

Tropical island forests under environmental change: policy, biodiversity, and use

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Abstract

We are witnessing large declines in biodiversity driven by anthropogenic environmental pressures, such as land-use change leading to ecosystem degradation and shifts in species assemblages. Addressing this crisis requires interdisciplinary approaches, including policy, ecological, and socio-ecological analyses. This thesis focusses on forests and islands, as they are inherently vulnerable to biodiversity loss.

First, it investigates how the 39 members of the Alliance of Small Island States considered forests in climate policy as a vehicle for simultaneously enhancing biodiversity. Content analysis of national climate action plans revealed that proposed forest-based climate solutions mostly failed to integrate biodiversity, representing a missed opportunity for tackling the climate and biodiversity crises together.

It further analyses how tree diversity and Nature's Contributions to People (NCP) linked to trees vary between urban, rural, and natural zones on the Afrotropical oceanic island of São Tomé. Tree surveys showed that abundance and species richness were significantly higher in the natural zone, especially for native and endemic species. The dominance of introduced species in the other zones further indicates how these have been subject to biotic homogenisation.

In contrast, the recognised potential of trees to deliver NCP varied among zones. Regulating and non-material contributions were concentrated in urban and rural zones, where introduced species abounded. Trees associated with delivering biomass-intense material contributions, namely “materials and assistance” and “energy”, were particularly abundant in the natural zone.

This thesis highlights the potential for aligning forest-based climate solutions with biodiversity. However, these measures need to consider anthropogenic gradients and specific contexts. On São Tomé Island, the protection and restoration of old-growth forests is a top priority for preserving native and especially endemic tree species. The ecological value of rural and urban zones needs to be enhanced, and introduced species should only be considered there when they are the sole providers of particular NCP. Enriching the scientific base regarding the integration of biodiversity conservation, societal needs, and climate targets can contribute to making forest strategies more sustainable.

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Abbreviations

ANOSIM	Analysis of similarities
AOSIS	Alliance of Small Island States
CBD	Convention on Biological Diversity
CICES	Common International Classification of Ecosystem Services
COP	Conference of the Parties
ENACT	Enhancing Nature-based Solutions for an Accelerated Climate Transformation
HFLD	High forest cover and low deforestation
ILK	Indigenous and local knowledge
IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature
LULUCF	Land use, land-use change and forestry
MA	Millennium Ecosystem Assessment
NAPA	National Adaptation Programme of Action
NBS	Nature-based solution
NBSAP	National Biodiversity Strategy and Action Plan
NCP	Nature's Contributions to People
NDC	Nationally Determined Contribution
NMDS	Non-metric multidimensional scaling
PCNM	Principal coordinates of neighbour matrices
PERMANOVA	Permutational multivariate analysis of variance
PERMDISP	Permutational multivariate analysis of dispersion
REDD	Reducing emissions from deforestation and forest degradation
UN	United Nations
UNEP	United Nations Environment Programme
UNFCCC	United Nations Framework on Climate Change

1 Introduction

1.1 Background

Global biodiversity loss has become evident for the last 100 to 200 years, understood to be a major consequence of anthropogenic environmental change (Ceballos et al., 2015; Le Roux et al., 2019). In terrestrial realms, the direct human drivers causing this decline are, in decreasing order of importance, land-use change, overexploitation, pollution, climate change, and species invasions (Jaureguiberry et al., 2022). These, in turn, are influenced by socio-cultural, economic, demographic, political, institutional, and technological changes (Díaz et al., 2019). Biodiversity loss can have serious implications for ecosystem resilience and functioning (Mori et al., 2013), and may negatively affect Nature's Contributions to People (NCP), which are important for good quality of life (IPBES, 2019).

Although biodiversity loss is a global phenomenon, it is prominent on islands, where extinction rates are the highest (Gray, 2019). Many islands are an integral part of biodiversity hotspots, which have been identified in areas that have lost 70 % or more of their primary vegetation and contain as endemics at least 0.5 % of the world's plant species (Myers et al., 2000). Islands are indeed a central aspect of the current biodiversity crisis. Despite only occupying 7.4 % of the land surface (Sayre et al., 2019), they hold between 15 and 20 % of known terrestrial biodiversity (Whittaker et al., 2017) and around half of all threatened species (Fernández-Palacios et al., 2021). There can be time lags between an event that represents a threat and species loss (Otto et al., 2017), which means that even without further anthropogenic pressures, more island endemics are likely to be lost unless countermeasures are implemented (Wearn et al., 2012).

The following sections explain the relevant background to this thesis by covering three main topics: The first one describes how interdisciplinary research, as conducted in this work, can contribute to improving the dialogue between biodiversity science and policy, in response to the biodiversity crisis. The second topic deals with forests and more specifically trees as possible solution approaches to anthropogenic environmental impacts, but also highlights the role of this vegetation type for terrestrial biodiversity and human well-being. The final section deals with islands as the model systems of this thesis. It highlights how island forests are paramount to the survival of island biota, and how this unique but vulnerable biodiversity sustains island people, who need to manage it.

1.1.1 Biodiversity science and policy

To halt biodiversity loss, multidimensional knowledge is fundamental. How to best generate such knowledge remains however debatable, as this can involve both science and policy and divergent theories about their relationships exist (Maas et al., 2022). Biodiversity science and policy can be regarded as two autonomous fields that may occasionally enrich each other (Figure 1.1) (Boswell and Smith, 2017). For instance, increased data sharing over more than two decades has allowed for great scientific progress on insular species distribution patterns, facilitating macroecological analyses (Fernández-Palacios et al., 2015). On the policy side, island governments have been active players in global environmental forums, developing progressive national policy documents without sufficiently involving scientists. The linear model, in contrast, assumes that science provides knowledge for policy to find solutions (Young et al., 2014), i.e. resulting in evidence-based policy (Nutley et al., 2007). For example, forest researchers may directly feed their knowledge into policy activities led by the Convention on Biological Diversity (CBD). This can cause tensions, however, with policy-makers sometimes asking scientists for precise recommendations (Ojanen et al., 2021). On the other hand, there is the reversed model that claims that political projects influence science (Smith, 2010), e.g. through providing funding schemes. This pathway is often criticised for lacking independence (Boswell and Smith, 2017), and it may be particularly problematic in tropical countries where national funds tend to be limited (Barber et al., 2014).

Increasingly, these three models of science-policy relations are being replaced by the concept of “co-production” (Miller and Wyborn, 2020). This approach acknowledges that science and policy are inseparable (Maas et al., 2022), leading to knowledge-producing processes that are non-linear, complex, sometimes iterative, and require diverse actors (Norström et al., 2020). In this case, policy is merely evidence-informed (Bandola-Gill et al., 2022). For instance, macroecology has the potential to co-produce knowledge with biodiversity policy. This can be facilitated by formal science-policy interfaces, such as the Intergovernmental Platform for Biodiversity and Ecosystem Services (IPBES) (Hof et al., 2015), which emerged in 2012 (Tinch et al., 2018). Forums and workshops that bring scientists and policy-makers together are promising ways forward, but these individuals must bring in the right type of information to adequately support such exchange formats (Young et al., 2014).

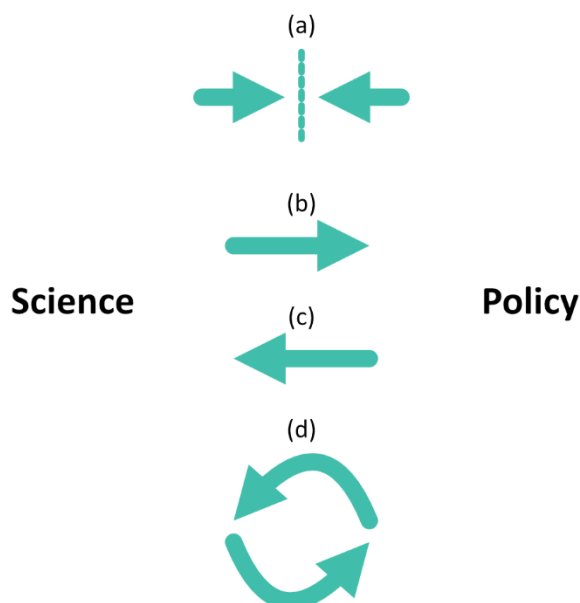


Figure 1.1. Four models showing the possible relations between biodiversity science and policy, in which they are regarded either (a) as isolated fields, (b) as science shaping policy, (c) as policy shaping science, or (d) as co-producing fields (modified from Boswell and Smith, 2017).

Knowledge co-production between science and policy can potentially make biodiversity conservation more effective when linked with trans- and interdisciplinary research (Young et al., 2014). More interdisciplinary research is needed to stimulate dialogues at science-policy interfaces. For instance, it may be insightful to analyse how policy documents integrate findings from biodiversity science, or analyse socio-ecological patterns that may have important messages for conservation policies. Eventually, the results from interdisciplinary work may allow for a more fruitful discussion in knowledge co-production processes.

1.1.2 Forests and trees

More dialogue between science and policy is also needed with regard to forest definitions. Forests have long been defined as land areas of more than 0.5 ha covered by over 10 % with a canopy of trees that are capable of reaching 5 m in height (FAO, 2000). Other definitions emphasise forest use over cover, focussing on timber production, carbon storage, or livelihood support, and yet others are based on the distinction of natural ecosystems vs. plantations, continuity vs. fragmentation, or native vs. introduced species (Chazdon et al., 2016). However, all these definitions fail to address the functional, structural, and compositional attributes, on which biodiverse, productive, and resilient forests depend (Vásquez-Grandón et al., 2018).

Being clear on what makes a forest is critical when determining strategies to tackle the biodiversity and climate crises, as the most significant environmental challenges. Especially in the current age in which forest restoration is a common policy objective, definitions play a big role (Chazdon et al., 2016). In this context, forests are increasingly gaining attention as nature-based solutions (NBS) for climate change mitigation. The aim is usually to enhance the quantity of carbon stocks via forest restoration. Yet, this could be achieved through monoculture plantations without considering forest quality, which is connected with biodiversity – an aspect that is particularly important for climate change adaptation (Seddon et al., 2021).

In the study of biodiversity loss and environmental change, forests are highly relevant because they are major habitats for species on land. For example, over half of the Earth's terrestrial biodiversity is found in tropical forests (Barlow et al., 2018; Pillay et al., 2022), but the human impact on these ecosystems is growing, resulting in forest degradation and loss (Lewis et al., 2015). Trees, as distinct plant growth form, are key structural elements of forests and significant primary producers; therefore declines can affect many taxonomic groups (Lindenmayer et al., 2014). Approximately one-third of all tree species are threatened with extinction, however (Rivers et al., 2023). Moreover, trees are essential components of urban ecosystems (Stagoll et al., 2012), yet urban tree cover is experiencing losses, particularly in Africa (Nowak and Greenfield, 2020).

Trees are vital to the health of not only our planet but also our people (Turner-Skoff and Cavender, 2019). In human-dominated landscapes, trees are often deliberately planted and maintained (Etongo et al., 2015) because they provide timber, erosion control, and spiritual value among other NCP (Martín-Forés et al., 2020; Sahle et al., 2021). Defined as “all the contributions, both positive and negative, of living nature (diversity of organisms, ecosystems, and their associated ecological and evolutionary processes) to people's quality of life” (Díaz et al., 2018), NCP are categorised into regulating, material, and non-material contributions (IPBES, 2019). The NCP conceptual framework, a relatively recent product of IPBES, supports inter- and transdisciplinary thinking, taking different interests, worldviews, and values into account. It recognises the importance of culture as the linking element between people and nature and encourages the inclusion of various knowledge systems (Díaz et al., 2018).

The NCP conceptual framework is understood to go beyond the ecosystem service concept, which gained popularity following the Millennium Ecosystem Assessment (MA) (Millennium Ecosystem Assessment, 2005b). The MA regards ecosystem services as “the benefits people obtain from ecosystems” (Millennium Ecosystem Assessment, 2005a) and distinguishes between supporting, regulating, provisioning, and cultural services. To enable a categorisation at finer resolution, the Common International Classification of Ecosystem Services (CICES)

was built on this. CICES however focusses on measuring final services, thus excluding supporting services, that underpin final services, and the resulting goods and benefits (Haines-Young and Potschin, 2018). Both the MA and CICES emphasise environmental-economic valuation, favouring an anthropocentric perspective (Bastos Lima and Palme, 2022).

Some critics have argued that the NCP approach lacks novelty, not sufficiently differing from its forerunner, the ecosystem service concept (Braat, 2018). Existing ecosystem service literature largely relates to economic and biophysical assessments, but it has, to some extent, also been inclusive of social sciences, value pluralism, culture, and indigenous and local knowledge. Nonetheless, NCP put more weight on these aspects and formalise some of the more recent trends in ecosystem service research, while also covering novel conceptual claims (Kadykalo et al., 2019): Diverse worldviews and knowledge systems are central to NCP, whereas ecosystem services align with a Western-scientific perspective (Bastos Lima and Palme, 2022). Accordingly, the NCP conceptual framework supports context-specific perspectives (Peterson et al., 2018), which are based on socio-cultural perceptions, or cosmologies, of humans and the environment. Hence, it may also represent a more effective communication tool. In addition, it is potentially more suitable for the study of relational values, which have gained little attention in the ecosystem service literature (Kadykalo et al., 2019). These values, linked to the cultural identity of people, may have implications for conservation rooted in legal rights (James, 2020). NCP also allow for more fluidity between categories (Kadykalo et al., 2019), which reflects the reality that some contributions cannot be unequivocally assigned to one group of NCP. However, this is what the ecosystem service concept pursues for economic valuation.

This thesis considers both NCP and ecosystem service literature but applies NCP for a number of reasons: Thanks to the fluidity between NCP categories (Kadykalo et al., 2019), supporting services as outlined in the MA are implicitly integrated, making this somewhat ambiguous category redundant, which facilitates communication between stakeholders. Compared to CICES focussing on final services and their sources, such as “cultivated terrestrial plants for nutrition, materials, or energy” (Haines-Young and Potschin, 2018), the 18 NCP reporting categories may also allow for greater applicability beyond economic and biophysical measurements, which typically correspond with Western thinking (Bastos Lima and Palme, 2022). Especially in contexts of forest dependency, benefits from nature are strongly linked to worldviews, values, and knowledge of local communities. The NCP approach has been explicitly suggested for the study of socio-ecological systems in which strong connections between humans and nature through culture exist (Ellis et al., 2019; Dean et al., 2021). Moreover, the pluralistic nature of NCP may be especially apt to encourage transformative change towards more sustainable pathways (Pascual et al., 2017). Finally, IPBES, as the most

influential science-policy platform for biodiversity, pushes this conceptual framework, e.g. in their global and regional assessments, and will continue to do so in the near future.

1.1.3 Islands as model systems

One of the most distinctive features of islands is their isolation, something that is particularly evident for marine islands (i.e. land surrounded by the ocean), which are the focus of this thesis. One-third of them are located in the tropics (Weigelt et al., 2013), which is relevant since tropical species are generally more sensitive to environmental change (Newbold et al., 2020). Darwin and Wallace categorised marine islands into ancient continental, recent continental, and oceanic islands. However, this broad classification system from the 19th century has been contested due to ambiguities (Whittaker et al., 2017). The newly proposed typology of islands distinguishes between continental, intra-oceanic arc, mantle-plume hotspot, composite terrane, and leftovers as the different geophysical settings providing substrate for flora and fauna. This also means that oceanic islands are in fact a relatively diverse group of islands that do not simply fall into one of these categories. What further influences insular biological communities is the way that they colonise islands, and there can be more than one type per island: deep-time vicariant, recent ice-sheet, recent land bridge, and overwater dispersed (Ali, 2017). For the purpose of this thesis, I will continue to broadly refer to oceanic islands, as the island biology literature is based on this traditionally accepted group. Since oceanic islands are typically said to host many endemics, they are especially interesting from a biological point of view.

For centuries, naturalists have been fascinated with islands, which facilitated major breakthroughs in evolutionary and ecological theories as “living laboratories” (Warren et al., 2015). This interest in island research is currently experiencing a renaissance (Fernández-Palacios et al., 2015). The same properties for which islands allowed major scientific progress in the past are also valid in the future (Santos et al., 2016): Islands are valuable study systems. When looking at them as a group, they can be seen as replicated entities (Warren et al., 2015) that also cover a wide range in area, remoteness, geology, altitude, and climate (Weigelt et al., 2013). In addition, islands are ideal models because they work like microcosms. They have closed boundaries, are small in size and are less complex than mainland study systems, which is why relatively complete data sets can be obtained for them (Kueffer and Kinney, 2017). Often, they also feature sharp environmental gradients (Norder et al., 2020), making them appear as microversions of continents (Kueffer and Kinney, 2017). Another advantage is that for many islands the timing of the first human occupation is relatively clear and hence the onset of anthropogenic impact (Dinapoli and Leppard, 2018; Norder et al., 2020). Therefore, as anthropogenic environmental influences are becoming more pressing than ever, islands can play

a pivotal role in understanding changes in biodiversity patterns. Such new findings ultimately set the ground for innovations in biodiversity conservation (Russell and Kueffer, 2019).

1.1.3.1 Island forests

Historically, land-use change and species invasions have been the major drivers of biodiversity loss on islands (Russell and Kueffer, 2019). Indigenous people populated some of them early on; however, large-scale transformations were often bound to the arrival of Western voyagers (Braje et al., 2017), typically starting around 1500 AD. Since then, over 60 % of all registered species extinctions concerned insular endemics (Whittaker et al., 2017). Many island ecosystems began to suffer from heavy deforestation, as the new settlers predominantly cleared lowlands and mid-elevations to grow agricultural export crops (Norder et al., 2020; Fernández-Palacios et al., 2021). It is also in these areas where most alien species got established (Ibanez et al., 2019). Hence, relatively intact ecosystems are nowadays largely limited to montane forests (Borges et al., 2018).

Deforestation and forest degradation are still high on islands, but the end products of land-use change have not necessarily remained the same, with urban expansion increasingly gaining relevance (Russell and Kueffer, 2019). In addition, introduced species continue to be severe threats to native biota (Moser et al., 2018), although there have been occasional success stories of their removal, such as in the case of invasive mammals (Jones et al., 2016). Overexploitation remains another crucial threat to biodiversity (Russell and Kueffer, 2019), as exemplified by the extinction of the heavily hunted Pinta Island tortoise (*Chelonoidis abingdonii*) from the Galápagos archipelago (Poulakakis et al., 2020). While pollution may only slightly increase as a driver of biodiversity loss in the future, the effect of climate change is projected to become more noticeable (Russell and Kueffer, 2019), likely interacting synergistically with other drivers. Due to changes in temperature, precipitation, and sea levels, island species will face more and more unfavourable conditions (Harter et al., 2015).

Whereas the forest proportion varies greatly across islands, that of their combined land area is still higher than that of the world's land area (Wilkie et al., 2004). Island forests are key ecosystems for global biodiversity conservation because they harbour extraordinarily high shares of endemic species (Wilkie et al., 2004; Kier et al., 2009). Native, usually montane forests are of particular importance to island biodiversity (Borges et al., 2018). Due to the high concentration of endemics, protecting island forests and their species is a cost-effective option towards global conservation (Kueffer and Kinney, 2017).

1.1.3.2 *Island biota*

Species richness on islands is typically low (Whittaker and Fernández-Palacios, 2007), in particular for oceanic islands whose initial colonisation depended on sea-crossings by few individuals (Cowie and Holland, 2006). Nonetheless, this is also where the rate of endemism is disproportionately high (Kier et al., 2009). Generally speaking, one-quarter of all vascular plant species are endemic to islands (Kreft et al., 2008). Especially for islands of volcanic origin, the topography tends to be steep and rugged, resulting in high habitat heterogeneity that promotes speciation (Kueffer and Kinney, 2017). Evolutionary adaptation to the unique environmental conditions of islands has given rise not only to many endemics but also to many bizarre species with morphological, behavioural, and ecological abnormalities (Baeckens and Van Damme, 2020). Flightlessness in insects and birds such as in the extinct dodo (*Raphus cucullatus*) of Mauritius (Maderspacher, 2022), naivety towards predators as observed in Lilford's wall lizard (*Podarcis lilfordi*) of the Balearic Islands (Cooper and Pérez-Mellado, 2012), dwarfism and gigantism including the giant seeds of the double coconut (*Lodoicea maldivica*) on the Seychelles (Bellot et al., 2020), and insular woodiness such as in the Hawaiian silversword *Argyroxiphium sandwicense* (Zizka et al., 2022) are just some examples of the so-called island syndromes (Fernández-Palacios et al., 2021).

Island species are more vulnerable to anthropogenic environmental changes than continental species. Apart from being affected by island syndromes and restricted distribution ranges (Rozzi et al., 2023), they are highly sensitive because of naturally small population sizes and low genetic diversity (Frankham et al., 2002). Moreover, the exposure of biodiversity to human pressures is enhanced on islands, where land-use change and species invasions have been more severe than on continents (Sanchez-Ortiz et al., 2019; Russell and Kueffer, 2019), and where rising sea levels and extreme weather events are expected to be most impactful (Bellard et al., 2014; Harter et al., 2015). In response, resident species may have limited possibilities to adapt. They can undertake range shifts to refugia on their islands, if available, or undergo rapid evolutionary adaptation, which can still be a reasonably slow process; or otherwise, they will eventually become extinct (Gillespie et al., 2008; Harter et al., 2015).

Island assemblages are susceptible to undergoing fundamental structural and compositional changes, not only because barriers to the influx of new species have been largely removed in times of globalisation (Gillespie et al., 2008), but also because land-use changes facilitate the introduction of broad-ranged generalists (Mitchell et al., 2022). Conserving the unique biota of islands implies counteracting biotic homogenisation, which is an important facet of the biodiversity crisis. This process describes the taxonomic, genetic, or functional assimilation in two or more localities (β -diversity), resulting from species introductions and extinctions (Olden et al., 2016). As such, it refers to species identities, not species richness, and is often but not

exclusively associated with an increase in alien species and a decrease in native species. Because of high endemism rates, changes in island species assemblages can disproportionately affect biotic homogenisation on a global scale. High introduction rates also tend to increase local biotic homogenisation, with potentially negative consequences for the stability of ecosystems (Wang et al., 2021).

1.1.3.3 *Island people*

While numerous species have been imported to islands accidentally, many others have been deliberately introduced to provide NCP. Island people in tropical latitudes are especially dependent on their natural resource pool (Balzan et al., 2016; Fedele et al., 2021), partly because their economies are fragile (McGillivray et al., 2010). Although some islands are uninhabited, many are densely populated. Just as for the number of species, the number of humans tends to increase with the island area; interestingly, it is unrelated to the island's distance from the mainland (Mologni and Burns, 2023). Altogether, islands host approximately 10 % of the world's human population, forming almost one-quarter of all nations (Global Island Database, 2023). Often, they are melting pots of cultures (Kueffer and Kinney, 2017), with great linguistic diversity (Tershy et al., 2015), but also great biocultural knowledge (Lauer, 2017). This traditional local knowledge influences the use of biodiversity and thus the recognition of NCP.

Islanders are the stewards of their biological heritage. Given that land is restricted and land uses are thus highly competitive (Wilkie et al., 2004), islanders tend to have stronger pressure to find a sustainable path for managing their flora and fauna. In a way, islands are paradigmatic sites for human-nature relations, in which local actors are crucial for biodiversity conservation (Kueffer and Kinney, 2017). Yet, financial means are typically tight among forest agencies and other relevant entities (Wilkie et al., 2004). This is one of the reasons why many islands are still heavily reliant on former colonial powers (Kueffer and Kinney, 2017), even though island nations are increasingly appreciating that networking can enhance their capacity for environmental action and make their political voices heard internationally (Dahl, 2017). The Alliance of Small Island States (AOSIS) is a coalition of island and low-lying coastal states that pursues this aim, especially in light of their vulnerability to climate change (Ourbak and Magnan, 2018).

1.2 Research gaps

Given that environmental concern can vary due to manifold worldviews (Ogunbode, 2013; Xiao et al., 2019), scientists and policy-makers are likely to focus on different aspects of environmental change (Skogen et al., 2018). These actors may develop their own silo of

thinking (Ojanen et al., 2021), having different views on the role of biodiversity and lacking a shared vision for the future. To improve options for communication between biodiversity science and policy, which ultimately allows for knowledge co-production, research must become more interdisciplinary (Young et al., 2014). Both policy and (socio-)ecological analyses can feed into widening scientific knowledge that concerns tropical island forests under environmental change.

1.2.1 Policy and the biodiversity-climate nexus

Biodiversity loss receives less attention than climate change in the public eye (Gardner et al., 2020). Nonetheless, the science-policy community increasingly recognises that the climate and biodiversity crises are intertwined (Pörtner et al., 2023). Climate change leads to habitat loss for many species (Nunez et al., 2019), and the decline of biodiversity, in turn, can worsen the climate crisis (Seddon et al., 2019; Shin et al., 2022). In December 2022, this nexus was highlighted during the 15th United Nations Biodiversity Conference (COP 15) in Montreal, Canada, perceived as an important policy window (Pettorelli et al., 2021). However, very little work had been done on the biodiversity-climate nexus prior to COP 15, which is when I engaged with this topic for Chapter 2.

A major outcome of COP 15 was the adoption of the Kunming-Montreal Global Biodiversity Framework, similar to the Paris Agreement on climate change in 2015. Its 2030 Targets 8 and 11 mention NBS (CBD Secretariat, 2023), for which forests are vital. There is much hope pinned on forests to jointly curb the global biodiversity and climate crises (Barber et al., 2020), but NBS carry the risk of fulfilling climate goals despite harming biodiversity (Seddon et al., 2019). It is thus necessary to assess if governments are already mainstreaming biodiversity into national climate policy frameworks to prevent negative outcomes from forest-based climate solutions and make sure that any potential synergies are explored. There is a clear need for better understanding the awareness of the biodiversity-climate nexus in environmental policies.

1.2.2 Biodiversity and its use across different conditions of nature

One key strategy in addressing biodiversity loss, potentially also tackling climate change, is spatial planning to promote ecosystem protection and restoration (Pörtner et al., 2023). This needs to happen along a continuum of land-use intensities, which can be divided into three broad conditions of nature on land (Obura et al., 2021): largely intact wild areas, such as natural forests, spaces shared by biodiversity and people, including agroforests, and heavily modified landscapes, such as cities. Arranged as mosaics, these conditions exist all over the planet (Locke et al., 2019). Biodiversity studies along anthropogenic gradients, however, often do not include

an urban component (Dampney et al., 2021; Soazafy et al., 2021), or they are restricted to urban-rural landscapes missing a natural baseline (Rija et al., 2014; Lowry et al., 2020).

Compared to most policy-makers working on environmental change, who tend to focus on large-scale or global analyses (Hof et al., 2015; Geijzenborffer et al., 2016), biodiversity scientists primarily deal with more localised aspects of environmental change (Estes et al., 2018; Teng et al., 2020). This is namely because land-use change, direct exploitation, and invasive alien species are widely accepted to be the most important drivers of terrestrial biodiversity loss (Jaureguiberry et al., 2022), which are easier to assess at smaller scales. Understanding how these drivers of biodiversity loss work is a major concern when developing conservation strategies, especially those that involve forests. From an ecological perspective, it is central to determine how biodiversity is influenced by these threats at smaller scales, which can eventually help clarify cross-scale interactions with macroecological patterns, a combined approach that may be particularly relevant in the face of environmental change (Teng et al., 2020). In this context, it is useful to assess how biodiversity changes along different levels of anthropogenic influence, taking biotic homogenisation into account, which frequently occurs at the expense of native species (Mitchell et al., 2022). Since humans often alter the environment to suit their needs, a more comprehensive picture is created if it is also assessed how biodiversity use, described here as NCP, shifts along this gradient. This may be especially important in regions where people rely more directly on natural resources.

1.2.3 Geographical bias

Biodiversity-related research has been growing since the 1980s but it is mostly concentrated in wealthy countries of Europe, Asia, and North America. Regions with weaker economies tend to be underrepresented in biodiversity studies, even if they contain higher levels of biodiversity, endemism, and threat (Tydecks et al., 2018). Particularly around the Equator, there appears to be a deficit in biodiversity publications, e.g. in Central Africa (Hickisch et al., 2019). Similar patterns are observable for the subcategory of conservation science, with a bias towards the USA, Australia, and the UK. In contrast, conservation research efforts have remained low in African countries over time, with some of them being almost entirely unstudied (Watson et al., 2017).

The study of species on tropical islands has led to iconic advances in evolution and ecology, such as the theory of natural selection observed in the finches of Galápagos Islands (Darwin, 1859). Similarly, the theory of island biogeography, which explores species-area relationships as well as relationships of immigration and extinction rates of island species, has been based on findings from the Florida Keys archipelago (MacArthur and Wilson, 1967). Despite the

importance of these works, tropical island species do not necessarily receive the attention they deserve according to their threat level (de Lima et al., 2011). Therefore, investigating biodiversity in tropical endemic-rich islands, especially in low- and middle-income contexts, helps balance out the current geographic bias in biodiversity research.

Focussing on individual drivers of biodiversity loss, the effects of land-use change on biodiversity are best known in temperate forests of North America and Europe. Despite possessing the second-largest connected area of forest, there is a “data vacuum over the Afrotropics” (Davison et al., 2021, p.5422). At the same time, this is also the area with one of the fastest urbanisation rates in the world (OECD/SWAC, 2020), so data gaps need to be filled urgently. In relation to the impact of invasive species, many studies have been conducted in North America and Western Europe. Yet, there is a lack of corresponding studies for oceanic islands (Bellard and Jeschke, 2016), even though these are known to be sensitive to the influence of introduced taxa.

If geographical biases regarding the effects of environmental change on biodiversity persist, data gaps will hamper progress in conservation. First, knowledge will remain incomplete, which means developed theories may be invalid, as findings from temperate regions often cannot be extrapolated to the tropics. Here, biodiversity levels are naturally higher (Mittelbach et al., 2007), and biodiversity takes longer to recover from disturbance (Newbold et al., 2020). Secondly, while the impact of environmental change on biodiversity will remain largely undocumented, so may be the threat status of many species. As a result, it will be unclear which species are already at the brink of extinction – numbers that could be relevant for policy-making – and windows of opportunities to counteract biodiversity loss may be closing.

1.3 Research aims

The goal of this thesis is to examine biodiversity in tropical island forests under anthropogenic environmental change, using policy, ecological, and socio-ecological analyses. Dealing with various scientific disciplines, this work may help create a sound vision for the future of tropical island forests. I first investigated how the AOSIS members consider biodiversity within forest-based climate solutions, by applying content analysis on their national climate policies. Then, I used field surveys to analyse the distribution of both biodiversity and its associated use in urban, rural, and natural zones of the Afrotropical island of São Tomé. This thesis therefore contains three results chapters with the following overarching aims and objectives:

Chapter 2:

To understand how 39 small island and low-lying coastal states in the tropics integrate biodiversity into their national climate action plans, the so-called Nationally Determined Contributions (NDCs). Specifically, I studied if governments view forest-based climate solutions as a vehicle to enhance biodiversity simultaneously, by asking the research questions below:

- (i) How many countries prioritise forests and/or biodiversity for climate change mitigation and adaptation?
- (ii) What is the range of forest-based climate solutions and biodiversity conservation measures being proposed?
- (iii) To what extent do forest-based climate solutions consider co-benefits and synergies with biodiversity conservation measures?

Chapter 3:

To evaluate the influence of land-use change on biodiversity patterns in the oceanic island of São Tomé, Central Africa. More precisely, I assessed tree diversity along urban, rural, and natural zones covering the entire island, by posing the following research questions:

- (i) How do tree assemblages change between urban, rural, and natural zones?
- (ii) To what extent do introduced species drive these changes?
- (iii) Are there differences in native biogeographic ranges across urban, rural, and natural zones?

Chapter 4:

To determine the effect of land-use change on recognised uses of biodiversity in the oceanic island of São Tomé, Central Africa. Particularly, I identified how NCP derived from trees change along urban, rural, and natural zones, by covering the following research questions:

- (i) Which NCP are recognised in tree species?
- (ii) How do recognised NCP vary between urban, rural, and natural zones?
- (iii) How do introduced, native, and endemic tree species differ in their recognised potential to deliver NCP?

1.4 Research design and methods

1.4.1 Thesis structure

This thesis consists of five chapters. The first and current chapter establishes the background on tropical island forests and the anthropogenic environmental changes they are exposed to, while also outlining the research gaps, research aims, research design and methods, and the thesis contributions. The second, third, and fourth chapters are the results chapters, answering the research questions described above. Chapter 2 has been published as a research article in *Environmental Science and Policy*. Chapter 3 is under review as a research article at *Ecology and Evolution* and Chapter 4 has been prepared as a research article for submission to *Ecosystems and People*. The fifth and final chapter serves to synthesise and discuss the findings from all results chapters. It also draws key conclusions about our understanding of biodiversity in tropical island forests, including future research needs and implications for policy and practice.

1.4.2 Methodology

This work follows an interdisciplinary approach to produce scientific knowledge that is potentially valuable in science-policy processes. It uses mixed methods and involves both primary and secondary data. Policy documents, thus secondary data, are the base for the content analysis in Chapter 2. Primary data collection is just as important, however, as there are signs of increasing neglect of fieldwork studies, while synthetic and modelling approaches are heavily on the rise (Ríos-Saldaña et al., 2018). Hence, Chapter 3 uses a biodiversity survey, that builds upon transect data on trees. Whereas I collected the data in the urban and rural zones myself with the help of local field guides, the data in the natural zone was generated by the “Threatened Flora of São Tomé e Príncipe” project team. Finally, Chapter 4 combines that same biodiversity survey with expert opinions on tree uses by this team.

