

# Chapter 7

## Species Ecology in the Gulf of Guinea Oceanic Islands: Distribution, Habitat Preferences, Assemblages, and Interactions



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**Abstract** The oceanic islands of the Gulf of Guinea (Príncipe, São Tomé, and Annobón) are an exceptional centre of endemism for flora and fauna. Remarkable progress has been made in biological research during the last few decades: from species being described and reported for the first time, to general patterns of species-habitat associations found across terrestrial, coastal, and marine taxa. Despite this increase in knowledge, key aspects of Gulf of Guinea species ecology remain poorly

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understood. This chapter reviews existing knowledge on the biodiversity of the islands, focusing on species distributions, population abundance estimates, traits, habitat associations and interactions. To promote these islands as ecological models, and to ensure the future of their endemic-rich biodiversity, it is essential to overcome current knowledge gaps and reduce existing taxonomic, spatial, and temporal biases in the information available. Therefore, future studies should favour systematic island-wide surveys and prioritize understudied areas and taxonomic groups. Moreover, long-term monitoring studies are urgently needed to assess biodiversity trends and to advise conservation actions. The future of ecological research and conservation of the unique biodiversity of these islands must increasingly rely on the development of local biodiversity-focused scientific expertise, through outreach, capacity building, and advanced training, paired with international collaborations and the development of local organizations.

**Keywords** Annobón · Conservation · Exotic species · Príncipe · São Tomé · Seasonality

## Introduction

The oceanic islands of the Gulf of Guinea (Príncipe, São Tomé, and Annobón) have long been recognized for the high levels of endemism of their flora and fauna (Jones 1994). This in itself makes them an important model of ecological research, but studying ecology in these unique islands may also provide invaluable insights into evolutionary and ecological processes, since islands can be used as natural experiments to extrapolate to wider scales (Whittaker et al. 2017).

The description of the biodiversity in the archipelago began in the late eighteenth century and was intensified during the late nineteenth and twentieth centuries (Cerfaco et al. 2022b). Since then, the islands have captured the imagination and efforts of biologists, prompting scientific studies across multiple disciplines, many of which aim to clarify different aspects of ecology (e.g., Lima 2016), such as species distributions and habitat associations. Up to the 1990s, virtually all zoological publications focused on taxonomy (Gascoigne 1993), and this is still mostly the case for plants (Stévant et al. 2022) and most invertebrates. Despite an increase in ecological research over the last few decades, key aspects of the ecology of species occurring in the Gulf of Guinea islands remain poorly documented, such as the influence community diversity and composition has on ecosystem processes. Progress is often halted by major knowledge gaps in areas fundamental to ecology, such as taxonomy. This has been the case for most invertebrates, as unresolved taxonomy halts progress in other areas of research. Take the example of terrestrial molluscs, in which an updated taxonomy opened the doors for several ecological studies (Panisi et al. 2022).

Here, we review existing information on the ecology of species from the oceanic islands of the Gulf of Guinea. Specifically, we address current knowledge on species distributions, population abundance, traits, habitat associations and interactions. We

also provide key references for each island and taxonomic group and identify current knowledge gaps to direct future research.

