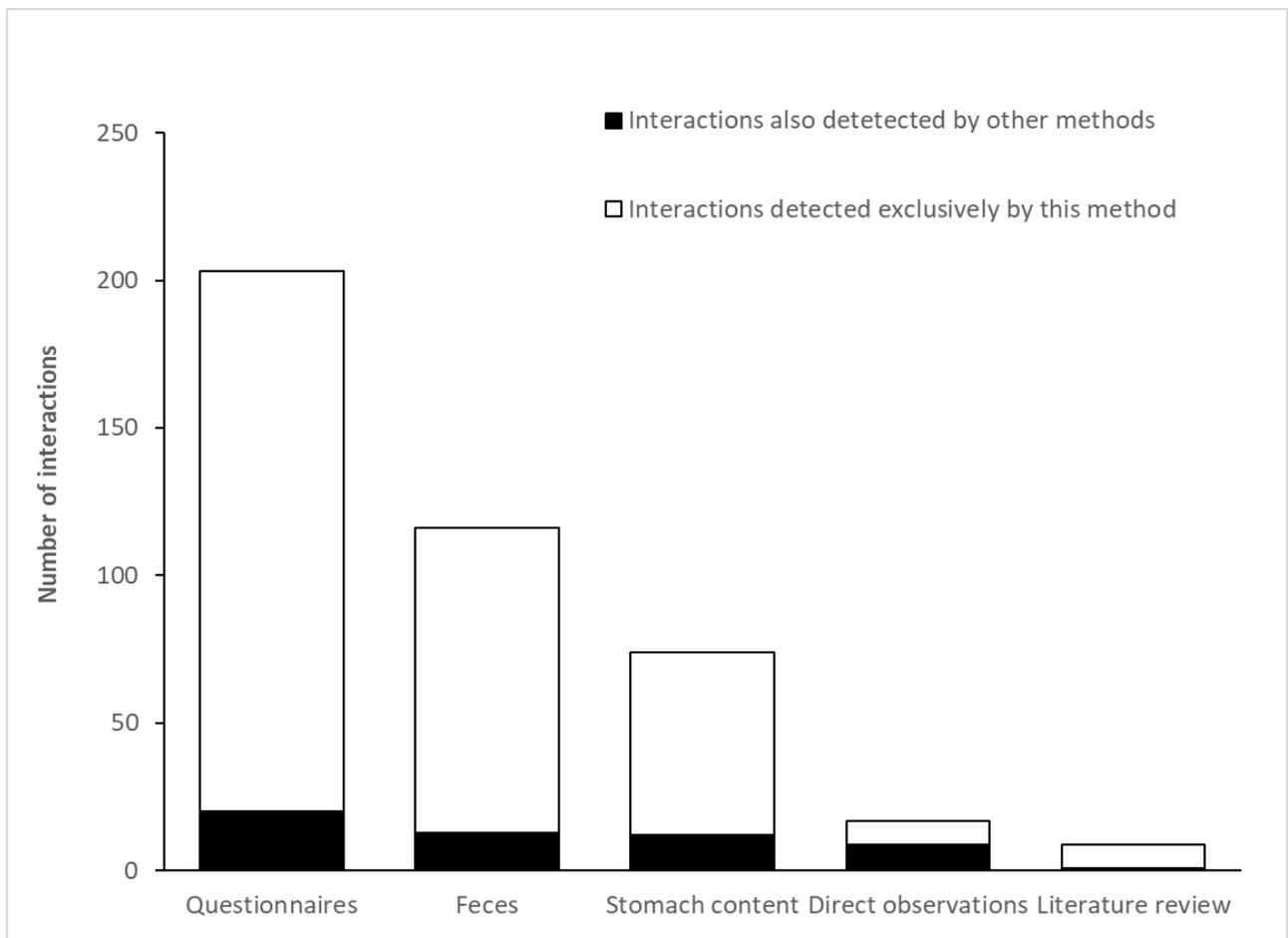
Figure 3.2 – Total and exclusive number of interactions detected by each sampling method.

