Classification, Distribution, and Biodiversity of Terrestrial Ecosystems in the Gulf of Guinea Oceanic Islands

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Chapter 3
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Abstract The oceanic islands of the Gulf of Guinea display a large diversity of environmental conditions and biological communities, whose interactions have contributed to the development of a great variety of ecosystems, from mangroves to montane grasslands. Human activities have extensively and profoundly altered many of these natural ecosystems over the past five centuries. We review key studies to propose an updated classification map of terrestrial ecosystems, taking advantage of up-to-date spatial information on abiotic gradients and biological distributions. To guide future research and conservation programs, we highlight challenges and pending questions regarding our understanding of the structure, integrity, and dynamics of terrestrial ecosystems in these islands.

Keywords Abiotic gradients · Biological communities · Introduced species · Novel ecosystems · Topography · Vegetation types

Introduction

The oceanic islands of the Gulf of Guinea (GGOI) comprise three islands: Príncipe, São Tomé (together forming the Democratic Republic of São Tomé and Príncipe), and Annobón (part of the Republic of Equatorial Guinea). Despite their small size (c. 1000 km^2), their combined human population is ca. 225,000 inhabitants (INEGE 2017; INESTP 2020), and they are also host to a rich endemic fauna and flora (Jones 1994).

The tropical humid climate, complex topography, altitudinal gradients, and isolation (distance to mainland from 220 to 350 km) are often invoked to explain the endemic-rich biodiversity of these islands (Jones 1994). The abiotic gradients generate a diversity of habitats with distinct biological communities, whose interactions contribute to the development of a great variety of natural ecosystems, from mangroves to montane grasslands (Monod 1960). Over the past five centuries, human activities have profoundly altered most of these natural ecosystems across large areas (Eyzaguirre 1986). Impacts have varied in intensity across time and space among the three islands, but agricultural land use in particular has intensified (Jones et al. 1991), which has likely facilitated the expansion of introduced species (e.g., Soares et al. 2020).

The first attempts to delineate the ecosystems of the GGOI date back to the first half of the twentieth century, and aimed at documenting vegetation types (Henriques 1917; Chevalier 1938–1939; Exell 1944). These studies relied almost entirely on variations in vegetation physiognomy and on the degree of human interference. These authors paid particular attention to defining altitudinal vegetation belts. Other studies tried to identify phytogeographical units based mostly on the co-distribution of plant species, but ended up having to rely heavily on abiotic proxies (Stévart 1998; Ogonovszky 2003). Phytogeographical units can be misleading for identifying ecosystems because biogeographical processes can lead to different species

assemblages in similar ecosystems. However, given the relatively small size of these islands, we can assume that the co-distributions of species within each island reflect environmental conditions and anthropogenic disturbances, while biogeographical processes, such as limited dispersal and speciation rates, are negligible.

Recently, many large-scale studies have inferred the integrity, distribution, and dynamics of ecosystems, taking advantage of the increasing availability of remote sensing data (e.g., Hansen et al. 2013; Gosling et al. 2020; Vancutsem et al. 2021). Unfortunately, these products are of little relevance for the GGOI, due to their coarse resolution and unavailability of high-quality aerial images without atmospheric obstructions, such as haze and aerosols.

In this chapter, we review the key studies that attempted to document the terrestrial ecosystems of the islands, and then propose an updated classification, taking advantage of up-to-date spatial information on abiotic gradients and biological communities to map proposed vegetation types. Finally, to guide future research and conservation efforts, we identify several challenges and pending questions regarding our understanding of the structure, integrity, and dynamics of the terrestrial ecosystems in the GGOI.

Ecological Setting and Previous Classifications

São Tomé Island

Abiotic Gradients

Rainfall measurements using remote sensing lack the accuracy required for a small and heterogeneous area like São Tomé (Chou et al. 2020). Thus, our understanding of rainfall patterns must still rely on the rough isohyets drawn from 50-year-old observations (Bredero et al. 1977). These isohyets show that annual rainfall varies strongly across the island, ranging from <1000 mm in the northeast to more than 7000 mm in the southwest (Fig. 3.1). Four seasons are recognized: a humid season from mid-September to mid-December, a mild dry season from mid-December to mid-march ("gravanito"), a humid season from mid-March to June, and a prolonged dry season from July to mid-September ("gravana").

The rainfall pattern can be explained by the rugged topography and the resulting rain shadow ("foehn effect"; Ceríaco et al. 2022). Elevation reaches a maximum of 2024 m at Pico de São Tomé, to the northwest of the center of the island, which is surrounded by a multitude of smaller peaks, ridges, and steep slopes. Overall, the island is divided by a north–south ridge, extending from Pico de São Tomé to Cabumbé, which separates the island into a wetter west flank and a drier east flank. Apart from the northeast and a few flat areas and gentle slopes in the south and southeast, the topography of most of the island is complex and dominated by steep ridges and mountains (Fig. 3.1).
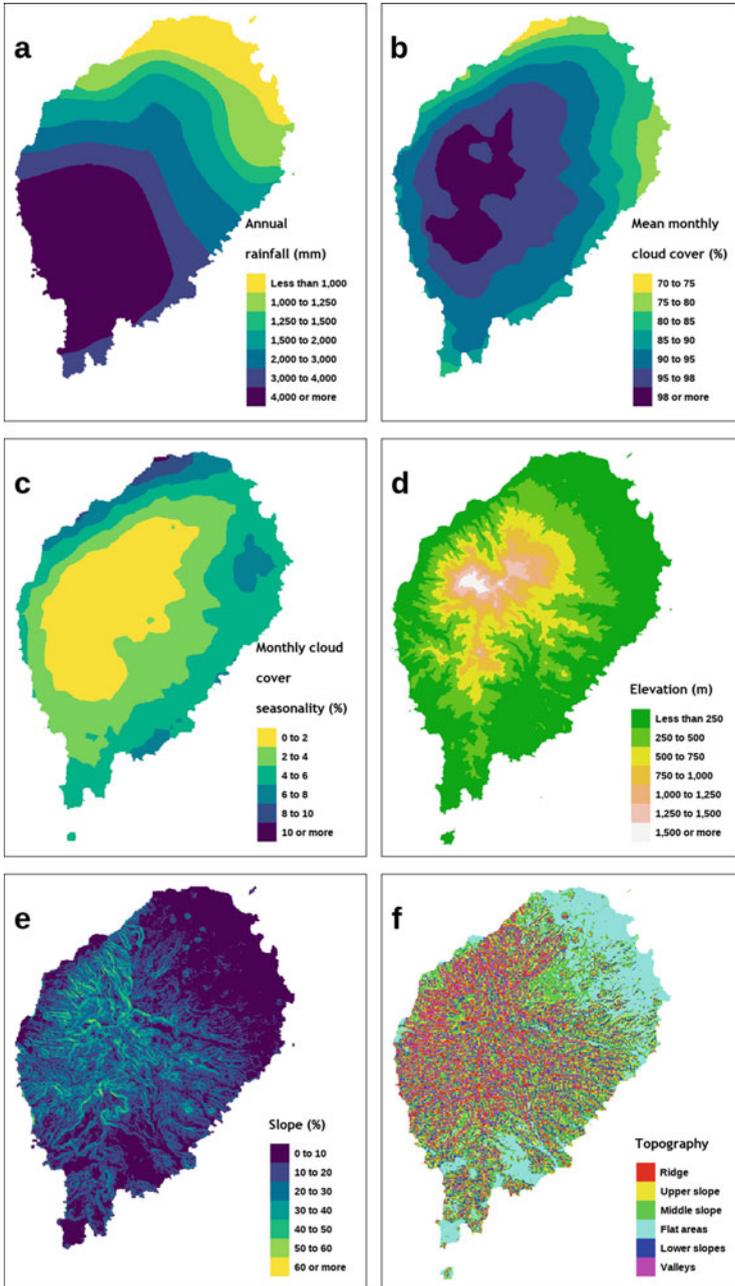
Fig. 3.1 Main physico-climatic gradients on São Tomé Island. Sources of data can be found on https://github.com/gdauby/stpa_ecosystems_review

Cloud cover influences biological processes and species distribution (Wilson and Jetz 2016). On São Tomé, according to remotely sensed data, the mean monthly cloud cover ranges from 70% in the extreme north to nearly permanent in the western highlands (Fig. 3.1). Rainfall and cloud cover do not fully coincide, although together they typify the constant high moisture on the west side of the island. Persistent cloud cover coincides with altitudes between 500 and 1500 m on the west flank, and above 1000 m on the south and east flanks as a result of the foehn effect. Intra-annual cloud cover varies little, but reflects the stronger seasonality in the north (Fig. 3.1).

São Tomé soils have been studied and mapped, and their properties are conditioned by topography and climate that often vary at fine scales (Cardoso and Garcia 1962). The most frequent soil types are highly weathered, such as Ferralsols and Lixisols, characteristic of tropical climates. Vertisols, Lithosols, and Fluvisols are noteworthy because they interact with vegetation. Vertisols are heavy clay soils frequently associated with grasslands and forests that develop deep wide cracks when dry, making them difficult to use for agriculture (Kovda 2020). This soil type is restricted to the dry north and northeast (Fig. 3.1). Lithosols are thin soils that have very little organic matter, and can be found everywhere on the island, often associated with ridges, steep slopes, and cliffs near the coast (Diniz and Matos 2002). Fluvisols, derived from alluvial deposits, are nutrient-rich, often associated with large riverbanks, and can be flooded or have weak drainage (IUSS Working Group WRB 2015).