Geographically, this thesis moves from many islands (global level) to one island (local level) from Chapter 2 to Chapters 3 and 4. This approach makes sense given that climate change is a global driver of environmental change, and thus it is interesting to see how different islands respond to this shared threat through policy. There is little islands can do in terms of mitigation, as their share in global greenhouse gas emissions is very low. Yet, they can turn to policy to draw attention to their need for climate change adaptation and use the opportunity to foster biodiversity conservation simultaneously, as political negotiations can open up new funding routes for instance. Consequently, I analysed policy documents from a number of island states submitted to the United Nations (UN). Land-use change, in contrast, is a complex driver of

environmental change that is worth being studied at smaller scales. By developing thorough conservation strategies, islands can reduce the threats to biodiversity with local measures. Thus, I use a field study to investigate how urban-rural expansion shapes biodiversity locally and how this compares to NCP associated with biodiversity along the resulting anthropogenic gradient.

1.5 Thesis contributions

This thesis produces scientific knowledge from interdisciplinary research that involves both policy and (socio-)ecological analyses, to potentially stimulate science-policy discussions about sustainable pathways for forests. More precisely, it discusses the role of tropical island forests within the broad themes of policy as well as biodiversity and its associated use. Thereby, it helps set the ground to improve conservation strategies in light of environmental change, particularly for vulnerable and endemic-rich oceanic islands such as São Tomé. It clarifies what potential future visions for these forests are, and how they can contribute towards halting biodiversity loss.

Chapter 2 illustrates to which degree the biodiversity-climate nexus has been considered within climate policy, as exemplified by the national climate action plans of 39 small island and low-lying coastal states in the tropics. Via content analysis on their NDCs, it demonstrates which sectors governments prioritise to achieve climate goals, and if they perceive forests as vehicles to create synergies and co-benefits between biodiversity and climate protection. Furthermore, this work identifies which specific types of forest-based climate solutions governments propose, and which are the most commonly cited ones, that may be suitable to help mitigate both the climate and biodiversity crises. It forms a final opinion on biodiversity inclusiveness in the present set of NDCs and an outlook about possible consequences.

Furthermore, this thesis assesses how tree diversity and uses associated with trees are distributed along different levels of human interference at an island scale, using the island of São Tomé as a model, in an attempt to inform conservation policies that might have synergies with forest-based climate solutions. Specifically, Chapter 3 investigates how anthropogenic influence changes the biodiversity patterns of the tree assemblage, i.e. species richness, abundance, composition, and structure across urban, rural, and natural zones (Figure 1.2). It also examines how native and introduced species are distributed along these zones, to assess biotic homogenisation. Reflecting on the results, I assess the ecological value of the different zones and consider measures to maintain or enhance tree diversity.

Chapter 4 adds expert elicitations to the tree surveys from Chapter 3, to reveal recognised uses of tree species in São Tomé. It determines which uses, described here through the conceptual

framework of NCP, are underpinned by trees and if the resulting NCP are distinct across urban, rural, and natural zones. These are further classified into broad groups, categories, and subcategories, which are also analysed for introduced, native, and endemic species. This research reveals which zones may contribute to meeting the needs of local people via tree-derived NCP, and how these could be supported alongside conserving biodiversity.

The findings from this research further highlight that, if national suggestions from climate policies are to be implemented, the distribution of biodiversity and its recognised uses need to be known in detail. Otherwise, if anthropogenic gradients are not taken into account, negative outcomes for biodiversity and the quality of life of people may follow. In addition, biodiverse forests are of importance in the discourse of forest-based climate solutions, due to providing greater resilience and higher carbon stocks in the long term.

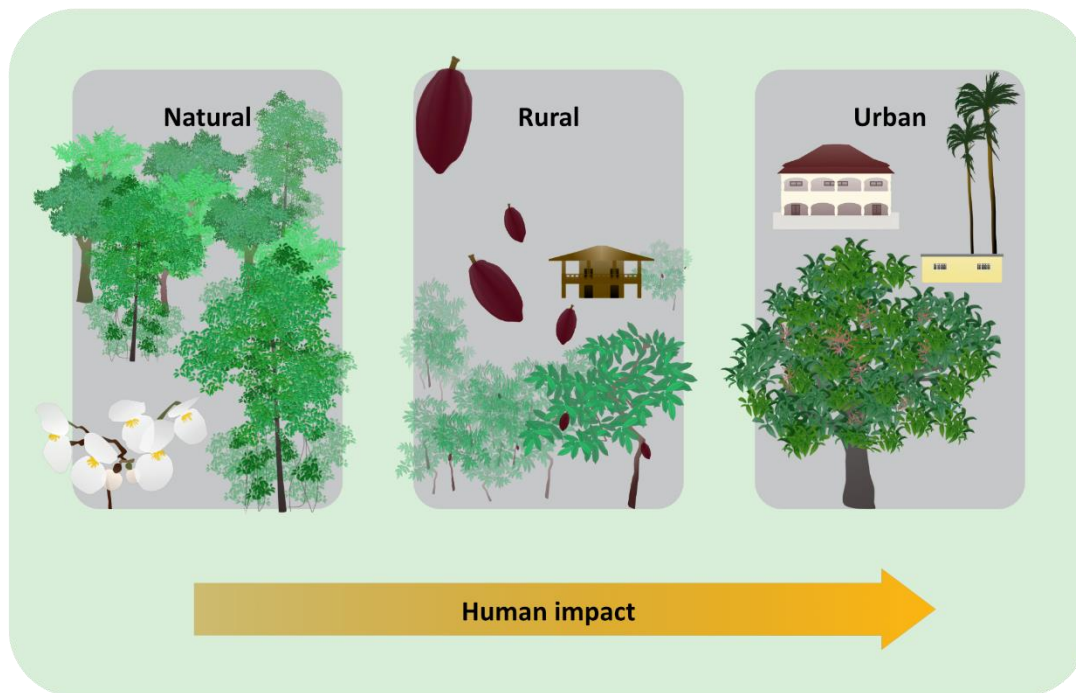


*Figure 1.2. Schematic diagram of the increasing human impact from the natural, to the rural, through to the urban zones of São Tomé Island. The natural zone has the highest diversity in trees and features many other organisms, showing a relatively high level of intactness. In contrast, the rural zone is dominated by cocoa trees (*Theobroma cacao*) managed by farms, while also being a space that is shared with the rural population. The urban zone is the most heavily modified landscape, as illustrated by the enhanced infrastructure and the prevalence of introduced species.*

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2 Limited integration of biodiversity within climate policy: Evidence from the Alliance of Small Island States

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Abstract

Climate change and biodiversity loss are deeply intertwined anthropogenic global crises, for which forests provide powerful nature-based solutions. Biodiverse forests are more resilient to climate change than monocultures, thereby enhancing long-term carbon storage and ecosystem-based adaptation. Awareness of these interdependencies is slowly growing, but we know little about how countries are considering biodiversity within climate policies. Island and low-lying coastal states are particularly vulnerable to climate change and biodiversity loss. Here we assessed if and how the members of the Alliance of Small Island States (AOSIS) are integrating biodiversity into their national climate action plans through forest-based climate solutions. Our analysis shows that these solutions are a missed opportunity for tackling the twin crises

together. Only five of the 39 countries explore co-benefits and synergies between forest-based climate solutions and biodiversity conservation measures. An additional nine mention them separately. Among these 14 countries, only a narrow range of interventions were proposed. While 28 AOSIS members prioritised forests for combating climate change, mostly for mitigation, only three prioritised their unique and globally important biodiversity. This omission is potentially risky, since mitigation measures, such as planting rapidly growing non-native trees, can have negative outcomes for biodiversity. Climate action plans must place a greater emphasis on concrete and measurable targets that create synergies with biodiversity conservation, including through the protection of old-growth forests and forest restoration. Our results highlight that forums such as the United Nations Climate Change Conferences need to continue pushing for a stronger integration of biodiversity into climate policies.

Keywords

Biodiversity co-benefits; Content analysis; Nationally Determined Contributions; Nature-based solutions; Paris Agreement; Tropical forest

2.1 Introduction

The climate and biodiversity crises are among the most pressing issues of our time (Ceballos et al., 2015; Ripple et al., 2020). Average rates of global warming may reach 1.5 °C above pre-industrial levels as early as 2030 and one in eight species are at risk of extinction (IPCC, 2018; IPBES, 2019). Solving these crises requires us to understand that climate change and biodiversity loss are mutually interdependent (CBD, 2019; Marquet et al., 2019). Some species are going extinct as a result of rising temperatures, as they are unable to shift their geographical distribution (Taylor and Kumar, 2016; Nunez et al., 2019). Lower levels of biodiversity, in turn, limit the ability of some ecosystems to combat climate change (Seddon, Turner, et al., 2019; Mori et al., 2021). The causes of both crises are also often shared, driven by issues such as intensive agriculture and loss of native forest (IPCC, 2018; IPBES, 2019). As a result, scientists and politicians have increasingly been calling for a joint approach to tackling the crises (CBD, 2019; Turney et al., 2020).

International policy processes have struggled to address climate change and biodiversity loss together (Seddon, Turner, et al., 2019; Turney et al., 2020). For example, the Convention on Biological Diversity (CBD) primarily deals with the conservation of biodiversity under the United Nations Environment Programme (UNEP), but although its secretariat has created an agenda item on “climate change and biodiversity”, parties still hesitate to implement activities

under this heading (Secretariat of the Convention on Biological Diversity, 2017). In contrast, the United Nations Framework Convention on Climate Change (UNFCCC) aims to stabilise atmospheric greenhouse gas concentrations but has largely failed to mainstream biodiversity, despite the United Nations (UN) being officially obliged to do so across all its environmental policies (Díaz et al., 2009; Kupika and Nhamo, 2016). These challenges reflect the constraints upon the CBD and UNFCCC to achieve direct cooperation as they have different mandates, members, and negotiators. Nonetheless, climate-biodiversity collaborations are slowly developing among these international governing bodies, as well as among scientific committees (Intergovernmental Panel on Climate Change, IPCC, and Intergovernmental Platform on Biodiversity and Ecosystem Services, IPBES). IPCC and IPBES held their first joint workshop in December 2020, which led to the release of a report (Pörtner et al., 2021). However, a coordinated policy approach that provides a balanced integration of climate change and biodiversity loss is still lacking (Deprez et al., 2019; Turney et al., 2020). Meanwhile, there has been growing interest in biodiversity under the international climate change policy framework (Veríssimo et al., 2014; Gardner et al., 2020). On a national level, the clearest opportunity for creating synergies is hence to ensure that biodiversity conservation is fully integrated within the mitigation and adaptation components of the Nationally Determined Contributions (NDCs) to the Paris Agreement (UNFCCC, 2015).

The international community has repeatedly stressed the importance for NDCs to include nature-based solutions (NBS) (Griscom et al., 2017; Seddon, Daniels, et al., 2020), which are defined as interventions that “are inspired and supported by nature, which are cost-effective, simultaneously provide environmental, social and economic benefits and help build resilience” (European Union, 2020). This umbrella term spans other well-established concepts, including ecosystem-based adaptation/mitigation, natural climate solutions, and green infrastructure (Seddon, Chausson, et al., 2020). NBS may contribute by more than one third to the climate change mitigation needed for reaching the Paris temperature goal (Griscom et al., 2017), as well as substantially contributing to adaptation (Chausson et al., 2020; Seddon, Daniels, et al., 2020). Yet, uncertainties remain with regard to estimates and cost efficiency of these solutions, which in practice often focus on mitigation (Griscom et al., 2017; Seddon, Chausson, et al., 2020).

Forests offer some of the most important NBS for both climate change mitigation and adaptation (Barber et al., 2020; Seddon, Daniels, et al., 2020). We use the term forest-based climate solutions to differentiate from NBS in the climate change discourse provided by other ecosystems, such as grasslands, river catchments, or agricultural fields (Seddon, Daniels, et al., 2020). As carbon sinks, forests actively capture and store atmospheric CO₂ (Pan et al., 2011), simultaneously aiding adaptation, by preventing soil erosion, supporting hydrological flows, and protecting coastal areas against storms (Pramova et al., 2012).

Since forests are among the most important habitat types for terrestrial species (Watson et al., 2018), forest-based climate solutions may offer co-benefits for and synergies with biodiversity conservation (Morita and Matsumoto, 2018; Chausson et al., 2020). Biodiversity co-benefits are additional positive outcomes resulting from policy measures aimed at combating climate change (cf. Grafakos et al., 2019). Synergies occur when the effect of implementing climate and biodiversity policy measures together is greater than their separate implementation (cf. Klein et al., 2007). Despite their potentially high impact, these synergistic relationships are often undervalued (Seddon, Turner, et al., 2019; Mori, 2020). Biodiversity may be an active player in the solution, not only a conservation target (Mori, 2020): Biodiverse biomes are more productive in terms of biomass, thus better mitigating climate change (Poorter et al., 2015; Mori et al., 2021), and facilitate ecosystem-based adaptation to climate change (CBD, 2019; Seddon, Turner, et al., 2019).

Island and coastal states hold unique and particularly vulnerable biodiversity (Kier et al., 2009; Friess et al., 2019), and are also expected to suffer disproportionately high impacts from climate change (Halstead, 2016). The Alliance of Small Island States (AOSIS) was formed in 1990 as a joint political voice for this vulnerable group of countries, which is recognised as a key player in the UN climate negotiations (Ourbak and Magnan, 2018). The NDCs represent an important opportunity to protect and enhance biodiversity in these countries. Here, we examine the extent to which the connections between climate change, forest-based climate solutions, and biodiversity conservation have been integrated in NDCs of AOSIS members. Specifically, we use NDCs to assess: (i) How many countries prioritise forests and/or biodiversity for climate change mitigation and adaptation; (ii) The range of forest-based climate solutions and biodiversity conservation measures being proposed; (iii) To what extent forest-based climate solutions consider co-benefits and synergies with biodiversity conservation measures. Finally, we provide some recommendations to ensure NDCs promote forest-based biodiversity co-benefits and synergies. This is especially relevant to overcome the climate-biodiversity gaps discussed at the 26th Conference of the Parties (COP 26) to the UNFCCC, which took place in Glasgow, UK, in November 2021.

2.2 Methods

2.2.1 Rationale

Island and low-lying coastal states, where the impacts from climate change and biodiversity loss are particularly prominent, represent an interesting case among UNFCCC parties. The focus and potential role of their NDCs is distinct from that of other country groups including industrialised

and emerging nations. With rising sea levels and extreme weather events posing severe threats to their survival (Halstead, 2016), AOSIS members are known to emphasise adaptation in the NDC context (Mbeva and Pauw, 2016). At the same time, their high levels of endemic and extinction-prone species are of global significance (Kier et al., 2009; Fordham and Brook, 2010). Any positive or negative change in AOSIS' biodiversity can have far-reaching implications for conservation and their NDCs have the potential to promote either direction. Furthermore, the role of biodiversity conservation for climate change adaptation is more widely accepted than its impact on mitigation (Hisano et al., 2018; Seddon, Turner, et al., 2019). It is therefore more likely that references to biodiversity will be found in the NDCs of the adaptation-oriented AOSIS members, compared to other groups. In addition, AOSIS have proven highly influential in climate negotiations and may thus be promising pioneers for such new approaches.

NDCs were chosen as study objects since the National Biodiversity Strategies and Action Plans (NBSAPs), as the counterpart under CBD framework, are internationally less recognised. Historically, climate negotiations are more advanced than the biodiversity ones, which can partially be explained by the existence of the clear ambitions covered in the Paris Agreement's long-term temperature goal (Legagneux et al., 2018; Mace et al., 2018). They also receive much greater attention in science and media (Veríssimo et al., 2014; Legagneux et al., 2018). It is thus wise to make use of the growing awareness of climate issues, which remain high on the policy agenda, and create synergies for biodiversity conservation under UNFCCC framework (Veríssimo et al., 2014; Gardner et al., 2020). Besides, if a country chooses to mention biodiversity in the NDC context, where there is no official requirement to do so, this effectively demonstrates its heightened interest in conservation. Another advantage of NDCs is their structural division into mitigation and adaptation action, which enables a detailed study of biodiversity integration under both components. Equally pivotal is that the UNFCCC allows for a clear split between biodiversity and forests, e.g. treating each as a separate priority for adaptation (UNFCCC, 2021a).

The inclusion of the forest sector in UNFCCC processes has a long-standing history, committing parties to land use, land-use change and forestry (LULUCF) activities, with stronger obligations for developed countries (UNFCCC, 2021b). For greenhouse gas accounting in NDCs, more and more parties are listing LULUCF as one of their categories of anthropogenic emissions and removals (UNFCCC, 2021a). Almost in parallel to LULUCF, the UN programme on reducing emissions from deforestation and forest degradation (REDD; later extended with the role of conservation, sustainable management of forests and enhancement of forest carbon stocks – REDD+) evolved. It shares the same goal, considering forest carbon sinks and sources for greenhouse gas mitigation, but uses an entirely different approach (Pistorius et al., 2017). As

an incentive-based mechanism, it builds on voluntary agreements between donors (developed countries) and receivers (developing countries). Consequently, not all parties mention REDD+, or elaborate on LULUCF as such, in their NDCs (Grassi et al., 2017; Hein et al., 2018). This is also true for AOSIS countries, that lack a joint vision for both institutions, despite the awareness that forests are becoming an increasingly important negotiation topic. For instance, individual country submissions on LULUCF to the UNFCCC have been more common in the past than joint statements by AOSIS (Betzold et al., 2012). Moreover, only 10 AOSIS members are partners of REDD+ currently (UN-REDD Programme Collaborative Online Workspace, 2021), likely due to weak interest and support of donors for REDD+ initiation in relatively small forests on islands.

The idea of incorporating biodiversity concerns into forest-based climate actions already emerged within REDD+ in the form of environmental safeguards, which, in contrast, have never been discussed under LULUCF (Pistorius et al., 2017). Yet, REDD+ only allows for limited biodiversity ambitions, namely co-benefits, as the focus for funding is mitigation (Gardner et al., 2012). NBS, which started to gain relevance in the mid-2010s, cover more: As a term originating from climate change adaptation in urban areas, it can refer not only to mitigation but also adaptation, and is often rooted in biodiversity conservation (Eggermont et al., 2015; Pauleit et al., 2017), setting the ground for synergistic approaches. This combination makes NBS attractive as NDC commitments for the adaptation-focused AOSIS members. Since many of them are rich in forests, NBS from forests may be of particular interest for their climate targets. The exploration of NBS in NDCs is thus the best option to study how AOSIS countries consider synergies between forest-based climate solutions and biodiversity.

2.2.2 Study area

The AOSIS consists of 44 tropical countries and territories. Guinea-Bissau, Belize, Guyana, and Suriname are low-lying coastal states, while the remaining are small island states (AOSIS, 2019). For this study, we only considered the 39 countries that are full members of the UN or participate within the UN (Figure 2.1). The five observer states of American Samoa, Guam, Netherlands Antilles, Puerto Rico, and United States Virgin Islands were excluded since they are not required to submit their own NDCs.

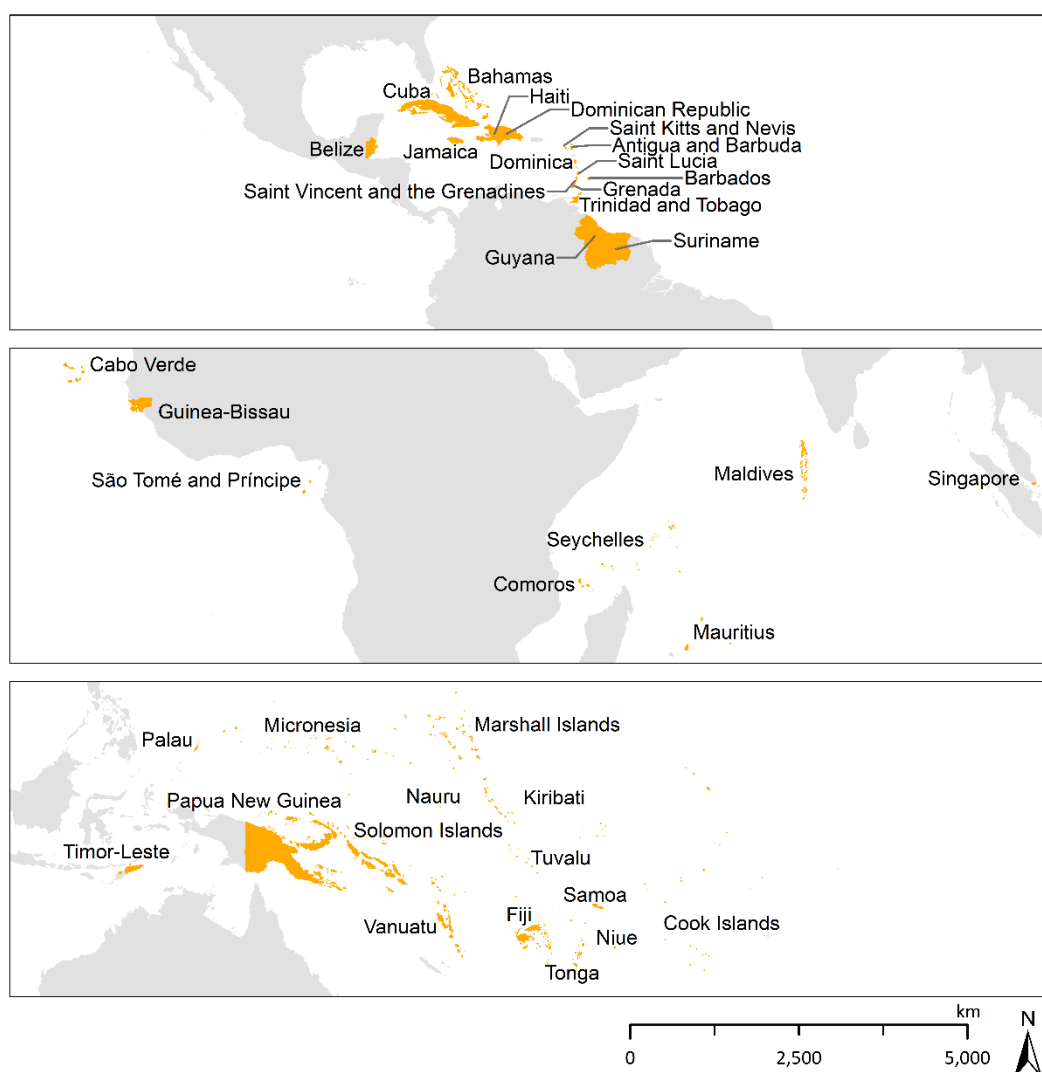


Figure 2.1. Location of the 39 Alliance of Small Island States (AOSIS) countries that are full members of the United Nations or participate within the United Nations (in orange), in the Caribbean (top), the African, Indian and South China Seas (middle), and the Pacific Ocean (bottom).

2.2.3 Data collection and analysis

NDCs were downloaded from the NDC registry website (UNFCCC, 2020) on 28 August 2020. The resulting set of 39 documents consisted mostly of first NDCs, but also updated first NDCs for Singapore and Jamaica and second NDCs for Suriname and Marshall Islands. The documents were in English, except for the NDCs of Comoros and Haiti, which were in French, and the NDC of Cuba, which was in Spanish. Apart from the NDC by the Dominican Republic, that provides an unofficial translation from Spanish into English, all documents were analysed in their original language.

To analyse NDCs, we conducted an iterative content analysis (Krippendorff, 2018), a commonly used method for qualitative data analysis, known for its transparency, reliability, and simplicity (Kuckartz, 2019). At its core stands the identification of categories – groups of similarly coded data (Kuckartz, 2019), which we determined through provisional and structural coding, followed by axial coding. Given that NDCs are policy documents and should be formulated in a clear, unambiguous manner, our analyses did not consider underlying, interpretive meanings (Berg et al., 2004; Bengtsson, 2016).

2.2.4 Preparatory work

Provisional coding allows data to be broken down according to broadly predefined codes. These are used to explore documents and identify key text segments (Saldaña, 2009). Thus, a list of provisional codes was first compiled concerning the main themes of this study, forests and biodiversity, which we translated into French and Spanish (App. A.1). This deductive approach helped to strengthen the focus of our investigation (Saldaña, 2009). The provisional codes were derived from REDD+ key activities, namely reducing emissions from deforestation, reducing emissions from forest degradation, conservation of forest carbon stocks, sustainable management of forests, and enhancement of forest carbon stocks, and their biodiversity safeguards (Gardner et al., 2012). For each activity, a range of synonyms was chosen to serve as provisional codes, in line with the literature. For instance, “forest conservation” was represented by “forests”, “trees”, “mangroves”, “conservation”, “preservation”, and “protection” (Donato et al., 2011; Crumpler et al., 2019). Considering the focus of the study, only terrestrial biodiversity was included, and particular attention was paid to “endemism”, as well as “co-benefits”, “synergies”, and “trade-offs”. The codes were used one after another, applying automatic text search to NDCs in NVivo 12 Plus software (QSR International Pty Ltd, 2018). Subsequently, relevant text passages (words, quasi-sentences, full sentences, and whole paragraphs) were highlighted by hand. These were the smallest meaning units that contained the predefined codes (Bengtsson, 2016).

2.2.5 Further coding and analysis

Next, we employed structural coding to classify data based on our research questions (Saldaña, 2009). For this purpose, we elaborated a coding frame directly linked to these questions by comparing units of text and labelling them with new codes (Saldaña, 2009; Bengtsson, 2016), as described below. In addition, we applied axial coding for the second research question. This is a method which creates linkages between codes to reorganise them in categories (Strauss and Corbin, 1990).

2.2.5.1 Prioritisation of forests and biodiversity

We started by checking which countries considered forests as a priority for climate change. Since NDCs usually have separate sections for climate change mitigation and adaptation, we used the codes “forestry as a mitigation priority sector” and “forestry as an adaptation priority sector” to differentiate between relevant text segments of these sections, and forests were considered a priority if words such as “priority”, “major”, “main”, or “focus” were contained. If countries did not apply this terminology but listed a concise number of target sectors instead, these were regarded as the country’s priority sectors. Similarly, the codes “biodiversity as a mitigation priority” and “biodiversity as an adaptation priority” were created to assess if biodiversity was prioritised in NDCs.

2.2.5.2 Forest-based climate solutions and biodiversity conservation measures

To distinguish types of forest-based climate solutions within countries, the following codes were used: “reducing deforestation and forest conservation”, “reducing degradation and sustainable forest management”, and “afforestation/reforestation” (Crumpler et al., 2019). This list was complemented by other forest-based climate solutions found in the NDCs and labelled as “other”. The code “biodiversity” was used to identify any kind of biodiversity conservation measures. To ensure replicability, the assignment of codes to text passages was iterated until results became stable (Guba and Lincoln, 1982).

Axial coding carried out by forming categories that merged deductive and inductive codes (Graebner et al., 2012) resulted in eight categories of forest-based climate solutions and three categories of biodiversity conservation measures linked to climate change (Table 2.1). The category “other sectors” was only indirectly linked to forests, while “forest assessment and monitoring” was regarded as a precursor for forest-based climate solutions.

Table 2.1. Categories and corresponding descriptions formed to distinguish different types of forest-based climate solutions and biodiversity conservation measures, respectively, which are proposed in the Nationally Determined Contributions (NDCs) of the 39 Alliance of Small Island States (AOSIS) members.

Category	Description
Forest-based climate solutions	
<i>Forest protection</i>	Includes forest conservation in general as well as the preservation, management, and expansion of protected areas, such as forest reserves.
<i>Forest (re-)growth</i>	Includes afforestation, reforestation, forest restoration and rehabilitation. Covers related terms such as forest (re-)growth, plantation, increased tree cover, enhancement of forests or forest carbon stocks, and promotion of particular species, such as indigenous or climate-resilient species.
<i>Reduction of deforestation and forest degradation</i>	Covers actions to decrease levels of deforestation and forest degradation, and the control of forest fires.

<i>Sustainable forest management</i>	Includes activities covered by the United Nations (2008) definition of “a dynamic and evolving concept, [...] intended to maintain and enhance the economic, social and environmental value of all types of forests, for the benefit of present and future generations”. This definition excludes general actions to reduce deforestation and degradation as these do not necessarily imply that the level of reduction is sustainable.
<i>Forest management</i>	Any type of management that did not fit into the aforementioned categories as well as forest management not specified in detail was placed into this category.
<i>Forest governance</i>	Includes governance, in the sense of rules, regulations, laws, strategies, policies, and programmes (Lemos and Agrawal, 2006; Fischer et al., 2020), actions not covered above, as well as market-based mechanisms such as REDD+ and certification schemes (e.g. FSC) (compare Nunan, 2019).
<i>Forest assessment and monitoring</i>	Includes forest inventories, assessment, and monitoring.
<i>Other sectors</i>	Covers any reference made to other sectors that were targeted to reduce pressure on forest resources such as energy, mining, agroforestry, and arboriculture sectors.
Biodiversity conservation measures	
<i>Biodiversity protection</i>	Includes conservation, management, and sustainable use of biodiversity, as well as the management and expansion of protected areas for biodiversity conservation.
<i>Biodiversity governance</i>	Includes integrative governance and management approaches, as well as consideration of the Convention on Biological Diversity (CBD) and other biodiversity-related instruments.
<i>Biodiversity resilience</i>	Covers management options that aim to improve biodiversity resilience.

Then we analysed which categories of forest-based climate solutions and biodiversity conservation measures were covered by each country. This was expressed in a joint heatmap, based on the presence-absence data for each country and category, using the function “heatmap.2” from the “gplots” R package (R Core Team, 2019; Warnes et al., 2020). Since measurable targets are vital to evaluate progress towards climate action (Seddon, Sengupta, et al., 2019), we used subcodes to evaluate which countries were proposing these for each of the forest-based climate solutions and biodiversity conservation measures.

2.2.5.3 *Links between forest-based climate solutions and biodiversity conservation measures*

We built a contingency table identifying which countries mentioned forest-based climate solutions and biodiversity conservation measures simultaneously in the NDCs, and carried out a Fisher’s exact test to assess the strength of the correlation between the two variables (Bower, 2003). Afterwards, we identified which categories were more frequently mentioned together and which countries made direct links between forest-based climate solutions and biodiversity conservation measures.

2.3 Results

2.3.1 Prioritisation of forests and biodiversity

Twenty-eight out of the 39 AOSIS members (71.8 %) included forests as a priority sector: 24 (61.5 %) for climate change mitigation and 14 (35.9 %) for adaptation. The mitigation goal of the Government of Jamaica (2020), for instance, comprised “the energy sector (supply and end-use) and land-use change and forestry” (p. 4), while Belize’s adaptation action stated that “[t]he sectors of focus are agriculture, forestry, fisheries and aquaculture, coastal and marine resources, water resources, land use and human settlements, human health, energy, tourism and transportation” (Government of Belize, 2016, p.11).

The prioritisation of forests contrasted with the lack of biodiversity prioritising. Only Mauritius, Singapore, and Timor-Leste (7.7 % of AOSIS members) declared biodiversity a priority, and they did so exclusively for adaptation. The Government of Mauritius (2016) considered biodiversity resilience in its priority adaptation actions, aiming for “[i]mprovement of the management of marine and terrestrial protected areas and expansion of protected area network including rehabilitation of wetlands, sea-grass, mangrove plantation, increase in tree coverage areas and coral reef rehabilitation/farming” (p. 4). No AOSIS state mentioned endemism as a factor to value its biodiversity in a global perspective of conservation.

2.3.2 Forest-based climate solutions and biodiversity conservation measures

Only Guinea-Bissau and Timor-Leste mentioned all eight categories of forest-based climate solutions (Figure 2.2). Forest protection and forest (re-)growth were the most frequently cited categories (20 countries each). Twenty-five AOSIS members (64.1 %) claimed to have forest-based climate solutions planned or in place. The Government of Guyana (2016), for instance, “will utilize a combination of conservation and sustainable management of its forests in the fight against climate change” (p. 6), which fits the categories of forest protection and sustainable forest management. Forest (re-)growth and reduction of deforestation and forest degradation were identified by the Government of Saint Vincent and the Grenadines (2016), that “intends to develop its GHG sinks through reforestation, afforestation, reduced deforestation and reduced forest degradation” (p. 4).

Eight countries quantified forest-based climate solutions (App. A.2), but only São Tomé and Príncipe and Singapore quantified forest-based adaptation targets. Six out of the 24 countries claiming that forests are a priority for mitigation and three out of 14 claiming them as a priority for adaptation did not suggest forest-based climate solutions. In contrast, Niue, the Seychelles,

and Saint Lucia expressed forest-based climate solutions without prioritising forests in the fight against climate change. The latter claimed that “[s]ignificant work is currently being conducted to improve forest inventory data, develop policies for forest management and protection and to identify reforestation projects” (Government of Saint Lucia, 2016, p.4).

No country covered all categories of biodiversity conservation measures and only 15 (20.5 %) proposed at least one (Figure 2.2). Biodiversity protection and biodiversity governance were the most mentioned categories (eight and seven times, respectively). To improve biodiversity resilience, the Government of Timor-Leste (2017) envisioned to “[m]aintain mangrove plantations and promote awareness raising to protect coastal ecosystems from impacts of sea level rise” (p. 19).