Similarly, eleven dispersers were recorded only by one sampling method. The questionnaires were the most important sampling method for the seeds dispersed by bats, non-flying mammals, and snake. Seed dispersal by birds was often captured by different sampling methods.
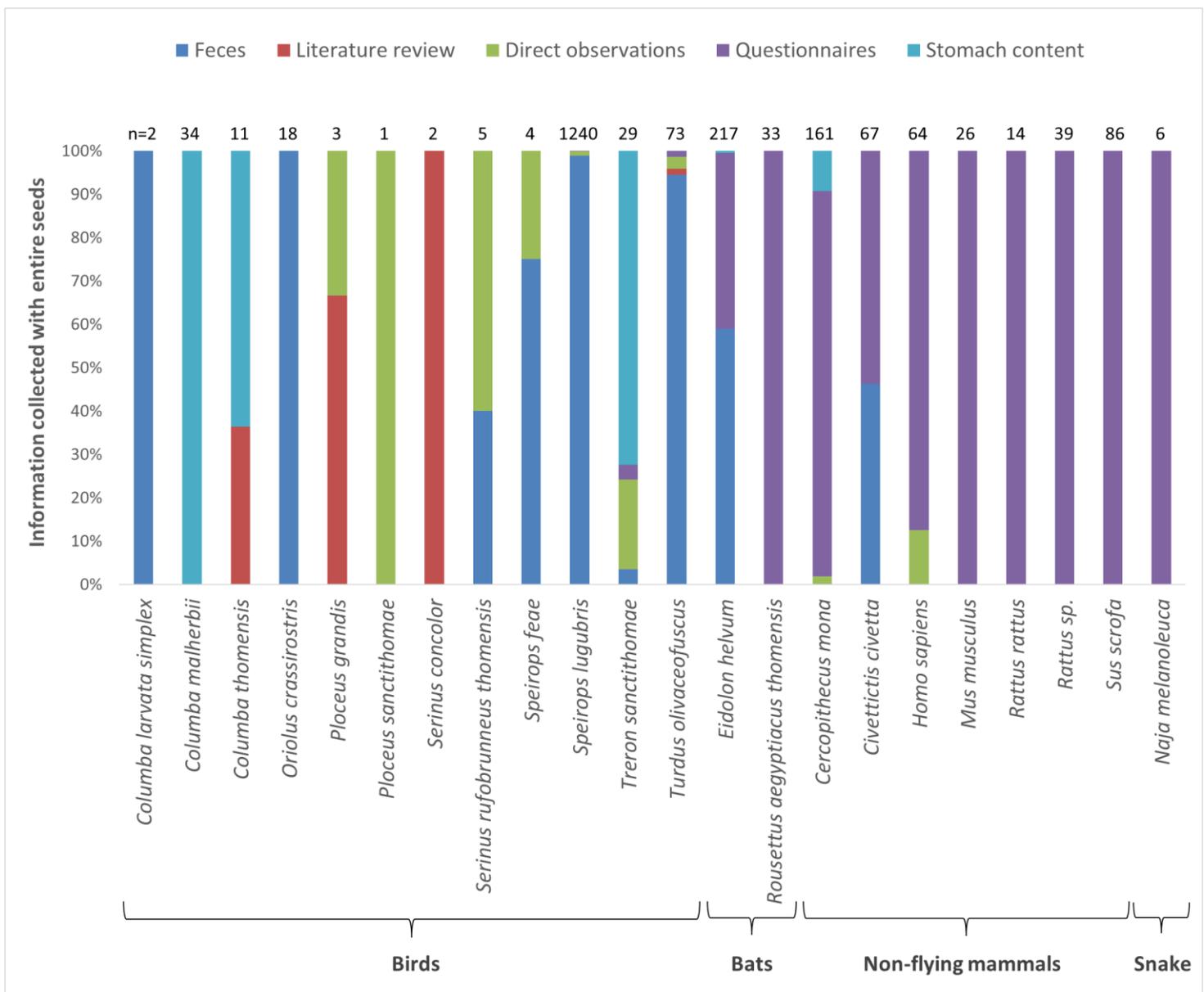
Figure 3.3 – Proportion of the information contributed by each sampling method to reconstruct the seeds dispersed by each disperser. The total number of samples with entire seeds is indicated in the top of each bar.