Human Disturbance

Around three-quarters of the native vegetation of São Tomé has been lost, most of which was converted into large plantations (Fig. 3.2a; Soares et al. 2020). This transformation started in the late fifteenth century when humans began colonizing the island, clearing large extents of forest mostly in the dry northern coastal areas to establish sugarcane plantations (Eyzaguirre 1986). In the early sixteenth century, the island became a top producer of sugar globally, developing a cash crop economy that collapsed later that century (Garfield 1979), slowing down the deforestation rate. Throughout the seventeenth and eighteenth centuries, the island became an important slave trading post and the traditional "gleba" agroforestry system (based on tree and root crops grown in dense mixed stands with minimal tillage) expanded (Eyzaguirre 1986). In the nineteenth century, the deforestation rate increased and expanded further inland and upland, giving way to intensive plantations dedicated mostly to coffee and cacao, but also to oil palm, coconut, quinine, and cinnamon. This period saw the spread of shade plantations that can be defined as plantations where a canopy is maintained above crops (typically cacao or coffee). The canopy is often composed of introduced tree species (typically of the *Erythrina* genus).

Deforestation in São Tomé reached its peak early in the twentieth century, when the island became the world's largest producer of cacao. For various reasons, this system became economically unsustainable and during the late 1930s many
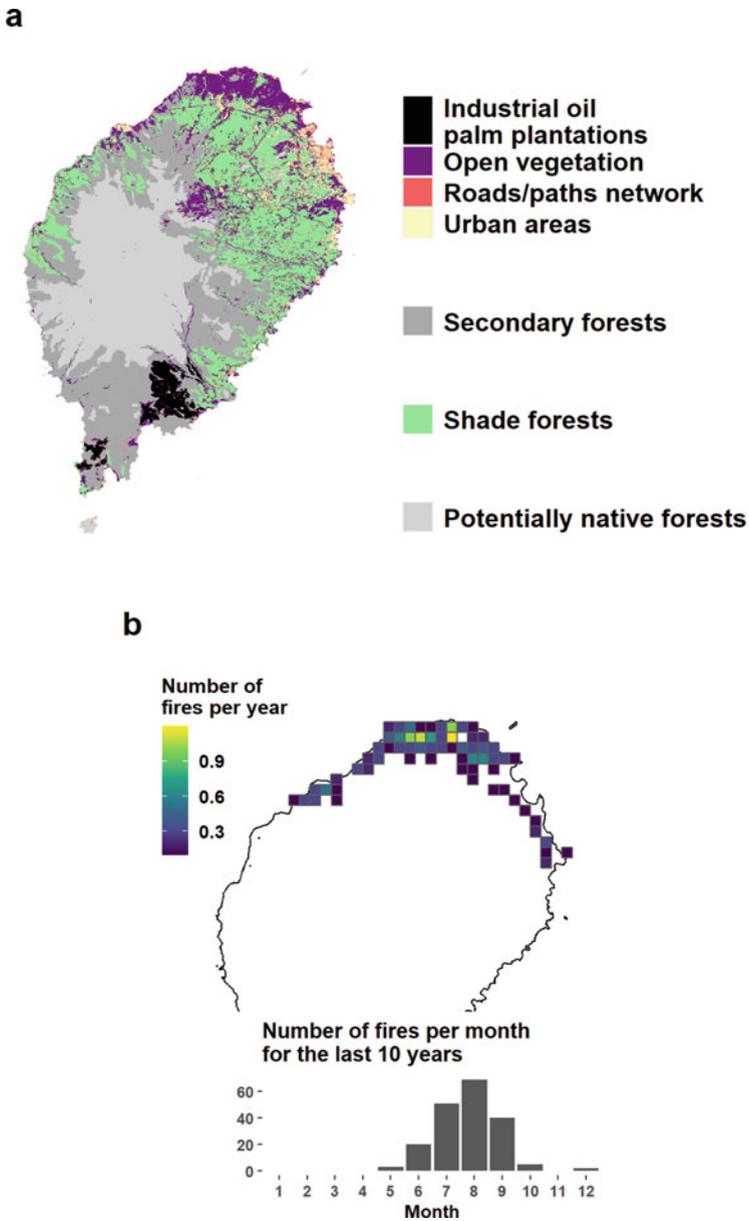
Fig. 3.2 (**a**) Degraded or transformed land cover on São Tomé. Note that the "open vegetation" category includes both agricultural lands and savanna-like vegetation (Adapted from Soares et al. 2020). (**b**) Annual fire frequency (data for the last 10 years). The inset barplot shows the distribution of fires along the year

Table 3.1 Total area and relative importance of transformed or degraded land cover in each island (Calculated from Norder et al. 2020; Soares et al. 2020; Frazer Sinclair and Yodiney dos Santos, unpublished data). Note that the open vegetation category also includes naturally open vegetation type

Land cover	Annobón	São Tomé	Príncipe
Open vegetation	2.8 km^2 (13.4%)	92.5 km^2 (10.9%)	6.6 km^2 (4.8%)
Urban areas	1.8 km^2 (8.5%)	23.3 km^2 (2.7%)	1.9 km^2 (1.4%)
Industrial palm plantations	–	23.4 km^2 (2.7%)	–
Roads/paths network	–	17.8 km^2 (2.1%)	2.9 km^2 (2.1%)
Secondary forest	–	240.6 km^2 (28.2%)	37.4 km^2 (26.8%)
Shade forest	–	218.6 km^2 (25.6%)	41.3 km^2 (29.6%)

plantations were abandoned, creating large extents of secondary forests in the higher altitudes, while the flatter lowland remained as plantations. Following independence in 1975, and especially after land privatization in the early 1990s, logging and residential areas expanded significantly, especially in the shade plantations. Meanwhile, swidden agriculture emerged to satisfy local food needs, producing horticultural crops such as potatoes, maize, cabbage, beans, and carrots (Eyzaguirre 1986). Strong demographic growth led to an increase in timber consumption (the main building material in the country), resulting in increasing pressure on forest resources (Salgueiro and Carvalho 2001). More recently, agro-industrial concessions to foreign companies have reconverted large areas of secondary forest to export crop plantations, such as oil palm, cacao, and coffee (Oyono et al. 2014).

This complex history led to the patchwork of land uses that characterizes the landscape on São Tomé (Fig. 3.2a, Table 3.1; Soares et al. 2020). Native forests (ca. 26.4% of the island) are mostly found in the rugged wetter areas at the center and southwest. Around these are mostly secondary forests (ca. 30.5%), resulting from agricultural abandonment, notably more widespread in the south. Agroforests (ca. 28.5%), comprising the traditional "glebas" but also more intensive shade plantations of cacao and coffee, are dominant in the northeast and in the south along the coast. The remainder of the island is characterized by non-forested land uses (ca. 14.5%), including urban areas and anthropogenic savannas in the northern coast and horticultural areas at higher altitudes. Terrain ruggedness predominantly shapes the extent of remaining native vegetation cover, suggesting that topography constrains human occupation across the island (Norder et al. 2020). Anthropogenic impacts have been felt mostly in the flat lowlands of the drier north, where fire maintains large extents of open vegetation, even though other areas are not spared. At higher altitudes, for instance, the distinct climate and fertile soil has promoted agricultural expansion of crops like quina, arabica coffee, cinnamon, and annuals, especially in the flatter areas around Monte Café.

Besides land-use change, human disturbance is also felt through more subtle modifications, namely through the exploitation of forest resources and the facilitation of introduced species. Logging (Espírito et al. 2020), hunting (Carvalho 2015), silviculture, and the gathering of other forest products such medicinal plants

(Madureira et al. 2008) are known to have impacts on the vegetation and overall functioning of forest ecosystems. Being at the crossroads of the Atlantic slave trade, having fertile soils and diverse ecological conditions, São Tomé was often used as an agricultural experimental ground, receiving crops from all over the world (Ferrão 2005), as well as many other species of flora (Figueiredo et al. 2011) and fauna (Dutton 1994). Agriculture greatly changed the ecology of the island, creating the conditions for many introduced species to expand across the island (Soares et al. 2020) that sometimes also became invasive in native undisturbed forests (Lima et al. 2014; Panisi 2017; De Menezes and Pagad 2020).