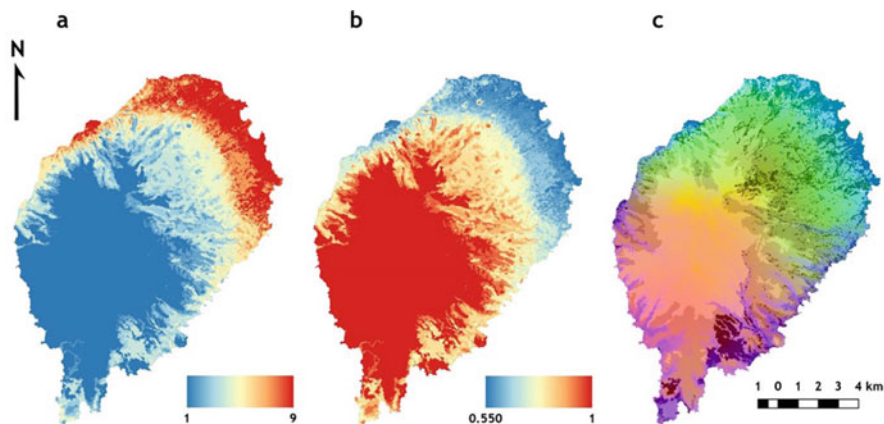
## Distribution

Information on the distributions of species on the oceanic islands of the Gulf of Guinea has been an important feature of initial studies. Some are even associated with the first descriptions of the islands themselves: a report of São Tomé in 1506, made by the Portuguese navigator Gonçalo Pires and written by Valentim Fernandes, describes an abundance of kites and the occurrence of a crocodylian that has since been extirpated from the island (Monod et al. 1951). However, much of the data on species distributions available today is still limited to the brief reports included in species descriptions (e.g. Ceríaco et al. 2015), species catalogues (e.g. Stévant and de Oliveira 2000; Csuzdi 2005; Sérgio and Garcia 2011; Mendes and Bivar-de-Sousa 2012), or studies focusing on various aspects of their biology (e.g. Drewes and Stoelting 2004). These are usually based on opportunistic observations, rather than on systematic surveys of the islands, and often only mention the islands where the species occur. When such studies provide details on the distribution of a given species, they tend to be biased towards well preserved accessible sites (Atkinson et al. 1991, Stévant et al. 2022).

Few studies have compiled geographically explicit information on species locations. Some exceptions include pteridophytes (Figueiredo 2002), endemic plants (Joffroy 2000; Stévant et al. 2022), land snails (Holyoak et al. 2020), and birds (Jones and Tye 2006). In some cases, information and even maps are shown, but details on how these were obtained are missing, as is the case for amphibians and reptiles (Pollo 2017) and threatened endemic birds (IUCN 2020a).

Even fewer species assemblages have been systematically surveyed across any of the islands. Some exceptions include plants (Fundação Príncipe 2019; Stévant et al. 2022), terrestrial snails (Tavares 2020), benthic reefs and fishes (Maia et al. 2018b), sea turtles (Ribeiro 2018; Hancock 2019), birds (Fundação Príncipe 2019; Soares et al. 2020), and bats (Rainho et al. 2010). Bird surveys informed some of the first island-wide assessments of the distribution of community traits, such as species richness, composition, and structure (e.g. Lima et al. 2013; Soares 2017; Fig. 7.1). Documenting plant species assemblages to classify vegetation is ongoing (Dauby et al. 2022), although the main gradients have been described (Monod 1960; Stévant 1998; Ogonovszky 2003).

The scarcity of historical records hampers the detection and quantification of temporal changes in the distribution of species on the oceanic islands of the Gulf of Guinea. However, sometimes even sporadic records allow assessing trends, such as the retraction of native species and the expansion of introduced species. For instance, localities linked to herbarium samples have provided convincing evidence for the disappearance of many plant species from large portions of the north of São Tomé and Príncipe, such as *Aerangis flexuosa* (Ridl.) Schltr, 1887. Interviews in rural and



**Fig. 7.1** Maps showing the distribution of (a) non-native bird species richness, (b) proportion of native bird species (Soares et al. 2020), and (c) compositional dissimilarity (Soares 2017). There was a clear opposing pattern in the distribution of non-native species richness and proportion of native species: non-native bird species thrive particularly well in land use types most influenced by humans (a), whereas native bird species dominate the best-preserved forests (b). Species composition largely coincides with the distinct land use types (c)

coastal communities suggest distribution areas for populations of giant land snails (Panisi 2017) and fishes (Maia et al. 2018a) have shifted. Historical distribution data reveal strong declines in the ranges of the endemic Obô Giant Land Snail *Archachatina bicarinata* (Bruguière, 1792) (Dallimer and Melo 2010), of the endemic São Tomé Shrew *Crocidura thomensis* (Bocage, 1887) (Lima et al. 2016), and of the number of beaches where sea turtles nest on São Tomé (Graff 1996; Ribeiro 2018). The number of recorded extinctions and extirpations is very small, with the only documented cases being an unknown species of crocodile on São Tomé (Ceríaco et al. 2018), an endemic subspecies of Olive Ibis on Príncipe (Lima and Melo 2021), and two orchid species (IUCN 2020). However, as for most other oceanic islands, vegetation clearance and the introduction of species are likely to have caused extinctions and extirpations before taxonomic studies started, and those may remain unknown, especially considering the poor fossil or subfossil record of the islands.