We found no consistent differences on the topological role of native and introduced dispersers, either in terms of the number of plant species dispersed (degree: $F_{1,20}=1.068$; $p=0.747$), resource selectiveness (selectiveness d': $F_{1,20}=0.031$; $p=0.862$) or overall importance as seed dispersers (species strength: $F_{1,20}=0.581$; $p=0.455$; Figure 3.4).
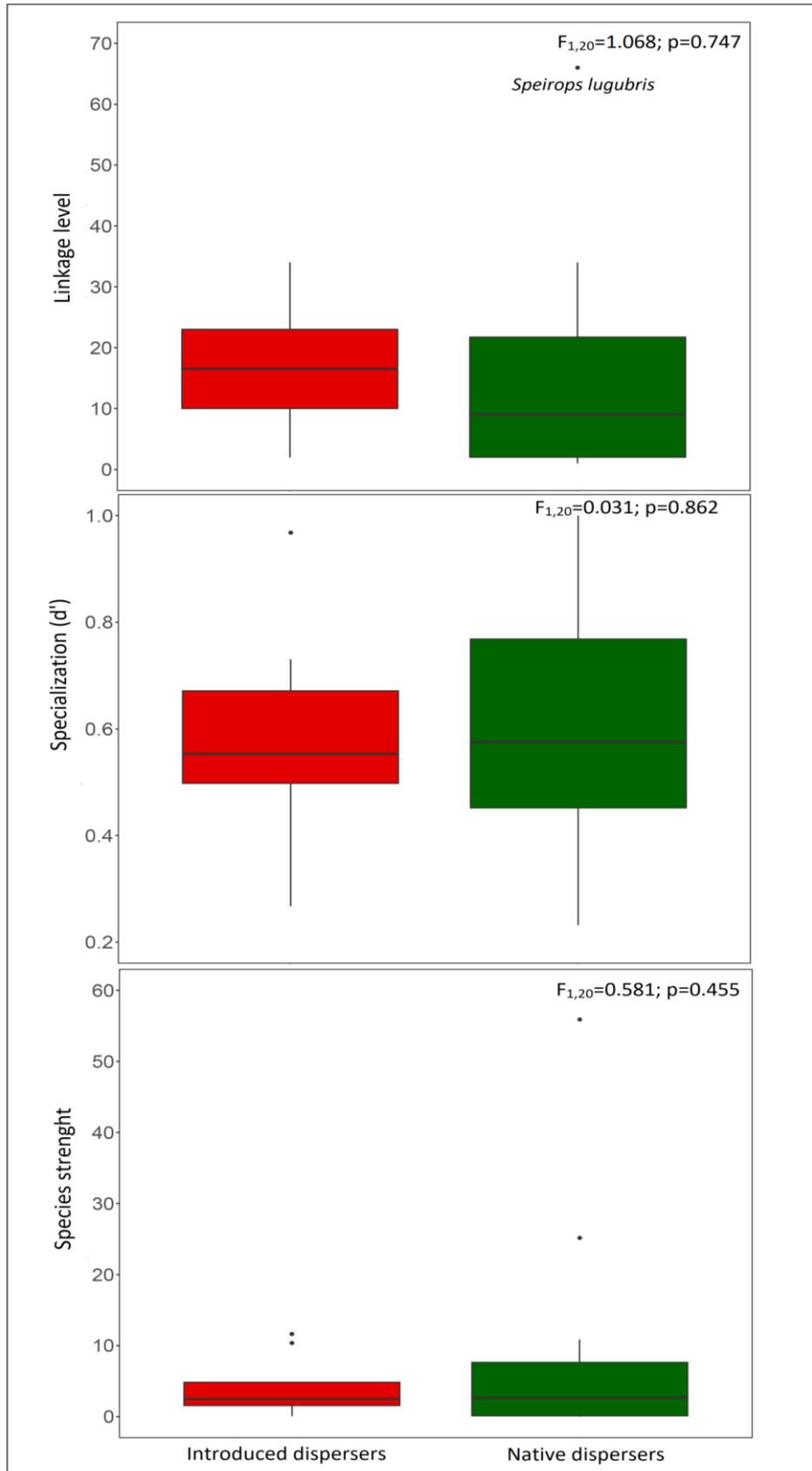
Figure 3.4 – Comparison between three key topological descriptors of species-level interaction patterns between native and introduced dispersers in São Tomé, namely linkage level, specialization (d') and species strength. No significant differences were found for any of the metrics computed.

As expected, the gape width of the introduced dispersers was on average seven times greater than that of the native seed dispersers ($F_{1,793}$= 842.6; p< 0.001).
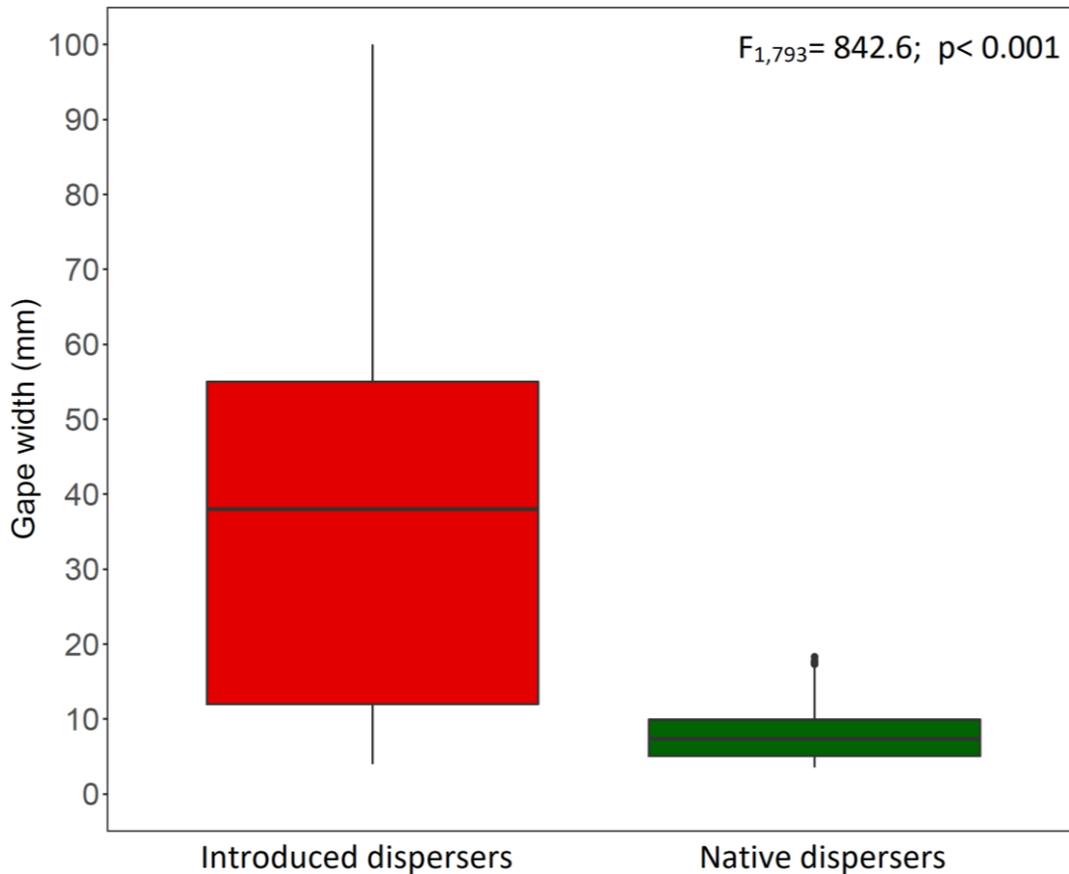
Figure 3.5 – Mean gape width (mm) of native and introduced seed dispersers.