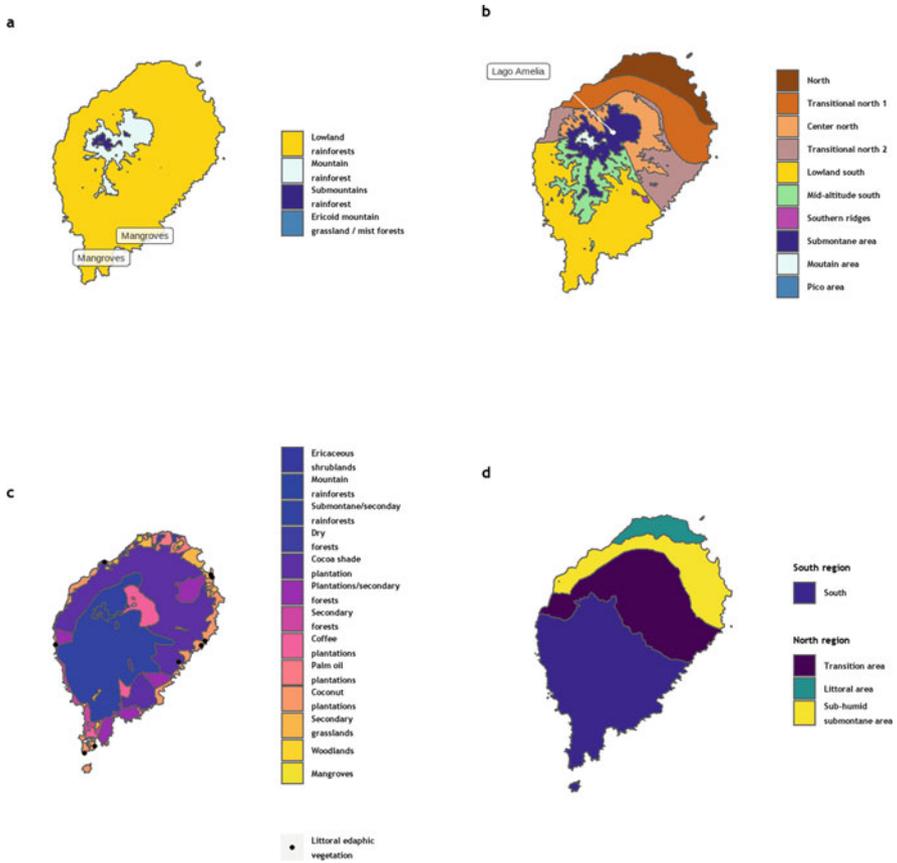## Previous Vegetation and Phytogeographical Classification

Previous works aimed to document vegetation types focused mostly on its physiognomy, the intensity and nature of anthropic impacts, and the use of abiotic gradients as proxies, such as altitude and precipitation (Table 3.2).

Chevalier (1938–1939) was the first to mention different vegetation types. However, it was Exell (1944) who proposed a delimitation and detailed description of several vegetation types. Exell recognized mangroves and coastal dunes as distinct and narrowly distributed vegetation types, and used three altitudinal belts to distinguish the remaining vegetation: low-altitude (mostly degraded) forests (up to 700 or 900 m), montane rainforests (between 800 and 1400 m), and mist forests (above 1400 m; Fig. 3.3).

Silva (1958) distinguished "primary" from "secondary" vegetation, and "climate-driven" from "edaphic-driven" vegetation, including summit shrubland and dry northern savannas in the latter (Fig. 3.3c). This approach also acknowledged the crucial role of human activities in transforming the landscapes of São Tomé.

Table 3.2 Key references proposing spatial delimitations of the islands in ecological, ecosystems, or phytogeographical units

References	Island(s)	Content	Criteria
Mildbraed (1922)	Annobón	Five vegetation types	Flora and vegetation physiognomy, elevation
Exell (1944)	São Tomé and Príncipe	Elevational belt	Abiotic gradients
Silva (1958)	São Tomé and Príncipe	Map of vegetation units	Elevation and land use
Monod (1960)	São Tomé and Príncipe	Documentation of vegetation type	Elevation, presence of endemic plant species
Peris (1962)	Annobón	Six vegetation types	Flora and vegetation physiognomy, elevation, agricultural activities
Stévart (1998)	São Tomé and Príncipe	Map of vegetation units	Elevation, annual rainfall, presence of orchids species
Diniz and Matos (2002)	São Tomé and Príncipe	Map of agro-ecological entities	Field observations, topography, edaphic properties, elevation

Fig. 3.3 Previous delimitations of vegetation types or phytogeographical territories on São Tomé Island. (a) According to Monod (1960) and Exell (1944); (b) According to Stévart (1998); (c) According to Silva (1958); (d) According to Diniz and Matos (2002). For the Diniz and Matos (2002) map, only the main regions are shown

Monod (1960) was especially interested in the altitudinal variation of vegetation. He extended previous classifications (Fig. 3.3a), highlighting the uniqueness of the high-altitude shrublands distributed in several small patches above 1900 m, which hosts some emblematic endemic plant species, such as *Erica thomensis* (Henriq) Dorr & E.G.H. Oliv. 1999 and *Lobelia barnsii* Exell 1944.

Stévart (1998) proposed a phytogeographical classification based on the distribution of orchid species and their auto-ecology (Fig. 3.3b). He was the first author to explicitly consider the rainfall pattern distinguishing the dry north and the wet south of the island, following the 3000 mm annual rainfall isohyet. He suggested that the area around Lagoa Amélia could be a distinct vegetation type. Stévart (1998) also pointed out that several ridges at lower elevation (below 800 m) in the southeast had a unique assemblage of orchid species. The floristic distinction of those ridges could

be driven by the combination of topographic position and high precipitation, although data were very limited at the time.

Diniz and Matos (2002) provided a detailed map of 109 agro-ecological units distributed in two main regions (Fig. 3.3d). Although their primary goal was to assess the potential of each unit for agricultural production, they also provide detailed descriptions of vegetation and flora in each unit. The northern region broadly corresponds to the area with <2000 mm of annual rainfall, and is divided into three sub-regions; the littoral plain with a semi-arid climate, the transition area with a sub-humid climate, elevations between 300 and 550 m with slopes that do not exceed 15%, and the mountainous more humid area. The southern region is described as more homogenous, being characterized by the steep transition between the central mountainous highland and the littoral band, composed of ridges and deep valleys.

Príncipe Island

Abiotic Gradients

The mainland of Príncipe Island has a maximum length of 18.5 km (north to south) and 11 km in its maximum width (east to west), with an area of approximately 139 km^2. It is located 220 km off the West African coast and 146 km north of São Tomé (Diniz and Matos 2002; Dallimer and Melo 2010). The north of the island is relatively flat, whereas the south-center has the largest elevated area (>500 m), including Pico do Príncipe that reaches 942 m, and multiple peaks surrounded by steep slopes and ridges (Fig. 3.4).

Just like São Tomé, our knowledge of rainfall patterns still relies on rough isohyets drawn several decades ago. Annual rainfall ranges from more than 4000 mm in the southeast to <2000 mm in the northeast, which is a remarkable contrast in such a small area. Cloud cover follows broadly the same pattern as annual rainfall, highlighting the elevated and rugged area around the Pico Príncipe (Diniz and Matos 2002). Four seasons are also recognized for Príncipe, following the same patterns found in São Tomé.

Soils have been studied and mapped (Diniz and Matos 2002). Bedrocks are predominantly volcanic, mostly in the north, while Phonolite rocks are more common in the south. As on São Tomé, the most frequent soils are highly weathered such as Ferralsols and Lixisols (Cardoso and Garcia 1962).

Human Disturbance

The history of land occupation on Príncipe is broadly similar to that of São Tomé. However, contrary to São Tomé, no large areas are regularly burned. A peculiarity in the history of Príncipe is the intense deforestation campaign that took place between
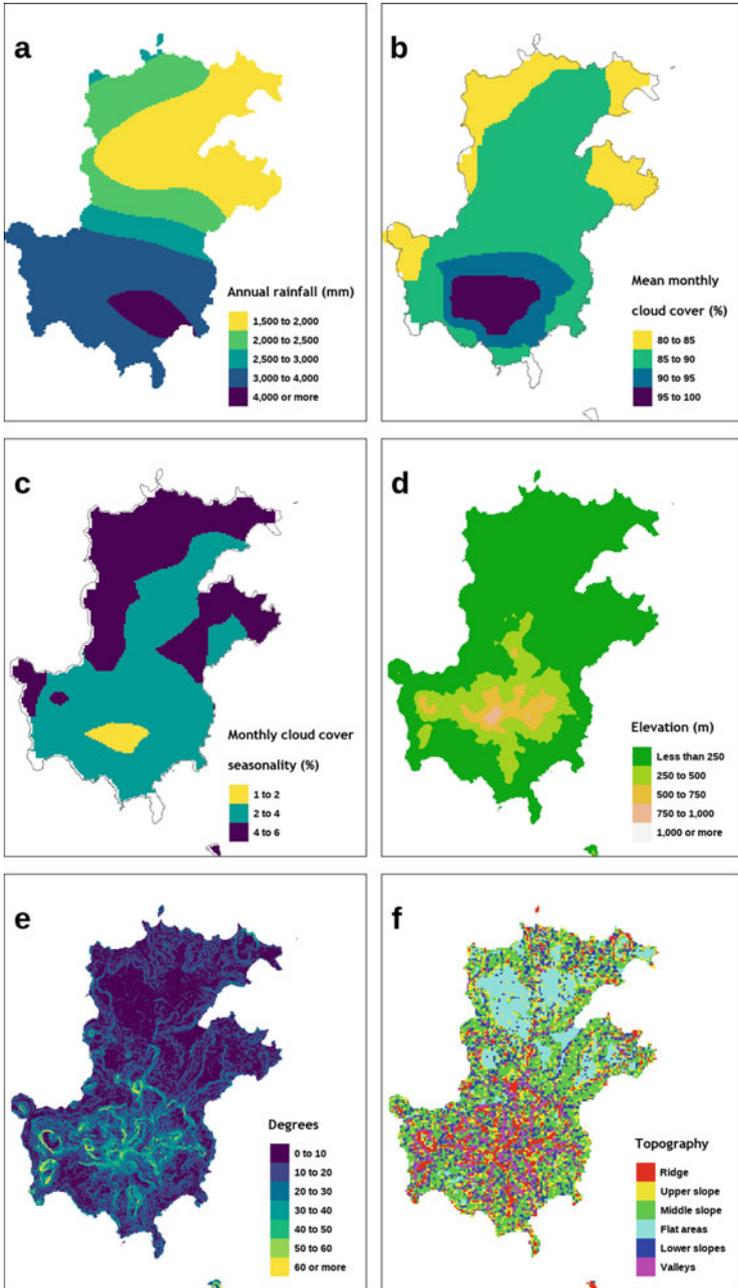
Fig. 3.4 Main physico-climatic gradients in Príncipe Island

1911 and 1916 to eradicate the tsetse fly vector of sleeping sickness (da Costa et al. 1916):

> The steps taken (...) consisted principally in the clearing away of herbaceous and bushy vegetation, in the opening out to the sun's rays of the margins of watercourses and swamps, straightening out and leveling the banks and the beds of these, draining and filling swamps, and forest fellings on a large scale.