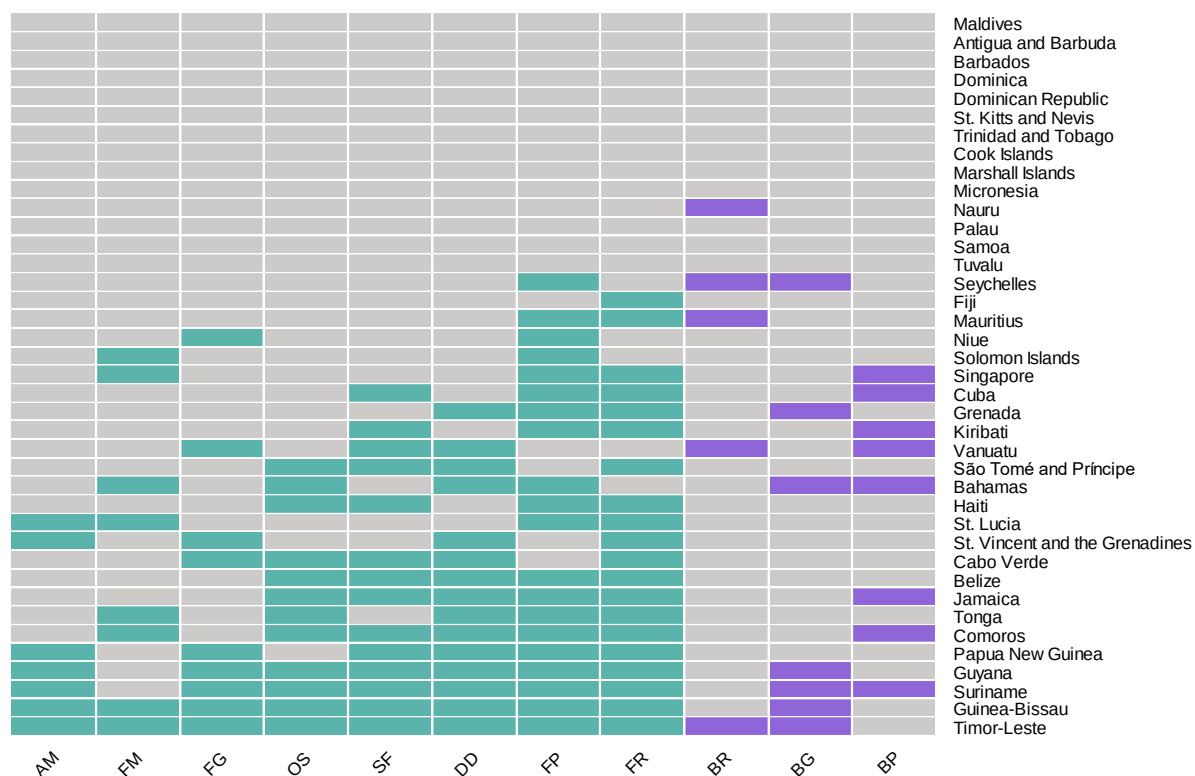


Figure 2.2. Heatmap of forest-based climate solutions (green) and biodiversity conservation measures (purple) suggested in the Nationally Determined Contributions (NDCs) of the 39 Alliance of Small Island States (AOSIS) members. AM: forest assessment and monitoring, FM: forest management, FG: forest governance, OS: other sectors, SF: sustainable forest management, DD: reduction of deforestation and forest degradation, FP: forest protection, FR: forest (re-)growth, BR: biodiversity resilience, BG: biodiversity governance, BP: biodiversity protection.

All three countries that considered biodiversity a priority for adaptation suggested biodiversity conservation measures (Table 2.2). Twelve countries proposed biodiversity conservation measures without making biodiversity a priority for combating climate change. Only two countries expressed quantified conservation measures in relation to biodiversity. The Government of Singapore (2020) aimed to implement “recovery plans for over 70 more animals [sic] and plant species” (p. 24). “100% representation of all ecosystems and biological species” was strived for by the Government of Suriname (2019, p.12).

Table 2.2. Categorised biodiversity conservation measures found in the Nationally Determined Contributions (NDCs) of Alliance of Small Island States (AOSIS) members. Whenever direct in-text links are present between forest-based climate solutions and biodiversity conservation measures, corresponding words are underlined and highlighted in bold in the quote.

Country	Category	Quote
Bahamas	Biodiversity protection	“These protected areas will conserve and protect habitats for Grouper and Bonefish spawning aggregations, coral reefs, sea grass meadows, mangrove nurseries and important migratory bird areas.”
	Biodiversity governance	“[...] The Bahamas acts not only under the UNFCCC but also the United Nations Conventions on Biological Diversity (CBD), and Convention to Combat Desertification (UNCCD) and other relevant multilateral and regional environmental agreements (MEAs) and initiatives.”
Comoros	Biodiversity protection	“Le gouvernement Comorien a planifié de renforcer ses actions pour la conservation de la biodiversité marine et terrestre. Ainsi, il est projeté de passer à un total de 50 000 ha environ de terre sous couvert végétale, principalement les forêts, d’aires protégées à l’horizon 2030.” [Translation: The Comorian government plans to reinforce its actions for the conservation of marine and terrestrial biodiversity . Hence, it is projected that protected areas will increase to a total of 50 000 ha of land under plant cover, mainly forests , by 2030.]
Cuba	Biodiversity protection	Main actions: “Enfatizar la conservación y uso racional de recursos naturales como los suelos, el agua, las playas, la atmósfera, los bosques y la biodiversidad, así como el fomento de la educación ambiental”. [Translation: Emphasise the conservation and the rational use of natural resources such as soils, water, beaches, the atmosphere, forests, and biodiversity, as well as the promotion of environmental education.]
Grenada	Biodiversity governance	“Grenada has shown its commitment to the reduction of its greenhouse gas emissions over the years by signing on to several international and regional initiatives and expressing commitment to a number of United Nations processes relative to Climate Change, Small Island Developing States, Biological Diversity, and the Millenium Development Goals [sic]. [...] Grenada has a National obligation to protect 17% of its terrestrial area as part of the Aichi Target under the convention on Biological diversity [sic].”
Guinea-Bissau	Biodiversity governance	“[The initiatives taken in the context of climate change] must be part of a consistent perspective of integration into a broader policy framework, developing strategic and programmatic approaches that integrate climate policy development, planning policy and action at national, regional and local levels, involving all sectors of the national economy and integrating all other dimensions of environmental management and natural resources, including biodiversity conservation, the sustainable management of land and water.”

Guyana	Biodiversity governance	Emissions Reductions Programme measures: “the conservation of an additional 2 million hectares through Guyana’s National Protected Area System and other effective area-based conservation measures as per Guyana’s commitment under the UNCBD, including the protection of conservancies and reservoirs and their watersheds and the watersheds upstream of new hydro-power sites”.
Jamaica	Biodiversity protection	“For example, the Integrated Management of the Yallahs and Hope River Watershed Management Areas (Yallahs-Hope) Project, [sic] aims to improve the conservation and management of biodiversity and the provision of ecosystem services within the region [...]. This will be done by implementing sustainable agriculture (including renewable power generation), forestry , land management and livelihood practices within targeted communities.”
Kiribati	Biodiversity protection	Kiribati Development Plan (KDP) 2012–2015: “The key objective of [key policy area] 4 is to facilitate sustainable development by mitigating the effects of climate change through approaches that protect biodiversity and support the reduction of environmental degradation by the year 2015.”
Mauritius	Biodiversity resilience	Priority adaptation actions: “Improve Marine and Terrestrial Biodiversity Resilience: Improvement of the management of marine and terrestrial protected areas and expansion of protected area network including rehabilitation of wetlands, sea-grass, mangrove plantation, increase in tree coverage areas and coral reef rehabilitation/farming”.
Nauru	Biodiversity resilience	“High priorities are given to actions that can contribute towards multiple development and resilience objectives simultaneously, often cross cutting across sectors. The priority actions are arranged under sectors targeting the following areas: water; health; agriculture; energy; land management and rehabilitation; infrastructure and coastal protection; biodiversity and environment; community development and social inclusion; and education and human capacity development.”
Seychelles	Biodiversity governance	“[Seychelles National Climate Change Strategy and Seychelles Sustainable Development Strategy] called for the mainstreaming of climate change adaptation into all sectoral plans and this has progressed in several sectors including tourism, health, finance, agriculture, biodiversity, fisheries, disaster management, and land-use planning. [...] A new Biodiversity law is currently being drafted which will update the existing laws related to the protection of biodiversity and strengthening of the capacity of those charged with their protection. There is a need to balance protected areas and room for development whilst developing a strong capacity for biosecurity.”
	Biodiversity resilience	“Also recently, the Seychelles Biodiversity Strategy and Action Plan (2015-2020) has been launched, and includes many cross-sectoral projects with climate change adaptation implications. Projects address issues such as sustainable tourism, watershed management, sustainable agriculture and fisheries, disaster planning, research and a shift toward ecosystem-based adaptation approaches to biodiversity conservation.”
Singapore	Biodiversity protection	“Singapore will conserve more native plants and animals by carrying out recovery plans for over 70 more animals [sic] and plant species, enhancing 30 hectares of forest , marine and coastal habitats, and restoring ecological habitats in at least half of its gardens, parks and streetscapes by 2030.”
Suriname	Biodiversity protection	“The 2017 – 2021 Policy Development Plan aim for the forest sector is to increase its contribution to the economy and the welfare of this and future generations, including through biodiversity preservation. [...] The protection and management of protected areas is the highest priority for biodiversity preservation in the [Policy Development Plan] 2017-2021. It states mangrove forests that protect the Atlantic coastline will be protected within a scheme coupled with improved land zoning and enforcement capacities. [...] Stakeholders note the large impact mining has on forests and biodiversity. The PDP speaks about the need to balance the need for development and the protection of the environment. Several

		projects have been initiated in the sector and the government expects to include the sector in the 2025 NDC update.”
	Biodiversity governance	“In accordance with the 2015 NDC unconditional contribution, Suriname has established 14% of its total land area under a national protection system and will continue to pursue the expansion of this system by increasing the percentage of forests and wetlands under protection to at least 17% of the terrestrial area by 2030, in line [sic] the UN CBD Aichi target. [...] This will lead to the expansion of the national network of legally protected areas to accomplish 100% representation of all ecosystems and biological species, according to the National Biodiversity Action Plan (Ministry of Labour, Technological Development and Environment, 2013), the National Forest Policy (2005) and the Suriname National REDD+ Strategy (2018).”
Timor-Leste	Biodiversity resilience	“Priority adaptation areas are identified in relation to food security, water resources, health, natural disasters, forestry, biodiversity and coastal ecosystem resilience, livestock production and physical infrastructure.” Adaptation measures: “Forests, Biodiversity and Coastal Ecosystems Resilience: - Maintain mangrove plantations and promote awareness raising to protect coastal ecosystems from impacts of sea level rise. - Include ecosystem management in national planning to develop sustainable, ongoing programme, nurseries and community awareness development – [1st] year assessment, [2nd] year plan, 3rd year implementation and maintenance. - Mangrove plantation and protection to enhance coastal resilience.”
	Biodiversity governance	“The Ministry of Commerce, Industry and Environment, in cooperation with the National University of Timor Lorosa'e (UNTL), has established a Center for Climate Change and Biodiversity (CCCB) with the aim to undertake climate related research, providing effective data to the Government of Timor-Leste, which is targeted to develop relevant policy and to undertake data-informed decision making. [...] Proposed Biodiversity Decree Law, which specifically targets biodiversity conservation concerns such as the protection of habitats and ecosystems, threat and management of invasive alien species, trade in species and the penalties, and other provisions.”
Vanuatu	Biodiversity protection	“Vanuatu’s INDCs is well aligned with the Government’s Priority Action Agenda Policy Objective 4.5 which is most relevant to Climate Change and states, “to ensure the protection and conservation of Vanuatu’s natural resources and biodiversity, taking climate change issues in consideration.””
	Biodiversity resilience	“The [National Adaptation Programme of Action] further recognised that the following core issues were relevant to all priorities and should be an integral part of any proposed activities; [...] Consideration of marine and terrestrial Biodiversity [sic] issues”.

2.3.3 Links between forest-based climate solutions and biodiversity conservation measures

There was a significant association between whether NDCs mentioned forest-based climate solutions and biodiversity conservation measures (Fisher’s exact test, p-value: 0.005): 14 countries (35.9 %) considered both, 13 (33.3 %) incorporated none, 11 (28.2 %) incorporated only forest-based climate solutions, whilst Nauru (2.6 %) solely mentioned biodiversity

conservation measures. Regarding the most frequently cited categories, “forest protection” or “forest (re-)growth” and “biodiversity protection” or “biodiversity governance” had the strongest link. Overall, Timor-Leste covered most categories, followed by the low-lying coastal states Suriname, Guinea-Bissau, and Guyana. However, only five countries established direct in-text links between forest-based climate solutions and biodiversity conservation measures (Table 2.2): Mauritius and Singapore mentioned forest (re-)growth to enhance biodiversity resilience and protection respectively, Comoros and Suriname connected biodiversity protection with forest protection, and Jamaica claimed that biodiversity protection should be promoted through forestry, but did not specify through which type of forest-based climate solution.

2.4 Discussion

Nature-based solutions provided by forests offer great synergistic potential for combating both climate change and biodiversity loss. However, thus far there has been limited exploration of the extent to which this potential has been translated into policy documents. Here we show AOSIS members do tend to prioritise forests for climate change mitigation and to a lesser degree adaptation but hardly any prioritise biodiversity for climate action. This represents a missed opportunity for AOSIS countries to tackle both challenges simultaneously, and risks unintended consequences for biodiversity conservation whilst solely focussing on meeting climate change mitigation obligations.

2.4.1 Mitigation- and adaptation-oriented prioritisation of forests and biodiversity

Most AOSIS members prioritise forests in their NDCs (cf. GIZ, 2021; Pauw et al., 2016). In general, AOSIS members concentrate on climate change adaptation (Mbeva and Pauw, 2016), perhaps because their own climate footprint is insignificant when compared to the world’s largest CO₂ emitting countries. What is more, they are among the countries that pay the highest price in terms of loss and damage from climate change (Halstead, 2016; Thomas and Benjamin, 2018). However, in our study, forests were predominantly used as a mitigation-oriented strategy, although their combined absolute forest area is small, which limits their potential contribution to the global CO₂ balance (Wilkie et al., 2004; Saatchi et al., 2011). Forest-based climate solutions may simply be among the most achievable mitigation solutions for these countries as many of them are rich in forests.

Biodiversity is a neglected topic in the NDCs, and rarely seen as a priority. This pattern is not surprising since the role of biodiversity for climate change mitigation is even less prominent than for adaptation (Hisano et al., 2018; Seddon, Turner, et al., 2019). The three countries

prioritising biodiversity in their adaptation action did not distinguish between biodiversity as a conservation target and biodiversity as a contributor to adaptation. Recognising that biodiversity can be part of the solution for both climate change mitigation and adaptation, and that further loss could indeed aggravate the climate crisis, would be crucial for promoting synergies between forest-based climate solutions and biodiversity conservation measures (Mori, 2020). Moreover, it is striking that we could not find any references regarding the high level of endemism in most AOSIS countries despite the global importance of conserving this endemism (Wilkie et al., 2004; Kier et al., 2009). Climate change will affect terrestrial endemic species 10 times more than terrestrial introduced species in terms of abundance, diversity, spatial distribution, habitat change, and physiology. In addition, climate change puts endemics from islands at a much greater extinction risk than those from mainland regions (Manes et al., 2021).

2.4.2 Country-level variation in forest-based climate solutions and biodiversity conservation measures

Nearly two-thirds of AOSIS members proposed forest-based climate solutions in their NDCs, which is broadly in line with global analyses. For instance, 77 % of all NDCs include forest landscape restoration within their NDCs (IUCN, 2017) and two-thirds of signatories to the Paris Agreement propose NBS that include forests (Seddon, Daniels, et al., 2020). Furthermore, an emphasis on forest (re-)growth and forest protection among NBS appears to be common in NDCs (Laurans et al., 2016; IUCN, 2017; Seddon, Sengupta, et al., 2019), which supports our findings. However, there is substantial variation among countries in their specific approach.

Interestingly, not all AOSIS members that mention forests as a priority for combating climate change also proposed forest-based climate solutions. In other words, prioritisation does not always translate into action. This raises the question if some countries are in favour of forest-based climate solutions but face constraints that prevent them from stating concrete commitments. In our analyses, the larger countries Timor-Leste, Guinea-Bissau, Suriname, Guyana, and Papua New Guinea were among those nations proposing the highest numbers of forest-based climate solutions. Analytical and financial capabilities may be key here (Röser et al., 2020; Griscom et al., 2020). In fact, many AOSIS countries make their targets conditional on external support (Rossi and Miola, 2017), which may not be equally accessible to all members. Allocation of international funds can be highly unbalanced, and often related to population size and low GDP, rather than need (Robinson and Dornan, 2017).

As high forest cover and low deforestation (HFLD) developing countries, Suriname and Guyana may generally be highly motivated to present a wide range of forest-based climate solutions in their NDCs. They explicitly referred to their HFLD status in their NDCs, with Suriname saying

that it intends to sustain its 93 % forest cover. The international community has increasingly recognised the importance of HFLD nations for the delivery of forest-based climate solutions. This is a process partially driven by the Krutu Declaration in 2019, which aims to support cooperation among HFLD nations and mobilise international climate finance for their needs. Other, smaller AOSIS members, namely the Bahamas, São Tomé and Príncipe, the Seychelles, and Samoa, also support the declaration but the lack of international finance might explain their comparatively low to non-existing range of suggested forest-based climate solutions. Contrastingly, a few AOSIS countries hardly have any forest area, such as Nauru or the Maldives, and therefore may refrain from setting forest-based targets.

Those AOSIS members that did propose biodiversity conservation measures in their NDCs only presented vague targets, mirroring insufficient links between NDCs and the Aichi biodiversity targets in 100 countries, and perhaps related to the lack of encouragement within the NDC process to include biodiversity-related measures (Watts et al., 2018). Furthermore, the connection of biodiversity conservation measures to climate change action was not always straightforward. This was exemplified by the Government of Comoros. They planned to step up their efforts for biodiversity conservation by expanding protected areas. This intention was described as a mitigation action but how it exactly contributed to reducing CO₂ emissions was not explained.

2.4.3 Co-benefits, synergies, and governance of forest-based climate solutions and biodiversity conservation measures

Ensuring that there are co-benefits and synergies between forest-based climate solutions and biodiversity conservation is a relatively new concept (Gardner et al., 2020; Mori, 2020). This is despite the fact that NBS, including forest-derived ones, predominantly have positive effects on biodiversity (Chausson et al., 2020). Indeed, here we show that the few AOSIS members referring to biodiversity conservation measures typically did not indicate whether forests play a central role for their successful implementation. The Government of Suriname (2019) did acknowledge that their “primary old-growth tropical forests are of global importance, not only in terms of forest carbon, but also because of the interconnectedness of biodiversity, forest conservation and climate change” (p. 11).

If the opportunities presented by natural climate solutions through forests can also be of benefit to biodiversity conservation, then it is important to begin to understand what mechanisms might enable this to happen most rapidly. Given that forest protection and forest (re-)growth were most frequently mentioned in AOSIS members’ NDCs, these mechanisms could be one way forward. If this is to be the case, NDCs should stress the importance of forest protection for

biodiversity conservation, such as through protected areas, and provide quantitative targets. Native tropical forests host large numbers of rare and threatened species that are at the risk of being lost irreversibly. Special attention should hence be given to the preservation of these ecosystems (Barber et al., 2020). Another asset is that intact old-growth forests are generally more resilient to environmental change than human-modified ecosystems (Thompson et al., 2009), as well as offering carbon storage levels above those of other forest types (Watson et al., 2018).

Forest (re-)growth can be beneficial for biodiversity conservation if implemented appropriately, such as by avoiding monoculture plantations of non-native species (Seddon, Turner, et al., 2019), or by connecting remaining habitat patches (Pawson et al., 2013; Newmark et al., 2017). A mix of species, including native and climate-resilient species, should be the preferred option for plantations to ensure long-term climate change mitigation and adaptation as well as biodiversity protection (Seddon, Turner, et al., 2019; Seddon, Sengupta, et al., 2019; Mori, 2020). If forests are cultivated, they should be managed sustainably and degradation as well as deforestation should be avoided as much as possible to preserve biodiversity. In particular, retention forestry is a useful practice in this regard, where key elements of the stand structure, such as dead wood or old trees, are kept in the harvesting process (Lindenmayer et al., 2012; Mori and Kitagawa, 2014). Compared to reforestation, forest restoration and rehabilitation are terms that are more inclusive of biodiversity conservation. Their usage in NDCs should thus be encouraged.

Another important aspect is forest and biodiversity governance, upon which any decision-making on a management level depends. For instance, our analyses indicates that biodiversity-related instruments such as the CBD or Aichi targets are currently not routinely noted in the NDCs, something that should change if the opportunities to exploit synergies between the international treaties are to be maximised. Governments must commit to more integrative approaches in their NDCs to link biodiversity governance and climate-oriented forest governance better. In theory, REDD+ policies provide opportunities for co-benefits as the so-called Cancun safeguards take biodiversity into account (Bodin et al., 2015) but the more relevant synergies are not actively sought. These policies must also be designed to avoid leakage that leads to biodiversity loss elsewhere (de Lima et al., 2013). In addition, REDD+ primarily focusses on climate change mitigation and not adaptation. Additional options would be to mention inclusive approaches for biodiversity conservation measures and forest-based climate solutions existing within forestry acts or policies, National Adaptation Programmes of Action (NAPAs), or NBSAPs for instance.

It must also not be forgotten that the uptake of forest- and biodiversity-based approaches may negatively affect local people. Some states mentioned livelihood strategies when relating to sustainable forest management or REDD+, e.g.: “Guyana is prepared to continue to sustainably manage, conserve, and protect [its forest carbon stocks] for the benefit of ourselves and all humanity. In return, we must obtain benefits to improve the wellbeing and quality of life of Guyanese” (Government of Guyana, 2016, p.3). It seems, however, that most AOSIS countries revealed a substantial backlog with regard to combining mitigation and livelihood strategies in the context of forests. More references were found for forest-based adaptation enabling a climate resilient development. “Maintain and restore healthy forest ecosystems by sustainable forest management, increasing afforestation and reforestation in order to increase the resilience of human communities” is what the Government of Belize (2016, p.13) claimed as an adaptation priority goal, for example. Often it remained unclear, however, how forests shall be used in particular to achieve human resilience.

Although NDC commitments of AOSIS countries may have a limited influence on mitigation on a global scale, they are still crucial for adaptation in these countries. At the same time, AOSIS countries are disproportionately important for biodiversity conservation, compared to other UNFCCC parties. AOSIS members could therefore deliberately use their NDCs as an opportunity to protect their unique and threatened biodiversity, by aiming for synergistic effects. In contrast, if forests are intended for mitigation purposes only, as was the case in most NDCs, approaches that are harmful for biodiversity, such as monocultures, may be supported. Further attention thus needs to be drawn to the endemic biodiversity of island states in climate negotiations. International financial support will be needed to realise synergies between biodiversity and climate protection.

2.5 Conclusions

Here we examine the extent to which biodiversity conservation is integrated into NDCs, using the example of AOSIS members. Although NDCs predominantly show what countries intend to do and not what they actually do, these documents allow us to draw relevant conclusions. Thus far, NDCs are a missed opportunity for tackling the inseparable climate and biodiversity dilemmas together. Especially in AOSIS countries, where biodiversity loss and climate change are severe issues, more inclusive approaches are necessary. Although it may seem an initial burden, exploring co-benefits and synergies, in particular between biodiversity conservation and forest-based adaptation, is highly relevant for the sustainable future of these and many other states. Creating climate-resilient ecosystems goes hand in hand with biodiversity protection and, in addition, ensures carbon sequestration in the long term (Osuri et al., 2020). Key to combating

climate change is promoting diversity at all ecological scales and connectivity between ecosystems so that forests can resist or recover from environmental change (Pawson et al., 2013; Oliver et al., 2015). More awareness of the essential role that biodiversity plays both for climate change adaptation and mitigation needs to be raised. As such, its protection and enhancement can be regarded as the foundation of forest-based climate solutions.

Using forest-based climate solutions as a vehicle, clear and meaningful targets must be set to achieve co-benefits and synergies with biodiversity conservation measures. This not only allows progress with individual NDCs to be quantified, but also allows comparisons to be made between countries, so that best practice and lessons learnt can be shared. In line with the finalisation of the Paris Rulebook, changes in the structure of NDCs are underway. As a result of the Covid-19 pandemic, some countries still need to submit their updated or second NDCs. However, the next round of NDCs was originally due before the COP 26, which has been postponed by one year, taking place in November 2021 instead. Overall, this delay may have provided a window of opportunity to rethink the climate-biodiversity gap within NDCs and beyond.

Author contributions

Lena Strauß: Conceptualization, Methodology, Formal analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Visualization. **Timothy R. Baker:** Conceptualization, Methodology, Writing – Review & Editing, Supervision. **Ricardo F. de Lima:** Conceptualization, Methodology, Writing – Review & Editing, Supervision, Funding acquisition. **Stavros Afionis:** Conceptualization, Methodology, Writing – Review & Editing. **Martin Dallimer:** Conceptualization, Methodology, Writing – Review & Editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in the paper.

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3 Widespread introduced species dominate the urban tree assemblage on the endemic-rich tropical island of São Tomé

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Abstract

The Afrotropics are experiencing some of the fastest urbanisation rates on the planet but the impact of city expansion on their rich and unique biodiversity remains understudied. Here we investigated how the tree assemblage changes between urban, rural, and natural zones on the endemic-rich oceanic island of São Tomé. Based on 81 transects, we assessed different responses of endemic, native, and introduced species. Tree species richness and abundance were highest in the natural zone, and the composition was significantly different compared to the urban zone. The assemblage of the rural zone was the most uneven and had the lowest beta diversity. The urban zone was dominated by introduced species (57.7 %), most of which were not from the Afrotropics, while the natural zone hosted almost exclusively native species (93.3 %), including many endemics (26.1 %). The depletion of the tree flora in the urban zone was most noticeable when compared to the natural zone. In contrast to native and endemic species, introduced species have clearly benefitted from urban and rural expansion. These findings highlight how humans are impacting the native tree species of São Tomé, and the need for measures geared towards the conservation of endemic and globally threatened tree species. Importantly, these include the protection of natural forests, withstanding the rising land demands for settlements and agriculture.

Keywords

Afrotropical forest; Anthropogenic gradient; NMDS; Oceanic island; Urban ecology; Urbanisation

3.1 Introduction

By 2100 urban areas around the globe will occupy around six times the area they covered in 2000 (Gao and O'Neill, 2020). City expansion, especially into intact or biodiverse areas, can have substantial environmental impacts, but our understanding of the effects of urbanisation on

biodiversity is dominated by studies concentrating on biotic or abiotic factors, city age or size, or management practices within cities themselves (Beninde et al., 2015). Research that extends beyond city boundaries also typically only reaches nearby rural hinterlands (Rega-Brodsky et al., 2022), which often support species assemblages that are already highly influenced by human interference. We rarely compare species assemblages in urban areas against those of natural or near-natural zones (Padilla and Sutherland, 2019). Thus, our understanding of the extent to which urbanisation impacts biodiversity is compromised.

The lack of natural or near-natural baselines helps to explain why even in well-studied temperate, industrialised regions, assessments of urban biodiversity come to surprisingly different conclusions (McKinney, 2008). Some studies claim reduced diversity, while others report that urban areas can be hotspots of plant diversity (Gillespie et al., 2017; Kantsa et al., 2013), often linked to habitat heterogeneity and to introduced species (Kowarik, 2011). Some cities have been shown to be more diverse and even to hold more rare and threatened species than their rural surroundings (Ives et al., 2016), such as the urban-restricted tree species *Grevillea caleyi* in Australia (Soanes and Lentini, 2019). However, urbanisation is also known to underpin global biotic homogenisation (Lokatis and Jeschke, 2022), because widespread species accustomed to anthropogenic environments proliferate, often at the expense of native species. The biogeographic origin of species can thus be linked to their spatial distribution across landscapes. Exploring homogenisation processes may advance our comprehension of urbanisation-induced biodiversity changes.

It is important to study the impact of urbanisation in the tropics, where it is happening very rapidly. The Afrotropics are particularly important in this regard as they have some of the fastest urbanisation rates (OECD/SWAC, 2020). Here, cities are often surrounded by agroforestry systems (Zomer et al., 2016), which can host high biodiversity, including forest-dependent species (Deheuvels et al., 2014). Therefore, we cannot expect that urban biodiversity patterns in tropical cities replicate those of temperate zones.

Oceanic islands are good study systems to assess the impacts of urbanisation on biodiversity, as they are characterised by a high proportion of range-restricted species that are often sensitive to anthropogenic changes (Whittaker et al., 2023). However, they are rarely considered in urban biodiversity research (Lowry et al., 2020). High extinction and introduction rates on islands have also led to biotic homogenisation (Castro et al., 2010), which may further exacerbate patterns linked to urbanisation. Trees are especially relevant for terrestrial ecosystems, contributing to primary production and defining habitat features that are key for other taxa. While the importance of tree and canopy cover in urban areas for delivering ecosystems services is relatively well studied, even in the tropics, we still know little about how tree species

assemblages are being altered by urbanisation. Here we investigated how tree assemblages responded to urbanisation by sampling across the urban, rural, and natural zones of the oceanic island of São Tomé, Central Africa. Focussing on the questions below, we expected distinct tree assemblages between zones and a strong influence of widespread introduced species on biodiversity patterns (de Lima et al., 2014).

1. How do tree assemblages change between urban, rural, and natural zones?
2. To what extent do introduced species drive these changes?
3. Are there differences in native biogeographic ranges across urban, rural, and natural zones?

3.2 Materials and methods

3.2.1 Study area

São Tomé is an oceanic island that, together with the smaller Príncipe, comprises the Democratic Republic of São Tomé and Príncipe. It is part of the Guinean Forests of West Africa Biodiversity Hotspot, hosting an endemic-rich but threatened biodiversity (de Lima et al., 2022). Isolated in the Gulf of Guinea, the country is a distinct bioregion, whose vascular flora is composed of approximately 14.5 % endemic species (Stévant et al., 2022), and is the best studied in the Afrotropics (Droissart et al., 2018). The climate is oceanic equatorial (mean annual temperatures 16.2-25.9 °C; mean annual precipitation 600-7,000 mm) with one main dry season between June and August, and a shorter one between December and January. Due to the mountainous centre and prevailing winds from the southwest, the island has a distinct rain shadow (Ceríaco et al., 2022). There is also a strong gradient of human impacts linked to ruggedness (Norder et al., 2020). Lowland forests have been largely converted to agriculture, while most remaining forest is found in the mountainous centre (Dauby et al., 2022). Urban areas, where around three quarters of the population reside, are mostly located near the coast in the drier northeast (Figure 3.1). As in other African countries, the population, economy, and politics are disproportionately centred around the capital (Güneralp et al., 2018). The urban population has increased five-fold since 1950; a rate that far exceeds that of Central Africa as a whole (UN-DESA, 2018).

3.2.2 Sampling design

3.2.2.1 Land classification

To assess the effect of urbanisation, we classified São Tomé into urban, rural, and natural zones, based on land-use (Soares et al., 2020) and urban area maps (Ministério das Infra-Estruturas, Recursos Naturais e Ambiente, 2018). Besides infrastructure and sealed surfaces, the urban zone included greenspaces such as public parks, home gardens, and secondary forest fragments. The rural zone comprised landscapes of low human population density with forested or non-forested plantations and areas of regenerating vegetation. This zone predominantly corresponds to shade plantations, an agroforestry system composed of tall trees shading understorey cash crops such as coffee (*Coffea* spp.) or cocoa (*Theobroma cacao*). The natural zone, most of which is protected as Obô Natural Park, spanned old-growth native and secondary forests with little human presence.

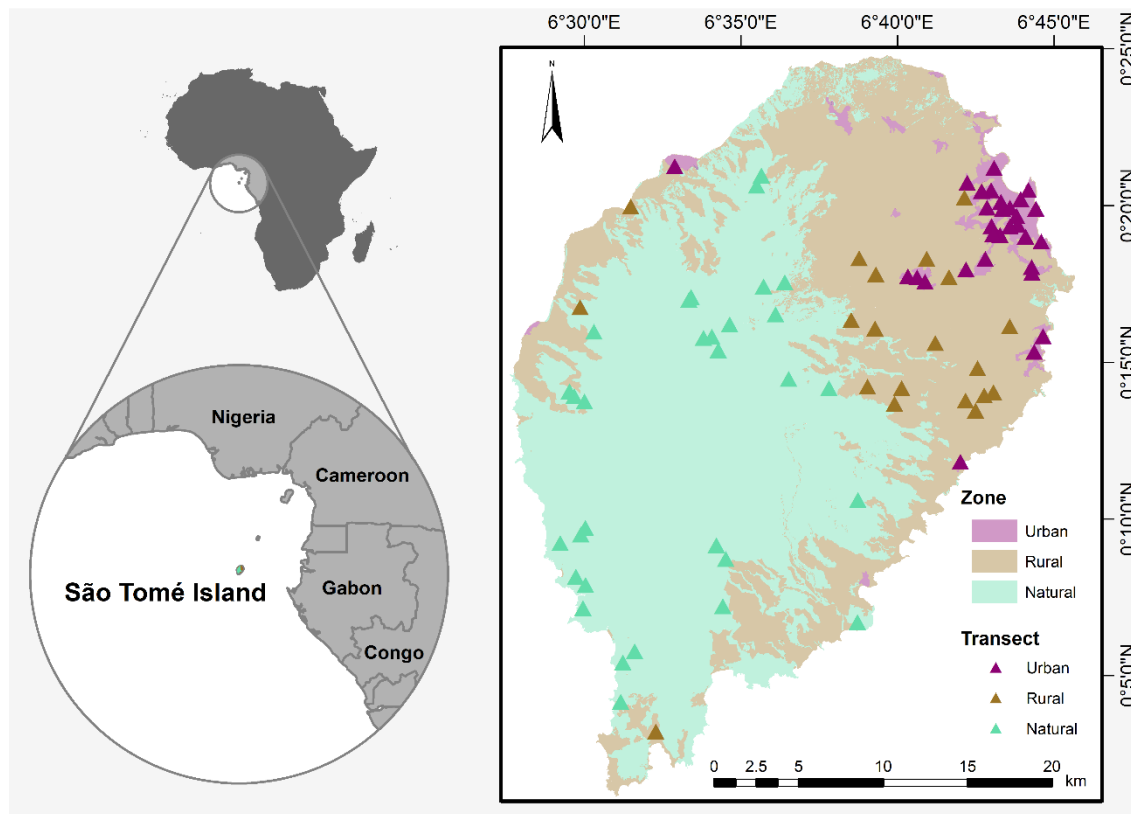


Figure 3.1. Location of São Tomé Island in Africa (top left) and in the Gulf of Guinea (bottom left), and of the 81 transects sampled across urban, rural, and natural zones of São Tomé (right). Zonation of the latter was based on Soares et al. (2020) and Ministério das Infra-Estruturas, Recursos Naturais e Ambiente (2018).