There was a statistically significant positive association between dispersers gape width and the size of the dispersed seeds (Figure 3.6), either when considering mean seed size ($F_{1,17}$=45.28; p<0.001) or maximum seed size ($F_{1,17}$=124.0; p<0.001). When considering weighed mean seed size (mean seed size weighted by the frequency of each dispersed seed species) no significant difference was found ($F_{1,17}$=0.876; p<0.362).

These differences were consistently different between native and introduced dispersers, with the latter dispersing on average larger seeds, both in terms of mean and maximum seed size (mean seed size: $F_{1,17}$=28.83; p<0.001; maximum seed size: $F_{1,17}$=15.92; p<0.001), but not in terms of the weighted mean seed size ($F_{1,17}$=0.425; p=0.523).
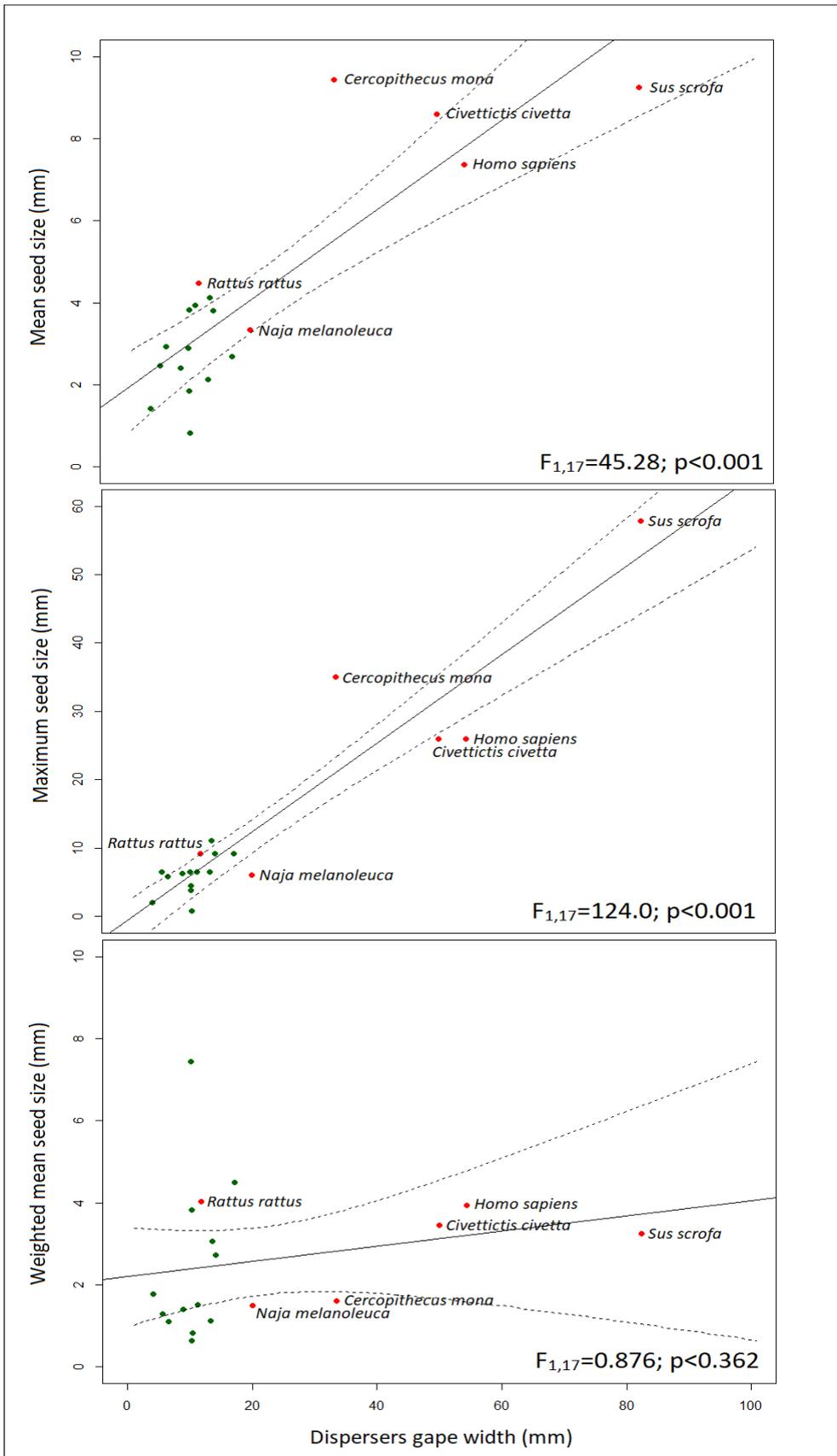
Figure 3.6 - Relationship between dispersers gape width and dispersers origin and the size of their dispersed seeds, namely: mean seed size, maximum seed size and weighted mean seed size (weighted by interaction frequency in all samples). Native dispersers are shown in green and introduced dispersers in red.