More than 15 km^2 of native forests in the northern part of the island were deforested (11% of the island), while many plantations were also being abandoned (da Costa et al. 1916; da Silva 2019).

Nearly all lowland forests in Príncipe have been disturbed by human activity (Fig. 3.5), creating a mosaic of native and secondary forest, as well as active and abandoned agricultural lands (Dallimer et al. 2012). Most of the remaining native vegetation occurs at mid and high elevation and is included in the Príncipe Natural Park, a protected area created in 2006 that covers around 21% of Príncipe, mostly in the south (Ministry of Infrastructure, Natural Resources and Environment 2016).
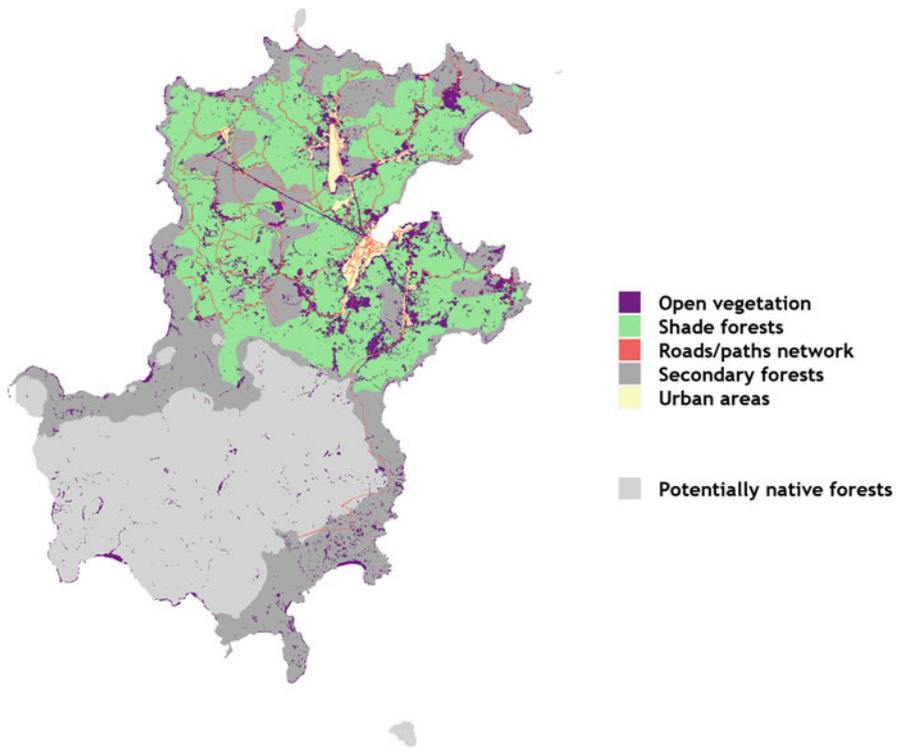
Fig. 3.5 Degraded or transformed land cover in Príncipe (Adapted from Frazer Sinclair and Yodiney dos Santos, unpublished data). Note that the "open vegetation" category includes both agricultural lands and savanna-like vegetation but also potentially natural edaphic open vegetation

The whole island was declared a UNESCO Man and Biosphere Reserve by 2012 (UNESCO 2021).

Previous Vegetation and Phytogeographical Classification

The distribution of forests on Príncipe was first depicted in a land cover map (IGC 1964) based on aerial photos and ground surveys. This map delimited the island according to land use in several categories, as natural forests or abandoned plantations, cacao plantations, coffee plantations, oil palm plantations, coconut plantations, agriculture, gardens, vegetable gardens or orchards, bush, undergrowth, or grasslands.

The native vegetation of Príncipe is similar to that of São Tomé, with plant families Rubiaceae, Euphorbiaceae, and Orchidaceae dominant (Figueiredo et al. 2011). It includes mangroves, but not savannas. Submontane forest is recorded only on the summit, at Pico do Príncipe, though Exell (1944) claimed that the composition of the vegetation at higher altitudes on Príncipe (namely Pico Papagaio; 680 m and Pico do Príncipe; 948 m) resembled that of lowland rainforest on São Tomé.

Diniz and Matos (2002) relied on climate, topography, and soil types to identify 28 agro-ecological units, which they described and delimited in detail. The vegetation is characterized by forests, ranging from primary ("obô") to secondary formations ("capoeira") and to strongly anthropized environments, including diverse types of plantations such as shaded cacao or coconut monocultures.

Forest tree communities were recently studied across the island, documenting floristic differentiation across north-south and altitudinal gradients (Fauna and Flora International 2018). These patterns were driven, at least partly, by a decrease in the relative abundance and diversity of tree species in secondary forests, highlighting the influence of past disturbances on forest tree composition.

Annobón Island

Abiotic Gradients

Of the three Gulf of Guinea Islands, Annobón is the smallest (17 km^2) and farthest from the mainland, located 360 km west of Gabon and 190 km southwest of São Tomé. Despite the small size, its geography is diverse. There is a 700 m wide crater at 150 m elevation, occupied by Lake A Pot, which has several adventitious cones, including the 400 m wide crater of Punta Manjob in the SE, the Quioveo and Santa Mina mountains, and northeast-southwest corridor that links the bays of San Pedro and Santa Cruz to the Anganchi river (Fig. 3.6). Santa Mina is the highest elevation at 613 m.

Annobón has an average temperature of 26 °C with little annual variation. Rainfall is primarily affected by the oceanic winds that cause a pronounced dry

season from May to October, while the rest of the year is wet (Juste and Fa 1994). No accurate rainfall data is available, but maximum precipitation is around 3000 mm (Juste and Fa 1994; Velayos et al. 2014). Remotely sensed data suggests that intra-annual variability in cloud cover is less pronounced than on Príncipe or São Tomé, even though there is still a north-south humidity gradient, ranging from <70% in the north to almost 90% in the south (Fig. 3.6).

The soils of Annobón have not been thoroughly studied and mapped. However, they are ultrabasic and have the same volcanic origin as those of Bioko with lower silica and higher proportions of ferromagnesian elements (De Castro and De la Calle 1985).

Human Disturbance

Humans have modified most of the vegetation on Annobón (Fig. 3.7), except for the high peaks of Santa Mina and Quioveo. San Antonio de Palé or "Ambo," located in the extreme north of the island, is the only permanent town. Most subsistence farms are on the fertile plains around the town, producing yuca (*Manihot esculenta* Crantz 1766), banana, and malanga (*Xanthosoma violaceum* Schott 1853). However, these small-scale plantations ("fincas") can now be found everywhere on the island, even in steep slopes (Velayos et al. 2014), and their encroachment in the montane forests of Quioveo and Santa Mina is set to cause irreversible damage. Other villages are temporarily occupied during the dry season or holiday months. More recently, the expansion of the airport and seaport must have had considerable environmental impacts.

## Previous Vegetation and Phytogeographical Classification

Only two studies attempted to delineate and document vegetation on Annobón. The first (Mildbraed 1922) proposed five vegetation types: (1) coastal "Sandstrand," (2) "Vorland," a savanna-like forest mixed with plantations, (3) "Buschwald," oil palm artisanal plantations mixed with others tree species, (4) lowland dry forest, "Trockener Wald," and (5) "Nebelwald," a cloud forest found mostly above 500 m that is rich in orchid and fern species, including tree ferns *Alsophila* spp.