3.2.2.2 *Sampling strategy*

We established 81 transects across the three zones. For the natural zone, 31 transects were purposefully selected to capture the diversity of well-preserved forest across altitudinal and rainfall gradients. For urban and rural zones, we used a stratified random sampling approach. First, we created a 500 x 500 m grid across the island and selected 30 grid cells in the urban zone and 20 in the rural zone. Fewer rural grid cells were selected as this zone is more uniform (de Lima et al., 2014). A transect was then established in each grid cell. If this was not possible, we targeted a new randomly selected grid cell. Across all zones, each transect consisted of four 5 x 50 m sections (0.1 ha) separated by less than 50 m, ensuring at least 200 m between transects. Sections were not in a straight line so that a homogenous patch of habitat could be sampled by avoiding obstacles such as roads or rivers/valleys (Benitez Bosco et al., 2018).

3.2.3 *Data collection*

3.2.3.1 *Tree sampling*

Fieldwork was carried out from October 2019 to August 2021. All trees with a diameter at breast height ≥ 5 cm were identified within each transect section (Benitez Bosco et al., 2018). Plants from the Arecaceae, Caricaceae, Musaceae, Pandanaceae, and Poaceae were not considered to be trees. We photographed and collected every species at least once to facilitate identification down to the lowest taxonomic level (Tropicos, 2023).

3.2.3.2 *Species origins*

We ascribed each taxon to a biogeographic realm (Udvardy, 1975) based on POWO (2023) and Figueiredo et al. (2011), or on author expertise if information was incomplete or doubtful. No realm was ascribed if data were unavailable. We distinguished introduced and native taxa, and classified as endemic if the native distribution was restricted to the oceanic islands of the Gulf of Guinea (App. B.1).

3.2.3.3 *Environmental parameters*

We selected spatially explicit environmental variables that best reflected physico-climatic gradients, based on availability and relevance, to explain differences in tree assemblages (Soares et al., 2020; Dauby et al., 2022). The resolution of altitude, precipitation, remoteness, slope, and topography was ~ 90 m (Soares et al., 2020), while for cloud cover it was 1 km (Wilson and Jetz, 2016). All variables were continuous, except for topography, which was categorical, distinguishing flat areas, valleys, middle slopes, upper slopes, and ridges. For each of the continuous variables, we used the mean of the values extracted at start and end points of transect sections to characterise each transect. For topography, we used the most frequent category

among these start and end points, or if categories were equally frequent, we used the one that occurred first along the transect.

3.2.4 Data analyses

Analyses were performed in R 4.2.2 (R Core Team, 2022). We used abundance data for each species in each transect to test for differences in community biodiversity metrics between zones. For species richness and Fisher's alpha index, we used one-way ANOVAs followed by Tukey HSD post-hoc tests, since data was normally distributed and homoscedastic. For abundance and Pielou's evenness index, we employed Kruskal-Wallis rank sum tests followed by pairwise Wilcoxon rank sum tests. Using "BiodiversityR" (Kindt and Coe, 2005), we created rank-abundance curves and Rényi diversity profiles to simultaneously compare species richness and evenness across zones (Oldeland et al., 2010). To account for different sample sizes, we calculated average abundance and species richness per transect for each zone. In addition, we created transect-based species accumulation curves to evaluate the variation in expected mean species richness between zones, and used Chao, first and second order Jackknife, and Bootstrap to estimate species richness.

We standardised data applying the "hellinger" method from the function "decostand" in "vegan" (Oksanen et al., 2022), and applied non-metric multidimensional scaling (NMDS) to visualise differences in the structure of tree assemblages between zones. We deemed stress values below 0.2 to be acceptable (Clarke, 1993). To help interpret the NMDS, we tested differences in location through permutational multivariate analysis of variance (PERMANOVA; permutations = 999) by using "adonis2" in "vegan" and "pairwise.adonis2" in "pairwiseAdonis" (Martinez Arbizu, 2017), and in dispersion through permutational multivariate analysis of dispersion (PERMDISP; permutations = 999) by using "betadisper" and "permutest.betadisper" in "vegan", complemented by an analysis of similarities (ANOSIM; permutations = 999) via "anosim" in "vegan". To understand how tree composition was linked to environmental characteristics, we superimposed all significant environmental variables as arrows on the NMDS, standardising continuous environmental variables using "standardise" from the function "decostand" in "vegan".

To examine whether species origins affected patterns across zones, we tested for differences in species richness and abundance for introduced and native species, and for endemic- and non-endemic species. This was done via one-way ANOVAs followed by Tukey HSD post-hoc tests when assumptions were met, or otherwise by Kruskal-Wallis rank sum tests followed by pairwise Wilcoxon rank sum tests. We also generated NMDS plots to visualise tree assemblage structures according to species origins and native ranges.

We calculated indicator values to identify associations between species and zones, using the multi-level pattern analysis of the function “multipatt” from “indicspecies” (De Cáceres and Legendre, 2009), and the argument “func = “IndVal.g”” for unequal group sizes. This function accounts for different niche breadths of species by exploring both individual zones and combinations.

To detect and quantify spatial autocorrelation, we used Moran’s I in “ape” (Paradis and Schliep, 2019). This was followed by variation and hierarchical partitioning via “rdacca.hp” (Lai et al., 2022). The former determined the unique and average shared contributions and the latter the overall importance of each predictor (or group of predictors), namely principal coordinates of neighbour matrices (PCNM) (Borcard and Legendre, 2002), environment (altitude, precipitation, remoteness, slope, topography, cloud cover), and zone (urban, rural, natural), towards explained variation (R-squared) in tree assemblages.

3.3 Results

We removed 21 individuals (0.32 %) only determined to family or higher, and 287 individuals (4.37 %) that were identified to genus, but for which we could not exclude the possibility that they may belong to already identified species. The final dataset contained 6,563 individuals, 6,436 belonging to 171 species, and 127 to undetermined species within six genera. For simplicity, all are referred to as species in the remainder of this work. There were between 17 and 240 individuals per transect. The mean number of species and individuals per transect was 15.0 ($\pm$ 5.7) and 81.0 ($\pm$ 51.6), respectively.

Species richness and abundance were highest in the natural zone (Figure 3.2a, Figure 3.2b). Abundance was higher in rural than in urban zones, but there was no difference in species richness. For Fisher’s alpha and Pielou’s evenness indices, transects in the rural zone had the lowest values (Figure 3.2c, Figure 3.2d). The natural zone had the most diverse profile, and the rural zone was the least diverse (Figure 3.3). This is due to the hyperdominance of cocoa tree in this zone, to which it was clearly associated, showing the highest indicator value (0.920). Species richness increased more rapidly and was highest in the natural zone (119 species), even though it was incompletely assessed in all zones (Figure 3.4).

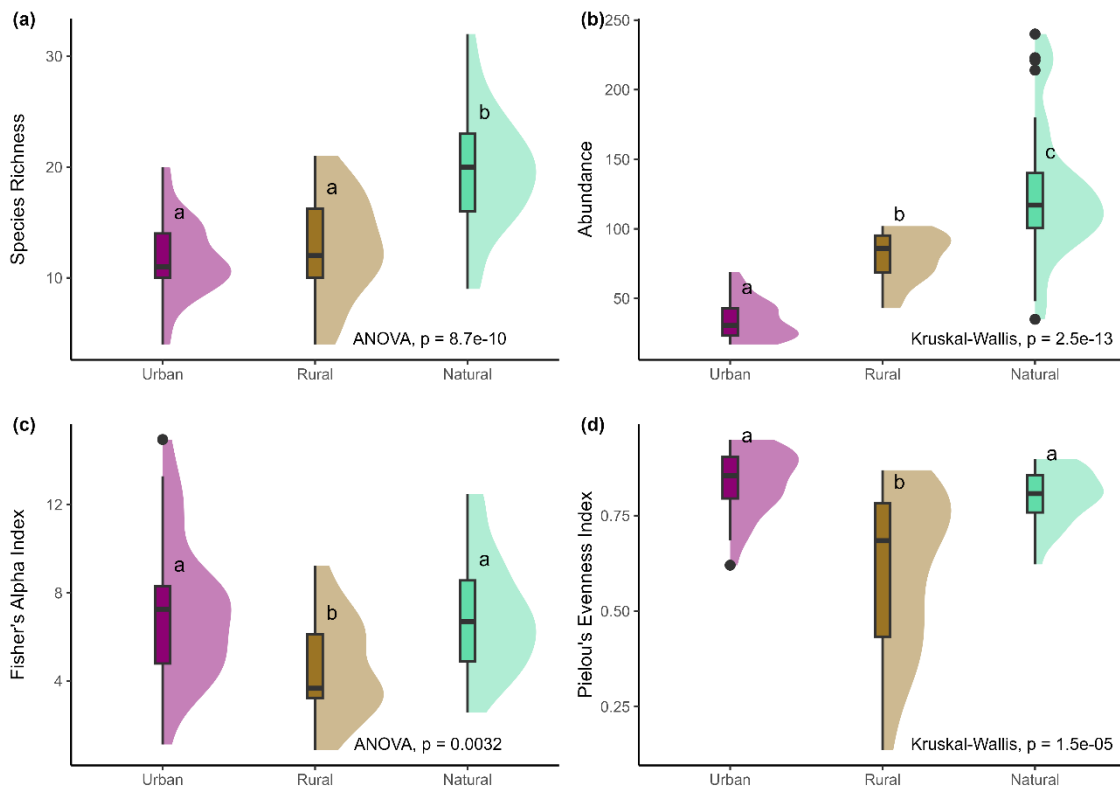


Figure 3.2. Violin box plots of (a) tree species richness, (b) abundance, (c) Fisher's alpha index, and (d) Pielou's evenness index per transect, showing the significance of relationships between zones. P-values ($df = 2$) of one-way ANOVA, (a) $F = 27.590$ and (c) $F = 6.192$, or Kruskal-Wallis rank sum tests, (b) $\chi^2 = 58.067$ and (d) $\chi^2 = 22.185$, at the bottom of each graph. Significant differences from Tukey HSD or pairwise Wilcoxon rank sum tests indicated by different superscript letters. Maximum width of violins scaled to 1.

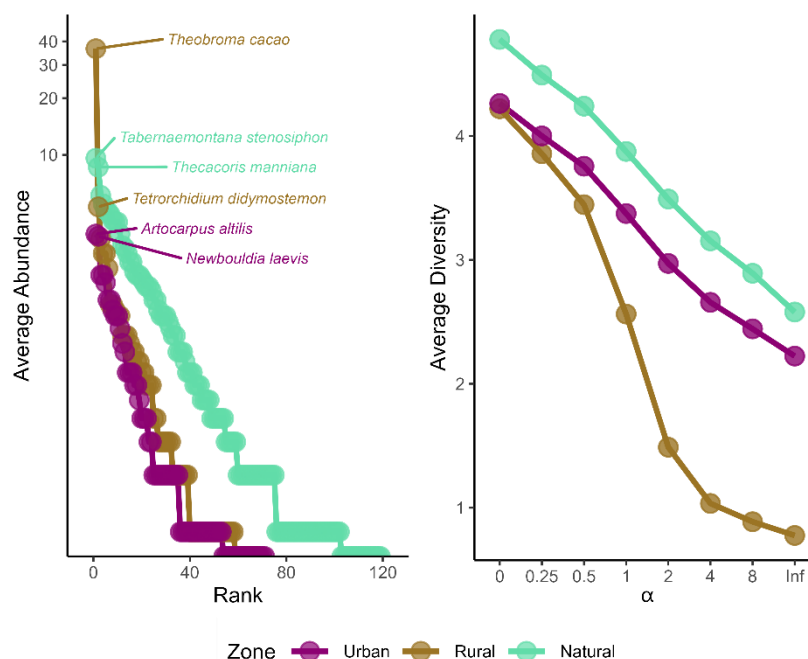


Figure 3.3. Rank-abundance curves on logarithmic scale (left), displaying the names of the two most abundant tree species for each zone, and Rényi diversity profiles (right), where the value of alpha stretches from zero to infinity (ranging between richness and evenness). 0: $\ln(\text{richness})$; 1: Shannon; 2: $\ln(1/\text{Simpson})$; Inf: $\ln(1/\text{BergerParker})$, which is the dominance of the most abundant tree species. Rank-abundance curves sort species by their abundance. A completely horizontal curve would determine perfect evenness among species. This logic is also true for Rényi diversity profiles. However, as a type of diversity ordering technique, a Rényi diversity profile orders the most common diversity indices. At one glance, it thereby enables cross-category comparisons between these different measures. Unlike rank-abundance curves, it does not give any information on the proportions of different species (Kindt and Coe, 2005; Oldeland et al., 2010). Abundance and diversity were averaged per transect for each zone.

Tree assemblages were distinct between all zones, but most notably between natural and urban zones (pairwise PERMANOVA: $F = 21.369$, $p = 0.001$; Figure 3.5a). Floristic similarity was always lower between zones than within zones (ANOSIM: $R = 0.719$, $p = 0.001$). Within zones, tree assemblages were equally similar among urban and rural transects (pairwise PERMDISP: $F = 6.019$, $p = 0.235$; App. B.2), and most distinct among natural transects ($p < 0.050$).

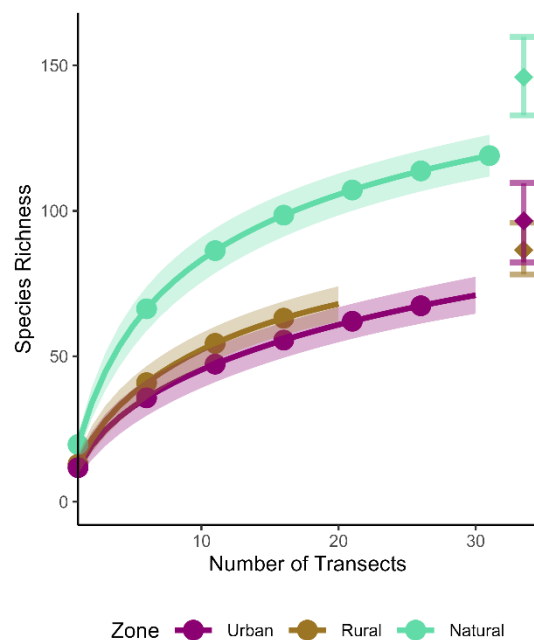


Figure 3.4. Sample-based species accumulation curves, grouped according to zones. The vertical bars indicate the interval between the minimum (Bootstrap) and maximum species richness estimator (second order Jackknife) per zone, while the diamond shapes show the respective mean.

Moran's I revealed spatial autocorrelation for species richness ($I = 0.240$, $p < 0.001$) and abundance ($I = 0.169$, $p < 0.001$). While 60.7 % of the variation in tree assemblages remained unexplained, 17.7 % was attributable to spatial factors (PCNM), 10.9 % to environment, and 10.8 % to zone (App. B.3). Within environment, precipitation and altitude were the most important variables (App. B.4). According to variation partitioning, PCNM had the highest unique fraction (8.4 %) and contributed to the highest shared fractions of the variation (App. B.5).

All six environmental variables yielded significant correlations with the NMDS axes (Figure 3.5b). The first axis was strongly and positively associated with cloud cover, remoteness, slope, ridges, and upper slopes, and negatively with flat areas, while the second axis had weak positive associations with precipitation and weak negative ones with altitude. Additionally, the natural zone was associated to ridges, upper slopes, higher altitude and precipitation, while the urban zone was linked to flat areas and lower altitude, and the rural zone to middle slopes and lower precipitation.

Biogeographic origins differed across zones (Figure 3.5c, Figure 3.5d). The richness and abundance of native and endemic species were significantly higher in the natural zone (App. B.6). In the urban zone, introduced species accounted for 57.7 % of the richness and 70.6 % of

the abundance, contrasting to 36.8 % and 68.3 % in the rural zone, and 6.7 % and 2.9 % in the natural zone, respectively. Endemics in the natural zone accounted for 26.1 % of the richness and 34.5 % of the abundance, contrasting to 7.4 % and 1.4 % in the rural zone, and 1.4 % and 0.6 % in the urban zone. Of all species, 72.3 % were exclusively Afrotropical and found across zones, even though many were more abundant in the natural zone. On the other hand, the urban zone showed the whole range of origins, including many species introduced from the Neotropics, Indomalaya, Australasia, Oceania, or multiple realms.

We identified 71 indicator species. The top urban zone indicator species was introduced from Indomalaya (mango, *Mangifera indica*), while those of the rural zone were introduced from the Neotropics (cocoa and coral tree, *Erythrina poeppigiana*; App. B.7). The top indicator species for rural and urban zones combined were from Oceania (breadfruit, *Artocarpus altilis*) and Indomalaya (jackfruit, *Artocarpus heterophyllus*). In contrast, the main natural zone indicator species were native Afrotropical species (*Homalium henriquesii* and *Casearia barteri*).

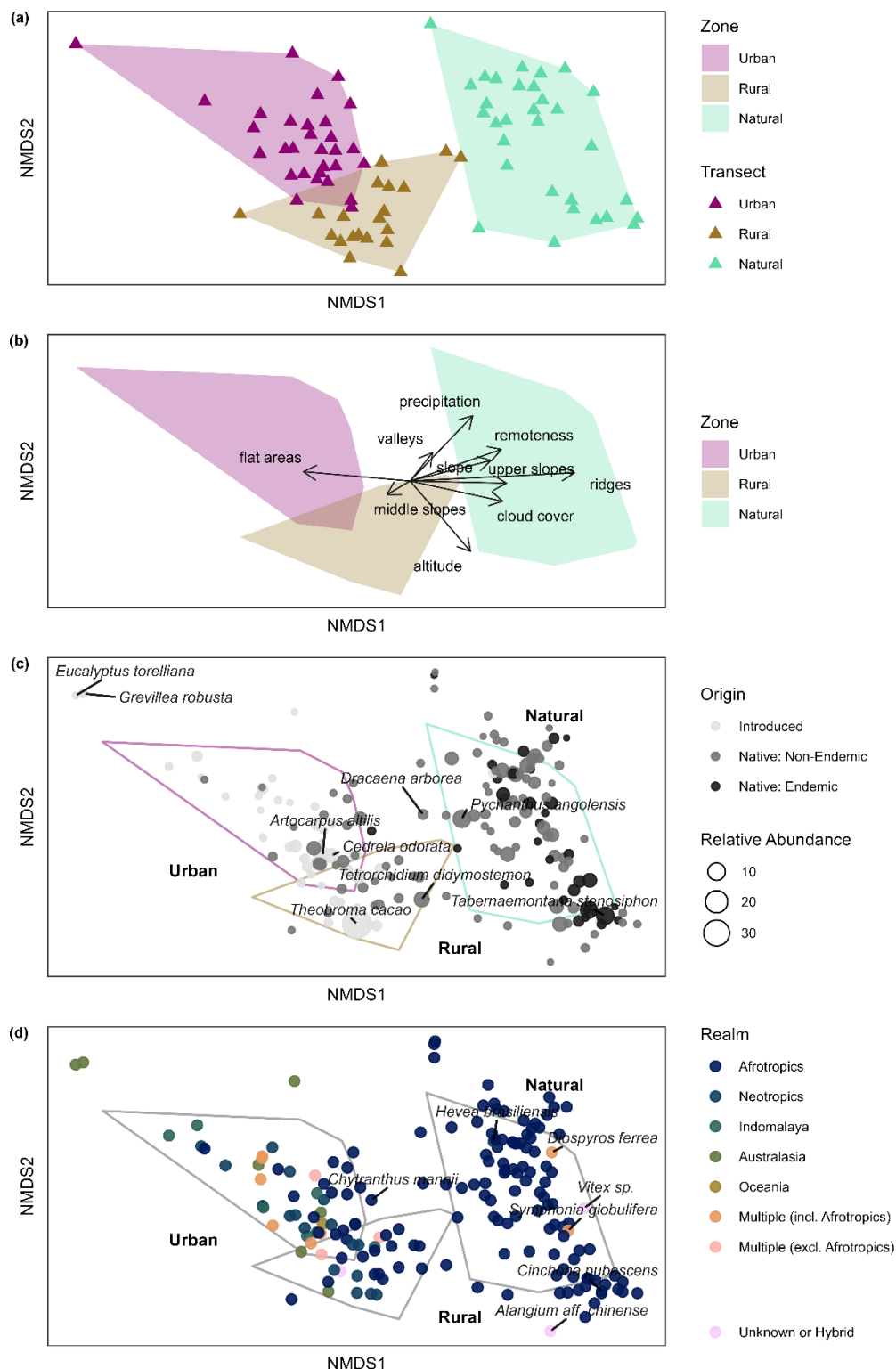


Figure 3.5. Non-metric multidimensional scaling (NMDS) plots based on Bray-Curtis dissimilarities of tree species abundances along transects (stress value = 0.126). In (a) and (b) minimum convex hulls for each zone are shown. In (c) and (d), these hulls are indicated by lines, and some minor random variation (“jitter”) has been added to avoid overlap between points (species). (a) Structural differences between transects. (b) Structural differences between transects, with fitted vectors of six environmental variables ($R^2 = 0.489$ to 0.698 , $p = 0.001$). (c) Structural differences between species, differentiated by origin and

sample relative abundance. The names of the two most abundant species of each zone and of those in outstanding positions are displayed: Dracaena arborea was a significant indicator for natural and rural transects combined (App. B.7); Eucalyptus torelliana and Grevillea robusta were only recorded in one transect in a tree nursery of the capital. (d) Structural differences between species, differentiated by realm (native range). The names of species with non-Afrotropical native ranges that are associated with the natural zone are displayed, as well as endemic species that are associated with non-natural zones.

3.4 Discussion

On the tropical oceanic island of São Tomé, urban and rural tree species richness were similar, but tree assemblages in both zones were less diverse than the natural tree assemblage. This was particularly noticeable for the richness and abundance of native and endemic species. Introduced species, in contrast, abounded in urban and rural zones, implying that tree assemblages in human-dominated landscapes have been subject to biotic homogenisation.

3.4.1 How do tree assemblages change between urban, rural, and natural zones?

The highest tree species richness and abundance were found in the natural zone. This pattern differs from other taxa on São Tomé, namely birds (Soares et al., 2020) and land snails (Tavares, 2021), which tended to have more species and higher abundances in land-use types with higher anthropogenic influence. This is not surprising since the response of biodiversity to anthropogenic interference is taxa-dependent (Barlow et al., 2007). The diversity patterns of tree species also contrast with the high plant diversity described for temperate urban areas (Gillespie et al., 2017; Kantsa et al., 2013). This might be explained by the combined effect of the tropics having younger cities (Aronson et al., 2014), higher natural tree diversity (Mittelbach et al., 2007), and less impoverished baselines than temperate areas (Wania et al., 2006).

The lowest evenness and Fisher's alpha were found in the rural zone, which is dominated by shade plantations, an agroforestry system that is heavily managed to produce a few crops shaded by a small subset of fast-growing species (Dauby et al., 2022). The rural tree assemblage of São Tomé might be particularly impoverished and uniform due to the history of intensive land-use change, which contrasts to many countries in continental Africa (Frynas et al., 2003).

Even though 16 species were shared across all zones, the assemblage structure was distinct between zones, and especially between urban and natural zones (Figure 3.5). As for São Tomé birds (Soares et al., 2020) and land snails (Tavares, 2021), native tree species, and notably the endemics, were clearly associated with natural settings, contrasting to the anthropogenic affinities of introduced taxa. Compared to those taxonomic groups, tree beta diversity was

higher in more natural settings, which might be explained by the high native species richness. However, it is not possible to distinguish whether native species are naturally absent from urban and rural zones, or if they have been removed by human actions, since trees in urban and rural zones are actively managed, being planted or removed to satisfy well-defined human needs (de Lima et al., 2014). Recent rapid urban expansion into rural areas (Muñoz-Torrent et al., 2022) may also help explain floristic similarities between the two zones. These specific circumstances all contribute to the difference between natural and both urban and rural tree assemblages.

Tree assemblages were also strongly determined by spatial components. Especially the correlations with precipitation and altitudinal gradients confirm that zone and space were not fully independent. This is understandable as native vegetation persists in rugged areas and at higher elevations (Norder et al., 2020), while rural and urban zones tend to occur in accessible drier areas at lower altitudes. The environmental differentiation of zones results from the ecological niche of humans, and intersects with that of tree species to explain current tree assemblages. Spatially, the latter may be further influenced by intra- or interspecific interactions, and by specific microhabitat requirements that were not captured by the environmental variables at the scale that they were assessed. This reinforces the abovementioned notion that tree assemblages in São Tomé were naturally rich and structured in diverse ecological niches, which thus far have not been fully described.

3.4.2 To what extent do introduced species drive these changes?

In São Tomé, 57.7 % of the tree species in the urban zone were introduced. Historically, this island being at the intersection of the Portuguese colonial routes may help explain this dominance. In many tropical regions, and especially on oceanic islands, introduced species are a legacy of colonialism (Abendroth et al., 2012) and are a testament to ecological changes associated with human settlement (Castro et al., 2010). As long-lived organisms, trees are often living proof of these legacies, and in São Tomé, many introduced tree species are prominent features of colonial streets and buildings. Other tropical cities do show similar proportions of introduced species (de Souza e Silva et al., 2020), but there is considerable variation, e.g. 79 % in Ethiopia (Koricho et al., 2020) and 36.4 % in Malawi (Chimaimba et al., 2020).

In the rural zone, over two-thirds of individual trees were introduced, which was mostly due to the hyperabundant cocoa trees, but there were also many native species, even though their abundance tended to be lower than in the natural zone. As such, the rural zone could potentially allow for the regeneration of native and endemic species, while it could also facilitate the expansion of introduced species, some of which might become invasive (de Lima et al., 2014).

The scarcity of introduced species in the natural zone is common to other island forests, such as in Trinidad (Arnold et al., 2021) and Madagascar (Osen et al., 2021).

3.4.3 Are there differences in native biogeographic ranges across urban, rural, and natural zones?

The natural zone was home to most Afrotropical species, which largely coincided with native species. Nevertheless, Afrotropical species were also well represented in rural and urban zones, in some cases by introduced species (Figure 3.5). In contrast, most non-Afrotropical species were associated with the urban zone, reinforcing the fact that this zone is characterised by biotic homogenisation through the introduction of widespread species (Lokatis and Jeschke, 2022). Many of these are useful species, such as the Indomalayan mango tree, which has been introduced across the tropics for its fruits and was the best indicator for the urban zone in São Tomé. The strong historical ties with Brazil facilitated the introduction of many Neotropical species, such as cocoa and coral trees, both of which are indicators of the rural zone.

Endemic species richness and abundance in the natural zone exceeded that of the rural and urban zones. These results contrast with those of temperate cities in Australia (Ives et al., 2016), Greece (Kantsa et al., 2013), and South Africa (Holmes et al., 2012). The scarcity of endemics in São Tomé urban and rural zones might be linked to island species struggling to adapt to anthropogenic environments, especially when they have to compete against numerous introduced species (Sánchez-Ortiz et al., 2020). This is not helped by most endemics being less valuable to humans, as they tend to have smaller or inedible fruits (Heleno et al., 2022) and to take longer to produce timber (de Lima et al., 2013). An exception to this is the rural and urban occurrence of *Chytranthus mannii* (Benitez Bosco et al., 2018), an endemic species planted for its edible fruits.

3.5 Implications and conclusions

In São Tomé, the conservation value of urban and rural tree assemblages is very low. They hold few species, most of which are introduced, widespread, and not threatened. The natural zone clearly has the highest value for conservation, hosting rich, abundant, and diverse tree assemblages that have most of the native, endemic, and threatened species. Hence, preserving the natural zone is the most important approach for conserving the island's biodiversity, counteracting biotic homogenisation. However, this could be complemented by species-specific conservation strategies targeting the few endemic and threatened species that have important populations outside the natural zones, and by exploring approaches to increase the ecological

value of rural and urban zones. We therefore propose that conservation strategies on the island should broaden out from the Obô Natural Park for better integration of rural and urban zones into national biodiversity action plans. These might introduce novel mechanisms for encouraging the diversification of native, endemic, and threatened tree species in rural zones and in urban planting programmes, as well as the celebration of their importance as a symbol of island identity and pride.

Tree diversity was higher in the natural zone, questioning the widespread notion that urban environments can be valuable for conservation. This may partly be due to most studies on urbanisation comparing cities with already highly modified rural hinterlands, rather than natural ecosystems. Thus, we call for using areas of low human interference as references to assess urban biodiversity, but also for a wider array of metrics that can capture subtle changes in biodiversity. Our results further suggest that the geographic bias of research towards temperate regions may be distorting the current perceptions of how urbanisation influences biodiversity.

Author contributions

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Conflict of interest statement

The authors declare that they have no competing interests.

Data availability statement

The data that support the findings of this study are available in the supplementary material of this article (Dataset S1, S2, S3, and Code S4).

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4 Native and introduced trees are recognised for different Nature's Contributions to People across an island anthropogenic gradient

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Abstract

Our planet is composed of landscapes heavily modified by humans, spaces shared by people and biodiversity, and almost intact wild areas. However, little is known about how these distinct land-use intensities influence Nature's Contributions to People (NCP). We studied the types and distribution of NCP associated with native and introduced trees on the Afrotropical oceanic island of São Tomé, distinguishing between urban, rural, and natural zones. Our results reveal that trees, regardless of their origin, were mainly recognised for material contributions, such as materials and assistance or energy. The biomass-intense subcategories of building materials, fuel wood, and charcoal were particularly relevant in the natural zone, which is dominated by native species and has numerous endemics. Compared to the natural zone, the recognised potential of regulating and non-material contributions by trees was considerably higher in urban and rural zones, where introduced species dominated. This means that a diversity of recognised NCP was supported across the different zones. The potential importance of introduced species for the provision of NCP highlights the need for including them in conservation efforts, rather than focussing solely on native and endemic species. By ensuring the persistence of species that are key to satisfying human needs, conservation measures are more likely to be accepted, and thus to be effective, especially in regions that are more directly dependent on natural resources.

Keywords

Afrotropics; Anthropogenic gradient; Ecosystem services; Land-use change; São Tomé; Urbanisation

4.1 Introduction

An important milestone in addressing global biodiversity loss is the Kunming-Montreal Global Biodiversity Framework. Its vision for 2050 is “a world of living in harmony with nature” (CBD Secretariat, 2023), which therefore allows for the sustainable use of biodiversity. This can

be achieved through biodiversity conservation and restoration activities that integrate human needs (Pörtner et al., 2023). However, to deliver this goal successfully, this integration will need to take into account the extent of human modification of each region. To this end, global terrestrial landscapes can be divided into three broad conditions: heavily modified landscapes (e.g. cities), spaces shared by people and biodiversity (e.g. agroforests), and almost intact wild areas (e.g. natural forests) (Locke et al., 2019). Inclusive appraisal and planning processes could improve how human needs and biodiversity conservation goals are aligned within these landscapes. But we first require a comprehensive understanding of how the benefits that nature provides to people are distributed (Schröter et al., 2023), for which the framework of Nature's Contributions to People (NCP) can serve.

The conceptual framework of NCP, initiated by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (Díaz et al., 2015), broadly distinguishes between regulating, material, and non-material contributions (IPBES, 2019). This inclusive approach integrates social sciences and humanities explicitly (Kadykalo et al., 2019), and highlights the role of culture in linking nature and people (Díaz et al., 2018). It supports a great variety of stakeholders, worldviews, and knowledge systems, including indigenous and local knowledge (Díaz et al., 2018; Kadykalo et al., 2019). Since the latter influences natural resource use (Brondízio et al., 2021), the framework is particularly suitable for low- and middle-income countries (Pineda-Guerrero et al., 2021), where many people rely more directly on NCP (Fedele et al., 2021).

Trees are important providers of material NCP, such as timber, fuel, nutrition, and medicine (Stringer et al., 2018). Food trees, for example, are popular with urban dwellers (Adeyemi and Shackleton, 2023), and medicinal trees are often integral to traditional rural healthcare practices (Furukawa et al., 2016). Trees can also support less tangible services, which may be harder to assess but whose value should not be ignored. They include the non-material contributions of ornamental trees enhancing urban aesthetics (Shackleton et al., 2015), and of sacred, old trees forming sites of spiritual reflection (Sahle et al., 2021). Further, trees are often cultivated to underpin regulating contributions, e.g. leguminous shade trees that improve soil fertility and microclimate in agroforestry systems (Muchane et al., 2020).