## Population Estimates

To date, there has not been an attempt to estimate plant population sizes. The first attempts to characterize plant species abundance on Príncipe provided valuable information on population dynamics of threatened species (Benitez et al. 2018). This study also revealed a higher abundance of species than previously thought, with high levels of regeneration for *Grossera elongata* Hutch, 1944, *Santiria balsamifera*

Oliv., 1886, and *Mesogyne henriquesii* Engl., 1894, and a lack of regeneration for *Strephonema* sp. nov. and *Carapa gogo* A. Chev. ex Kenfack, 2011.

The scarcity of quantitative surveys has resulted in very few reliable population size estimates for animal species. These include estimates made for birds (Dallimer and King 2007; Dallimer et al. 2009, 2010, 2012; Fundação Príncipe 2019), particularly for species of conservation concern, such as the Critically Endangered Dwarf Olive Ibis *Bostrychia bocagei* (Chapin, 1923) (Azevedo 2015), all pigeon species on São Tomé (Carvalho 2014), the Endangered Grey Parrot *Psittacus* sp. on Príncipe (Valle 2015), and the undescribed Príncipe Scops-Owl *Otus* sp. (Freitas 2019). Recent studies have also attempted to estimate population sizes for the Hawksbill Turtle *Eretmochelys imbricata* (Linnaeus, 1766) (Hancock 2019) and the Obô Giant Land Snail (Panisi 2017; Fundação Príncipe 2019), both on Príncipe and on São Tomé. On land, the difficult terrain and dense vegetation have greatly hampered the use of methods to account for detectability, such as distance sampling (but see: Dallimer and King 2007). In marine ecosystems abundances are even harder to sample, partly because many of the important species in these environments are migratory and have complex life cycles.

The very few long-term population studies that have been conducted include attempts to determine population trends of reef fishes, sea turtles, seabirds, and the Grey Parrot on Príncipe. The study of reef fish on São Tomé revealed worrisome declines (Maia et al. 2018b). Underwater visual census and photo-quadrats across six sites around São Tomé allowed researchers to explore the relative importance of exposure, depth, and topographic complexity as drivers of fish and benthic reef communities. Species richness, abundance, and biomass of reef fish were higher in deeper sites, which suffer less influence from human activities and are under the direct influence of a constant thermocline resulting from the intrusion of cold waters from the Benguela current.

Breeding female sea turtles have been monitored on Príncipe and São Tomé since the early 1990s (Ribeiro 2018; Hancock 2019). However, incomplete temporal and spatial coverage has led to high levels of uncertainty and hindered the quantification of critical parameters to estimate abundances. Recent advances in population modeling are overcoming this problem (Hancock et al. 2019), and standardized surveys carried out on both islands since 2012 will allow even more accurate estimates in the future. Techniques such as genetic analyses have also been used to estimate operational sex-ratios and assess population changes over time, such as reductions in effective population sizes in the Olive Ridley Turtle *Lepidochelys olivacea* (Eschscholtz, 1829), and migration rates in the Green Turtle *Chelonia mydas* (Linnaeus, 1758) (Hancock et al. 2019).