The second study (Peris 1962) proposed six vegetation types: (1) coastal, subdivided into rocky and sandy shores, (2) open vegetation strongly transformed by human activities, which was divided into herbaceous savanna-like vegetation, large-leaved savanna-like vegetation, cassava plantation, and shrubland, (3) dry forest, equivalent mostly to "trockener Wald," (4) wet forest, also included in "trockener Wald" but distinguished by the presence of *Olea welwitschii* Gilg & G. Schellenb. 1913, (5) *Hymenophyllum* spp. cloud forest in the peaks of Santa Mina and Quioveo (see Fig. 3.8), and (6) tree fern areas in the summit of Santa Mina.
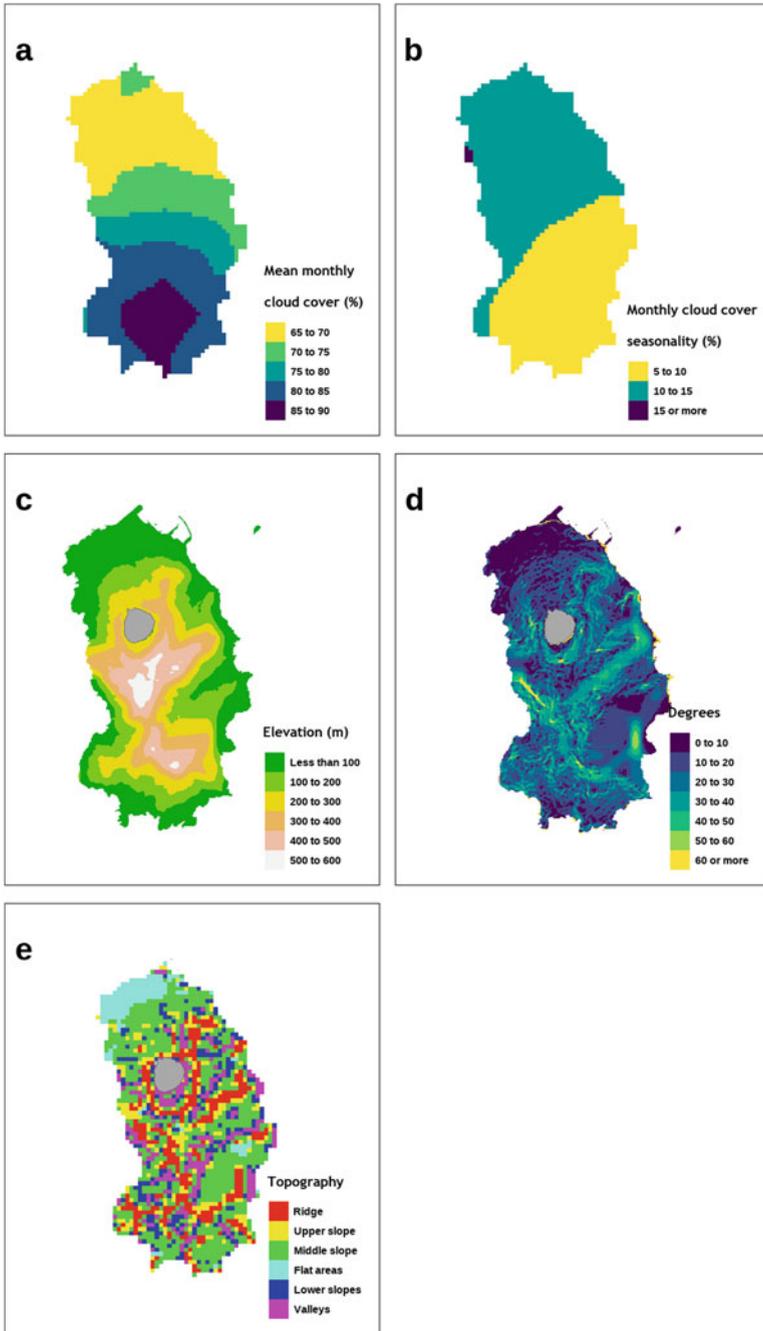
Fig. 3.6 Main physico-climatic gradients in Annobón island. The dark gray polygon represents the crater lake A Pot
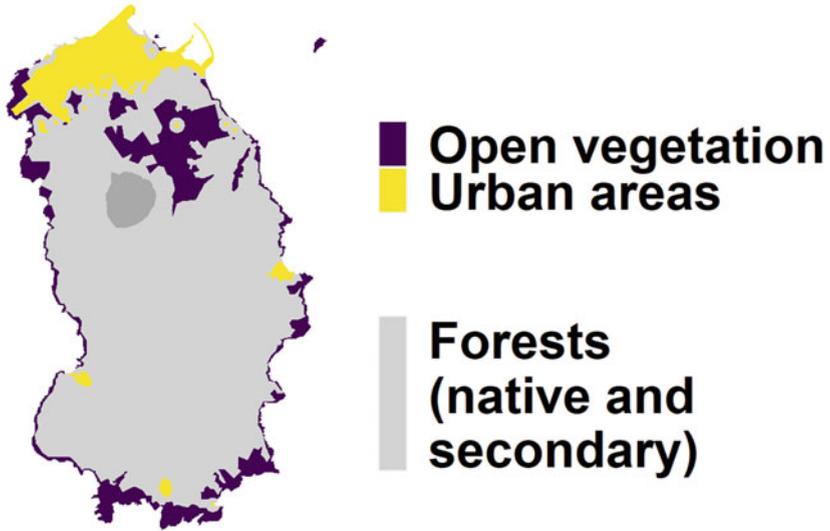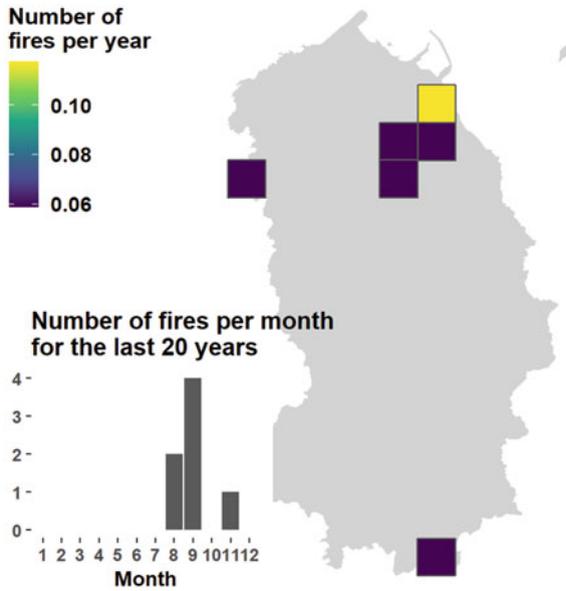
Fig. 3.7 (**a**) Degraded or transformed land cover on Annobón (Adapted from Norder et al. 2020). Note that the "open vegetation" category includes both agricultural lands and savanna-like vegetation but also naturally open vegetation type. (**b**) Annual fire frequency (data for the last 20 years). Inset barplot shows the distribution of these fires during the year

Fig. 3.8 Examples of terrestrial ecosystem types from the oceanic islands of the Gulf of Guinea. From top left to bottom right: (**1**) Mesic old-growth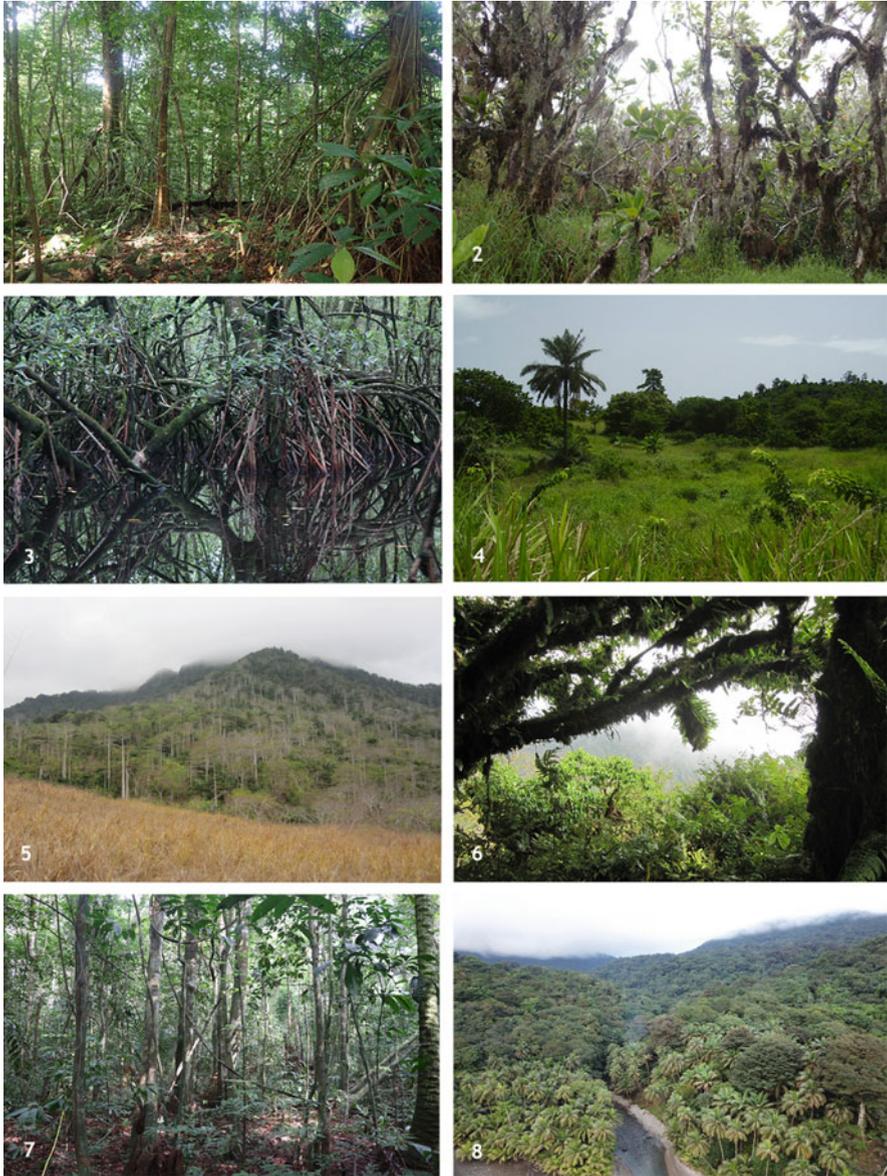 lowland rainforest in southwest São Tomé, where upper strata is dominated by *Uapaca vanhouttei* Pax 1908; (**2**) Vegetation on the Pico Pequeno characterized by small trees and shrub and the largest known population of *Erica thomensis* (Henriq.) Dorr & E.G.H. Oliv. 1999, endemic to this area; (**3**) typical mangrove with *Rhizophora* L. 1753 stilt roots in São Tomé; (**4**) the mosaic of lowland deciduous forest and savanna in the north of São Tomé; (**5**) lowland semi-deciduous forest in the background and savanna in the forefront, in Annobón; (**6**) rainforest in Annobón on the Quioveo peak above 500 m. According to the new classification, it is lowland rainforest, but the abundance of ferns and epiphyte suggests it is instead submontane rainforest similar to what can be found above 800 m in São Tomé; (**7**) Lowland

Classification Synthesis

Ecosystems are by definition open, dynamic, and scale-dependent, emerging from the interactions between organisms and the physical environment. Assuming that classifications are necessarily a simplification of reality, it makes sense to use variations in environmental conditions and biological communities to classify terrestrial ecosystems. Our goal here is to provide an updated classification, based on previous attempts and current knowledge, offering baselines for management and future scientific research on the dynamics of biodiversity.