Trees are under enormous pressure in the Afrotropics, which have the highest proportion of threatened species globally (39.5 %) (BGCI, 2021). Land-use change is a key driver of tree diversity loss here (Rivers et al., 2023). Consequently, entire ecosystems may be degraded, since trees are vital structures of ecological communities (Lindenmayer et al., 2014). These changes may ultimately affect the supply of NCP in this region. At the same time, the conversion of forested ecosystems can promote biotic homogenisation, not only caused by the

loss of unique native species but also by the introduction of widespread species (Mitchell et al., 2022). Some of the latter can become invasive, thereby exacerbating degradation processes (Pyšek et al., 2020).

Typically, conservation focusses on native, especially threatened and endemic species because introduced species are commonly regarded as harmful to ecosystems (Sax et al., 2022). Nevertheless, introduced species may also be valued because of their perceived contributions to people (Schlaepfer, 2018; Castro-Díez et al., 2019), especially in urban contexts (Schlaepfer et al., 2020). For instance, *Eucalyptus* spp. and *Acacia* spp. have been introduced across the tropics for their timber but they have also been critically viewed for their altering effects on natural ecosystems (Wells et al., 2023). These dualities must be considered to set the right management priorities in each context (Vimercati et al., 2020). Understanding how people in urban, rural, and natural settings make use of endemic, native, and introduced species is therefore key to defining successful conservation strategies.

Islands are good places to study these interactions because they are often simplified and threatened systems that contain large proportions of both endemic and introduced species (Kueffer and Kinney, 2017). On oceanic islands in particular, the impact of human modification also tends to be relatively recent and thus discernible (Rull, 2023). Here we aim to find out how tree-derived NCP change between urban, rural, and natural zones, hypothesising that NCP composition is not equal across this gradient (Shumi et al., 2021). For instance, we expect an emphasis on timber in natural forests (Gamfeldt et al., 2013; Harrison et al., 2014), and on food crops in rural plantations (Rasmussen et al., 2018). We use the oceanic island of São Tomé (Central Africa) as a model system since it hosts many endemic and introduced species (Stévant et al., 2022), as well as a strong gradient of anthropogenic disturbance (Dauby et al., 2022). Specifically, we assess:

1. Which NCP are recognised in tree species?
2. How do recognised NCP vary between urban, rural, and natural zones?
3. How do introduced, native, and endemic tree species differ in their recognised potential to deliver NCP?

4.2 Materials and methods

4.2.1 Study area

The Democratic Republic of São Tomé and Príncipe is a lower-middle-income country (UN-DESA, 2019), where many urban and rural people rely directly on natural resources (de Lima et

al., 2022). Out of the two main islands, São Tomé is by far the larger and more populous one. It lies in the Gulf of Guinea ($0^{\circ} 14' \text{ N}$, $6^{\circ} 36' \text{ E}$; Figure 4.1), approximately 250 km west off the coast of Gabon, and the climate is oceanic equatorial (Ceríaco et al., 2022). São Tomé is a volcanic island that has always been isolated from the mainland, which helps explain its flora rich in endemics (c. 14.5 % for vascular plants; Stévant et al., 2022). The island is included in the biodiversity hotspot of the Guinean Forests of West Africa (Myers et al., 2000).

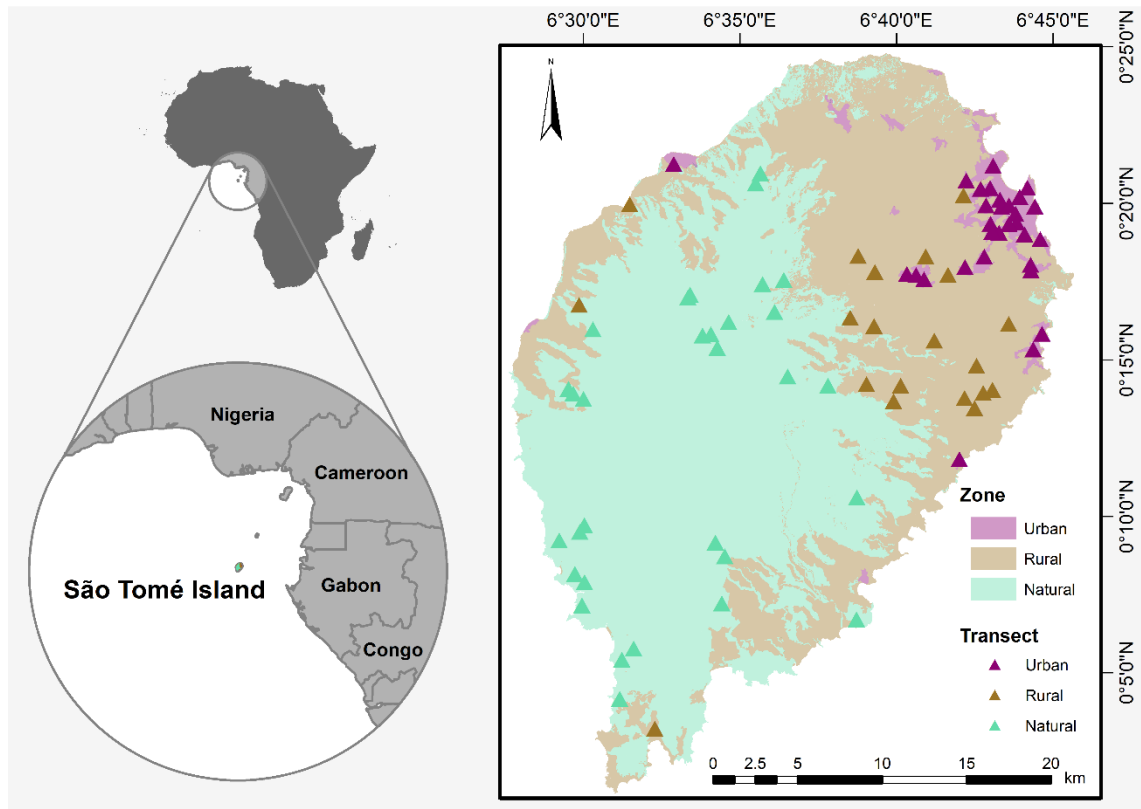


Figure 4.1. São Tomé Island. Top left: Position in Africa. Bottom left: Position in the Gulf of Guinea. Right: Location of sampled transects ($n = 81$) across zones, based on Ministério das Infraestruturas, Recursos Naturais e Ambiente (2018) and Soares et al. (2020).

São Tomé was uninhabited when it was discovered by the Portuguese in 1470 (Muñoz-Torrent et al., 2022). Subsequent human colonisation led to the loss of a high share of the original vegetation, creating a strong gradient of anthropogenic influence. Much of the lowland forest has been converted to plantations to produce cash crops, such as sugar, coffee, and cocoa, while well-preserved forest can still be found in the mountainous centre of the island (Dauby et al., 2022). A fast-growing population coupled with a marked rural exodus has promoted urban expansion, mostly close to the coast (Muñoz-Torrent et al., 2022).

4.2.2 Framework

Within the IPBES concept of NCP, the three broad groups of regulating, material, and non-material contributions embrace 18 reporting categories (IPBES, 2019), which we subcategorised to allow for analysis at fine resolution (Table 4.1). Our subcategories were based on ecosystem services listed for sub-Saharan Africa, mostly in the context of urban green infrastructure (du Toit et al., 2018) and trees in agricultural landscapes (Kuyah et al., 2016). As these references used the ecosystem services approach, we assigned subcategories to the equivalent NCP (Bastos Lima and Palme, 2022).

Table 4.1. Broad groups and reporting categories of the Nature's Contribution to People conceptual framework (IPBES, 2019) to which subcategories were assigned. These originated, partially modified, from du Toit et al. (2018); exceptions are noted as ^F for Festin et al. (2019), ^K for Kuyah et al. (2016), and ^R for Rose et al. (2022).

Broad group	Reporting category	Subcategory
Regulating	1 Habitat creation and maintenance	•Habitat •Maintenance of functional diversity
	2 Pollination and dispersal of seeds and other propagules	•Pollination
	3 Regulation of air quality	•Air quality regulation
	4 Regulation of climate	•Microclimate^K •Carbon sequestration and storage^K
	5 Regulation of ocean acidification	•Carbon sequestration and storage^K
	6 Regulation of freshwater quantity, location, and timing	•Regulation of water flow and runoff •Watershed protection and contribution to rainfall
	7 Regulation of freshwater and coastal water quality	•Water purification and waste treatment
	8 Formation, protection, and decontamination of soils and sediments	•Soil fertility^K •Sediment trapping •Soil decontamination^F
	9 Regulation of hazards and extreme events	•Noise reduction •Windbreaks •Erosion prevention •Flood control^K
	10 Regulation of detrimental organisms and biological processes	•Bio-control^K
Material	11 Energy	•Fuel wood •Charcoal^R
	12 Food and feed	•Crop food •Non-crop food •Livestock fodder
	13 Materials and assistance	•Building materials •Wood tools

		•Fibre •Manure^K •Ornamental products^K
	14 Medicinal, biochemical, and genetic resources	•Medicinal plants •Biochemicals^K •Genetic resources^K
Non-material	15 Learning and inspiration	•Education •Aesthetic value
	16 Physical and psychological experiences	•Recreation •Tourism •Stress relief
	17 Supporting identities	•Social cohesion •Supernatural beliefs and spiritual value •Place of spiritual reflection •Sense of place •Heritage, cultural, and historical values
Cross-cutting	18 Maintenance of options	-

4.2.3 Study design

4.2.3.1 Zonation

There were three levels of anthropogenic impact on São Tomé Island: While the urban zone faced the highest human pressure, hosting approximately 75 % of the island's inhabitants in 2.8 % of its area (UN-DESA, 2018), the rural zone included much smaller scattered (*luchans*) and clustered settlements (*roças*) in a matrix of agroforestry. In contrast, the natural zone covers 56.9 % of the island and is virtually uninhabited, being visited almost solely to extract natural resources, such as timber, medicinal plants, and quarry species (de Lima et al., 2022). The spatial classification of these zones was based on maps of urban areas (Ministério das Infra-Estruturas, Recursos Naturais e Ambiente, 2018) and other land-use types (Soares et al., 2020). The official definition of urban areas in São Tomé comprises “[...] the district and regional capitals (cities) and all villages, as well as the entirety of the district of Água Grande” (Instituto Nacional de Estatística, 2015, transl.). Since this would include large areas of agroforest, we modified it, to classify these as rural zone. Apart from secondary forest fragments, urban greenspaces contained home gardens, public parks, squares, and some avenues. The vegetation of the rural zone was characterised by both young secondary forests and plantations, typically coffee (*Coffea* spp.) or cocoa (*Theobroma cacao*), that were mostly shaded by large trees. Less accessible and wetter areas formed the natural zone, where mature secondary forests and old-growth native forests prevailed.

4.2.3.2 *Sampling strategy*

To enable stratified random sampling, we laid a 500 x 500 m grid over the map, and randomly selected 30 grid cells in the urban zone and 20 in the rural zone. The reduced number for the latter was justified by the expected lower habitat heterogeneity (de Lima et al., 2014). One transect in the field was established in each selected cell. If this was not feasible within the cell limits, a new grid cell was chosen. In addition, 31 transects were directly established in well-preserved forest patches of the natural zone, representing gradients of precipitation and elevation. All 81 transects kept a minimum distance of 200 m from one another and each had four sections measuring 5 x 50 m (0.1 ha). Sections of the same transect were ideally no more than 50 m apart, but not automatically in a straight line, ensuring ecosystem homogeneity and exclusion of glades, rivers, roads, or other obstacles (Benitez Bosco et al., 2018).

4.2.4 Data collection

4.2.4.1 *Tree survey data*

Between October 2019 and August 2021, transects were sampled for all trees with a minimum diameter at breast height of 5 cm (Benitez Bosco et al., 2018). Trees were identified following the taxonomy of Tropicos (2023) to the highest possible level of taxonomic resolution. Arecaceae, Caricaceae, Musaceae, Pandanaceae, and Poaceae were excluded from the sampling, as they are not considered to be trees. Identification was confirmed based on photographs and herbarium samples that were collected for all potentially distinct species.

4.2.4.2 *Data on recognised species contributions*

The authorship team assessed the recognised potential of each tree species to underpin each NCP. We took this approach since the authors (ES, MCM, TS, GD, and RFdL) are the only experts globally familiar with the tree species and their associated uses on the island. Indeed, 11 of the species in this study had not been identified prior to 2021, and many have ambiguous local names (Stévant et al., 2022). IPBES distinguishes between Indigenous and local knowledge holders (ILK-holders), Indigenous and local knowledge experts (ILK-experts), and Experts on Indigenous and local knowledge (Experts on ILK). While the first type refers to someone from a local community with that particular knowledge, the second one has cross-regional knowledge of ILK issues and contexts being from a local community him-/herself. The third type represents an outsider who has acquired knowledge of ILK issues and contexts (Hill et al., 2020). In São Tomé, this knowledge refers to local rather than Indigenous people, as the inhabitants have been on the island for several generations but not prior to another ethnic group (Wheeler and Root-Bernstein, 2020). Local knowledge can vary substantially among ILK-holders (Vallet et al., 2023), influenced by globalisation processes such as urbanisation and the

availability of imported products (Aswani et al., 2018; Arjona-García et al., 2021). Referring to the few remaining ILK-experts and Experts on ILK, included among the authors, was hence the most accurate approach to acquiring aggregated local knowledge from across the whole island of São Tomé.

Having worked as a parataxonomist for over 30 years, ES is both an ILK-holder and ILK-expert. He was most qualified to evaluate which NCP subcategories each tree species was recognised for in São Tomé. Furthermore, we anticipated timber, which concerned several NCP subcategories (fuel wood, charcoal, building materials, wood tools, and ornamental products), and medicine to be key NCP worth exploring in more detail (Stévant et al., 2022; de Lima et al., 2022). Therefore, where appropriate, ES also assessed the timber quality (good, medium, low, very low) and described the medicinal applications (supported by Figueiredo et al., 2011). Medicinal uses were subsequently assigned to nine treatment categories: digestive, respiratory, genitourinary, cardiovascular, dermal, anti-inflammatory/analgesic, metabolic, febrile, or other (modified from Stévant et al., 2022). All this information was then double-checked by other team members, especially by ethnopharmacologist MCM, who is an Expert on ILK, regarding medicinal data. Some NCP established in the literature (Figueiredo et al., 2011; e.g. non-crop food such as edible fruits from *Diospyros ferrea* or Cape fig, *Ficus sur*) were excluded as they were not known to have those uses in São Tomé.

Resulting information referred to recognised rather than actual use (Shumi et al., 2021). To enhance the comparability among regulating, material, and non-material contributions, we used numbers of tree individuals and tree species identified with underpinning NCP (Schlaepfer et al., 2020; Shumi et al., 2021). Each individual/species could be recognised for multiple NCP. Contributions were considered on the level of NCP broad groups, reporting categories, and subcategories.

4.2.4.3 Data on species origins

We determined whether species were native or introduced using “Plants of the World Online” (POWO, 2023), complemented by Figueiredo et al. (2011) and expertise from the “Threatened Flora of São Tomé e Príncipe” team (Critical Ecosystem Partnership Fund, 2021). Native species were split into endemic and non-endemic, depending on whether their native distribution was restricted to the Gulf of Guinea oceanic islands.

4.2.5 Data analyses

To estimate the recognised potential of trees to provide NCP in our study area, we calculated their individual and species numbers per transect, and then summed up these metrics per NCP

subcategory, NCP reporting category, and NCP broad group. Many species were associated with several subcategories and therefore several reporting categories. We hence determined the level of overlap between reporting categories by computing the Bray-Curtis similarity index (1 – distance) on binary data (Fisher et al., 2023) via “vegdist” in *vegan* (Oksanen et al., 2022). This index ranges between 0 (dissimilar) and 1 (similar).

To investigate NCP associated with trees along the urban-rural-natural gradient, we compared the numbers of individuals and species for NCP reporting categories between zones. We analysed these metrics, both individually and summed up as a total, against species abundance and richness across zones. Depending on data normality and homoscedasticity, we used one-way ANOVAs followed by Tukey HSD post hoc tests or Kruskal-Wallis rank sum tests followed by pairwise Wilcoxon rank sum tests, according to zones (Anderson et al., 2020). We adjusted the p-values of pairwise Wilcoxon rank sum tests via Bonferroni correction to control for multiple comparisons (Hending et al., 2020). The same procedure was undertaken for the abundances of trees recognised for supporting certain timber qualities across zones.

To visualise structural differences between and within zones, non-metric multidimensional scaling (NMDS) was conducted based on the abundances of trees recognised for supporting different subcategories on transect level. We analysed this against NMDS of abundance-based tree assemblages on transect level. All data were standardised prior to NMDS, using the “hellinger” method from “decostand” in “*vegan*”. We further calculated if similarities of transects were greater between or within zones (analysis of similarities, ANOSIM; permutations = 999), using “anosim” in “*vegan*”. Then, we analysed differences in dispersion (permutational multivariate analysis of dispersion, PERMDISP; permutations = 999) and location (permutational multivariate analysis of variance, PERMANOVA; permutations = 999) of transects for subcategories according to zones, using “permutest.betadisper” in “*vegan*” and “pairwise.adonis2” in “*pairwiseAdonis*” (Martinez Arbizu, 2017), respectively. We applied indicator analysis to all subcategories to assess linkage (high fidelity and specificity) with specific zones, using “multipatt” from “*indicspecies*” (De Cáceres and Legendre, 2009). In addition, we repeated NMDS, ANOSIM, PERMDISP, and PERMANOVA for proportional abundances of both introduced and endemic tree species recognised for supporting different subcategories on transect level, as well as for abundances of trees recognised for underpinning different medicinal treatment categories on transect level.

To analyse statistical differences in the number of species identified with underpinning NCP subcategories according to species origin, we employed Mann-Whitney U tests, as data consisted of two independent groups and did not meet assumptions of normality and homogeneity. We first divided each number of species per subcategory by the total number of

species, for native and introduced species, respectively, to test both the whole dataset and each NCP broad group separately. To test each subcategory individually, we divided each number of species per subcategory and transect by the total number of species, for native and introduced species, respectively. Moreover, to examine the importance of origin according to multi-use of species, we divided the number of species per number of subcategories (between 0 and 9) by the total number of species, for native and introduced species, respectively, and tested these two variables via Mann-Whitney U test. We used R for all analyses (R Core Team, 2022) and significance levels were set to $p \leq 0.05$.

4.3 Results

We removed 21 individuals (0.32 %) that were only identified to family or higher, and 287 individuals (4.37 %) identified to genus, which could belong to other identified species. As a result, 6,563 tree individuals formed our final dataset, of which 6,436 were from 171 species and 127 were from unidentified species of six genera, giving a total of 177 tree taxa. For simplicity, all are referred to as species in the remainder of this work.

4.3.1 Which NCP are recognised in tree species?

The data obtained for the 177 tree species covered all three NCP broad groups, as well as 11 out of 17 NCP reporting categories, and 25 out of 41 NCP subcategories. Of the 177 species, five were not recognised for underpinning any NCP (*Alangium* aff. *chinense*, *Anthocleista scandens*, *Diospyros ferrea*, *Phyllocosmus* aff. *sessiliflorus*, *Trilepisium madagascariense*). All the remaining 172 were recognised for material contributions. Of these, 130 were recognised for material contributions only, ten for a combination of material and regulating contributions, 23 for a combination of material and non-material, and the remaining nine for a combination of all broad groups. These nine “superspecies” were *Acacia auriculiformis*, *Cassia siamea*, kapok tree (*Ceiba pentandra*), *Erythrina variegata*, *Eucalyptus torelliana*, silky oak (*Grevillea robusta*), mango tree (*Mangifera indica*), guava (*Psidium guajava*), and mombin (*Spondias mombin*). This means that no species were recognised just for non-material or regulating contributions, or a combination of them.

There were many more trees recognised for material contributions (6555 individuals and 172 species) than for non-material (1726 individuals and 32 species) or regulating contributions (399 individuals and 19 species; Figure 4.2). Considering their low abundance, trees identified with regulating contributions were nevertheless relatively species-rich. “Materials and assistance” followed by “energy”, both material contributions, were the NCP reporting

categories associated with the highest numbers of individuals and species (App. C.1). Similarly, “building materials” followed by “fuel wood” were the most abundant and species-rich NCP subcategories. There were numerous subcategories only associated with one species: “noise reduction” (silky oak) and “erosion prevention” (mango tree) for regulating contributions; and “wood tools” (West Indian cedar, *Cedrela odorata*), “manure” (coral tree, *Erythrina poeppigiana*) and “ornamental products” (West Indian cedar) for material contributions. The non-material contributions of “tourism”, “place of spiritual reflection”, and “heritage, cultural, and historical values” were exclusively associated with the kapok tree.

The overlap in tree species between associated NCP reporting categories was overall low but there were exceptions: The most similar pairs were identified among material contributions, namely “energy” and “materials and assistance” (Bray-Curtis similarity index: 0.88; App. C.2), followed by “materials and assistance” and “medicinal, biochemical, and genetic resources” (0.71).

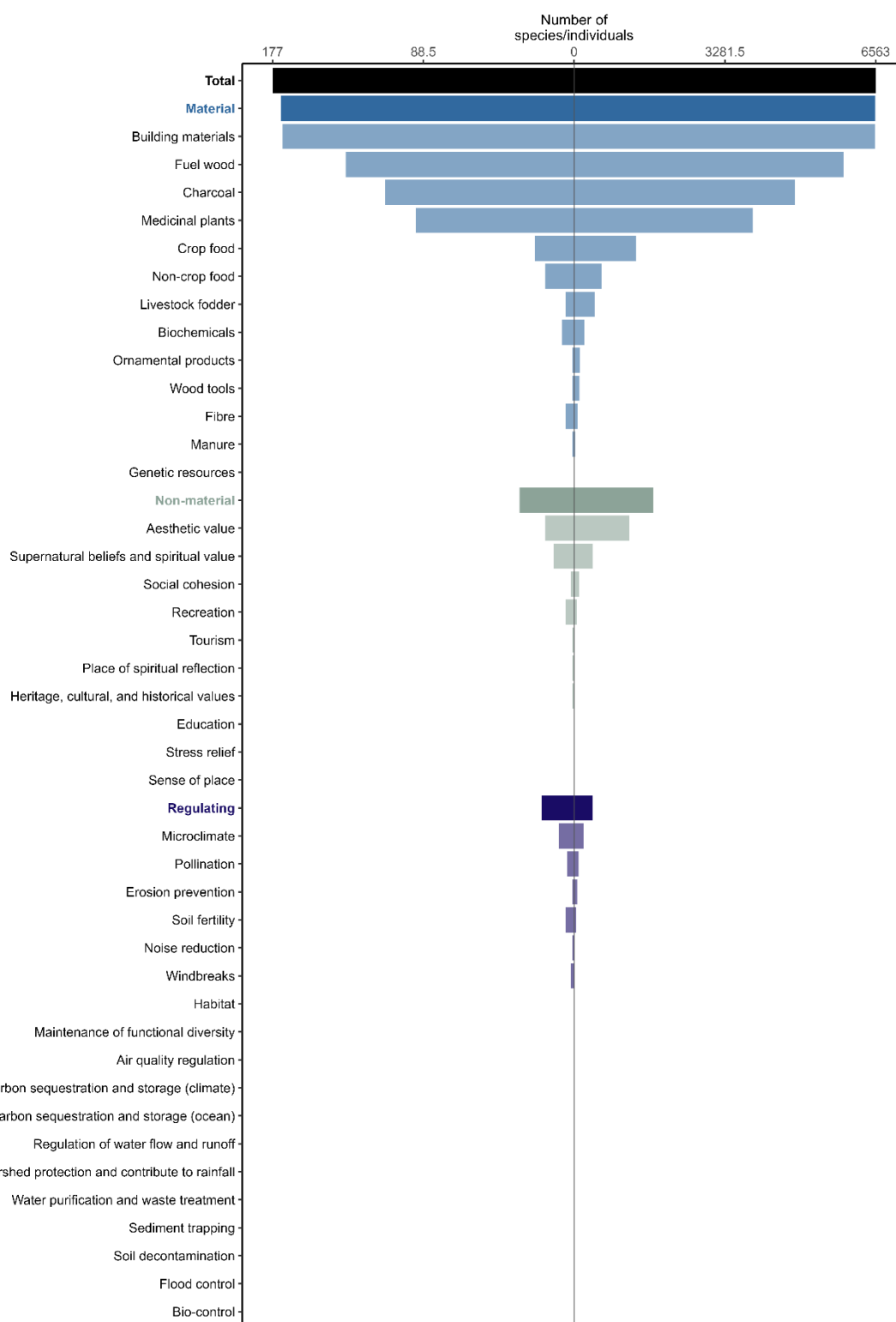


Figure 4.2. Number of species (left) and individuals (right) of trees recognised for supporting total contributions, broad groups, and subcategories according to the Nature's Contribution to People conceptual framework, based on expert opinions, along 81 transects on São Tomé Island. Label colours: blue = material contributions; olive = non-material contributions; violet = regulating contributions. Note changes in the scale of the X axis.

4.3.2 How do recognised NCP vary between urban, rural, and natural zones?

The number of tree individuals and species identified with different NCP reporting categories varied substantially across zones. The abundance of trees recognised for “supporting identities” and “regulation of hazards and extreme events” was significantly higher in the urban zone (Figure 4.3g, Figure 4.3j), as was that for “food and feed”, “learning and inspiration”, and “formation, protection, and decontamination of soils and sediments” in the rural zone (Figure 4.3e, Figure 4.3f, Figure 4.3l), and that for “materials and assistance” and “energy” in the natural zone (Figure 4.3b, Figure 4.3c). In contrast, the abundance of trees recognised for “materials and assistance”, “energy”, and “medicinal, biochemical, and genetic resources” was significantly lower in the urban zone (Figure 4.3b, Figure 4.3c, Figure 4.3d), as was that for “food and feed”, “learning and inspiration”, and “regulation of climate” in the natural zone (Figure 4.3e, Figure 4.3f, Figure 4.3h). The species richness of trees recognised for underpinning NCP reporting categories was only equal across zones for “medicinal, biochemical, and genetic resources” (App. C.3).

The total abundance of all NCP reporting categories associated with trees was lower in the urban zone than in the other two zones (Figure 4.3a). This pattern was similar to that of tree abundance across zones (Figure 4.3m), although in that case abundance was also significantly higher in the natural zone than in the rural zone. The total species richness of all reporting categories associated with trees was equal between zones (App. C.3a). This again was similar to the pattern of species richness across zones (App. C.3m), in which the number of species was however significantly higher in the natural zone than in the other two zones.

For the number of tree individuals recognised for providing the 11 NCP reporting categories, only “materials and assistance” and “energy” (Figure 4.3b, Figure 4.3c) followed the same pattern of tree abundance (Figure 4.3m). For the number of tree species, “materials and assistance” (App. C.3b) was the only reporting category following the same pattern of tree species richness (App. C.3m).

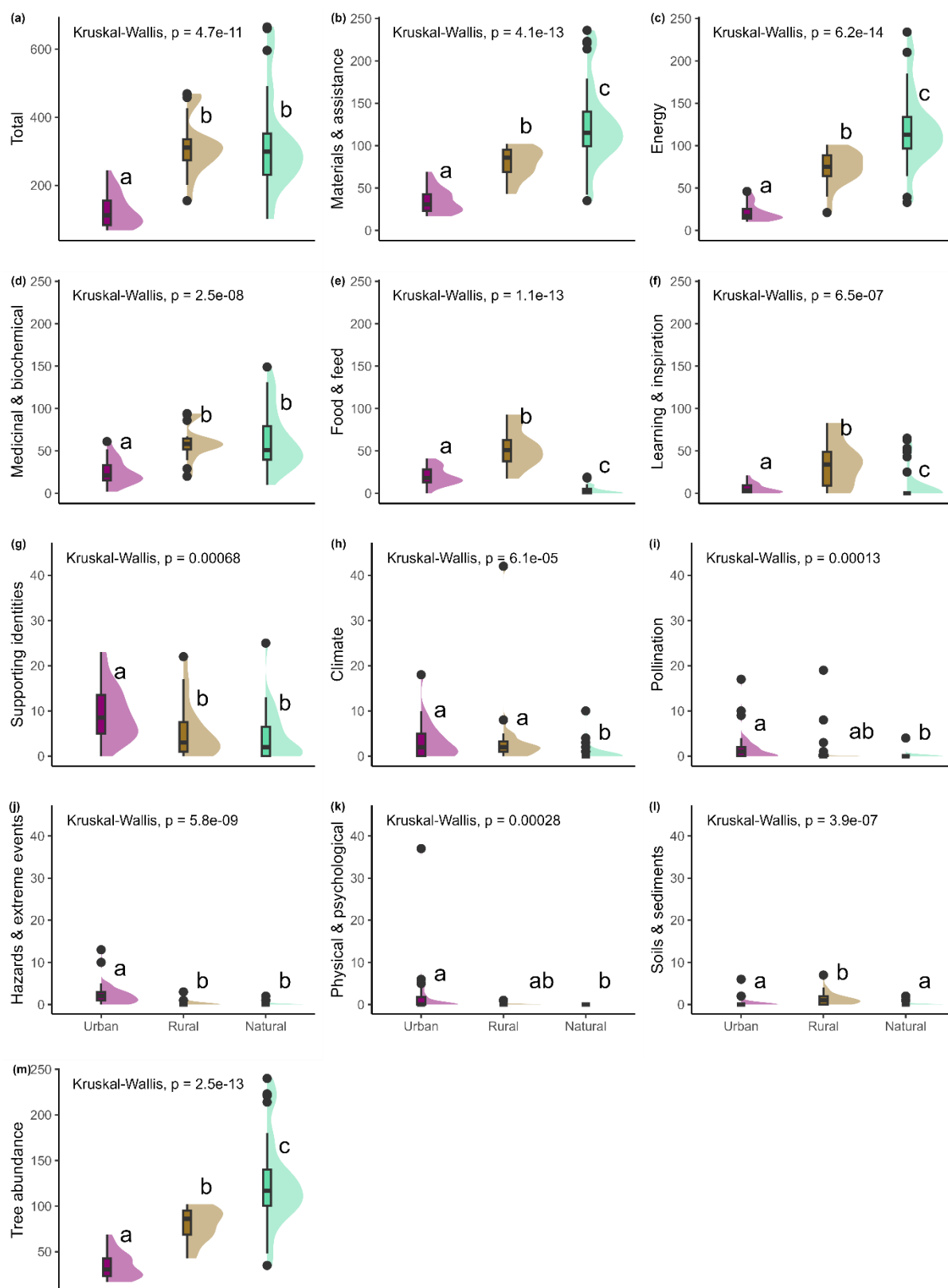


Figure 4.3. Violin box plots on transect level according to zones for the number of tree individuals identified with supporting different reporting categories of Nature's Contributions to People, (a) in total and (b-l) individually, versus (m) tree abundance. P-values ($df = 2$) of Kruskal-Wallis rank sum tests, (a) $\chi^2 = 47.555$, (b) $\chi^2 = 57.066$, (c) $\chi^2 = 60.807$, (d) $\chi^2 = 35.049$, (e) $\chi^2 = 59.645$, (f) $\chi^2 = 28.506$, (g) $\chi^2 =$

14.582, (h) $\chi^2 = 19.399$, (i) $\chi^2 = 17.869$, (j) $\chi^2 = 37.916$, (k) $\chi^2 = 16.377$, (l) $\chi^2 = 29.494$, and (m) $\chi^2 = 58.067$, at the top of each graph. Significant differences from pairwise Wilcoxon rank sum tests (following Bonferroni correction) indicated by different superscript letters. Maximum violin width is scaled to 1. Graphs b-l were ordered according to total abundance of each graph. Note changes in the scale of the Y axes.

Assemblages of trees recognised for supporting different subcategories were distinct between all zones (Table 4.2). The natural zone had the lowest variety among transects for these assemblages, while for tree assemblages, it had the greatest variety among transects. For the former, two clusters linked to elevation could be distinguished in the natural zone (App. C.5).

Table 4.2. Comparison of results of analysis of similarities (ANOSIM), pairwise permutational multivariate analysis of dispersion (PERMDISP), and pairwise permutational multivariate analysis of variance (PERMANOVA) for assemblages based on the abundances of trees recognised for supporting subcategories of Nature's Contributions to People (NCP) and for abundance-based tree assemblages.

	Assemblages of trees recognised for underpinning NCP subcategories	Tree assemblages
ANOSIM	The similarity was higher within zones than between zones ($R = 0.784$, $p = 0.001$).	The similarity was higher within zones than between zones ($R = 0.719$, $p = 0.001$).
Pairwise PERMDISP	Within zones, assemblages were most similar among natural transects ($F = 11.810$, $p < 0.005$; App. C.4), while the similarity among rural and urban transects was equal ($p = 0.155$).	Within zones, assemblages were most distinct among natural transects ($F = 6.019$, $p < 0.050$; App. B.2), while the similarity among rural and urban transects was equal ($p = 0.235$).
Pairwise PERMANOVA	Assemblages were distinct between all zones, but most notably between urban and natural zones ($F = 87.070$, $p = 0.001$; Figure 4.4a).	Assemblages were distinct between all zones, but most notably between urban and natural zones ($F = 21.369$, $p = 0.001$; Figure 3.5a).

“Building materials”, “fuel wood”, “charcoal”, and “medicinal plants”, as the NCP subcategories identified with the highest numbers of tree individuals, were common to all zones (Figure 4.4b). “Windbreaks” was only associated with three natural transects (linked to the presence of *Olea capensis*) and one urban transect (linked to the presence of *Eucalyptus torelliana*), and “noise reduction” only with that same urban transect (linked to the presence of silky oak), thus both subcategories taking distant positions in Figure 4.4b. Indicators for specific zones associated with more than five species were “crop food”, “non-crop food”, “aesthetic value”, and “microclimate”, simultaneously indicating rural and urban zones (App. C.6). There were no indicators for the natural zone.