Local seabird colonies are the most important in the tropical Eastern Atlantic (BirdLife International 2020), primarily due to the large breeding colonies on the Tinhosas islets (Monteiro et al. 1997; Valle et al. 2016; Bollen et al. 2018; Lima and Martins 2020). These small islets (<25 ha) host around 140,000 breeding pairs of Sooty Tern *Onychoprion fuscatus* (Linnaeus, 1766), 10,000 pairs of Brown Noddy *Anous stolidus* (Linnaeus, 1758), and important breeding populations of Black Noddy *Anous minutus* Boie, 1844, and Brown Booby *Sula leucogaster* (Boddaert,

1783). Large population decreases have been reported for these colonies, but it is not yet clear whether these represent real declines or natural variations between years. Breeding and non-breeding seabird population sizes were first assessed in 1997, for most islets and small islands around Príncipe and São Tomé (Monteiro et al. 1997). More recently, the Tinhosas have been monitored quarterly to refine population estimates and trends, and to gain a better understanding of the breeding seasonality of these species (Valle et al. 2016; Bollen et al. 2018; Lima and Martins 2020).

Finally, the population of Grey Parrot on Príncipe has so far been the only one targeted by a population viability analysis (Valle 2015). Counts suggest that the species has recovered since the 2005 trade ban, now numbering around 8000 individuals, and that adult survivorship is critical to ensure population persistence, since the species can sustain relatively high levels of chick harvesting.

## Species Traits

From early on, researchers showed an interest in describing the temporal trends in the evolution and selection of species traits (Hortal et al. 2015). Many initial descriptions of biodiversity provided the first data on species traits that are vital for ecological studies. Biological collections, in particular, play a fundamental role in enriching trait databases, and can even lead to unexpected discoveries. In the oceanic islands of the Gulf of Guinea, morphological analyses of more than 2500 plant specimens collected in 2019 and 2020 have yielded many new species, while rediscovering rare species and finding new records for the islands (Stévant et al. 2022). Despite strong research effort in the 2000s (Figueiredo et al. 2011), ongoing studies on orchids are still leading to the description of new species, especially for the genus *Tridactyle*. Moreover, museum specimens allow the quantification of traits and trait variability, which are key to understanding the ecological function of species (e.g., Heleno et al. 2021). These collections are particularly relevant for species that might be harder to find and offer a historical reference that allows an assessment of temporal changes in traits, an aspect that remains poorly explored in these and other islands.

Species traits can be measured not only on museum specimens but also in the field, on living specimens that are not collected. This has begun to be carried out extensively in plants, but the amount of information available varies greatly between islands and specific groups (Exell 1944; Figueiredo et al. 2011; Sérgio and Garcia 2011; Klopper and Figueiredo 2013; Velayos et al. 2014), and, overall, information about plant traits remains scarce. This is not surprising considering that much of the plant taxonomy remains unresolved, and many species are still being reported and described as new to the islands (Benitez et al. 2018; Stévant et al. 2022). Ongoing work focused on threatened plant species has been collecting important information on species traits (Stévant et al. 2019).

A new checklist of land snails of São Tomé and Príncipe provided some information on these species' traits (Holyoak et al. 2020). Despite limitations, both on the

types of the traits characterized and on the number of species that have been assessed (Tavares 2020), this remains one of the few studies providing species traits for invertebrate taxa.

Sea turtle and bird traits have been studied much more extensively on the islands. The long-term monitoring of sea turtles in Príncipe and São Tomé since the 1990s collected data on female size that captured both spatial and temporal variation (Ribeiro 2018; Hancock 2019). Bird banding activities on the islands, although sporadic, have allowed collecting trait data, mostly on activity, morphometric measurements, and coloration, which have improved our understanding of sexual dimorphism, spatial trait variability, and daily and annual life cycles (King and Dallimer 2003; Madeira 2018).

High endemism rates and island syndromes hinder the use of the increasingly available global trait databases to assess species traits for island species, which have to be gathered locally (e.g., Covas 2016). In addition, behavioural, physiological, and life-history traits are often less easily recorded than morphological traits and remain an important knowledge gap (Hortal et al. 2015). Finally, to interpret current ecosystems under the lens of long-term ecology it is also vital to understand which species are native (Nogué et al. 2017).

## Habitat Associations

Until recently, local information on species-habitat associations was very scarce (e.g., Exell 1944; de Naurois 1994), but the situation has greatly improved since the 1990s. Some of the first studies from this period reported associations between species occurrence and local environmental variables, producing brief descriptions of habitat preferences (e.g., Atkinson et al. 1991; Joffroy 2000; Jones and Tye 2006). This was followed by more detailed and accurate descriptions for the best-studied groups, such as mammals (e.g., Dutton and Haft 1996) and birds (e.g., Dallimer and King 2007).