Methodology

Spatial Information

We compiled previous classifications (Table 3.2) and mapped key ones, using QGIS (QGIS Development Team 2021) and R (R Core Team 2021) for georeferencing and analyzing spatial data. We retrieved several spatial features from Open Street Map (OSM) database using *"osmdata"* R package (Padgham et al. 2017) and other freely available shapefiles (see https://github.com/gdauby/stpa_ecosystems_review for further details on codes and data sources).

Synthetic Classification Mapping

We first considered abiotic gradients that drive potential natural ecosystems (e.g., temperature, rainfall, topography), and then vegetation types or proxies of anthropogenic impacts (e.g., secondary vegetation, shade tree plantation, fire frequency, urban area). This approach requires defining thresholds for characterizing ecosystems for continuous abiotic gradients, and acquiring spatial information on the distribution, nature, and intensity of human impacts. Thus, one map presents "potential natural ecosystems," which can be discussed in terms of potential vegetation types. A second map presents the developmental stages, resulting from natural or anthropogenic land-use changes. To analyze the relative importance of developmental stages in each ecosystem, we estimated the total area and proportion of each stage in each potential natural ecosystem. Spatial analyses were conducted in R using the packages "sf" (Pebesma 2018), "cleangeo" (Blondel 2019), and "sp" (Bivand et al. 2013) (see R codes here: https://github.com/gdauby/stpa_ecosystems_review).

Fig. 3.8 (continued) moist forest from the north of Príncipe, partly secondarized as indicated by the presence of *Elaeis guineensis* Jacq. 1763; (**8**) Lowland wet forest from the south of Príncipe. Photo credits: (1) G. Dauby, (2) D. U. Ikabanga, (3) Paula Chainho, (4) R. F. de Lima, (5,6) P. Barbéra, (7) L. Benitez, (8) T. Stévart

Annobón was excluded from this analysis because rainfall data was missing, but we still discuss similarities with the other islands.

Mapping Non-Forested Areas

To evaluate developmental stages of terrestrial ecosystems on Príncipe and São Tomé, an important first step was to identify forested and non-forested areas. To do so, we uploaded very high-resolution satellite images (sentinel-2) (https://peps.cnes.fr/rocket/) from the long dry season to minimize cloud cover. Then, we used eCognition software (Trimble Inc.) to segment spectrally homogeneous non-forest polygons based on thresholding normalized difference vegetation index. The resulting polygons were manually checked using Google Earth and added to a vector layer, which was combined with the land cover types retrieved from OSM, namely polygons identified as "scrub" and various built categories (residential, commercial). We also selected the "roads" tag polylines to be converted into polygons by adding a 10 m buffer. The final shapefiles distinguished non-forested "urban areas," "roads and path network," and "any other non-forested areas," which included agricultural land, deforested wastelands, but also naturally open vegetation types that could not be distinguished at fine scale.

High-quality satellite images were not available for Annobón, so we used the OSM shapefile to extract buildings and forest polygons. The "buildings" shapefile was edited based on Google Earth, and a 100 m buffer was added to identify areas impacted by urban activities.

Ecosystem Delimitations

The methodology is based on principles from the Ecosystemology approach recently proposed by Senterre et al. (2021). We defined regional-scale ecosystems based on relevant available abiotic gradients, namely altitude, precipitation, distance to coast, and cloud frequency. Within each of these units, we identified the distribution and extent of stand-scale units using abiotic gradients at a finer scale, such as topography, and soil features including humidity and salinity (Table 3.3). Thresholds were set based on the literature and on personal experiences and observations of the authors. Regional- and stand-scale ecosystems were listed, and their features discussed.

In parallel, we gathered spatial information on the distribution of human impacts on São Tomé and Príncipe (Fig. 3.2; Table 3.2), which were not included in the classification process, but were overlaid over the regional-scale units (Supp. Mat.). We estimated that secondary forests and shade plantations together cover over half of São Tomé and of Príncipe (28 and 27%, and 26 and 30%, respectively), while native vegetation covers around one-third or less (27 and 35%, respectively). Similar information was not available for Annobón, but recent observations suggest that native vegetation is mostly restricted to the highest peaks.

Table 3.3 Total area and relative importance of each stand-scale ecosystem defined for São Tomé and Príncipe

Ecosystem type	São Tomé	Príncipe
Montane forests	7.9 km^2 (0.9%)	–
Mesic	3.3 km^2 (0.4%)	–
On steep slope	3.1 km^2 (0.4%)	–
On ridge	1.5 km^2 (0.2%)	–
Montane low forest, grasslands, and shrublands	0.7 km^2 (0.1%)	–
Submontane rainforest	80.1 km^2 (9.4%)	0.8 km^2 (0.6%)
Mesic	39.9 km^2 (4.7%)	0.2 km^2 (0.1%)
In valley	4.5 km^2 (0.5%)	0.04 km^2 (0%)
On ridge	7.8 km^2 (0.9%)	0.1 km^2 (0.1%)
On steep slope	28 km^2 (3.3%)	0.5 km^2 (0.3%)
Lowland deciduous forests and woodlands	344.2 km^2 (40.4%)	43.4 km^2 (31.1%)
Mesic	248.6 km^2 (29.2%)	43.1 km^2 (30.9%)
On Vertisols	51.4 km^2 (6%)	–
In valleys	10.4 km^2 (1.2%)	0.1 km^2 (0.1%)
On steep slope	21.6 km^2 (2.5%)	0.2 km^2 (0.1%)
On Fluvisols	12.1 km^2 (1.4%)	–
Lowland moist and wet rainforests	459.7 km^2 (54%)	92.2 km^2 (66.2%)
Mesic	329.6 km^2 (38.7%)	74.3 km^2 (53.3%)
On ridge	30.7 km^2 (3.6%)	4.8 km^2 (3.4%)
On steep slope	63.6 km^2 (7.5%)	9.3 km^2 (6.7%)
In valleys	24.2 km^2 (2.8%)	3.8 km^2 (2.8%)
On Fluvisols	11.6 km^2 (1.4%)	–
Coastal ecosystems	10.4 km^2 (1.2%)	2.6 km^2 (1.9%)
Undifferentiated shores	9.2 km^2 (1.1%)	2.1 km^2 (1.5%)
Mangroves	0.9 km^2 (0.1%)	0.02 km^2 (< 0.1%)
Sandy shores	0.3 km^2 (< 0.1%)	0.4 km^2 (0.3%)
Palustrine areas	0.1 km^2 (< 0.1%)	0.1 km^2 (< 0.1%)

All classifications produced in this chapter and associated resources are accessible online (https://github.com/gdauby/stpa_ecosystems_review).

Coastal Ecosystems

The coasts of São Tomé, Príncipe, and Annobón are approximately 204, 100, and 35 km long respectively, and include mangroves, other palustrine areas, sandy coasts, and cliffs.

At the interface between terrestrial, freshwater, and marine realms, mangroves are the most distinctive coastal ecosystems on the islands (Herrero-Barrencua et al. 2017; Afonso 2019). On São Tomé, at least 14 mangroves areas persist (Fig. 3.8). Malanza and São João dos Angolares are the largest, and Malanza and Praia das

Conchas are the only ones within a protected area. In Príncipe, mangroves persist at Praia Caixão, Praia Grande, and Praia Salgada. Even though there is no estimate of the lost mangrove area, past distribution was certainly wider, especially in the north of São Tomé (Herrero-Barrencua et al. 2017). Mangroves are absent on Annobón (Juste and Fa 1994).

Other estuarine ecosystems often occupy similar conditions surrounding mangroves, some of which might have resulted from mangrove degradation on São Tomé. Sandy coasts are sparsely distributed across the three islands and host distinct psammophile communities.

Cliffs are frequent but their distribution and associated biota are poorly characterized. In the south of São Tomé, dense populations of *Pandanus thomensis* Henriq. 1887 frequently colonize them. Given its distinct edaphic properties, this ecosystem might be less impacted by human activities than others, but its vulnerability to invasive species remains unknown.

At least 15% of the coast of São Tomé and 12% of that of Príncipe have been strongly impacted and transformed into urban areas or roads. More than 50% of coastal ecosystems on São Tomé and 13% in Príncipe are covered by, or are next to secondary forests or shade plantations (Supp. Mat.).