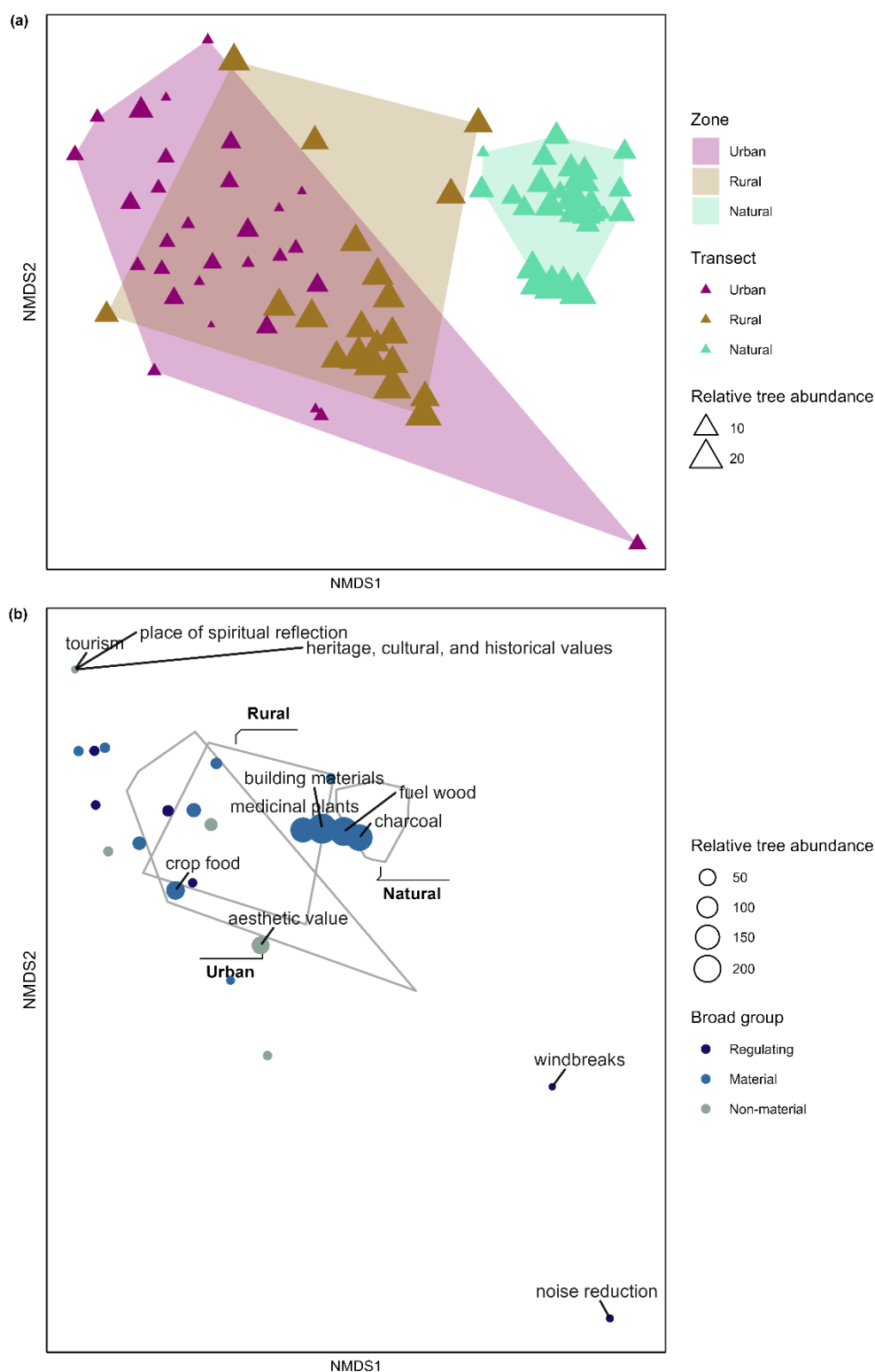


Figure 4.4. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities of the abundances of trees recognised for supporting different subcategories of Nature's Contributions to People per transect ($k = 2$, stress value = 0.125): (a) Structural differences between 81 transects; transects in each zone are united by the minimum convex polygon. (b) Structural differences between 25 subcategories; convex hulls connect outer transects of each zone. The names of the six subcategories with

the highest sample relative tree abundances (accumulated numbers from 81 transects) and of those in distant positions are displayed.

Concerning the 171 tree species recognised for providing timber, the abundance of those with good quality timber (eight species) was low across zones (Kruskal-Wallis rank sum test: $\chi^2 = 2.386$, $p = 0.303$; App. C.7). The most abundant timber trees in the urban and rural zone were of very low quality, and in the natural zone of low quality.

Assemblages of trees recognised for underpinning medicinal treatment categories (ANOSIM: $R = 0.496$, $p = 0.001$) did not much resemble those recognised for underpinning NCP subcategories (Table 4.2). Assemblages were also distinct between all zones, but most notably between rural and natural zones (pairwise PERMANOVA: $F = 45.891$, $p = 0.001$, App. C.8a), and the similarity among transects within all three zones was equal (PERMDISP: $F = 0.396$, $p = 0.675$). Of the 93 medicinal tree species, the 67 species associated with supporting “anti-inflammatory/analgesic” treatments and the 46 species associated with supporting “metabolic” treatments were particularly abundant towards urban and rural zones (App. C.8b), while the 37 species identified with providing “digestive” treatments abounded towards both urban and natural zones. Regarding plant parts, bark was recognised the most for medicinal uses, followed by leaves (App. C.9).

4.3.3 How do introduced, native, and endemic tree species differ in their recognised potential to deliver NCP?

Of 25 NCP subcategories, ten were only associated with introduced species and one (“wood tools”) only with native species. The species that had no recognised NCP were all native, one of which was endemic (*Phyllocosmus* aff. *sessiliflorus*).

There was no significant difference between the proportion of native and introduced species recognised for providing material NCP subcategories (Mann-Whitney U test: $W = 57.500$, $p = 0.418$). However, regulating ($W = 3.000$, $p = 0.018$) and non-material subcategories ($W = 4.000$, $p = 0.009$) were associated with higher proportions of introduced species (Figure 4.5).

“Charcoal” and “wood tools” were the only NCP subcategories whose proportions were more associated with native than with introduced species, while 18 of the 25 subcategories showed the opposite trend (Figure 4.5). There was no significant difference between the proportion of native and introduced species recognised for providing different numbers of NCP subcategories (Mann-Whitney U test: $W = 52.500$, $p = 0.879$).

The abundance of introduced tree species recognised for delivering regulating, material, and non-material contributions was significantly higher in the urban and rural zones than in the natural zone (App. C.10). In the latter, the abundance of native tree species recognised for delivering material contributions was highest.

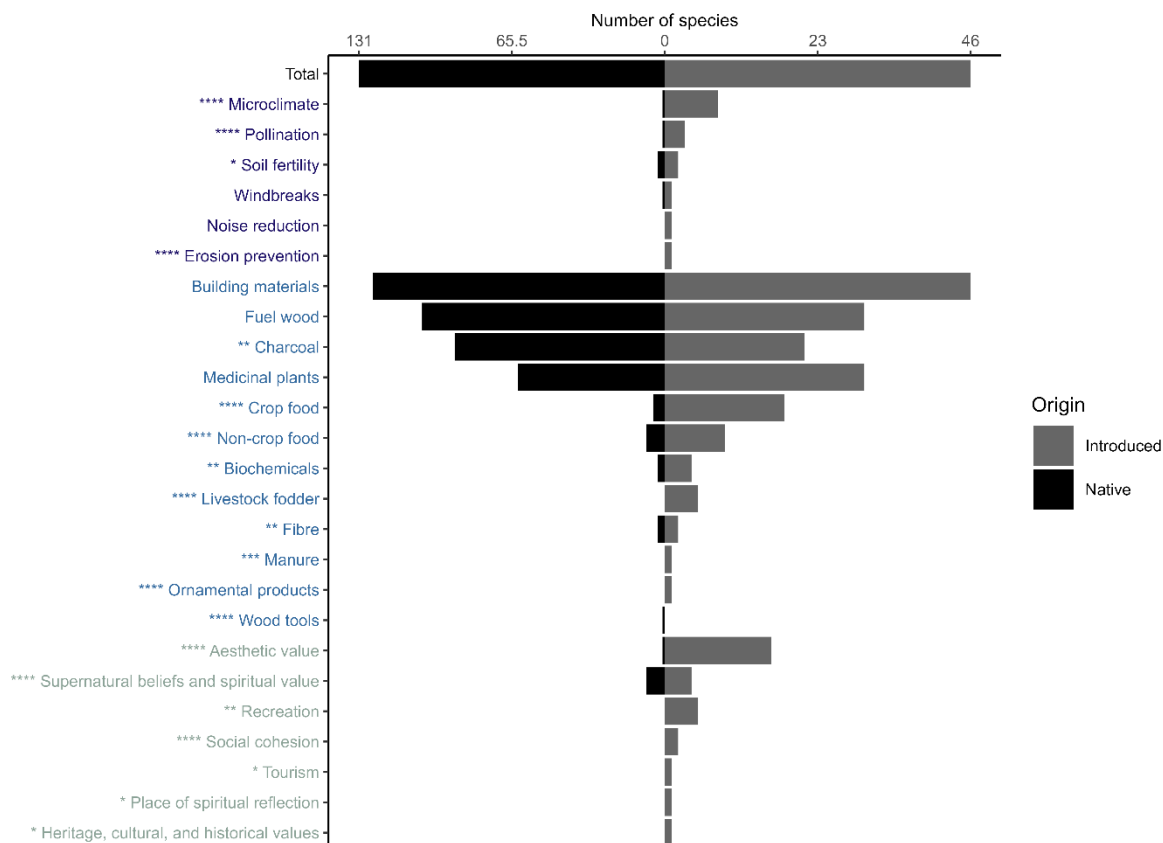


Figure 4.5. Number of native ($n = 131$) vs. introduced tree species ($n = 46$) recognised for supporting different subcategories of Nature's Contributions to People. Subcategories ordered according to broad groups and joint standardised numbers of native and introduced species. Label colours: violet = regulating contributions; blue = material contributions; olive = non-material contributions. Note changes in the scale of the X axis. Native and introduced subcategories with significant differences between each other for standardised transect data are marked by asterisks (significance levels = *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$, ****: $p \leq 0.0001$).

Assemblages of introduced tree species recognised for underpinning NCP subcategories (ANOSIM: $R = 0.545$, $p = 0.001$; pairwise PERMANOVA: $F = 13.220$, $p = 0.001$, App. C.11a) resembled assemblages of trees recognised for underpinning NCP subcategories (Table 4.2). However, natural transects were the least similar (pairwise PERMDISP: $F = 11.670$, $p < 0.005$), while the similarity among rural and urban transects was equal ($p = 0.252$). The resemblance with assemblages regardless of species origin was not true for assemblages of endemic tree

species identified with underpinning NCP subcategories (ANOSIM: $R = 0.152$, $p = 0.084$).

Hereby, assemblages were only distinct between urban and natural zones (pairwise PERMANOVA: $F = 3.143$, $p = 0.019$, App. C.11c), while similarity was only distinct between urban and natural transects (pairwise PERMDISP: $F = 7.484$, $p < 0.001$).

The highest mean proportional abundances of introduced species across transects were associated with the subcategories “livestock fodder” (63.0 %), “crop food” (60.4 %), and “aesthetic value” (53.1 %), dominated by one or more introduced species across most urban and rural transects (App. C.11b). In contrast, the highest mean proportional abundances of endemic species across transects were identified with “supernatural beliefs and spiritual value” (18.5 %), “non-crop food” (17.6 %), and “charcoal” (12.9 %), demonstrating relatively high proportions across most natural and some rural transects (App. C.11d). “Microclimate” was represented by one endemic species (*Carapa gogo*) in two rural and six natural transects, contributing to the high differentiation of this subcategory (App. C.11d).

4.4 Discussion

Most tree species were associated with providing material NCP, while non-material and regulating contributions were recognised on a much lower level. “Materials and assistance” and “energy” were the most abundant NCP reporting categories, coinciding with the high tree abundance in the natural zone. Despite their lower tree abundance, rural and urban zones had the recognised potential to disproportionately contribute to NCP diversity thanks to the higher prevalence of introduced tree species.

4.4.1 Which NCP are recognised in tree species?

The recognised potential of trees to provide NCP was generally high in São Tomé. Only five tree species were not recognised for any NCP, while all others were associated at least with material contributions. This high material use of trees is not surprising because energy, food, and medicine derived from trees are known to be an essential part of daily life in São Tomé (de Lima et al., 2022; Stévant et al., 2022), and in many parts of Africa (Reed et al., 2017; Lhoest et al., 2019). The direct reliance on natural resources, such as these, is likely to be linked to low levels of income (Fedeles et al., 2021) since around two-thirds of people on the island live on less than US \$ 3.2 per day (World Food Programme, 2022).

Material contributions had a high recognition rate, of which “materials and assistance” and “energy” were associated with the largest number of species and individuals. In fact, most species were linked to these NCP reporting categories, so much so that they are also the

contributions with the greatest overlap of species. Since they are particularly biomass-intense, abundance is key, as opposed to species identity. The high species richness implies that people may resort to most species for the same purpose. This suggests NCP redundancy, which may ensure the persistence of a certain contribution if environmental perturbations impair some of the associated species (Mori et al., 2013). Accordingly, “building materials” and “fuel wood” were the NCP subcategories associated with the highest numbers of species, and many species were recognised for multiple purposes, such as ockna (*Treculia africana*), which was recognised for both of these. The high similarity between material reporting categories further indicates the occurrence of multipurpose species, which are usually appreciated in areas where space is restricted (Tekalign et al., 2017).

Compared with material contributions, few species in São Tomé were recognised for non-material contributions and even less for regulating contributions. These species also tended to be more specialised in underpinning the two NCP broad groups. The scant recognition of non-material and regulating contributions may be connected to them being less obvious (Sutherland et al., 2018). It may also reflect the relatively recent history of human colonisation of the island (de Lima et al., 2022), meaning that people may not yet appreciate some of these tree-derived contributions. Regulating contributions such as “carbon sequestration and storage” existed, but they were not recognised. Some studies in nearby African countries confirm a general lack of local awareness of regulating contributions (Lhoest et al., 2019; Gouwakinnou et al., 2019), but findings are not consistent across the continent. It has also been argued that rural residents are more aware of regulating contributions due to their closer contact with nature (Mengist et al., 2022), but in other circumstances, urban residents showed greater appreciation (Constant and Taylor, 2020). Higher education, lower resource dependency, and the experience of awareness campaigns may improve chances for recognising regulating contributions (Zhang et al., 2016; Lhoest et al., 2019).

4.4.2 How do recognised NCP vary between urban, rural, and natural zones?

The composition of trees recognised for providing NCP differed between the three zones in São Tomé. Most NCP reporting categories were predominantly associated with rural and urban zones, despite the natural zone being the most biodiverse. The latter was particularly important for material contributions, while the other two zones were more relevant for non-material and regulating contributions. This also implies that the natural zone has mostly trees recognised for NCP that can be extracted and used in other zones. In contrast, those that are non-transferable between zones, and oftentimes exclude highly extractive uses, have to be provided by trees that coexist with people in the rural and urban zones. This includes “aesthetic value” and “microclimate”, which were indicators of these zones, supported by few tree species that had

been widely planted. As in other tropical agroforestry systems, the hyperabundant cocoa tree is appreciated for its aesthetics (Schroth et al., 2015) and shading trees, including the coral tree, optimise the microclimate (Mortimer et al., 2018) in the rural zone. Besides, ornamental and shading trees are among the most valued NCP for urban quality of life (Olivero-Lora et al., 2020; Shackleton et al., 2015), not least because trees can help to reduce the urban heat island effect (Turner-Skoff and Cavender, 2019), which is particularly useful in the hot climate of urban areas in São Tomé.

Assemblages of trees recognised for underpinning NCP were particularly distinct among transects of the urban zone but also of the rural zone. Urban areas, for instance, have been shown to be able to hold complex ecosystems that can provide a multiplicity of NCP (du Toit et al., 2018; Shackleton et al., 2015), facilitated by their high spatial heterogeneity (Behm, 2020). More importantly, this variation of recognised NCP within urban and rural zones is likely determined by tree management, which may fluctuate widely across these spaces. For example, the socio-economic status of the neighbourhood could be an explanatory factor, shaping people's needs for NCP and influencing the extent and quality of greenery (Wilkerson et al., 2018). Overall, trees with diverse human uses may be more likely to persist in human-dominated landscapes in the long term (Huang et al., 2023).

Trees identified with supporting “food and feed” were least abundant in the natural zone and most abundant in the rural zone. Due to high demand, such trees are convenient in close proximity to settlements, e.g. wild foods were mostly harvested up to 5 km from communities in South Africa (Makhubele et al., 2022). In addition, the history of plantations in São Tomé explains the prevalence of “food and feed” in the rural zone, mostly due to the cocoa tree (Dauby et al., 2022). Interestingly, a study from Ghana revealed equal food tree biomass and higher feed tree biomass in natural forests than in agroforests (Dampney et al., 2021). In São Tomé's natural zone, the low abundance of trees that could support “food and feed” may reflect an insufficient familiarisation with the native species there, linked to the distance from settlements and the recent human occupation of the island (de Lima et al., 2022). However, the native pool of such tree species could also generally be much smaller in São Tomé than in African mainland regions (Gaisberger et al., 2017; Leakey et al., 2022). In contrast, the rural and urban zones of the island appeared to have been enriched with associated tree species, as “crop food” and “non-crop food” were indicators there.

“Materials and assistance” and “energy” were the only contributions that showed the same pattern as tree abundance between zones, being highest in the natural zone, decreased in the rural zone, and lowest in the urban zone. This pattern may be because space in rural and urban zones is taken by uses that are less compatible with the occurrence of trees. Many rural farmers

may also prefer short-term profit from unshaded agriculture since trees take years to produce valuable timber (Arvola et al., 2020). Accordingly, trees identified with timber of very low quality were most abundant in the rural zone, typically fast-growing species serving as fuel. The number of trees recognised for producing timber of good quality was nevertheless low across zones, which could be a sign of general overexploitation.

Zones were the same regarding the number of tree species recognised for “medicinal, biochemical, and genetic resources”, but they varied in terms of medicinal applications. Most medicinal tree species in São Tomé have anti-inflammatory, analgesic, anti-rheumatic, and digestive indications (Stévant et al., 2022). In the urban and rural zones, there were many trees associated with “anti-inflammatory/analgesic” treatments, which may often substitute costly Western medicine in deprived communities (Aremu and Pendota, 2021). Both urban and natural zones had many trees that could be used for “digestive” treatments. This may be connected to the low availability of basic hygiene facilities in urban zones (Quispe-Coica and Pérez-Foguet, 2022), and to the natural forest being viewed as particularly powerful (Muñoz-Torrent et al., 2022), its tree species thus being more effective for certain digestive applications. The bark appeared to be the most important plant part, as commonly used in other African medicinal contexts (Furukawa et al., 2016). Bark harvesting can however affect tree physiology, representing a threat to its survival (Mohammed et al., 2022).

4.4.3 How do introduced, native, and endemic tree species differ in their recognised potential to deliver NCP?

While the origin of tree species did not affect their recognised potential to provide material contributions, introduced species were associated with regulating and non-material contributions. These results partially coincide with those of a global review that also presented higher regulating but lower material contributions for introduced than native species, and mixed outcomes for non-material contributions (Castro-Díez et al., 2019). NCP supported by introduced species were also associated with a higher number of trees in urban and rural zones. This was particularly evident for the subcategories “livestock fodder”, “crop food”, and “aesthetic value”. Introduced species tend to be highly adaptable generalists, and therefore can be easy to grow in rural and urban zones (Sánchez-Ortiz et al., 2020). These characteristics enabled the first settlers in São Tomé to establish cash crops and greening initiatives successfully. Similar patterns, including introduced ornamentals in urban settings, can be observed in other regions shaped by a colonial past, such as the Caribbean (Hunte et al., 2019).

Ten NCP subcategories were only associated with introduced species, seven of which were with a single species. These preferences may be rooted in culture (Araia and Chirwa, 2019). Even

though no culture knows and makes effective use of all tree species, the recognition of native species might be particularly poor in São Tomé. Since Santomeans descend from a recent colonisation of displaced people, they might have transferred some uses from their place of origin onto native species (Medeiros et al., 2012). Yet, they might be better equipped to recognise the uses of trees that arrived with people, especially compared with mainland Africans, who have established long-term relationships with their native flora and might have had less contact with introduced plants (Hoffman, 2013). There, many multipurpose species are also native (Lelamo, 2021), whereas we found no difference in São Tomé. The nine “superspecies”, linked to all three NCP broad groups, were even introduced (however, the kapok tree might be native) (POWO, 2023).

Endemic tree species were mostly associated with “supernatural beliefs and spiritual value”, alongside “non-crop food” and “charcoal”, predominantly in the natural zone. This makes sense considering that endemics are often poorly known and not planted, while the natural zone is commonly connected with mystical powers in São Tomé (Muñoz-Torrent et al., 2022).

Understanding NCP linked to native, endemic, and threatened species, and to the natural zone, where most of them occur, might help reveal new means to promote their conservation and to counteract introduced species and biotic homogenisation.

4.5 Implications and conclusions

In São Tomé, sustainable management of trees recognised for material contributions may be vital, since local people are likely to depend on them. However, knowledge about the actual use of these trees is poor, which calls for studies that directly target this aspect. Further research should explore the possibility of replacing introduced species with native or even endemic species that provide similar contributions, or of simply enhancing these species in rural and urban areas to counteract biotic homogenisation. It might also be insightful to explore the implications of NCP that exclude one another, i.e. trees associated with both highly extractive (e.g. building materials) and non-extractive uses (e.g. aesthetic value). A clearer picture of the values that different stakeholders attribute to trees, influencing use and management decisions, could boost the effectiveness of biodiversity conservation.

In addition, raising awareness about the regulating and non-material contributions of trees in urban and rural settlements might help counter their overall insufficient recognition. Regarding material contributions, some associated introduced species, such as breadfruit (*Artocarpus altilis*) or guava, are deeply interwoven with Santomean culture, but limiting their spread to the most human-modified environments could be a viable conservation goal. The main concern for conservation is maintaining the natural zone, where trees recognised for supporting building

materials, fuel wood, and charcoal are predominantly native. If these were to be extracted on a large scale, species survival and the overall wealth of important forest ecosystems would be affected. Our results can inform the sustainable management of the natural zone and the restoration of some forest resources in the rural zone. It is crucial for conservation to understand what values people place on introduced, native, and endemic tree species, and how the diversity of these species varies across anthropogenic gradients, considering that trees providing NCP are essential for the human quality of life and are more likely to persist in urban and rural landscapes.

Author contributions

LS, RFdL, TRB, MD, TS, GD, LBB, and MCM designed the research; LS, RFdL, ES, PS, MCM, TS, GD, and LBB performed the research and collected data; LS analysed the data; LS, RFdL, TRB, and MD interpreted the data; LS wrote the original draft of the manuscript; RFdL, TRB, and MD reviewed and edited the manuscript.

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5 Synthesis and conclusions

5.1 Introduction

As anthropogenic environmental change is intensifying, more pressure is being put on tropical forests, especially on islands (Fernández-Palacios et al., 2021). To understand how to prevent further loss of their unique biodiversity, island-based interdisciplinary research, ideally aimed at enriching science-policy dialogues, can be beneficial (Young et al., 2014). A solid vision for the future of tropical island forests may arise from recognising that forests can be viewed from different angles. Policies concerning environmental change often make suggestions on how forests can support climate protection and hence nature-based solutions (NBS) (Seddon et al., 2019). It remains largely unexplored, however, if national climate policies acknowledge the synergistic potential of forests to contribute to resolving both the climate and biodiversity crises. Knowledge about environmental change impacts on forest biodiversity can add to the climate policy perspective on forests, by providing information on distributional patterns of species and their uses.

One of the major drivers of forest biodiversity loss is land-use change (Jaureguiberry et al., 2022), becoming increasingly relevant as urbanisation is growing across the globe. Assessing biodiversity along different levels of human impact is key in this context but studies tend to lack either a natural or an urban component. The implications of urban expansion are particularly unclear for tropical regions, such as in Africa, which has one of the fastest urbanisation rates (OECD/SWAC, 2020). How species patterns compare with the potential human use of this biodiversity across anthropogenic gradients is even less known but especially needed in areas where people depend on natural resources more directly, e.g. on islands (Balzan et al., 2016). Such outcomes would be crucial for developing effective conservation strategies and enabling humans to live in harmony with nature by 2050, as strived for by the Kunming-Montreal Global Biodiversity Framework (CBD Secretariat, 2023a).

Against this background, the present thesis employed an interdisciplinary, mixed-methods approach to investigate tropical island forests under anthropogenic environmental change, using policy, ecological, and socio-ecological analyses. First, it aimed to clarify how the national climate action plans of island and low-lying coastal states consider biodiversity within forest-based climate solutions. Second and third, it examined how the distribution of biodiversity and its associated use, respectively, change along an urban-rural-natural gradient on the Afrotropical island of São Tomé.

5.2 Contributions to research

Hereafter, I will summarise the contributions that this thesis has made to research, as described in depth in the second, third, and fourth chapters. This will set the ground for drawing out key points that deserve further discussion. An overview of the results chapters can be found in Table 5.1.

NBS supported by forests can create win-win situations for climate and biodiversity protection but how this nexus is considered in national climate action plans remains largely unclear. Using content analysis, Chapter 2 showed that only 14 of 39 Alliance of Small Island States (AOSIS) members integrated biodiversity in their Nationally Determined Contributions (NDCs): Five of them explored co-benefits and synergies between forest-based climate solutions and biodiversity conservation measures, while the rest mentioned them separately. Only a small range of concrete interventions were proposed, most importantly forest protection and (re-) growth. Hence, these NDCs can be regarded as a missed opportunity to jointly address the intertwined climate and biodiversity crises. This is worrying considering some forest-based climate solutions bear the risk of being implemented as potentially harmful for biodiversity.

At the same time, understanding how urban expansion affects biodiversity is crucial, as cities are growing rapidly, such as in the Afrotropics. Yet, there is a lack of studies comparing urban biodiversity levels with natural or near-natural baselines. Hence, Chapter 3 was based on field surveys along urban, rural, and natural zones in São Tomé. It revealed that tree species richness and abundance were significantly higher in the natural than in both the rural and urban zones. Furthermore, native and endemic species dominated the natural zone, contrasting with the urban zone, where introduced species were most common. The low ecological value of urban and rural tree assemblages contradicts with the notion that urban biodiversity can benefit conservation, as found in many studies from temperate regions.

To create sustainable pathways connecting climate, biodiversity, and society, it is also essential to know how Nature's Contributions to People (NCP) are distributed along the terrestrial conditions of nature, namely heavily human-modified landscapes, spaces shared by people and biodiversity, and almost intact wild areas. Chapter 4 therefore builds upon the data from Chapter 3 but includes expert opinions on the recognised uses of the assessed trees in São Tomé. The findings demonstrate that tree species were mostly associated with material contributions. Regulating and non-material contributions were recognised much less, and they were predominantly linked with urban and rural zones, where introduced species were most abundant. This potential relevance of introduced species for urban and rural dwellers means that conservation efforts are likely to be more effective if they are aligned with human needs.

Table 5.1. Summary of studies conducted as per Chapters 2, 3, and 4. Abbreviations: AOSIS: Alliance of Small Island States; NDCs: Nationally Determined Contributions; NCP: Nature's Contributions to People.

Chapter	Objective	Justification	Key findings	Importance	Implications for policy and practice
2: <i>Limited integration of biodiversity within climate policy: Evidence from the Alliance of Small Island States</i>	Analyse if and how AOSIS members integrate biodiversity into their NDCs.	Forests can provide powerful nature-based solutions to address the deeply intertwined climate and biodiversity crises jointly. Little is known about how this nexus is considered in climate policies, however.	• Only 14 member states mentioned biodiversity within forest-based climate solutions in their NDCs, five in the form of co-benefits/synergies and nine as separate issues. • A narrow range of interventions were proposed, most commonly forest protection and (re-)growth. • Forests were more often prioritised for climate change mitigation than adaptation, while biodiversity was hardly prioritised at all.	The NDCs are a missed opportunity for tackling the twin crises together. The lack of biodiversity integration can lead to risky outcomes, including forest monocultures for climate change mitigation.	• Concrete, measurable targets that include synergies with biodiversity are needed. • The protection of old-growth forests and forest restoration are the most promising approaches to creating biodiversity-inclusive interventions. • Forums such as the United Nations Climate Change Conferences should push for a stronger integration of biodiversity into climate policies.
3: <i>Widespread introduced species dominate the urban tree assemblage on the endemic-rich tropical island of São Tomé</i>	Assess how the tree assemblage changes between urban, rural, and natural zones on São Tomé Island.	Although the Afrotropics are among the most rapidly urbanising regions in the world, the effects of urban growth on their biodiversity remain understudied.	• Tree species richness and abundance were highest in the natural zone, where the composition was most distinct from the urban zone. • The rural tree assemblage was the most uneven and had the lowest beta diversity. • The urban zone was dominated by introduced, non-Afrotropical species, and the natural zone hosted almost exclusively native species, including many endemics.	Compared to the natural zone, the ecological value of urban and rural tree assemblages was very low. Here, introduced species have benefitted from the anthropogenic impact, contributing to global biotic homogenisation.	• The protection of the forest in the natural zone is the most important conservation strategy, to be accompanied by specific approaches for endemic and threatened species. • Measures to enhance the ecological value of rural and urban zones should be implemented. • Natural or near-natural zones should be used as a reference when assessing urban biodiversity.

4: <i>Native and introduced trees are recognised for different Nature's Contributions to People across an island anthropogenic gradient</i>	Examine the types and distribution of NCP associated with trees across urban, rural, and natural zones on São Tomé Island.	Heavily modified, shared, and almost intact spaces define our terrestrial world. Yet, it is largely unclear how NCP are influenced by these conditions of nature.	• Trees were mostly recognised for material contributions. • The recognised potential of regulating and non-material contributions by trees was much lower, and mostly linked to urban and rural zones, where introduced species were most abundant. • The natural zone was mostly associated with biomass-intense material NCP, such as “materials and assistance” and “energy”.	A diversity of recognised NCP was supported across the different zones. Introduced species may be especially important for the supply of NCP in urban and rural zones.	• Introduced species identified with providing NCP should be considered in conservation efforts, but their spread should be limited to the most human-modified zones. • Material contributions should be managed sustainably in the natural zone, or they should be promoted in other zones. • Understanding the recognised potential of introduced, native, and endemic tree species for NCP across anthropogenic gradients is important to create effective conservation strategies that align with human needs.
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5.2.1 Policy integration at the biodiversity-climate nexus

Regarding the integration of climate and biodiversity agendas, the 26th United Nations Climate Change Conference (COP 26) in 2021 did not achieve any major milestones, apart from mentioning biodiversity in the Glasgow Leaders' Declaration on Forests and Land Use (The National Archives, 2021) and recognising the interdependencies between the climate and biodiversity crises in the Glasgow Climate Pact (UNFCCC, 2021). This nexus only truly started to gain momentum during COP 27 in Sharm el-Sheikh in November 2022, which dedicated a whole day to biodiversity. It included the launch of a partnership on Enhancing Nature-based Solutions for an Accelerated Climate Transformation (ENACT), hosted by the International Union for Conservation of Nature (IUCN), to focus on the links between climate change, biodiversity loss, and land degradation (Nature-Based Solutions Initiative, 2022). The 15th United Nations Biodiversity Conference (COP 15) then took place in Montreal in the following month (IISD, 2022). The biggest achievement of COP 15, the Kunming-Montreal Global Biodiversity Framework, incorporates climate change in the context of NBS in its 2030 vision, namely Targets 8 and 11. However, forests are not part of the descriptions of these targets. Islands, as being particularly vulnerable to both biodiversity loss and climate change, are not referred to either. They only appear under Target 6, as priority sites for the reduction of invasive alien species (CBD Secretariat, 2023b). As the outcomes of the climate COP 27 and the biodiversity COP 15 indicate, the collaboration between the United Nations Framework on Climate Change (UNFCCC) and the Convention on Biological Diversity (CBD) has started to come along but has not developed to its full potential yet (Terton et al., 2022). Chapter 2 was published approximately one year before these two events, which is when some delayed submissions of NDCs were still happening. Regardless, no further climate action plans have been written by AOSIS members after COP 27 and COP 15.

My work, as laid out in Chapter 2, has shown that the NDCs of most AOSIS members currently fail to acknowledge the interdependencies between biodiversity and climate, lacking suggested measures tailored to this nexus. One crucial aspect of why biodiversity has not been fully integrated yet is the insufficient awareness of the biodiversity-climate nexus. This is a deficit that has been worked on since the first joint workshop in 2020 between the two most influential environmental science-policy interfaces, the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) and the Intergovernmental Panel on Climate Change (IPCC) (Pörtner et al., 2021). The explicit aim of these interfaces is to synthesise such knowledge for policy-makers (Förster, 2022), to which the ENACT partnership may also contribute (IUCN, 2022a). Another reason for the hesitation of countries may be uncertainties with regard to forest-based climate solutions. This concerns, for example, evidence about how these solutions

benefit biodiversity, or how climate change may negatively influence their overall effectiveness (Pettorelli et al., 2021). Finally, financial constraints may discourage members from looking beyond climate change mitigation/adaptation in their NDCs, as external funds are not necessarily aligned with biodiversity conservation goals (Robinson and Dornan, 2017).