In recent years, a few studies have used geographically explicit information on environmental variables to model the distribution of terrestrial snails and birds on Príncipe (Fundação Príncipe 2019; Rebelo 2020) and on São Tomé (Lima et al. 2017; Panisi 2017; Soares 2017). Some of these studies have also assessed how local variables, often related to the vegetation, affect the distribution of species and species assemblages at smaller scales. Most of these have focused on vertebrates, such as amphibians (e.g., Strauß et al. 2018) and birds (e.g., Lima et al. 2013; Carvalho et al. 2015; Margarido 2015; Lewis et al. 2018; Alves 2019; Freitas 2019), but also on land snails (Panisi 2017; Rebelo 2020; Tavares 2020).

Native species, and especially endemic and threatened species, tend to be strongly associated with ecosystems that have been less disturbed by human activities. This pattern is common to terrestrial, coastal, and marine realms, and to distinct groups, including birds (Lima et al. 2013; Soares et al. 2020), tree frogs (Strauß et al. 2018),

sea turtles (Hancock 2019), land snails (Panisi 2017; Tavares 2020), and even earthworms (Csuzdi 2005) in the Gulf of Guinea.

In terrestrial groups, species distributions are strongly determined by land use, which in turn has been shaped mostly by topography (Jones et al. 1991; Norder et al. 2020). The best-preserved native forests, on which most native species depend, tend to persist in rainy, remote, and rugged areas (e.g., Soares et al. 2020). However, some native species, and even a few endemics, managed to adapt to novel ecosystems created by humans, including some birds (Dallimer et al. 2009; Lima et al. 2013; Carvalho 2014; Alves 2019), mammals (Rainho et al. 2010), frogs (Strauß et al. 2018), and land snails (Tavares 2020). Among novel ecosystems, those that maintain dense tree cover and mimic the structure of the native vegetation seem to be preferred by native species (Jones and Tye 2006; Lima et al. 2014). These include secondary forests, which result from vegetation regrowth after logging and agricultural abandonment, and agroforest systems, such as coffee and cocoa shade plantations, which integrate trees and agricultural crops (Jones et al. 1991; Oyono et al. 2014; Dauby et al. 2022). Unfortunately, it is also clear that many taxa do not cope well in these novel ecosystems (e.g., Fundação Príncipe 2019; Soares et al. 2020). In contrast with native terrestrial species, introduced species tend to be associated with more intensive land uses, many of which are located in the drier lowlands (Jones et al. 1991). On São Tomé, introduced birds are mainly small granivore species that rely on anthropogenic land uses (Soares et al. 2020), while introduced mammals seem to be less restricted to these environments (Dutton 1994).

Altitude might be less relevant to explain the distribution of mobile terrestrial organisms with broad ecological niches, such as most birds (e.g., Soares et al. 2020; but see: Dallimer et al. 2009; Lima et al. 2017), but it is crucial for other groups, such as snails (Tavares 2020), and notably plants (Exell 1944; Monod 1960; Stévant et al. 2022). Since plants are key components of terrestrial ecosystems, altitude has thus fundamental implications for how ecosystems are distributed across the islands (Dauby et al. 2022).

In reef ecosystems, depth and wave exposure appear to be the most important factors to explain changes in fish diversity (Tuya et al. 2018) and in the composition of fish and benthic communities (Morais and Maia 2017; Maia et al. 2018b). For highly mobile marine megafauna, such as sea turtles and cetaceans, species distributions vary among groups and appear to be related mostly to ecosystem type, food availability, depth, and sea surface temperature. For example, species of cetaceans that are quite similar, such as the Pantropical Spotted Dolphin *Stenella attenuata* (Gray, 1846), and the Common Bottlenose Dolphin *Tursiops truncatus* (Montagu, 1821), show clearly distinct habitat preferences related with bathymetry (Picanço et al. 2009). In the case of sea turtles, the habitat associations are strongly related to life stage. Juvenile Green and Hawksbills sea turtles feed on seagrasses or algal beds and coral and/or rocky reefs respectively, all year long (Monzón-Argüello et al. 2011; Ferreira et al. 2018; Hancock et al. 2018). By contrast, most adult turtles are found in coastal waters only during the reproductive season and are seldom observed feeding. The northern beaches of São Tomé are dominated by the Olive Ridley, which is extremely rare in the south of the island and on the island of Príncipe