4. Discussion

This study contributes with novel information on a very poorly known and vital ecosystem function for the long-term dynamics of São Tomé forests. In addition to the avian seed dispersers, we revealed for the first time, six introduced mammals (*Cercopithecus mona*, *Civettictis civetta*, *Homo sapiens*, *Mus musculus*, *Rattus rattus*, *Sus scrofa*) and one introduced snake (*Naja melanoleuca*) as seed dispersers in São Tomé.

Two of the most commonly dispersed plants, *Cecropia peltata* and *Rubus rosifolius*, are introduced and have at least some invasive potential (Global Invasive Species Database, 2017).

Characterization of the São Tomé seed dispersal

Previous work on seed dispersal in São Tomé forest birds revealed nine avian seed dispersers. All of these were endemic to the Gulf of Guinea islands, and the São Tomé Speirops was the most common disperser (Coelho, 2016).

Due to the typical paucity of land mammals in oceanic islands, birds are often the most relevant dispersers (Traveset *et al.*, 2014). However, bats have also been reported as important dispersers in other islands (McConkey and Drake, 2002). Here we revealed for the first that *Eidolon helvum* can be almost as important for seed dispersal as the São Tomé Speirops, namely by being a key disperser of the introduced *Cecropia peltata*.

Unfortunately, the large proportion of species of unknown origin reflects, on one hand the difficulty in assembling the great plant diversity of the island in comprehensive reference collections, and, on the other hand, the still very incipient knowledge about the São Tomé flora. This knowledge gap is reflected in the large number of plant species (24%) that could be identified to the species level, but that could not be confidently determined as native or introduced in the island. This high proportion of plants with unknown origin hinders our capacity to assess the real impact of alien plants and mammals as disruptors of native seed dispersal networks.

On the effects of compiling dispersal interactions from multiple sampling methods

Community-level studies are intrinsically challenging due to the sampling effort needed to fully capture the community structure (Costa *et al.*, 2016). Seed dispersal in São Tomé is particularly difficult to study due to the steep terrain with very limited access, the high canopy of most

forests, the diversity of animal guilds involved in seed dispersal and the lack of adequate baseline information about the islands flora. To minimize these problems and try to assemble an overall seed dispersal network as comprehensive as possible, we decided to collate evidence of seed dispersal interactions collected from five complementary sampling methods. Overall, very few interactions have been recorded by two or more sampling methods. Normally, studies about seed dispersal interactions collect data using a single sampling protocol, usually by observing fruit consumption on focal plants (Debussche and Isenmann, 1989) (Olesen *et al*., 2010) (Schleuning *et al*., 2014), or by identifying undamaged seeds in animal droppings (Costa *et al*., 2014) (Heleno *et al*., 2013). Here we implemented five sampling methods which revealed very different sets of dispersers and dispersed plants. This has two very important implications. The first is that combining information from multiple sources might be very important to detect most interactions, as these sources are largely complementary. The second is that not all sources have the same degree of accuracy or are subject to the same biases. For example, dropping and stomach analyses are subject to biases related to the capture frequency of different species (e.g. high canopy bird species might be underrepresented in mist netting captures). On the other hand, results from questionnaires are mostly directed for conspicuous animals, chiefly those that are targeted by hunters, and also by large-fruited and abundant plant species. Finally, it is very important to keep in mind that the intrinsic quality of the information provided by each method is not the same. Questionnaires are vulnerable to taxonomic errors (for example in São Tomé it is very common to have several plants with a single or having the same common name), and to the lack of rigor in describing observed interactions, likely motivated by the desire of hunters to contribute to the study or by the difficulty in distinguishing between frugivory and seed dispersal. In the case of stomach contents, there will be cases where seeds found in the stomach will not remain viable until being naturally dispersed due to the continuation of the digestive process (Traveset, 1998).

The best way to assume that an animal is dispersing a certain seed is to obtain seeds retrieved from droppings and confirming its viability and recruitment probability in the field, although such as rarely been attempted (Carlo and Yang, 2011). Therefore, our results suggest that a combination of methods is desirable, particularly when there are several animal guilds involved in seed dispersal, but also that a rigorous "quality check" of the retrieved data, based on a deep knowledge of both animals and plants is paramount to minimize biases and safeguard data quality.