Given that AOSIS members' contribution to climate change mitigation can only be small because of their size, the NDCs are nonetheless a great opportunity to stress their need for both climate change adaptation and the protection of their unique, globally important flora and fauna. After all, most NBS have positive outcomes for biodiversity (Chausson et al., 2020). For instance, forest protection and (re-)growth can simultaneously promote climate change mitigation/adaptation and biodiversity. Nevertheless, there are mitigation measures that are potentially detrimental to biodiversity, such as plantations of monocultures. Relying on a single species, these are less resilient to environmental perturbations, and thus no viable long-term solutions (Seddon et al., 2019). It is therefore essential to consider biodiversity in NDCs explicitly.

Biodiversity plays a pivotal role in the adaptation of AOSIS members, due to the intertwinings between biodiversity and climate. Being at particular risk of loss and damage from climate change (Thomas and Benjamin, 2018), these countries rely even more on resilient ecosystems. This resilience is determined by diversity at different ecological scales, including intraspecific such as genetic variability, interspecific such as functional redundancy, and in the ecosystem context such as landscape heterogeneity and connectivity (Oliver et al., 2015). In this way, ecosystem functions and services can be maintained to help these countries deal with the changing patterns in temperature and rainfall, more pronounced extreme weather events, and rising sea levels. It is important to implement biodiversity-inclusive NBS rather sooner than later, with some island states already being heavily affected by climate change, e.g. Tuvalu losing land to submersion (Farbotko, 2010), and many island endemics being at risk of extinction (Gray, 2019).

5.2.2 Spatial planning to integrate biodiversity and climate

Chapter 2 revealed that forest protection and (re-)growth were the forest-based climate solutions cited by most countries. At the same time, these solutions are known to potentially benefit biodiversity. Therefore, forest protection and (re-)growth may represent good starting points for the integration of climate and biodiversity. Forest (re-)growth is, however, a relatively broad term, encompassing several concepts that do not necessarily consider the forest quality in terms of function, structure, and composition (Vásquez-Grandón et al., 2018): While afforestation and reforestation theoretically refer to (re-)plantations of any tree species, forest rehabilitation and

restoration imply the inclusion of biodiversity to some degree. Yet, as long as there are no universally agreed-upon definitions, there is no guarantee that such forests are truly biodiverse and able to be productive and resilient.

Whereas clear definitions are one aspect of ensuring that forest protection and restoration can be put into action effectively, these proposed policy interventions also need to become spatially explicit. The importance of spatial planning for biodiversity conservation has generally been acknowledged (Pörtner et al., 2023). In line with its 2050 vision to live in harmony with nature, the Kunming-Montreal Global Biodiversity Framework dedicates Target 1 to this aspect. Accordingly, land-use change should be addressed by planning or managing all terrestrial areas by 2030, thereby reducing losses in biodiversity-rich areas to a bare minimum (CBD Secretariat, 2023b). Translating measures of forest protection and restoration into maps facilitates planning processes but may also reveal further challenges arising from climate and biodiversity integration, due to the level of detail needed.

Solid spatial planning requires knowledge from site-based assessments, revealing the current levels of biodiversity in multiple environments, to inform which areas are to be protected, restored, or further developed. Specifically, this concerns understanding how ecosystems and their components are structured to guide spatial planning. Linking assembly theory and restoration ecology is considered crucial in this context (Audino et al., 2017). Chapter 3 demonstrated that, in São Tomé, tree assemblages are distinct between zones. Due to the much higher species richness and abundance, preserving the forests of the natural zone, where also most native and endemic species reside, is indispensable to achieving considerable outcomes for climate and biodiversity protection. Endemic-rich forests have been found to offer substantial carbon sequestration potential in other tropical regions but this relationship cannot be taken for granted (Reside et al., 2017). Typically, biodiversity metrics in such contexts lack distinctions between endemic, native, and introduced species (Key et al., 2022).

In contrast, for the tree assemblages of the urban and rural zones, where introduced species are ubiquitous, a change needs to happen to bring any major benefits for biodiversity, even though the rural zone may be reasonably contributing to carbon sequestration and storage. Measures of forest restoration in these areas will be necessary to fully integrate climate and biodiversity. These interventions may include enhancing the ecological value and promoting native, endemic, and threatened species in rural and urban zones. This would also align with the recent trend of “bringing nature back into cities”, which is a process not only depending on conservation aspects, ecological/economic feasibility, and social acceptability. It should also incorporate culture and thus local knowledge, although this link is typically rather made for remote than urban areas (Mata et al., 2020). In fact, the presence of both public and private ownership can

make urban forests more diverse (Sousa-Silva et al., 2023), i.e. counting in local perspectives could contribute to resilience. As Chapter 4 has shown, Santomeans might however have stronger ties with introduced species and hardly any tree species were associated with climate regulation. It is therefore questionable if trees are valued for climate change mitigation/adaptation, at least on the level of ecological communities. Governmental and non-governmental bodies may hence be required to put more emphasis on this aspect to promote the resilience of urban ecosystems.

Despite best efforts to promote biodiversity conservation and simultaneously allow for climate change mitigation/adaptation, there are some less predictable factors to consider: The principle of environmental stationarity is not given, as climate change is progressing, and current conservation strategies may be outdated in the future. In some circumstances, protected areas may no longer fulfil their present roles due to shifting species ranges (Hoveka et al., 2022). However, the Obô Natural Park, as a protected area, is already the highest region of São Tomé, limiting chances for more suitable climate refugia. At these high elevations, but also if species compositions are managed to include native and endemic species in urban and rural areas, another potential problem is the risk of hybridisation between evolutionarily related species that previously did not occupy the same space (Gómez et al., 2015). As a consequence, endemics may be lost. Furthermore, introduced species thought to be tolerable in conservation strategies could turn out to be invasive, especially under shifting climate regimes (Wallingford et al., 2020).

5.2.3 Biotic homogenisation as another layer of complexity

Chapter 3 supported evidence that urban and rural zones were subject to biotic homogenisation, as they had few endemics and were dominated by introduced species. This is connected to São Tomé's land-use history, and the low species richness, typical of islands (Whittaker and Fernández-Palacios, 2007). It is particularly concerning to observe such a strong sign of homogenisation in zones with greater anthropogenic influence, given that the natural ecosystems of many islands contain high numbers of endemic species. Therefore, in island settings, it becomes even more pressing to analyse how introduced and endemic species are distributed across different land-use types (Mitchell et al., 2022), and to take appropriate species- or ecosystem-based conservation action. The Afrotropics in general experience very high rates of urbanisation, in response to the massive human population growth. The associated land-use change increases the danger of losing native and endemic species, as they have very limited time to adapt. The urban-rural expansion into wild areas can also cause other related problems, such as facilitating the spread of diseases from introduced to native and endemic species (Young et al., 2017).

Integrating findings from biodiversity assessments is key to ensuring effective conservation strategies. However, since humans have been shaping the globe based on their needs, chances for success are likely to be greater when the distribution of NCP is also considered, especially in economically weaker regions, where people tend to rely on nature more directly (Fedele et al., 2021). In Chapter 4, the potential importance of introduced species for NCP in urban and rural zones in São Tomé showed how societal aspects must be accounted for, as introduced species may provide distinct benefits to people compared to native species. In some cases, the full potential of the latter might not have been identified yet. If an introduced species is indeed the sole provider of a certain NCP, but ideally also of other NCP, it may be worth considering in urban planting schemes alongside the generally preferable native species.

Besides, when discussing species selection for forest-based climate solutions, some introduced species could be favoured due to their adaptive capacity to climate change (Sjöman et al., 2016). This approach has however also been criticised because of the associated risks, e.g. introduced species becoming invasive (Ennos et al., 2019). Instead, more effort might have to be put into identifying diverse native species that are equally adaptable, even if planting success may depend on seedlings from nurseries rather than direct seeding (Palma and Laurance, 2015). There are positive examples, from Ethiopia for instance, in which cities were able to preserve native and endemic species while fostering climate change mitigation/adaptation (Muluneh and Worku, 2022).

Nonetheless, insular endemics such as in São Tomé may not be suitable for making urban areas more resilient, due to their high susceptibility to anthropogenic modification and climate change, while introduced species may benefit from both impacts (Manes et al., 2021; Mitchell et al., 2022). Hence, a vulnerability assessment for tree species can be a good starting point (Brandt et al., 2016). In response to the increasing pressure from climate change, possibilities and priorities might change in the future. In order to maintain NCP and enable climate change mitigation/adaptation, a functionalist approach may have to be chosen over a compositionalist approach, which aims for the historical state of ecosystems (Pettorelli et al., 2018). For instance, tree diversity in urban areas may have to be maximised based on functional traits rather than nativeness (Paquette et al., 2021). This means biodiversity conservation and climate change mitigation/adaptation in human-modified spaces, especially in heat-afflicted lowlands, may not always represent a win-win situation. In summary, meticulous effort must be put into finding the best possible compromise in species selection and promotion across space, to achieve a balance between climate, biodiversity, and society, especially in vulnerable places like endemic-rich islands.

5.2.4 Including human needs in the biodiversity-climate nexus

Chapter 3 highlighted how using strong baselines is important to inform conservation policies. Comparing urban only with rural zones would have led to a gross underestimate of the urbanisation effect on tree diversity. Similarly, assessing how humans might benefit from biodiversity along the complete range of terrestrial ecosystem conditions is important to inform how to sustainably manage this diversity, as indicated by Chapter 4. Without evaluating the natural zone, I would have missed where currently the greatest recognised potential of material NCP lies. This contrasts with biodiversity-rich protected areas, such as those located in the natural zone of São Tomé, often being regarded as separate from people (Obura et al., 2021), when in fact they provide valuable NCP complementary to those from spaces that are more intensively managed by humans. Equally, human-dominated places such as cities are sometimes perceived as having little value for conservation or restoration, although there are at least some options for promoting their biodiversity and associated NCP. This in turn might have indirect benefits for the effective conservation of natural zones. If we ensure that urban and rural zones can provide some NCP, this might reduce the pressure over some resources in natural zones, and thus contribute to their long-term persistence.

A truly sustainable path requires extension of the biodiversity-climate nexus to the multiple sectors of society (Pörtner et al., 2023). Importantly, solutions must be found that integrate the needs of people across the continuum of almost intact, shared, and heavily modified spaces, to avoid trade-offs between biodiversity conservation and NCP supplies (Obura et al., 2021). This particularly matters in low- and middle-income countries, such as São Tomé and Príncipe, where people rely more directly on NCP for their livelihoods. These communities need to be better integrated into conservation processes, in which they are important players due to their direct dependence on natural resources and their influence on how these are managed (Dawson et al., 2021). Understanding sociocultural values is thus crucial to enabling effective conservation (Franco-Moraes et al., 2021; Ihemezie et al., 2023).

5.3 Suggestions for future research

Chapter 2 clearly demonstrated that biodiversity was not sufficiently integrated into the latest set of NDCs by the AOSIS members. Therefore, one major aim would be to improve the knowledge regarding the biodiversity-climate nexus, which could incentivise countries to integrate biodiversity into forest-based climate solutions. For instance, the evidence base for the positive effects of biodiverse forests on climate change mitigation and adaptation could be broadened. It should also be analysed how to evaluate or quantify progress achieved via biodiversity integration into these solutions, to establish monitoring frameworks that would

become relevant after their implementation. Furthermore, it is important to study how climate change could impact the effectiveness of forest-based climate solutions over time (Pettorelli et al., 2021). In addition, it must be clarified what the chances are to realise measures for mitigation and adaptation simultaneously, while effectively integrating biodiversity (Seddon et al., 2020), especially in spatially restricted places.

Another important takeaway from this thesis is that the effect of urbanisation on biodiversity may be much less understood than previously thought. Chapter 3 revealed that the tree diversity of both urban and rural zones was highly impoverished in São Tomé, compared to the natural zone, where most endemic and native species resided. These outcomes contradict those of many temperate studies that have described urban biodiversity as high. There the situation may however be different, as in temperate regions natural biodiversity levels are generally lower (Mittelbach et al., 2007), species may recover from environmental change faster than in the tropics (Newbold et al., 2020), studied baselines may be more impoverished (Wania et al., 2006), and cities tend to be older (Aronson et al., 2014). There is a pressing need to balance out this current geographic bias, caused by a lack of research in tropical regions, where urbanisation is accelerating the most (Padilla and Sutherland, 2019; Rega-Brodsky et al., 2022; Shackleton et al., 2021). To some degree, this divide is also reflected in high-income countries presenting more related studies than low- and middle-income countries. Therefore, insufficient research funds may largely explain this gap, as financial donors may not set priorities according to needs (McDonald et al., 2020). In addition, scientific efforts should be stepped up to compare biodiversity levels in urban areas with those of natural or near-natural areas, as information on the complete picture is rare. This shortcoming might also be connected to the shifting baseline syndrome, which describes how the current generation's perceptions of nature intactness have changed in response to the lack of historical information or personal experience (Soga and Gaston, 2018).

Furthermore, Chapter 4 revealed the recognised potential of trees to provide NCP across the three terrestrial conditions of nature on São Tomé Island. Additional research activities need to be undertaken to clarify the actual use of these NCP, and to understand where overexploitation is likely to occur. Household interviews or other participatory approaches that enable some sort of quantification could be suitable methods. Gathering this type of data may be relatively straightforward for material and non-material contributions, in contrast to regulating contributions (Boerema et al., 2017), which appear to miss the direct link with local people (Sutherland et al., 2018). For São Tomé, I found a big deficit regarding the recognition of regulating contributions, which therefore may require biophysical assessments. Besides, in-depth analyses of the timber quality and medicinal treatments illustrated that NCP are a field that could be explored much further when looking at individual categories. Equally, it might be

interesting to examine the supply chains of NCP across zones, as flows between them can be expected.

Another point worth investigating would be the attitudes and behaviours of the stakeholders mentioned in Chapters 2 and 4. These are influenced by the complex set of human values, which can be categorised into anthropocentric, biocentric, and relational value orientations (Ihemezie et al., 2021). Consequently, more insights should be obtained into the values and motivations of policy-makers, here the governments that are part of AOSIS. What motivates them to suggest forest-based climate solutions? What are their attitudes towards biodiversity? The same is true for those in charge of spatial planning. With reference to Chapter 4, it can be useful for conservation to study the values of authorities, farmers, and local people, as these likely influence their decisions of planting and maintaining trees, whether they are native or introduced. In this context, it may also be relevant to examine people's socio-economic and ethnic backgrounds (Cuni-Sanchez et al., 2016; Wilkerson et al., 2018).

As pointed out earlier, biodiversity, climate, and societal needs should be taken into consideration to maximise synergies and achieve sustainability across anthropogenic gradients (Figure 5.1). In Chapters 3 and 4, I studied tree diversity and NCP associated with trees in São Tomé. Hence, the missing component would be climate, to be measured in the form of NBS involving trees. One question would be how carbon-rich these trees are in heavily modified, shared, and almost intact spaces. This can be answered by calculating carbon stocks (Lewis et al., 2013). What is more difficult to measure is the adaptation potential of trees (Morecroft et al., 2019).

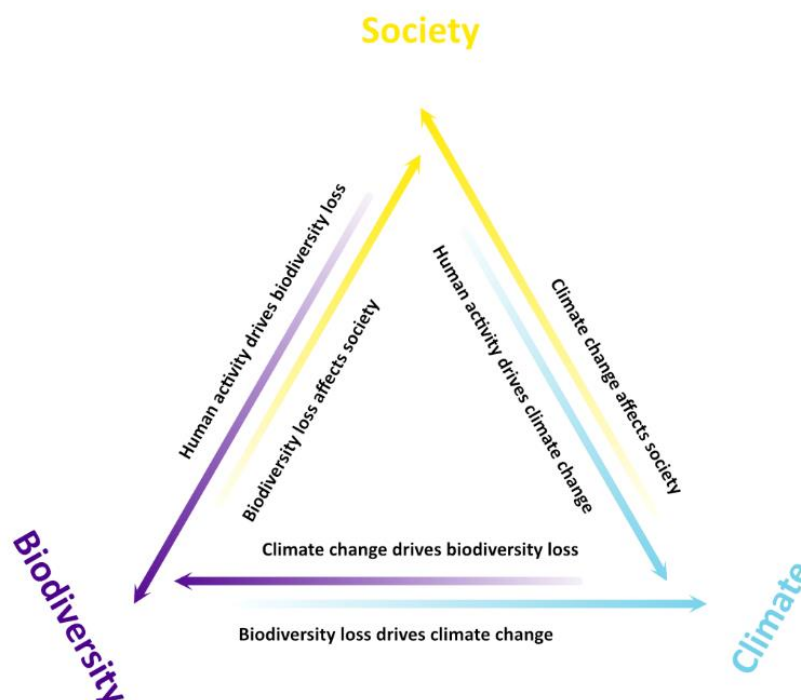


Figure 5.1. Simplified illustration of the biodiversity-climate-society nexus and the mutual relationships between each pair of the three components (modified from Pascual et al., 2022; WWF, 2022).

5.4 Implications for policy and practice

There are often time lags until the effects of environmental change on biodiversity become apparent. Hence, the precautionary principle should be followed for biodiversity conservation and use. Policies and practices need to be initiated as early as possible to avoid preventable species loss (Essl et al., 2015), especially on endemic-rich islands.

5.4.1 The biodiversity-climate nexus in policy and governance

As the biodiversity and climate crises are highly interrelated, addressing them jointly will clearly bring multiple benefits. AOSIS members should hence take the time now to integrate biodiversity, in particular via forest-based climate solutions, into their new NDCs more adequately, with the next round being due in 2025. Much integrative work also remains to be done across national environmental policies. Suggested measures in NDCs should not only be mirrored in National Adaptation Plans but also in National Biodiversity Strategies and Action Plans (NBSAPs) (Deprez and Rankovic, 2021; Terton et al., 2022), prepared by the parties to the CBD. Since AOSIS members have proven to be forerunners in the UNFCCC negotiations in the past (Ourbak and Magnan, 2018) and are particularly vulnerable to anthropogenic

environmental changes, it is to be expected that they continue pushing for a more progressive approach in the NDCs, despite currently showing some deficits with regard to biodiversity integration. A major question is therefore, how all UNFCCC parties can be encouraged to take this step in the future, considering that the international community needs to act together to tackle both crises and that funding opportunities remain an important barrier to promoting this integrated approach.

First, the UNFCCC should improve the implementing guidelines of the Paris Agreement, i.e. the Paris Rulebook, in terms of NDC structure. For instance, a section dealing with the integration of biodiversity could be made mandatory in NDCs. To ensure that biodiversity-inclusive interventions become effective, measurable targets, that can be monitored, should be the norm and not the exception as they were in the NDCs of AOSIS members. The results of Chapter 2 further imply that another major goal at the international policy level would be to raise awareness for the biodiversity-climate nexus among UNFCCC parties. This process should be backed up by more NBS-related research, which could be coordinated by a specified scientific body (Pettorelli et al., 2021), to reduce uncertainties about the interrelationships between biodiversity and climate. In addition, the UNFCCC should signal that adequate funding would be available for the integration of biodiversity into forest-based climate solutions on the ground.

Direct collaboration between the UNFCCC and the CBD will be increasingly desirable, also in terms of joint financial mechanisms (Terton et al., 2022). These could help balance out the chronic underfunding of biodiversity conservation compared to climate change mitigation/adaptation (Pettorelli et al., 2021). The institutional setup does not make collaboration particularly easy so far, although a Joint Liaison Group of the Rio Conventions, i.e. the UNFCCC, the CBD, and the United Nations Convention to Combat Desertification, exists. This group does not meet regularly enough, however (UNFCCC, 2016). While the Paris Agreement and the Kunming-Montreal Global Biodiversity Framework can be regarded as highly complementary, the former misses cross-references to biodiversity. In contrast, the Kunming-Montreal Global Biodiversity Framework mentions NBS to address climate change. If climate policy-makers were encouraged to read the latter, they might be more inclined to consider biodiversity concerns in climate goals and be inspired to develop a decade-long framework for concrete climate targets in a similar fashion (Streck, 2023).

Due to their broader scope, the United Nations Sustainable Development Goals could be a useful framework for reducing incoherence across biodiversity and climate goals (Deprez and Rankovic, 2021). Furthermore, science-policy platforms such as IPBES and IPCC, which have begun to work together, play a special role in the co-production of knowledge, thus having the potential to contribute to more coherent and effective policies in this context. Crucial policies

would be those that tackle the joint root causes of climate change and biodiversity loss, e.g. unsustainable agri-food systems (Deprez and Rankovic, 2021) among other global production and consumption systems (Förster, 2022). Furthermore, policies should address the removal of agricultural subsidies that can be harmful to both biodiversity and climate (IPBES, 2019).

Far-reaching, systemic shifts across institutions, structures, and individual mind-sets, involving social, economic, political, and technological change, need to happen to address the global, interconnected environmental crises, while also taking more immediate human needs into account (IPBES, 2019). In line with this, transformative governance is required to achieve sustainability for the biodiversity-climate-society nexus, which consists of both biophysical and social dimensions. In this way, win-win situations between biodiversity conservation, climate change mitigation/adaptation, and NCP promotion are possible (Pascual et al., 2022). Especially at larger scales, synergies and co-benefits can be created through an increased effort focussed on integrated spatial planning (Pörtner et al., 2021).

5.4.2 Forest protection and restoration across space

Preserving old-growth forests is the most important strategy to protect biodiversity- and carbon-rich ecosystems (Di Sacco et al., 2021). In São Tomé, these are the forests that persist predominantly in the mountainous centre of the island, where most of the native flora and fauna, including many endemics, can be found. Despite implementation challenges, the Obô Natural Park, which covers the majority of these forests, contributes to ensuring their conservation. Human impact is however present across the whole island to varying degrees, even though most of the natural zone is difficult to access. Selective logging, charcoal production, and hunting occur there, largely because the enforcement of laws and regulations has been poor. Theoretically, this would call for the restoration of some of these forests but budgets for this park have been tight compared to the needs for effective implementation, especially considering the growing human pressures on natural resources.

One major problem of forest restoration is space, a strong limiting factor on small islands. As São Tomé's human population is projected to grow further (UN-DESA, 2018), the situation becomes even more pressing. Nonetheless, the national government proposed forest (re-)growth as one of the targets in their NDCs. The strong land use competition will complicate the implementation of this target. Reducing agricultural land to enable the plantation of new forests bears a considerable risk of spreading “leakage” to native forests. An alternative is to intensify agricultural practices to make land available for this purpose (Latawiec et al., 2015). São Tomé's agroforests of shaded cocoa plantations are already intensively used but they can still be diversified to increase their productivity while improving their value for biodiversity. For

example, more shading tree species could be used, including endemics such as *Carapa gogo* or *Chytranthus mannii*. In addition, unforested smallholdings can be turned into agroforestry plots that include horticulture and assisted natural regeneration can be implemented in the buffer zone of the Obô Natural Park and other secondary forests. This is already happening as part of “The Restoration Initiative” project in São Tomé and Príncipe, the country’s first initiative on Forest and Landscape Restoration, aiming for ecosystem functionality and climate change mitigation (IUCN, 2022b).

NBS are increasingly being considered within urban areas (Frantzeskaki et al., 2019). While forest restoration may be less realistic in such densely populated environments, it is there that trees can make a big difference in terms of NCP provision and climate change adaptation. After all, large parts of the human population face urban heat island effects (Turner-Skoff and Cavender, 2019), which is also true for São Tomé’s capital, where the climate is already naturally hot. To integrate biodiversity, climate-resilient trees of preferably native origin could be planted that provide cooling but also habitats for native wildlife (Oke et al., 2021). Additionally, it is worth noting that the more NCP trees offer, the more likely they are to survive in human-modified ecosystems in the long run (Huang et al., 2023). Urban planting schemes could help realise efforts that align biodiversity, climate, and human needs.

5.5 Conclusions

Tropical island forests are particularly vulnerable to anthropogenic environmental change, which drives them towards the core of the biodiversity crisis. This thesis shows that interdisciplinary research benefitting from policy and (socio-)ecological analyses can be an important step in addressing this biodiversity loss. NDC policy-makers from island states proposed forests as climate solutions but hardly considered biodiversity. After the climate COP 27 and the biodiversity COP 15, ignoring the interrelations between the climate and biodiversity crises can no longer be acceptable. Suggestions to protect and restore forests should not remain empty phrases on paper, they ought to be put into action and they should go beyond carbon stocks. This will only be possible if spatially explicit assessments of biodiversity and associated NCP feed into the process, a work to be done by (socio-)ecological science. Spatial planners will then be needed to create a sound vision for protected and restored forests, one that allows humans to live in harmony with nature.

It is important to acknowledge that people are currently shaping our planet, even if at varying degrees across space, but that measures can be accommodated that contribute to the halting of the climate and biodiversity crises. Understanding the continuum of intact, shared, and heavily modified spaces, overlaid by patterns of biotic homogenisation, is paramount to prevent further

biodiversity loss, enhance climate change adaptation and mitigation, and cater to societal needs, especially in tropical environments. Here, the biodiversity-climate-society nexus will gain more relevance in the future, and islands can take on a pioneering role in this learning process. They are equipped with highly engaged policy-makers who are well aware of the vulnerability of their countries while providing the perfect ground to study this highly complex nexus.

5.6 References

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Appendix A Supplementary material Chapter 2

Title: Limited integration of biodiversity within climate policy: Evidence from the Alliance of Small Island States

List of keywords

App. A.1. Preliminary concepts and provisional codes applied on the Nationally Determined Contributions (NDCs) of the 39 Alliance of Small Island States (AOSIS) members during first cycle coding as well as corresponding sources and French and Spanish equivalents. Asterisks () indicate a wildcard for words with identical stems but multiple beginnings and/or endings.*

	Preliminary concepts	Provisional codes	Sources	French equivalent	Spanish equivalent
Forests	Forest conservation Sustainable forest management	*forest* tree* mangrove* conserv* preserv* protect*	Crumpler et al., 2019; Donato et al., 2011	forêt* sylv* arbre* mangrove* conserv* préserv* protég* protèg* protection*	bosque* selva* árbol* mangl* conserv* preserv* prote*
	Deforestation Forest degradation	*forest* degrad* logging wood* timber	Ahenkan and Boon, 2011; Putz and Redford, 2010	*forest* dégrad* défrichage* *bois*	*forest* degrad* tala* mader* leña*
	Afforestation Reforestation	*forest* restor* rehabilitat* plant*	Crumpler et al., 2019; Putz and Redford, 2010; UNEP-WCMC, 2014	*forest* restaur* réhabilit* plantation*	*forest* restaur* rehabilit* plantaci*
	Climate and forests	carbon CO2 biomass sequest* REDD*	Mach et al., 2014; UNEP-WCMC, 2014	carbon* CO2 biomasse séquestr* REDD	carbon CO2 biomasa secuestr* REDD
Biodiversity	General	*benefit* trade* synerg*	CBD, 2019	*bénéfice* compromis* synerg*	*beneficio* precio* sinerg*
	Biodiversity conservation Biodiversity restoration	divers* flor* faun* plant* animal* vegetation* genet* genes* species ecosystem* habitat* conserv* preserv* protect* restor* rehabilitat* recover* CBD	UNEP-WCMC, 2014; United Nations, 1992	divers* flor* faun* plant* anima* végéta* génétique* gène* espèce* écosystème* écosystémique* habitat* conserv* préserv* protég* protèg* protection* restaur* réhabilit*	divers* flor* faun* planta* animal* vegeta* genetic* gen* especie* ecosistema* ecosistémic* hábitat* conserv* preserv* prote* restaur* rehabilit* recuper* CBD

	Endemism	endemi* restricted- range range- restricted	UNEP- WCMC, 2014	récup* CBD endém*	endemismo endémic*
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Quantification of forest-based climate solutions

App. A.2. Concrete measures of forest-based climate solutions for climate change mitigation and adaptation of those Alliance of Small Island States (AOSIS) members that provide a quantification in their Nationally Determined Contributions (NDCs).

Country	Mitigation solution	Adaptation solution
Cabo Verde	Afforestation and reforestation of 10,000 ha (unconditional) plus 10,000 ha (conditional) by 2030 (400 trees per ha)	
Comoros	Reduction of deforestation by 45% until 2030; afforestation of 11,116 ha by 2019 (6% of its territory); reforestation of 2,200 ha per year for five years (2015-2019); reforestation of ca. 12,000 ha between 2018 and 2030	
São Tomé and Príncipe		Reduction of illegal and indiscriminate tree felling by 15% until 2030
Singapore		Plantation of one million trees by 2030
Guyana	Reduction of damage during tree felling by about 10% and damage from skid trails by about 35% (Reduced Impact Logging); low rate of illegal logging at less than 2% of production	
Haiti	Afforestation and reforestation of 2,500 ha per year from 2016 to 2030 (unconditional); plantation of 100,000 ha between 2020 and 2030 (conditional); plantation of energy forests (10,000 ha until 2030)	
Suriname	Annual deforestation rates below 0.1%	
Timor-Leste	Afforestation and reforestation of one million trees per year	

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Appendix B Supplementary material Chapter 3

Title: Widespread introduced species dominate the urban tree assemblage on the endemic-rich tropical island of São Tomé

App. B.1. Biogeographic origin and realm (native range) of the 177 tree taxa registered in 81 transects in São Tomé.