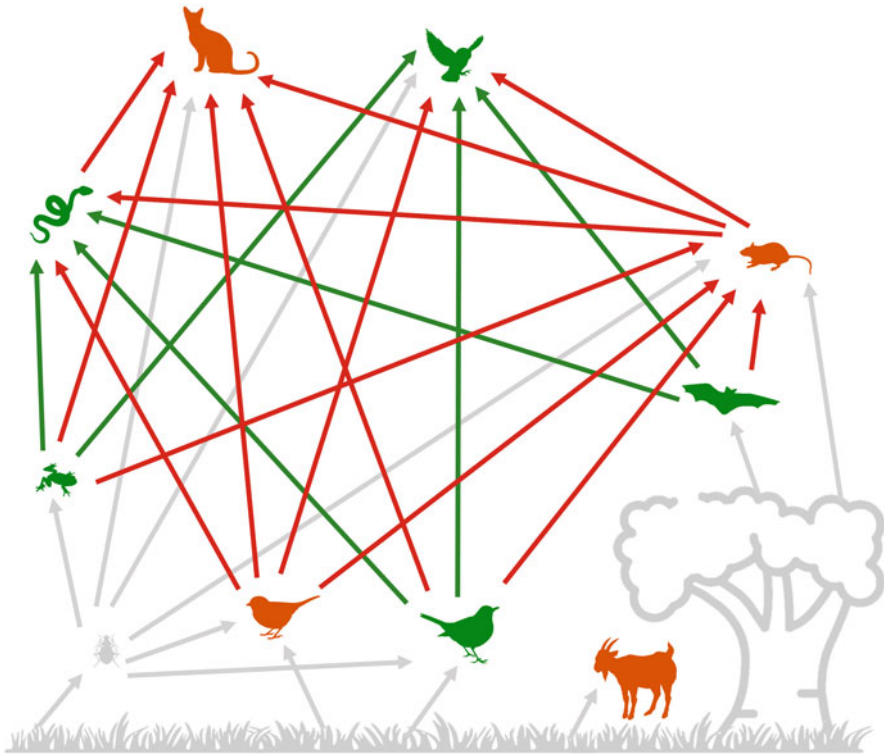
(Hancock et al. 2015). On the other hand, the Green Turtle is clearly the dominant nesting sea turtle species on Príncipe, and on the eastern and southern shores of São Tomé. This is linked to the preference of Green Turtle for narrow and steeper beaches associated with strong erosive processes, while Olive Ridley prefers unobstructed access to wide beaches with gentle slopes. The Hawksbill Turtle typically prefers small, protected beaches composed mainly of coralline sand and surrounded by vegetation, hence occurring mostly on the Rolas Islet off São Tomé, and along the northern coast of Príncipe (Hancock 2019).

## Species Interactions

Interactions between species are often complex, but they are the structure that supports biodiversity, and thus their study is fundamental to understand ecosystem functioning (Thébault and Fontaine 2010). Since they rely on detailed knowledge of basic aspects of the ecology of species and are often difficult to quantify, few species interactions have been studied in-depth on these islands, and the information available in the literature is often still limited to brief descriptions (e.g., Jones and Tye 2006; Wirtz and d’Udekem d’Acoz 2008; Vasco-Rodrigues et al. 2017).