Non-coastal Wetlands

Non-coastal wetlands include all habitats that are seasonally or permanently inundated by freshwater. We distinguished riverine forests, waterfalls, lowland swamp, and montane swamps.

Riverine forests can be defined as areas that are influenced by river soaking and flooding. Their distribution, extent, and associated biological communities are poorly characterized in the GGOI. Their width is expected to be small, considering most valleys are narrow, but this influence can be larger, particularly in flatter areas.

Waterfalls display specific geomorphic and micro-habitats features with strong but very localized, environmental heterogeneity and originality (Clayton and Pearson 2016). They also act as natural barriers, dividing streams and their associated biotas into distinct populations. Their biota characteristics and ecosystem functions have rarely been investigated in tropical regions, but some studies have highlighted their ecological and conservation significance (Baker et al. 2017). The distribution and ecological characteristics of waterfalls in the GGOI are not well known and deserve further attention, especially since they may be threatened by dams in the near future.

Lowland swamps are infrequent and small on São Tomé but seem to be somewhat more widespread in the northern plateau of Príncipe. This situation contrasts with continental central Africa, where swamp forests are frequent and harbor specific biological communities (e.g., Boupoya et al. 2017), but almost nothing is known about swamp forests in the GGOI. We do know, however, that large areas of Príncipe's swamps were drained during the tsetse eradication campaign in the early twentieth century (da Costa et al. 1916).

The only significant example of a montane swamp is the Lagoa Amélia, at c. 1400 m on São Tomé. Floristically, there is no evidence that this area has a distinct assemblage, but it represents a unique combination of environmental conditions in the GGOI, being a super humid, high-altitude swamp.

Inland Uplands

Inland uplands represent almost the entirety of the GGOI. In São Tomé and Príncipe, we divided them first by elevation, by thresholds at 800 m, 1400 m, and 1800 m, and then by the 2000 mm annual rainfall threshold. This allowed us to distinguish (1) lowland deciduous forests, (2) lowland moist and wet forests, (3) submontane rainforests, (4) montane forests, and (5) montane shrublands and grasslands. For each of these, we identified abiotic factors that may exacerbate or mitigate the local influence of temperature or water availability relative to the mesic environment. Namely, we considered specific soil types, slopes with steep gradients, and specific topographic categories, such as valleys and ridges. Steep slopes ($> 30°$) are likely to have superficial soils (Lithosols), increased susceptibility to erosion (landslides), and distinct micro-climate due to stronger (or weaker) insolation, depending on the aspect (Chapin III et al. 2011). They are also less directly threatened by anthropogenic activities.

Lowland Deciduous Forests

Occurring up to 800 m of elevation and registering <2000 mm of rainfall annually, these ecosystems are mostly found on the flat or gentle slopes of northern São Tomé. Given the limited rainfall, lower cloud frequency, and higher temperatures, water availability is probably the main limiting factor for vegetation growth. Vegetation composition and physiognomy also support the local influence of edaphic or topographical features. As such, we distinguished (1) forests on flat terrain and Fluvisols, (2) forests on flat terrain and Vertisols, (3) forests in valleys, and (4) forests on steep slopes. Almost none of this native forest vegetation remains, but we can assume the vegetation type in mesic conditions should have been a (semi)-deciduous or dry forest.

Fluvisols occur along large rivers on flat terrain, and are usually susceptible to occasional flooding. Native vegetation must have been moist semi-deciduous forest with higher frequency of species tolerant to poorly drained soils. This is the most disturbed ecosystem on São Tomé; ca. 23% are covered by roads and urban areas, and more than 30% by open agricultural land (Supp. Mat.). Fluvisols are infrequent on Príncipe (Diniz and Matos 2002).

Forest on flat terrain and Vertisols is only found on São Tomé, where it corresponds mostly to savanna-like vegetation. Soil moisture on Vertisols is highly variable, leaving plants vulnerable to drought. However, it is noteworthy that there are no indications that these savannas existed when human colonization started on

São Tomé, 500 years ago. It has been proposed that any such areas originally covered by the dry forest were lost to fires and sugarcane plantations (Diniz and Matos 2002). Later on, sugarcane production was mostly abandoned, but forests could not reestablish due to changes in soil properties and to regular fires during the dry season (Fig. 3.2). Nowadays, more than half of this area has open vegetation, mainly savanna-like but also agricultural lands, and around 15% has been converted to urban areas or to roads. Several plant communities occur in this mosaic of forest and savannas, where the landscape is locally dominated by the African baobab *Adansonia digitata* L. 1759. This complex mosaic might present some similarities with the north of Annobón, nowadays mostly occupied by urban areas.

In large and narrow valleys, particularly in the extreme north of São Tomé, water is less limited thanks to run-off from the central highlands. Floristic composition (Diniz and Matos 2002, personal observations) suggests that this specific topography holds distinct plant communities. This stand-scale ecosystem may also be significant for conservation as it might host the last remnant of lowland moist forests in the north of São Tomé, as almost all of these have been converted to shade cacao plantations, urban areas, and roads.

The forests surrounding the large valleys of São Tomé occur on the steep slopes, occupying a significant area (Table 3.3) that is less directly impacted by human activities, although most of these are nevertheless secondary forests.

Lowland Moist and Wet Rainforests

This regional-scale ecosystem includes all areas up to 800 m of elevation and above 2000 mm of annual rainfall, which are less limited by water availability due to lower seasonality. We considered topographic and soil features to distinguish forests (1) in valleys, (2) on ridges, (3) on steep slopes, and (4) on Fluvisols. Natural vegetation in mesic conditions is undoubtedly rainforest that still occupies most of São Tomé and Príncipe, even if most is secondary. On São Tomé, industrial palm plantations occupy more than 5% of this ecosystem. Overall, we estimate that native forests persist in <40% of its original area.

Forests in valleys occupy 4% of this region-scale ecosystem in Príncipe and 5% in São Tomé.

Forests on ridges have limited extent both on Príncipe and São Tomé but also seem to have been less impacted, due to their lower accessibility and reduced potential for agriculture. The biological communities here are poorly known. It has been suggested that lowland peaks, such as the Pico Maria Fernandes on São Tomé and Morro Fundão on Príncipe, host distinct plant assemblages that are more closely related to submontane vegetation than to surrounding lowland forests (Stévart 1998; Ogonovszky 2003). Biota and physico-climatic similarities of lowland ridges between the GGOI are likely and should be assessed. Indeed, these specific habitats are covered by low and open vegetation, close to those occurring on mainland inselbergs. However, the proximity to the ocean should increase moisture even

during dry seasons, allowing for the development of a distinct vegetation type in these rocky places.

Forests on steep slopes occupy a significant extent and also seem to have been less impacted than other forest types due to their lower accessibility and potential for agriculture.

Forests on Fluvisols have only been identified in the large watersheds of Iô Grande and Xufe-Xufe on São Tomé. These correspond to flat lowland areas near the coast and that have thus been strongly impacted by human activities, namely by agricultural development.

Submontane Rainforest

Submontane rainforests include areas between 800 and 1400 m, and apart from mesic conditions, we distinguished forests (1) on ridges, (2) on steep slopes, and (3) in valleys. On São Tomé, we estimated that 9% of the potential area for submontane rainforest is currently non-forested, most of which is agricultural, while 15% is secondary forest and 2.5% shade forest. The extent on Príncipe is very limited (Table 3.3) but has been spared from human activities. A small portion of this territory (>5%) appears to be non-forested, probably due to natural treeless Lithosols. Annobón has no area above 800 m and thus submontane rainforests may not occur there (but see discussion).

Forests on ridges are often characterized by the endemic gymnosperm *Afrocarpus mannii* (Hook.) C.N. Page 1989. They represent nearly 10% of submontane forests on São Tomé, while forests on steep slopes represent almost 35%. Both these forest types are likely to be spared from direct human disturbances, even though natural disturbances, such as landslides, are probably frequent.

Montane Forests

The area between 1400 and 1800 m is restricted to São Tomé and includes mainly montane rainforests. This ecosystem is almost intact, although introduced plant species can be locally abundant (e.g., tree species *Cinchona* spp. L. 1753). We distinguished (1) forests on ridges, (2) forests on slopes and plateau, and (3) montane grasslands.

Montane forests on ridges occupy nearly 20% of this region and are similar to submontane ridge forests, as indicated by the sun-loving tree *Afrocarpus mannii*, but also by herbs such as *Begonia thomeana* C. DC. 1892 and *Mapania ferruginea* Ridl. 1887. Forests on slopes and plateaus remain poorly documented because of their limited accessibility, even though they represent nearly half of this region. Both submontane and montane forests are characterized by forest species like *Palisota pedicellata* K. Schum. 1897, *Homalium henriquesii* Gilg ex Engl. 1921 *Tabernaemontana stenosiphon* Stapf 1895, and *Craterispermum cerinanthum* Hiern 1877 (formerly *C. montanum* Hiern 1877 but considered as synonym by

Taedoumg (2020)). However, certain montane forest species, such as *Symphonia globulifera* L. f. 1782, can also be found on ridges at lower elevations, indicating that the transition between submontane and montane forest depends on the local topography, a topic that surely deserves attention in future studies. The physiognomy and the floristic composition of the montane grassland have been relatively well described, but its precise extent is unknown.