Disruptive potential of introduced dispersers

Large terrestrial dispersers are less likely to overcome the dispersal barrier posed by the ocean and naturally colonize oceanic islands (Paulay, 1994). Therefore, these are usually absent from such islands were the typical native dispersers are birds and reptiles (Whittaker and Fernández-Palacios, 2007). Such consistent bias on the dispersal ability of species is responsible for the typical disharmony of oceanic islands biota and it might lead to different functional traits in native and introduced species. Here we calculated three key species-level descriptors to look for consistent patterns in the interactions established by native and introduced dispersers and we did not find any consistent differences in any of the metrics considered (linkage level, specialization and species strength). This means that "topologically", i.e. considering the position of nodes and vertices in the networks, regardless of their biological identity, both groups of dispersers tend to interact equally within the dispersed plants. However, as expected, native and introduced dispersers consistently differ in that the latter tend to have consistently larger gape widths than native dispersers. Moreover, we found that introduced dispersers disperse on average species with larger seeds, and also that they disperse species with a greater maximum seed size. Both differences were actually driven by differential gape width of native and introduced dispersers. Interestingly, when evaluating differences on the weighted size of dispersed seeds, i.e. by the frequency of interaction of each dispersed seed species, there were no significant differences either associated with the dispersers gape width or origin.

Taken altogether, these results show that both native and introduced animals tend to disperse many small seeds and only a few large seeds, and therefore they do not differ neither on the overall (i.e. weighted) size of the dispersed seeds, or on their topological role within their communities. Nevertheless, when considering only the dispersed species, regardless of their frequency, introduced dispersers show to disperse on average species with larger seeds, and to more frequently disperse very large seeds (maximum seed size). We argue that such dispersal events, even if infrequent, might be disproportional important if they confer an advantage for large-seeded plant species to recruit further away from the parent plant (Howe, 1989; Nathan and Muller-Landau, 2000; Peres and Van Roosmalen, 2002). If larger introduced animals have a greater gape width and disperse larger seeds than their native counterparts, such biological invasions are likely to favor the recruitment of large seeded plants, likely affecting the stability of the seed dispersal network and plant recruitment patterns. In the long term, this is likely to result on a competitive advantage of large seeded plants which might result in changes on São Tomé plant regeneration patterns and potentially affect forest composition. Other studies have also reported an association between gape width and body size (Levey, 1987), and therefore we believe that the tendency for introduced dispersers dispersing larger seeds, might not be specific

to São Tomé, but likely a common pattern of islands across the World. An example of this shift in the composition of the plant communities is the introduction of the invasive Argentine ant in South Africa: this species outcompeted two native ant species that were the key dispersers of large-seeded plants, negatively affecting their regeneration (Christian, 2001).

The main species level descriptors failed to reveal any difference on the interaction patterns established by native and introduced dispersers. Large frugivores might consume a wider range of foods items, including small and large seeded fruits (Kitamura *et al*., 2002; Wheelwright, 1985), however our analyses did not reveal any difference on the number of plants dispersed, on their selectiveness for resources or on importance for the plant community. This lack of differences is most likely a consequence of the high variability in the feeding behavior across the different species, as illustrated by the high contribution of the native São Tomé Speirops for seed dispersal (dispersing at least 66 plant species). A further factor likely hindering the detection of significant differences between the role of native and introduced dispersers on islands in the interaction release observed on islands that's promotes the widening of the niche breaths (Traveset *et al*., 2015) and the emergence of island super-generalists on islands (Olesen *et al*., 2002).

Interestingly, species descriptors exclusively based on the topological description of interactions patterns (of nodes and links), failed to detect differences on the functional roles of native and introduced dispersers. However a biological analyses of the "types of nodes" being dispersed by both groups (in this case seed size), revealed that their role was different. Taken together, these results highlight the limitations of exclusive network analyses and call for the combination of topological and biological assessments of species roles in their communities.

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6. Supplementary information

TABLE S1 – Taxonomic characterization of the seed dispersers species included in this study, including their origin in the archipelago and their conservation status IUCN Red List (IUCN, 2017). Not Evaluated (NE), Least Concern (LC), Nearly Threatened (NT) and Vulnerable (VU). *Species described by (Leventis and Neves, 2009; Rainho *et al.*, 2010).