We drafted a qualitative vertebrate food web for terrestrial ecosystems in São Tomé and Príncipe, distinguishing native and non-native species (Fig. 7.2). This was based solely on information on trophic interactions described for the islands for introduced mammals (Dutton 1994), birds (Jones and Tye 2006), bats (Rainho et al. 2010), shrews (Ceríaco et al. 2015; Lima et al. 2016), amphibians and reptiles (Ceríaco et al. 2018), the undescribed Príncipe Scops-Owl (Freitas 2019), and on more generic sources for other species (IUCN 2020). Nevertheless, even this simplistic approach, which excludes humans from the equation, illustrates major disruptions of trophic interactions by non-native species. Beyond the obvious changes in the topography of trophic interactions, the impact of introduced species is further heightened by their distinctive traits (Capellini et al. 2015). This food web provides a starting point for studies to deepen our understanding of trophic linkages and how they may be disrupted by introduced species.

A more quantitative, community-level approach enabled building a multi-guild seed dispersal network for São Tomé (Heleno et al. 2021). This showed that non-native species can disrupt this important component of ecosystem functioning, especially large mammals, which are seldom native on oceanic islands. Other quantitative studies at the community level have assessed how reef microhabitats mediate fish agonistic interactions (Canterle et al. 2020), and how land use and host species influence richness, prevalence, and co-infection patterns of haemosporidian bird parasites (Reis et al. 2021). A quantitative, species-specific study used stable isotopes to reveal that juvenile São Tomé Green Turtles adapt their diet preferences to the available food sources and, in contrast with expectations, are not strict herbivores (Hancock et al. 2018). Further quantitative studies at the community and species level across terrestrial and marine ecosystems are sorely needed.



**Fig. 7.2** Generalized São Tomé and Príncipe terrestrial vertebrate food web. Each icon represents a group of native or non-native species in the same trophic level. Arrows signal energy transfers through trophic interactions. Green symbolizes native species and interactions, red symbolizes non-native ones and grey symbolizes non-vertebrate components of the food web, namely plants and invertebrates. Native herbivores include fruit bats, pigeons, and parrots, while non-native include several ungulates, Rock Pigeon *Columba livia* J.F. Gmelin, 1789, and Laughing Dove *Streptopelia senegalensis* (Linnaeus, 1766). Native omnivores include several species of pigeons and perching bird species, while non-native include rodents, Mona Monkey *Cercopithecus mona* (Schreber, 1775), African Civet *Civettictis civetta* (Schreber, 1776), Pig *Sus scrofa* Linnaeus, 1758, fowls, and other bird species. Native insectivores include amphibians, geckos, skinks, shrews, bats, and a few bird species, while non-native include geckos, skinks; the Palm Swift *Cypsiurus parvus* (M.H.K.Lichtenstein, 1823), an insectivore that colonized the islands recently. Native carnivores include Dwarf Olive Ibis *Bostrychia bocagei* (Chapin, 1923), owls, and Black Kite *Milvus migrans* (Boddaert, 1783), while Cattle Egret *Bubulcus ibis* (Linnaeus, 1758) is the only non-native carnivore bird. Snakes are the only native vertebrates, while Cat *Felis catus* Linnaeus, 1758, Dog *Canis familiaris* Linnaeus, 1758, and Least Weasel *Mustela nivalis* Linnaeus, 1766 are all non-native vertebrates. Humans have been omitted from the figure, but they participate in all trophic levels that are represented. Decomposers have also been omitted

## Concluding Remarks

Species are still being described from the Gulf of Guinea on a regular basis (Lima 2016), clearly showing that much taxonomic work is still needed to understand the biodiversity of these islands. In recent years, careful reviews combined with intensive island surveys and advances in molecular analyses have led to the description of several new endemic species. Terrestrial vertebrates are certainly the best-studied taxa, but since 2000 two amphibians (Uyeda et al. 2007; Bell 2016), six reptiles (Ceríaco et al. 2022a), and one mammal species (Ceríaco et al. 2015) have been newly described as endemic to the islands. Many widespread species have also been reported for the first time, including plants (Stévant et al. 2019), land snails (Holyoak et al. 2020), fishes (Costa et al. 2022), and birds (Lima and Melo 2021). A few have also regained species status (e.g., Melo et al. 2010), while many others remain undescribed, even among plants (e.g. Stévant et al. 2022), land mammals (Rainho et al. 2022), and birds (Melo et al. 2022). This incomplete knowledge is a serious handicap to develop a more in-depth understanding of the ecology of the islands.