Montane Low Forest, Grasslands, and Shrublands

We consider this ecosystem above 1800 m as distinct from the Montane Forests because of its specific physiognomy characterized by the frequency of shrubby vegetation and smaller trees on ridges. Grass mat is also abundant along the ridges, but these grasslands can also be observed at lower altitude along ridges. The presence of plant taxa such as *Erica*, *Lobelia*, and the tree *Balthasaria mannii* (Oliv.) Verdc. 1969 makes this ecosystem as the most distinct in the GGOI, showing affinities to biological assemblages observed in other mountains ranges, such as on Bioko and in East Africa (Monod 1960). In addition to its unique species assemblage, the upper montane area of São Tomé also seems to display distinct abiotic properties. The "prevalent mist" of the "mist rainforests" is impressive but might be less important for the development of this specific community than the superficial soils (Exell 1944). Indeed, as Monod (1960) described, the area above 1800 m is often above the clouds and therefore tends to be relatively dry (especially during the dry season), while the montane and submontane forests at lower altitude remain wetter thanks to the nearly permanent mist (Fig. 3.1). Monod (1960) even noticed (in August, hence at the end of the dry season) that the vegetation was dry enough to be vulnerable to fires.

Besides ecotourism activity (which may bring seeds of invasive species, foster clearings along ridges, and provoke accidental fires during the dry season), this ecosystem has been mostly spared from direct human degradation. However, it may very well be one of the most threatened, considering its narrow distribution (ca. 0.66 km^2), the impact of climate change, and the spread of invasive species, in particular *Cinchona* spp. trees. This genus has been considered among the most invasive in many tropical islands (Jäger 2015), and especially in naturally treeless environments (Jäger et al. 2007). We do not know if these taxa are replacing native plant populations, but it is the dominant species (mono-dominant locally) along several ridges. This may be the consequence of vegetation clearings in the past and *Cinchona* plantings (Monod 1960).

Discussion

Defining ecosystems as discrete units is a simplification (Boitani et al. 2015) but can be useful to facilitate our understanding of a complex reality (Senterre et al. 2021). While the delineation of some ecosystems is straightforward, it is often not the case because transitions are usually not abrupt (Exell 1944; Monod 1960). The classification we propose tries to improve on existing classifications based on the best available data, to provide better baselines for management, and for testing hypotheses regarding biodiversity dynamics. This synthetic classification is thus likely to evolve as more data become available, namely regarding the distribution of ecosystems, and specifically of vegetation types on different islands. For future reference, all maps and spatial information are available on an open-access portal (https://github.com/gdauby/stpa_ecosystems_review).

Below, we point out several pending questions and challenges that became apparent during this exercise and that could help guide future research on the terrestrial ecosystems of the GGOI.

Is It Still Valid to Define Ecosystems Based on Altitude?

Most changes in large units of natural vegetation in the GGOI, and in the distribution of species, appear to be associated with altitude, explaining why the first naturalists (Exell 1944; Monod 1960) focused on the influence of this environmental gradient on biological communities. Altitude (i.e., a proxy for temperature pattern) interacts with topography and rainfall, creating micro-environmental conditions that can affect vegetation at a fine scale, and that remain poorly understood due to their subtle variations and complex effects on the distribution and abundance of species. Moreover, the intensity of anthropogenic disturbances interacts with this natural complexity, further complicating our understanding of ecosystem dynamics. As an example, these disturbances (and deforestation in particular) are typically more intense in the lowlands, where several populations of native species might have already been extirpated. In this scenario, their current distributions are artificially correlated with altitude, misguiding our understanding of the ecology of those species.

Even if altitude is still the best available proxy for delimiting large natural vegetation types, it may be hard to understand, or even misleading when trying to infer drivers of species distribution. For example, if those drivers are linked to precipitation or moisture, (sub)montane species may persist as satellite populations at lower altitudes where micro-habitats are sufficiently humid, such as deep valleys or riverine areas. Setting a threshold of 800 m for submontane forest, as we did, means this forest type does not occur on Annobón where the maximal altitude is 600 m. However, the description of the floristic and physiognomic features of the forest above 500 m (Peris 1962) does suggest some similarities with submontane

forests found on São Tomé. If confirmed, this would suggest that humidity matters more than altitude for defining submontane forest. Comprehensive surveys of biota and physical features are still required across the islands to improve our understanding of the distribution of vegetation types and underlying environmental drivers.

What Is the Extent of Novel Ecosystems?

All three islands have high proportions of introduced species, whose frequency and abundance vary between ecosystems. Increasing proportions of introduced species can lead to changes in ecosystem functioning (Wardle et al. 2011). These taxonomic and functional turnovers can lead to the development of "novel" ecosystems resulting from human intervention; i.e., the ecosystem becomes self-sustaining in an alternative stable state (Hobbs et al. 2009; Morse et al. 2014). Applying these concepts for characterizing altered ecosystems is key for conservation and management, especially in oceanic islands where ecosystems are more prone to the threats posed by introduced species (Sax and Gaines 2008; Morse et al. 2014). Novel ecosystems, such as secondary vegetation and plantations, cover most of the GGOI and are far from homogenous, presenting a wide variety of species assemblages. The functioning of these new assemblages, whether they differ from that of native ecosystems and affect ecosystem services, remains to be investigated.

Which Factors Drive the Establishment of Novel Ecosystems?

The development of novel ecosystems results from the expansion of introduced species, which often but not always results from anthropogenic land-use changes (Morse et al. 2014). Novel ecosystems in the GGOI, and their accompanying introduced species, are probably more widespread in active and abandoned lowland agricultural areas, where historical land-use changes have been more significant (Muñoz-Torrent et al. 2022). This has already been shown for GGOI birds (Soares et al. 2020), and mollusk species assemblages (Panisi et al. 2022), for which invasion success is highest in the lowland areas. Nevertheless, although less abundant and diverse than in the lowlands, introduced species also occur in highland ecosystems where native vegetation largely dominates. Similar patterns are expected for other groups, such as plants. For example, species of *Cinchona* can be locally dominant in lower strata of montane and submontane forests, where it was planted for bark production (Chevalier 1938–1939). Populations of this species persist in old-growth forests, but it is unknown if they are spreading and replacing native species. In Estação Sousa on São Tomé, few individuals persist (unpublished results) in an area that was a plantation over 100 years ago (Chevalier 1938–1939). It is crucial to assess the vulnerability of highland ecosystems to introduced species,

since these endemic-rich and diverse ecosystems have so far been the least impacted by human activities (Muñoz-Torrent et al. 2022).

How to Prioritize Conservation Efforts?

An understanding of the distribution of endemic and threatened species across ecosystems is necessary for allocating conservation efforts. Unfortunately, this information remains insufficient for several areas and clades (Stévart et al. 2022; Nève et al. 2022). Available data suggest that endemism tends to be higher in submontane and montane ecosystems (Stévart et al. 2022). On the other hand, lowland ecosystems are the most impacted and are often undersampled. For example, the extreme north of São Tomé hosts a complex mosaic of forest and savannas that is probably the best example of a novel ecosystem in the GGOI. Most scientists have focused on endemic-rich ecosystems, which at least partly explains why flora and fauna in the extreme north remain undersampled (Stévart et al. 2022). However, recent fieldwork (unpublished results) has led to the identification of some endemic plants, including two putative new species, suggesting that native biodiversity persists in these ecosystems. These discoveries highlight the importance of these areas for conservation, emphasizing the urgent need for further studies in novel ecosystems, particularly since native populations persisting in these areas may be some of the most vulnerable to extinction.

How to Improve Ecosystem Monitoring Through Space and Time?

Efficient ecosystem monitoring cannot rely solely on field observations, as these demand too many resources. The use of remote sensing data can help extend current assessments, in particular to document vegetation features and dynamics, but so far, these have been limited by their coarse resolution, which are not appropriate to study the complex landscapes of the GGOI. The availability of spectroscopic data and analytical tools is constantly improving and, in combination with in situ observations, might enable meaningful ecosystem monitoring in the near future (Cavender-Bares et al. 2020). For example, hyperspectral images could help characterize the dynamics of introduced plant species and thus infer the distribution of novel ecosystems.

The Need for a Unified Classification of Ecosystems for Central Africa

Island ecosystems are ideal natural experiments to test hypotheses regarding the links between biodiversity and ecosystem properties (Pimm 1984). To investigate these hypotheses, it is useful to define ecosystem units that are transferable across regions. In practice, such classification is challenging because there is no clear definition on how ecosystems should be identified (but see Senterre et al. 2021), despite international initiatives such as the Red List of Ecosystems (Keith et al. 2013). We support the development of an ecosystem classification that can be shared between the GGOI and continental Africa, as it would allow comparative studies that could greatly improve our understanding of regional biogeography and patterns of species diversity.

Conclusions

The three GGOI present similar humidity gradients, increasing from the northeast to the southwest due to the rugged topography and resulting foehn effect. These gradients, along with altitude and anthropogenic disturbance, can be used to identify distinct ecosystems and their distributions, and help to explain differences between islands. The high concentration of biotic and abiotic complexity in these small island territories creates unique combinations of features that shape ecosystem properties, making them ideal for studying the dynamics of tropical ecosystems. However, much of what is known about the GGOI is based mostly on São Tomé: by far the best known but also the most diverse island. Overcoming existing knowledge gaps will require multidisciplinary, collaborative frameworks and research agendas, which in turn rely on long-term observatories and capacity building. We hope that the synthetic ecosystem classification we have presented in this chapter, together with all the underlying resources that we have made available, will foster the future research needed for a better understanding and conservation of the tropical ecosystems of the GGOI.

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