Species	Common name	Family	Distribution in São Tomé	Conservation status
Columba larvata simplex (Temminck, 1809)	Lemon dove (Mucanha)	Columbidae	Endemic subspecies	LC
Columba malherbii (Verreaux and Verreaux, 1851)	Bronze-naped pigeon (Rola)	Columbidae	Endemic	NT
Columa thomensis (Bocage, 1888)	Marron pigeon (Pombo-do-mato)	Columbidae	Endemic	EN
Oriolus crassirostris (Hartlaub, 1857)	São Tomé oriole (Papa-figos)	Oriolidae	Endemic	VU
Ploceus grandis (Gray, 1849)	Giant weaver (Camussela)	Ploceidae	Endemic subspecies	LC
Ploceus sanctithomae (Hartlaub, 1848)	São Tomé weaver (Tchin-tchintxoló)	Ploceidae	Endemic	LC
Serinus concolor* (Bocage, 1888)	São Tomé grosbeak (Anjolô)	Fringillidae	Endemic	CR
Serinus rufobrunneus thomensis (Gray GR, 1862)	São Tomé/Príncipe seed-eater (Pardal)	Fringillidae	Endemic subspecies	LC
Zosterops feae (Hartlaub, 1866)	São Tomé white-eye (Neto-do-olho-grosso)	Zosteropidae	Endemic	NE
Speirops lugubris (Hartlaub, 1848)	São Tomé speirops (Olho-grosso)	Zosteropidae	Endemic	LC
Treron sanctithomae (Gmelin, 1789)	Green pigeon (Cécia)	Columbidae	Endemic	VU

Turdus olivaceofuscus (Hartlaub, 1852)	São Tomé thrush (Tordo)	Turdidae	Endemic	NT
Eidolon helvum* (Kerr, 1792)	Straw-coloured fruit bat (Morcego-grande-da fruta)	Pteropodidae	Native	VU
Rousettus aegyptiacus thomensis* (E. Geoffroy, 1810)	Egyptian fruit bat (Morcego-pequeno-da-fruta)	Pteropodidae	Endemic subspecies	VU
Cercopitecus mona (Schreber, 1774)	Mona monkey (Macaco mona)	Cercopithecidae	Introduced	LC
Civettictis civetta (Schreber, 1776)	African civet (Lagaia)	Viverridae	Introduced	LC
Homo sapiens (Linnaeus, 1758)	Man (Homem)	Hominidae	Introduced (colonist)	LC
Mus musculus (Linnaeus, 1758)	House mouse (Rato)	Muridae	Introduced	LC
Rattus rattus (Linnaeus, 1758)	Ship rat (Rato)	Muridae	Introduced	LC
Sus scrofa (Linnaeus, 1758)	Wild boar (Porco selvagem)	Suidae	Introduced	LC
Naja melanoleuca (Hallowell, 1857)	Black cobra (Cobra-preta)	Elapidae	Introduced	LC

TABLE S2 – Characterization of the topological role of dispersers within the seed dispersal network using three key species-level descriptors, Linkage level, Specialization (d'), and Species strength.

	Disperser species	Linkage level	Specialization (d')	Species strength
Introduced	*Cercopithecus mona*	34	0.7301697	11.625148842
	Civettictis civetta	14	0.9681243	2.993214497
	Homo sapiens	10	0.5016218	2.496818886
	Mus musculus	19	0.4869766	1.654776412
	Rattus rattus	10	0.6513605	1.168022329
	Rattus sp.	20	0.5456312	2.518769028
	Sus scrofa	32	0.5616723	10.352522579
	Naja melanoleuca	2	0.2675334	0.101781261
Native	*Columba larvata simplex*	2	0.6614574	0.141299825
	Columba malherbii	34	0.7812003	25.161403366
	Columba thomensis	8	0.7304429	3.536782959
	Oriolus crassirostris	10	0.4180521	3.046794682
	Ploceus grandis	1	0.5689239	0.025000000
	Ploceus sanctithomae	1	0.2323018	0.001402525
	Serinus concolor	2	1.0000000	2.000000000
	Serinus rufobrunneus thomensis	3	0.5821754	0.116461326
	Speirops feae	2	0.4320530	0.021707093
	Speirops lugubris	66	0.7844213	55.915717356
	Treton sanctithomae	22	0.5119829	10.837467581
	Turdus olivaceofuscus	29	0.3253546	8.259067129
	Eidolon helvum	21	0.9090272	5.770733989
	Rousettus aegyptiacus thomensis	13	0.5448592	2.255108336

TABLE S3 – Identity of the plant species and morphotypes dispersed in São Tomé and represented in Figure 3.1. Species origin follows (Figueiredo *et al.*, 2011).