Furthermore, ecological studies have been biased towards certain groups, such as terrestrial vertebrates, and notably birds. This bias occurs because the taxonomy of these groups is mostly resolved, both locally (Jones and Tye 2006) and globally (Billerman et al. 2020). Such studies have been particularly relevant for the recognition of the biological importance of these islands at the global scale (e.g. Le Saout et al. 2013). Conversely, very few ecological studies have been dedicated to invertebrate groups, exceptions including very recent research on land snails (Panisi et al. 2022) and mosquitoes (Reis et al. 2021). Biases persist even within taxonomic groups, since studies tend to focus on conspicuous and easily detectable species. Even among birds, the existence of the Príncipe Scops-Owl was only confirmed in 2016 (Verbelen et al. 2016), and the taxonomy of the Gulf of Guinea Storm Petrel remains uncertain (Flood et al. 2019). Although often rarer and harder to find, threatened and endemic species are targeted by more studies than expected (Lima et al. 2011), because they tend to be the focus of conservation studies (e.g., Lima et al. 2017).

There are also important spatial research biases, within and across the islands. The most evident is the scarcity of studies on Annobón, the smallest and least accessible of the main islands. Within Príncipe and São Tomé, the most remote areas have also been less surveyed. Marine species are often less known, simply because they are more challenging to study. This is especially true for those living away from the coast and at greater depths.

Finally, there are also multiple temporal biases. Certain groups tend to be studied primarily during certain seasons, as it is the case for plants (e.g., Benitez et al. 2018) and sea turtles (Ribeiro 2018; Hancock 2019), which are mostly monitored during the breeding season. Out of convenience, many other taxa tend to be studied during the dry seasons, such as birds (Lima et al. 2017), even though this is not their breeding season (Madeira 2018). These biases may ultimately constrain the broader

understanding of the ecology of the islands and a conscious effort to study species throughout the year would help alleviate this bias.

Relatively few studies have addressed community ecology, focusing instead on individual species, even when multiple species are included in the same study. In some cases, this has resulted from methodological limitations to gather comparable data from multiple species simultaneously. Nevertheless, in recent years, there have been several community ecology studies, including birds (Lima 2012; Soares et al. 2020), land snails (Tavares 2020), plants (Fundação Príncipe 2019), and bird–plant interactions (Heleno et al. 2021).

To promote these islands as models for understanding ecological processes, it is necessary to overcome knowledge gaps and research biases, which generate uncertainty and limit extrapolation to broader contexts. To do so, future studies should include systematic island-wide surveys, or prioritize understudied areas, such as Annobón, less accessible areas within the islands, and marine environments. Likewise, research must focus on understudied taxonomic groups, such as invertebrates. For most of these groups many fundamental ecological aspects, such as distribution and environmental associations, remain fully unknown. Furthermore, studies at the community level and focusing on species interactions are needed to understand the functioning of ecosystems and ultimately help protect the unique biodiversity of these islands.

To ensure the future of the endemic-rich biodiversity of these islands, it is evident that protecting remaining natural ecosystems and preventing the degradation of human-modified ecosystems, such as secondary forests, are key priorities. Additionally, the over-exploitation of native species and the introduction and spread of non-native species must be curbed, and conservation strategies need to be continuously refined and implemented. These include Red Listing (IUCN 2020), species-specific action plans for threatened species (e.g., Ndag’ang’a et al. 2014a, b; Panisi et al. 2020; Fundação Príncipe 2021), the expansion of the existing network of protected areas (BirdLife International 2020), and their management plans. Long-term monitoring studies are urgently needed to assess biodiversity trends, promptly identify declines, and inform conservation actions.

Finally, it is crucial to raise public awareness about the unique biodiversity of these islands, both internationally and locally. Local biodiversity education has greatly improved in recent years (Ayres et al. 2022), but the development of local scientific expertise through outreach, capacity building, and advanced training is still lacking and should be promoted through international collaborations.

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