Plant species	Origin in São Tomé	Species code in the Network
Achyranthes aspera	Introduced	1
Aframomum daniellii	Unknown	2
Alchornea cordifolia	Unknown	3
Alchornea sp.	Unknown	4
Annona muricata	Introduced	5
Anthocleista scadens	Native	6
Anthocleista sp.	Unknown	7
Antidesma vogelianum	Native	8
Artocarpus altilis	Introduced	9
Artocarpus heterophylla	Introduced	10
Aulacocalyx pallens	Native	11
Averrhoa carambola	Introduced	12
Bridelia micrantha	Native	13
Browallia americana	Introduced	14
Carica papaya	Introduced	15
Cecropia peltata	Introduced	*Cecropia peltata*
Cestrum laevigatum	Introduced	17
Chenopodium sp.	Introduced	18
Chrysophyllum albidum	Unknown	19
Chrysophyllum sp.	Unknown	20
Cinnamomum burmanni	Introduced	21
Citrus sp.	Introduced	22
Coffea arabica	Introduced	23
Cola acuminata	Unknown	24
Croton stellulifer	Native	25
Dacryodes edulis	Unknown	26
Desmodium adscendens	Unknown	27
Dicranolepis thomensis	Native	28
Discoclaoxylon occidentale	Native	29
Discoglypremna caloneura	Unknown	30
Elaeis guineensis	Unknown	31
Eriobotrya japonica	Introduced	32
Erythrina sp.	Unknown	33
Erythrococca molleri	Native	34
Ficus chlamydocarpa	Native	35
Ficus exasperata	Unknown	36
Ficus kamerunensis	Native	*Ficus kamerunensis*
Ficus mucuso	Unknown	38
Ficus sp.	Unknown	39
Harungana madagascariensis	Unknown	*Harungana madagascariensis*
Landolphia landolphioides	Unknown	41
Leea tinctoria	Native	42
Lycopersicon esculentum	Introduced	43
Maesopsis eminii	Unknown	44
Mangifera indica	Introduced	45
Margaritaria discoidea	Unknown	46

Milicia excelsa	Unknown	47
Morinda lucida	Unknown	48
Musanga cecropioides	Unknown	49
N1	Unknown	50
N2	Unknown	51
N3	Unknown	52
N4	Unknown	53
N5	Unknown	54
N6	Unknown	55
N7	Unknown	56
N8	Unknown	57
N9	Unknown	58
N10	Unknown	59
N11	Unknown	60
N12	Unknown	61
N13	Unknown	62
N14	Unknown	63
N15	Unknown	64
N16	Unknown	65
N17	Unknown	66
N18	Unknown	67
N19	Unknown	68
N20	Unknown	69
N21	Unknown	70
N22	Unknown	71
N24	Unknown	72
N25	Unknown	73
N27	Unknown	74
N28	Unknown	75
N29	Unknown	76
N30	Unknown	77
Oxyanthus speciosus	Unknown	78
Passiflora quadrangularis	Introduced	79
Pauridiantha floribunda	Native	80
Pavetta monticola	Unknown	81
Pentaclethra macrophylla	Unknown	82
Persea americana	Introduced	83
Phyllanthus sp.	Unknown	84
Physalis peruviana	Introduced	85
Pseudagrostistachys africana	Unknown	86
Psidium guajava	Introduced	87
Psychotria subobliqua	Native	88
Psydrax acutiflora	Native	89
Psydrax subcordata	Native	90
Pupalia lappacea	Unknown	91
Pycnanthus angolensis	Unknown	92
Rauvolfia caffra	Native	93
Rauvolfia vomitoria	Native	94
Rubus pinnatus	Unknown	95
Rubus rosifolius	Introduced	*Rubus rosifolius*
Sabicea ingrata ingrata	Native	97
Santiria trimera	Unknown	98

Schefflera mannii	Unknown	99
Scytopetalum klaineanum	Unknown	100
Seed_08	Unknown	101
Seed_09	Unknown	102
Seed_14	Unknown	103
Seed_18	Unknown	104
Seed_20	Unknown	105
Seed_23	Unknown	106
Seed_24	Unknown	107
Seed_25	Unknown	108
Seed_27	Unknown	109
Seed_29	Unknown	Seed_29
Seed_30	Unknown	111
Seed_33	Unknown	112
Seed_34	Unknown	113
Seed_36	Unknown	114
Seed_39	Unknown	115
Seed_40	Unknown	116
Seed_41	Unknown	117
Seed_45	Unknown	118
Seed_46	Unknown	119
Seed_48	Unknown	120
Seed_50	Unknown	121
Seed_53	Unknown	122
Seed_54	Unknown	Seed_54
Seed_55	Unknown	124
Seed_57	Unknown	125
Seed_58	Unknown	126
Seed_61	Unknown	127
Seed_62	Unknown	128
Seed_63	Unknown	129
Seed_65	Unknown	130
Seed_66	Unknown	131
Seed_67	Unknown	132
Seed_68	Unknown	133
Seed_72	Unknown	134
Sem_03	Unknown	135
Sem_05	Unknown	136
Sem_06	Unknown	137
Sem_11	Unknown	138
Shirakiopsis elliptica	Native	139
Solanum americanum	Introduced	140
Solanum macrocarpon	Unknown	141
Solanum terminalle	Unknown	142
Solanum wrightii	Introduced	143
Sorindeia grandifolia	Unknown	144
Spondias cytherea	Introduced	145
Spondias mombin	Unknown	146
Sterculia tragacantha	Unknown	147
Tabernaemontana stenosiphon	Native	148
Tamarindus indica	Introduced	149
Tarenna eketensis	Native	150

Terminalia catappa	Introduced	151
Tetrorchidium didymostemon	Unknown	152
Theobroma cacao	Introduced	153
Treculia africana	Unknown	154
Trema guineense	Unknown	155
Trema orientalis	Unknown	156
Trichilia grandifolia	Native	157
Uapaca guineensis	Unknown	158
Zea mays	Introduced	159