Family	Taxon	Origin	Realm	Notes
Anacardiaceae	<i>Lannea welwitschii</i>	Native	Afrotropics	All information was extracted from POWO (2023), except for the following markings:
	<i>Mangifera indica</i>	Introduced	Indomalaya ^T	
	<i>Pseudospondias microcarpa</i>	Native	Afrotropics	
	<i>Sorindeia grandifolia</i>	Native	Afrotropics	
	<i>Spondias dulcis</i>	Introduced	Australasia	
	<i>Spondias mombin</i>	Introduced	Neotropics	
Anisophylleaceae	<i>Anisophyllea cabole</i>	Native	Afrotropics	* Not listed and assumed as “Introduced” based on native range. + Listed as “Native” or “Native (Endemic)” but might be introduced based on current distribution and on being widely cultivated in the island. ~ Listed as “Introduced” but might be native based on current distribution.
Annonaceae	<i>Annona muricata</i>	Introduced	Neotropics	
	<i>Annona squamosa</i>	Introduced	Neotropics	
	<i>Cananga odorata</i>	Introduced	Multiple realms (Indomalaya, Australasia)	
	<i>Greenwayodendron</i> aff. <i>suaveolens</i>	Native [^]	Afrotropics	
	<i>Monodora myristica</i>	Native	Afrotropics	
	<i>Xylopia aethiopica</i>	Native	Afrotropics	
	<i>Xylopia quintasii</i>	Native	Afrotropics	
	<i>Xylopia</i> sp. nov. Sao Tome [#]	Native (Endemic) ^T	Afrotropics	
Apocynaceae	<i>Cascabela thevetia</i>	Introduced	Neotropics	
	<i>Funtumia africana</i>	Native	Afrotropics	
	<i>Funtumia elastica</i>	Native+	Afrotropics	
	<i>Rauvolfia caffra</i>	Native	Afrotropics	
	<i>Rauvolfia dichotoma</i>	Native (Endemic)	Afrotropics	
	<i>Rauvolfia vomitoria</i>	Native	Afrotropics	
	<i>Tabernaemontana stenosphon</i>	Native (Endemic)	Afrotropics	
Araliaceae	<i>Astropanax mannii</i>	Native	Afrotropics	
	<i>Polyscias quintasii</i>	Native (Endemic)	Afrotropics	
Asparagaceae	<i>Dracaena arborea</i>	Native	Afrotropics	
Asteraceae	<i>Vernonia amygdalina</i> [#]	Native+	Multiple realms (Afrotropics, Neotropics)	
Bignoniaceae	<i>Crescentia cujete</i>	Introduced*	Neotropics	

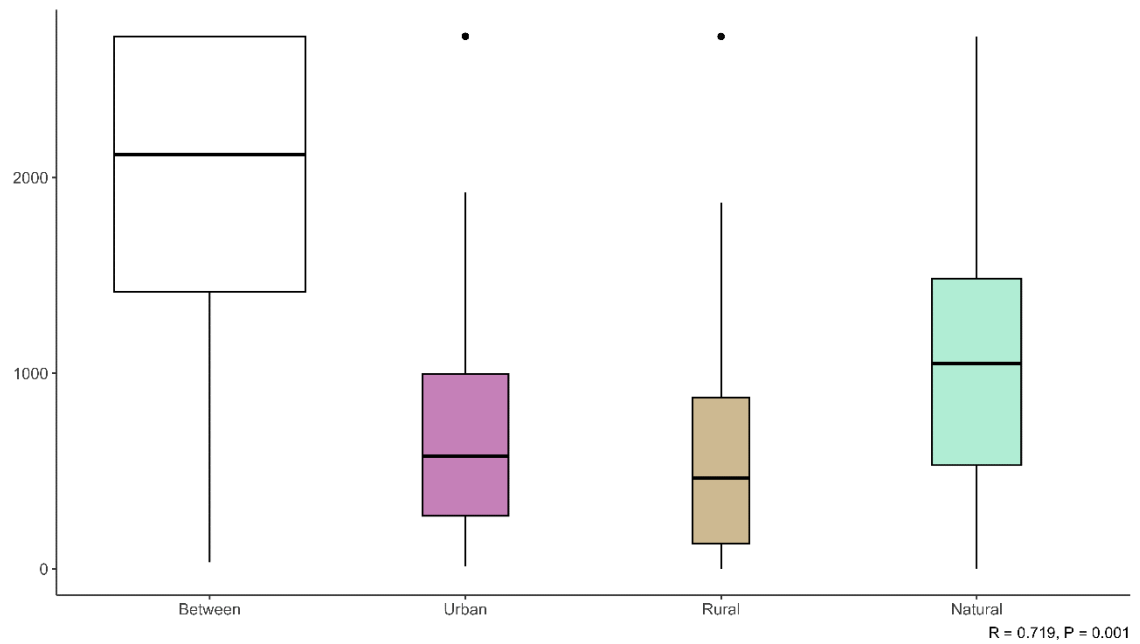
	<i>Newbouldia laevis</i>	Native+	Afrotropics	^ Listed as “Native” or not listed but might be a distinct and endemic species.
Burseraceae	<i>Dacryodes edulis</i> [#]	Introduced ^T	Afrotropics	
	<i>Santiria balsamifera</i>	Native (Endemic)	Afrotropics	
Cannabaceae	<i>Celtis gomphophylla</i>	Native	Afrotropics	^F Based on Figueiredo et al. (2011).
	<i>Celtis prantlii</i> [#]	Native	Afrotropics	
Clusiaceae	<i>Symphonia globulifera</i>	Native	Multiple realms (Afrotropics, Neotropics)	
Combretaceae	<i>Terminalia catappa</i>	Introduced	Multiple realms (Afrotropics, Indomalaya, Australasia, Oceania)	^T Based on ongoing work by the authors.
Cornaceae	<i>Alangium</i> aff. <i>chinense</i>	Native ^T	Unknown	
Ebenaceae	<i>Diospyros ferrea</i>	Native	Multiple realms (Afrotropics, Indomalaya, Australasia)	
Ehretiaceae [#]	<i>Ehretia cymosa</i>	Native	Afrotropics	The realm is unknown for taxa that could not be determined to the species level.
Euphorbiaceae	<i>Anthostema aubryanum</i>	Native	Afrotropics	
	<i>Croton stellulifer</i>	Native (Endemic)	Afrotropics	
	<i>Discoclaoxylon occidentale</i>	Native (Endemic)	Afrotropics	Species are listed as endemic if their distribution is restricted to the oceanic islands of the Gulf of Guinea.
	<i>Discoglyprena caloneura</i>	Native	Afrotropics	
	<i>Euphorbia grandifolia</i>	Native ^T	Afrotropics	
	<i>Grossera elongata</i>	Native (Endemic)	Afrotropics	The taxonomy was based on Tropicos (2023).
	<i>Hevea brasiliensis</i>	Introduced	Neotropics	
	<i>Klaineanthus gabonii</i> [#]	Native	Afrotropics	
	<i>Macaranga monandra</i>	Native	Afrotropics	Scientific family or species names not accepted by POWO (2023) are indicated by [#] .
	<i>Manihot glaziovii</i> [#]	Introduced	Neotropics	
	<i>Pseudagrostistachys africana</i>	Native	Afrotropics	
	<i>Shirakiopsis elliptica</i>	Native	Afrotropics	
	<i>Tetrorchidium didymostemon</i>	Native	Afrotropics	
Fabaceae	<i>Acacia auriculiformis</i>	Introduced*	Australasia	
	<i>Albizia chinensis</i>	Introduced*	Multiple realms (Indomalaya, Australasia)	
	<i>Albizia falcata</i> [#]	Introduced	Australasia	
	<i>Albizia lebbeck</i>	Introduced	Indomalaya	
	<i>Cassia siamea</i> [#]	Introduced	Indomalaya	
	<i>Cynometra mannii</i>	Native	Afrotropics	

	<i>Dialium guineense</i>	Native+	Afrotropics
	<i>Erythrina fusca</i>	Introduced	Multiple realms (Afrotropics, Neotropics, Indomalaya, Australasia, Oceania)
	<i>Erythrina poeppigiana</i>	Introduced	Neotropics
	<i>Erythrina variegata</i>	Introduced	Multiple realms (Afrotropics, Indomalaya, Australasia, Oceania)
	<i>Lonchocarpus sericeus</i>	Native	Multiple realms (Afrotropics, Neotropics)
	<i>Millettia barteri</i>	Native	Afrotropics
	<i>Millettia griffoniana</i>	Native	Afrotropics
	<i>Pentaclethra macrophylla</i>	Native	Afrotropics
	<i>Tamarindus indica</i>	Introduced	Afrotropics
Gentianaceae	<i>Anthocleista scandens</i>	Native	Afrotropics
Hypericaceae	<i>Harungana madagascariensis</i>	Native	Afrotropics
Ixonanthaceae	<i>Phyllocosmus</i> aff. <i>sessiliflorus</i>	Native (Endemic) ^T	Afrotropics
Lamiaceae	<i>Gmelina arborea</i>	Introduced*	Indomalaya
	<i>Vitex</i> sp.	Native ^T	Unknown
Lauraceae	<i>Cinnamomum burmannii</i> [#]	Introduced	Multiple realms (Indomalaya, Australasia)
	<i>Cinnamomum verum</i>	Introduced	Indomalaya
	<i>Persea americana</i>	Introduced	Neotropics
Lecythidaceae	<i>Scyttopetalum klaineianum</i>	Native	Afrotropics
Malvaceae	<i>Ceiba pentandra</i>	Introduced~	Neotropics
	<i>Cola acuminata</i>	Introduced ^T	Afrotropics
	<i>Glyphaea brevis</i>	Native	Afrotropics
	<i>Pachira glabra</i>	Introduced	Neotropics
	<i>Sterculia dawei</i>	Native	Afrotropics
	<i>Theobroma cacao</i>	Introduced	Neotropics
Melastomataceae	<i>Memecylon myrianthum</i>	Native ^T	Afrotropics
Meliaceae	<i>Carapa gogo</i>	Native (Endemic)	Afrotropics
	<i>Cedrela odorata</i>	Introduced	Neotropics
	<i>Trichilia grandifolia</i>	Native (Endemic)	Afrotropics
Moraceae	<i>Artocarpus altilis</i>	Introduced	Oceania

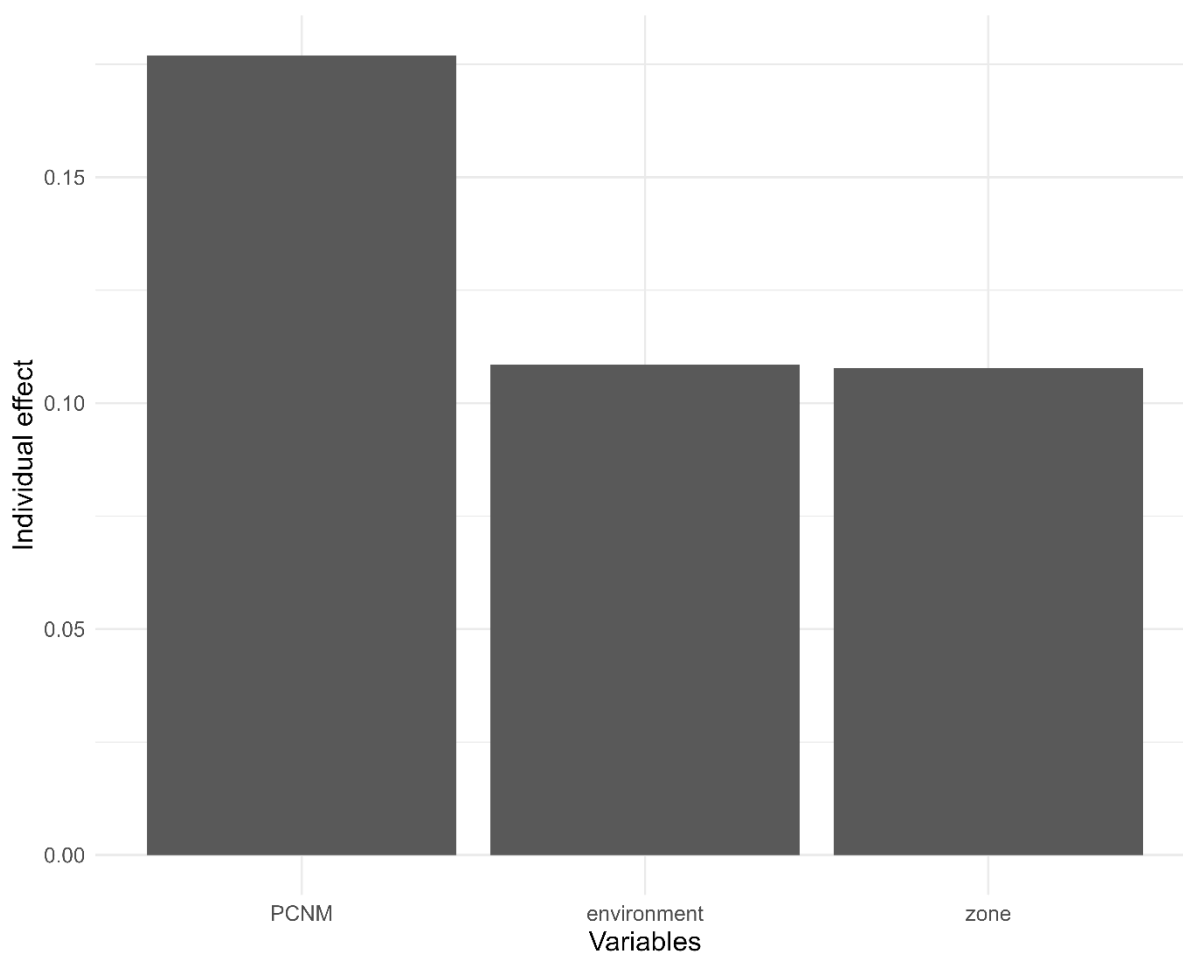
	<i>Artocarpus camansi</i>	Introduced*	Australasia
	<i>Artocarpus heterophyllus</i>	Introduced	Indomalaya
	<i>Castilla elastica</i>	Introduced	Neotropics
	<i>Ficus chlamydocarpalo</i>	Native	Afrotropics
	<i>Ficus exasperata</i>	Native	Multiple realms (Afrotropics, Indomalaya)
	<i>Ficus mucuso</i>	Native	Afrotropics
	<i>Ficus sur</i>	Native	Afrotropics
	<i>Ficus thonningii</i>	Native	Afrotropics
	<i>Mesogyne insignis</i>	Native^	Afrotropics
	<i>Milicia excelsa</i>	Native	Afrotropics
	<i>Treculia africana</i>	Native+	Afrotropics
	<i>Trilepisium madagascariense</i>	Native	Afrotropics
Moringaceae	<i>Moringa oleifera</i>	Introduced*	Indomalaya
Myristicaceae	<i>Pycnanthus angolensis</i>	Native	Afrotropics
	<i>Staudtia pterocarpa</i>	Native (Endemic)	Afrotropics
Myrtaceae	<i>Eucalyptus torelliana</i> [#]	Introduced*	Australasia
	<i>Eugenia brasiliensis</i>	Introduced	Neotropics
	<i>Eugenia uniflora</i>	Introduced	Neotropics
	<i>Psidium guajava</i>	Introduced	Neotropics
	<i>Syzygium guineense</i>	Native ^{T^}	Afrotropics
Ochnaceae	<i>Campylospermum reticulatum</i>	Native	Afrotropics
	<i>Campylospermum vogelii</i>	Native	Afrotropics
	<i>Idertia axillaris</i>	Native	Afrotropics
	<i>Rhabdophyllum arnoldianum</i>	Native	Afrotropics
	<i>Rhabdophyllum calophyllum</i>	Native	Afrotropics
Olacaceae	<i>Heisteria parvifolia</i>	Native	Afrotropics
	<i>Strombosia grandifolia</i>	Native	Afrotropics
	<i>Strombosia</i> sp. nov. Sao Tome [#]	Native (Endemic) ^T	Afrotropics
Oleaceae	<i>Olea capensis</i>	Native	Afrotropics
Oxalidaceae	<i>Averrhoa bilimbi</i>	Introduced*	Australasia
Phyllanthaceae	<i>Amanoa</i> cf. <i>bracteosa</i>	Native ^T	Afrotropics ^T

	<i>Antidesma vogelianum</i>	Native	Afrotropics
	<i>Bridelia micrantha</i>	Native	Afrotropics
	<i>Cleistanthus libericus</i>	Native	Afrotropics
	<i>Maesobotrya glabrata</i>	Native (Endemic)	Afrotropics
	<i>Margaritaria discoidea</i>	Native	Afrotropics
	<i>Protomegabaria stapfiana</i>	Native	Afrotropics
	<i>Thecacoris manniana</i> [#]	Native (Endemic) ^F	Afrotropics
	<i>Uapaca vanhouttei</i>	Native ^T	Afrotropics
Primulaceae	<i>Rapanea melanophloeos</i> [#]	Native	Afrotropics
Proteaceae	<i>Grevillea robusta</i>	Introduced	Australasia
Putranjivaceae	<i>Drypetes glabra</i>	Native (Endemic)	Afrotropics
	<i>Drypetes henriquesii</i>	Native (Endemic)	Afrotropics
	<i>Drypetes principum</i>	Native	Afrotropics
Rhamnaceae	<i>Lasiodiscus rozeirae</i>	Native (Endemic)	Afrotropics
	<i>Maesopsis eminii</i>	Native	Afrotropics
	<i>Ziziphus abyssinica</i>	Native+	Afrotropics
Rhizophoraceae	<i>Cassipourea gummiflua</i>	Native	Afrotropics
Rubiaceae	<i>Aidia quintasii</i>	Native (Endemic)	Afrotropics
	<i>Aulacocalyx pallens</i>	Native	Afrotropics
	<i>Belonophora coffeoides</i>	Native	Afrotropics
	<i>Bertiera racemosa</i>	Native	Afrotropics
	<i>Cinchona pubescens</i> [#]	Introduced	Neotropics
	<i>Coffea canephora</i>	Introduced ^F	Afrotropics
	<i>Craterispermum cerinanthum</i>	Native	Afrotropics
	<i>Hymenodictyon biafranum</i>	Native	Afrotropics
	<i>Morinda lucida</i>	Native	Afrotropics
	<i>Oxyanthus speciosus</i>	Native	Afrotropics
	<i>Pauridiantha floribunda</i>	Native	Afrotropics
	<i>Pauridiantha insularis</i>	Native (Endemic)	Afrotropics
	<i>Pavetta monticola</i>	Native (Endemic)	Afrotropics
	<i>Pouchetia</i> aff. <i>parviflora</i>	Native (Endemic) ^T	Afrotropics

	<i>Psychotria grumilea</i> [#]	Native (Endemic)	Afrotropics
	<i>Psychotria venosa</i>	Native	Afrotropics
	<i>Psydrax sanguinolenta</i> sp. nov. [#]	Native ^T	Afrotropics ^T
	<i>Psydrax subcordata</i> [#]	Native	Afrotropics
	<i>Rothmannia urcelliformis</i>	Native	Afrotropics
	<i>Tarenna nitiduloides</i>	Native (Endemic)	Afrotropics
Rutaceae	<i>Citrus × aurantium</i>	Introduced	Hybrid
	<i>Zanthoxylum gillettii</i>	Native	Afrotropics
	<i>Zanthoxylum thomense</i>	Native	Afrotropics
Salicaceae	<i>Casearia barteri</i>	Native	Afrotropics
	<i>Homalium henriquesii</i>	Native	Afrotropics
	<i>Ophiobotrys zenkeri</i>	Native	Afrotropics
Sapindaceae	<i>Allophylus africanus</i>	Native	Afrotropics
	<i>Allophylus grandifolius</i>	Native	Afrotropics
	<i>Blighia sapida</i>	Native+	Afrotropics
	<i>Chytranthus mannii</i>	Native (Endemic)+	Afrotropics
Sapotaceae	<i>Chrysophyllum africanum</i> [#]	Native	Afrotropics
	<i>Chrysophyllum albidum</i> [#]	Native+	Afrotropics
	<i>Manilkara obovata</i>	Native	Afrotropics
	<i>Synsepalum revolutum</i>	Native	Afrotropics
	<i>Synsepalum</i> sp. nov. 1 Sao Tome [#]	Native (Endemic) ^T	Afrotropics
	<i>Synsepalum</i> sp. nov. 2 Sao Tome [#]	Native (Endemic) ^T	Afrotropics
Simaroubaceae	<i>Hannoa klaineana</i> [#]	Native	Afrotropics
Solanaceae	<i>Cestrum laevigatum</i>	Introduced	Neotropics
Stilbaceae	<i>Nuxia congesta</i>	Native	Afrotropics
Thymelaeaceae	<i>Dicranolepis thomensis</i>	Native (Endemic)	Afrotropics
	<i>Peddiea thomensis</i>	Native (Endemic)	Afrotropics
Urticaceae	<i>Cecropia peltata</i>	Introduced	Neotropics
Violaceae	<i>Rinorea chevalieri</i>	Native (Endemic)	Afrotropics
Vitaceae	<i>Leea tinctoria</i>	Native (Endemic)	Afrotropics



App. B.2. Analysis of similarities in tree assemblages based on dissimilarity ranks between zones ("Between") and within zones ("Urban", "Rural", "Natural"), with associated R- and p-value. The R-value can range between 1 (high dissimilarities between zones) and close to 0 (equal dissimilarities between and within zones).



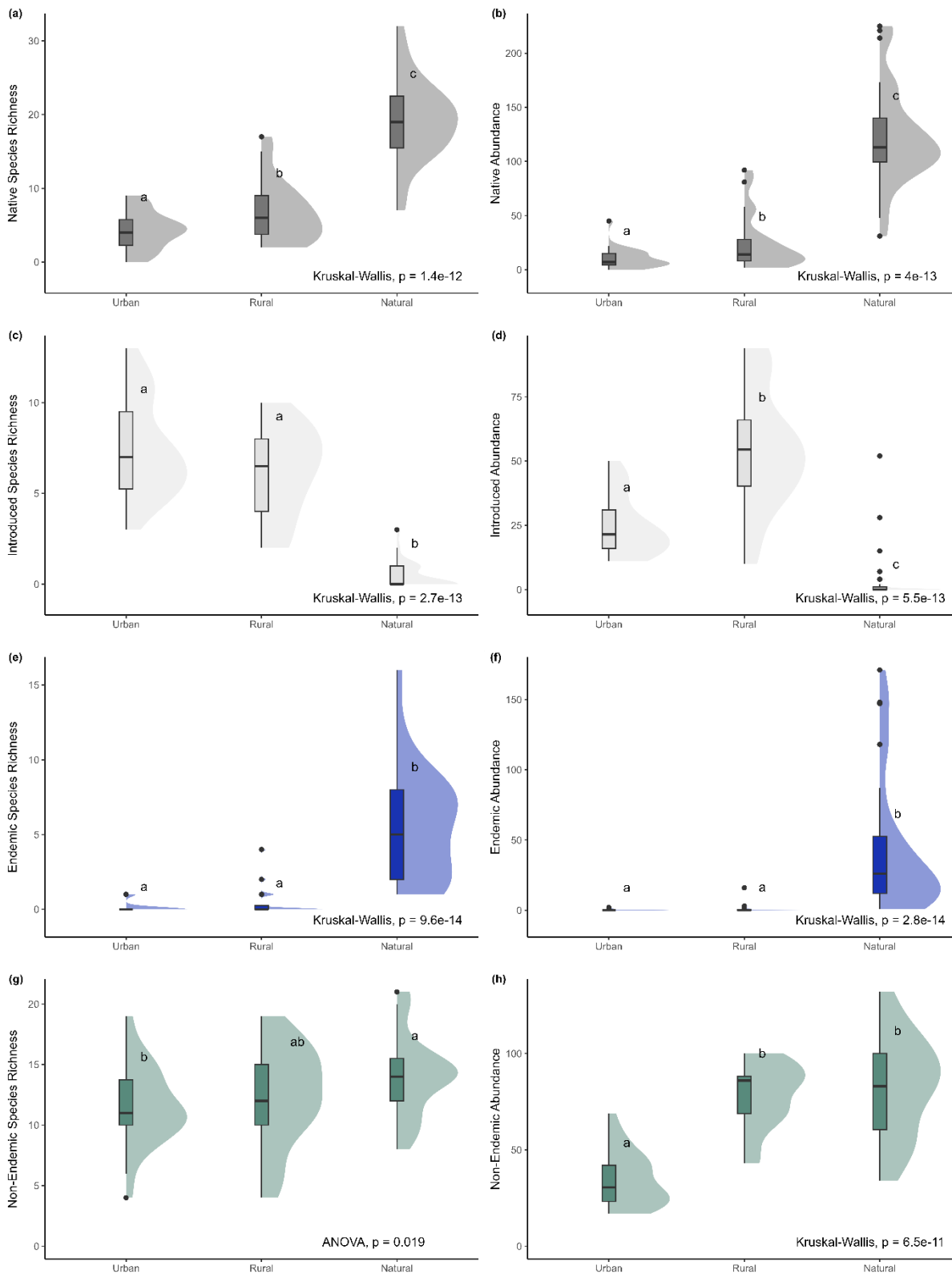
App. B.3. Hierarchical partitioning, combining unique and common fractions, of PCNM (principal coordinates of neighbour matrices), environment (altitude, precipitation, remoteness, slope, topography, cloud cover), and zone (urban, rural, natural) towards explained variation (R-squared) of tree assemblages.

App. B.4. Hierarchical partitioning, combining unique and common fractions, of environmental variables: altitude, precipitation, remoteness, slope, topography, cloud cover.

	Individual effect (%)
Altitude	20.52
Precipitation	24.19
Remoteness	17.07
Slope	9.61
Topography	14.41
Cloud cover	14.10
Total (%)	100.00

App. B.5. Variation partitioning between environment (altitude, precipitation, remoteness, slope, topography, cloud cover), zone (urban, rural, natural), and PCNM (principal coordinates of neighbour matrices) explaining variation (R-squared) of tree assemblages.

		Fraction of explained variation (%)
Unique to	environment	3.66
	zone	1.88
	PCNM	8.41
Common to	environment and zone	1.96
	environment and PCNM	2.71
	zone and PCNM	6.15
	environment, zone, and PCNM	14.56
Total explained variation (%)		39.32



App. B.6. Violin box plots of tree species richness and abundance of native (a and b), introduced (c and d), endemic (e and f), and non-endemic taxa (g and h) per transect, showing the significance of relationships between zones. P-values (df = 2) of one-way ANOVA, (g) $F = 4.147$, or Kruskal-Wallis rank sum tests, (a) $\chi^2 = 54.572$, (b) $\chi^2 = 57.111$, (c) $\chi^2 = 57.904$, (d) $\chi^2 = 56.473$, (e) $\chi^2 = 59.957$, (f) $\chi^2 = 62.395$, and (h) $\chi^2 = 46.902$, at the bottom of each graph. Significant differences from Tukey HSD or

pairwise Wilcoxon rank sum tests indicated by different superscript letters. Maximum width of violins scaled to 1.

App. B.7. Significant indicator values (significance levels = *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$, ****: $p \leq 0.0001$) of tree taxa for the urban, rural, and natural zone, as well as for combinations of them.

Taxon	Indicator value	Significance level
URBAN		
<i>Mangifera indica</i>	0.810	**
<i>Newbouldia laevis</i>	0.750	**
<i>Annona muricata</i>	0.616	**
<i>Terminalia catappa</i>	0.577	**
<i>Spondias mombin</i>	0.528	*
<i>Chrysophyllum albidum</i>	0.516	**
<i>Gmelina arborea</i>	0.447	**
RURAL		
<i>Theobroma cacao</i>	0.920	**
<i>Erythrina poeppigiana</i>	0.775	**
<i>Tetrorchidium didymostemon</i>	0.708	**
<i>Cecropia peltata</i>	0.635	**
<i>Pseudospondias microcarpa</i>	0.543	**
<i>Celtis gomphophylla</i>	0.533	**
<i>Macaranga monandra</i>	0.440	*
<i>Albizia lebbbeck</i>	0.420	**
NATURAL		
<i>Homalium henriquesii</i>	0.803	**
<i>Casearia barteri</i>	0.778	**
<i>Pauridiantha floribunda</i>	0.724	**
<i>Antidesma vogelianum</i>	0.680	**
<i>Scytopetalum klaineanum</i>	0.672	**
<i>Thecacoris manniana</i>	0.672	**
<i>Oxyanthus speciosus</i>	0.657	**
<i>Chrysophyllum africanum</i>	0.648	**
<i>Santiria balsamifera</i>	0.622	**
<i>Xylopia</i> sp. nov. Sao Tome	0.599	**
<i>Craterispermum cerinanthum</i>	0.596	**
<i>Syzygium guineense</i>	0.596	**
<i>Uapaca vanhouttei</i>	0.596	**
<i>Cleistanthus libericus</i>	0.587	**
<i>Drypetes henriquesii</i>	0.568	**
<i>Greenwayodendron</i> aff. <i>suaveolens</i>	0.568	**
<i>Grossera elongata</i>	0.568	**
<i>Heisteria parvifolia</i>	0.539	**
<i>Protomegabaria stapfiana</i>	0.539	**
<i>Symphonia globulifera</i>	0.539	**
<i>Psychotria venosa</i>	0.532	**
<i>Rhabdophyllum arnoldianum</i>	0.525	**
<i>Cassipourea gummiflua</i>	0.520	**
<i>Aulacocalyx pallens</i>	0.508	**
<i>Croton stellulifer</i>	0.508	**
<i>Synsepalum revolutum</i>	0.508	*
<i>Klaineanthus gabonii</i>	0.506	**
<i>Amanoa</i> cf. <i>bracteosa</i>	0.475	**

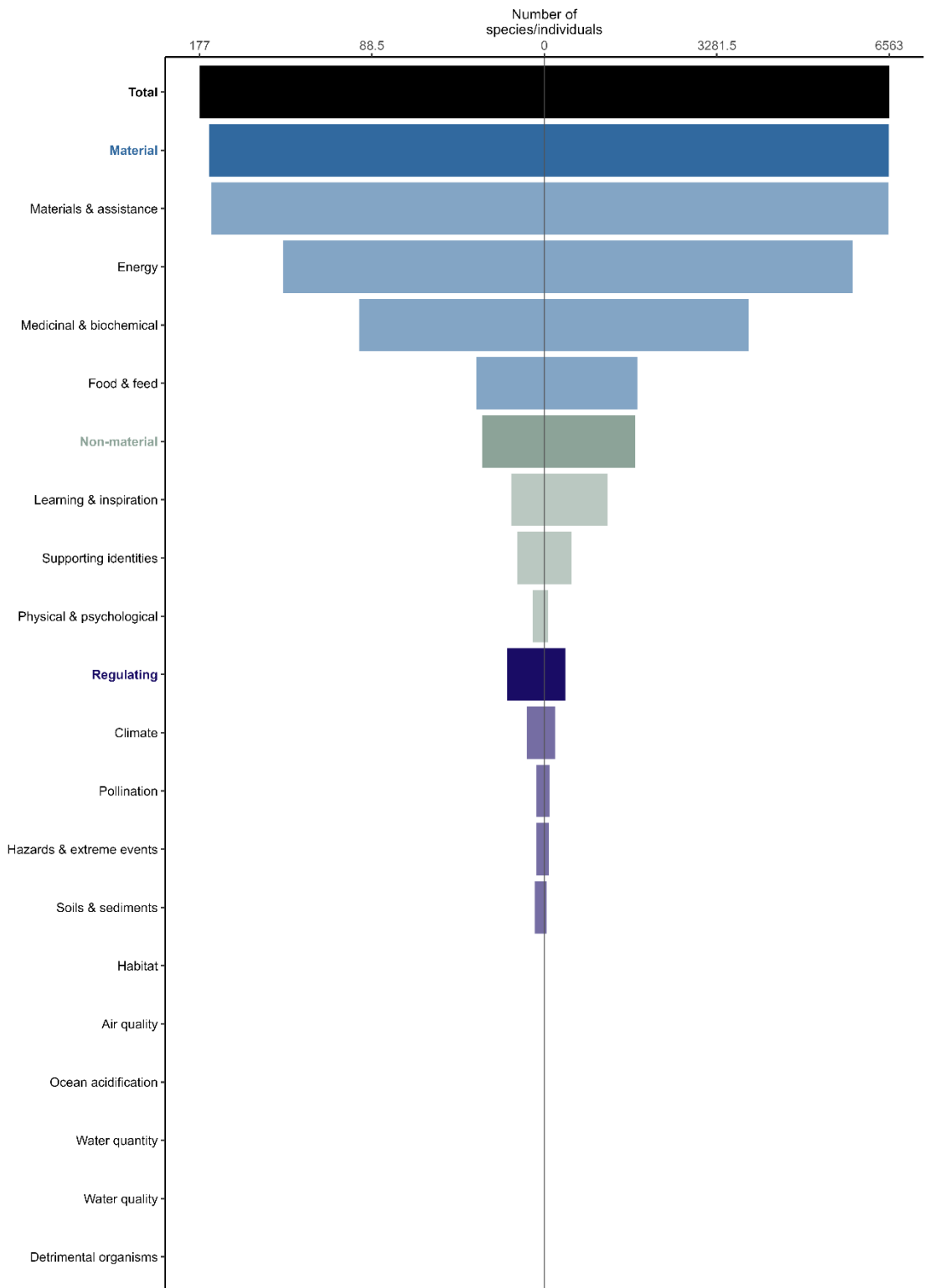
<i>Psydrax sanguinolenta</i> sp. nov.	0.475	**
<i>Rauvolfia dichotoma</i>	0.475	**
<i>Staudtia pterocarpa</i>	0.475	*
<i>Aidia quintasii</i>	0.440	**
<i>Blighia sapida</i>	0.440	**
<i>Maesobotrya glabrata</i>	0.440	**
<i>Tabernaemontana stenosphon</i>	0.440	*
<i>Hannoa klaineana</i>	0.424	*
<i>Synsepalum</i> sp. nov. 1 Sao Tome	0.421	*
<i>Drypetes glabra</i>	0.402	*
<i>Pavetta monticola</i>	0.402	*
<i>Strombosia</i> sp. nov. Sao Tome	0.402	*
<i>Dicranolepis thomensis</i>	0.359	*
<i>Discoclaoxylon occidentale</i>	0.359	*
<i>Discoglypsemna caloneura</i>	0.359	*
<i>Pseudagrostistachys africana</i>	0.359	*
URBAN and RURAL		
<i>Artocarpus altilis</i>	0.854	**
<i>Artocarpus heterophyllus</i>	0.775	**
<i>Cedrela odorata</i>	0.705	**
<i>Morinda lucida</i>	0.663	**
<i>Milicia excelsa</i>	0.663	**
<i>Ficus exasperata</i>	0.648	**
<i>Dacryodes edulis</i>	0.583	**
<i>Psidium guajava</i>	0.469	*
<i>Castilla elastica</i>	0.444	*
URBAN and NATURAL		
<i>Dracaena arborea</i>	0.496	*
RURAL and NATURAL		
<i>Pycnanthus angolensis</i>	0.737	**
<i>Funtumia africana</i>	0.534	**

References

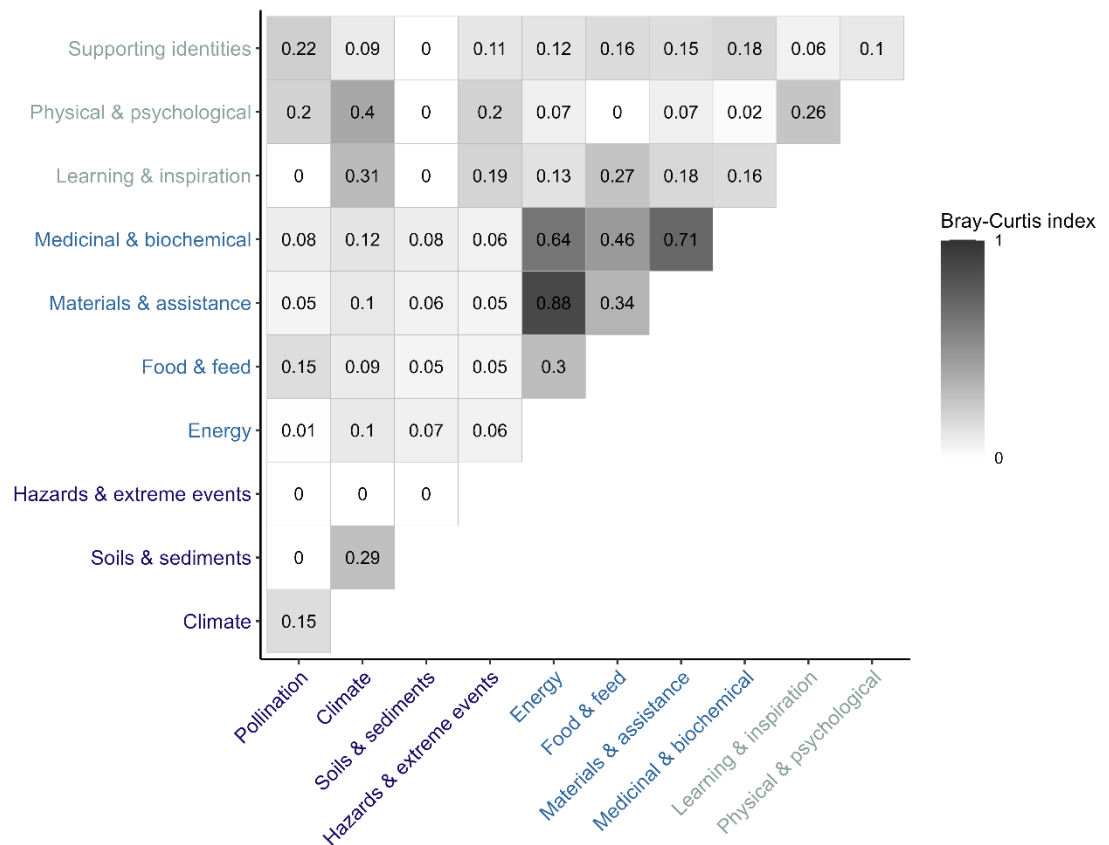
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Appendix C Supplementary material Chapter 4

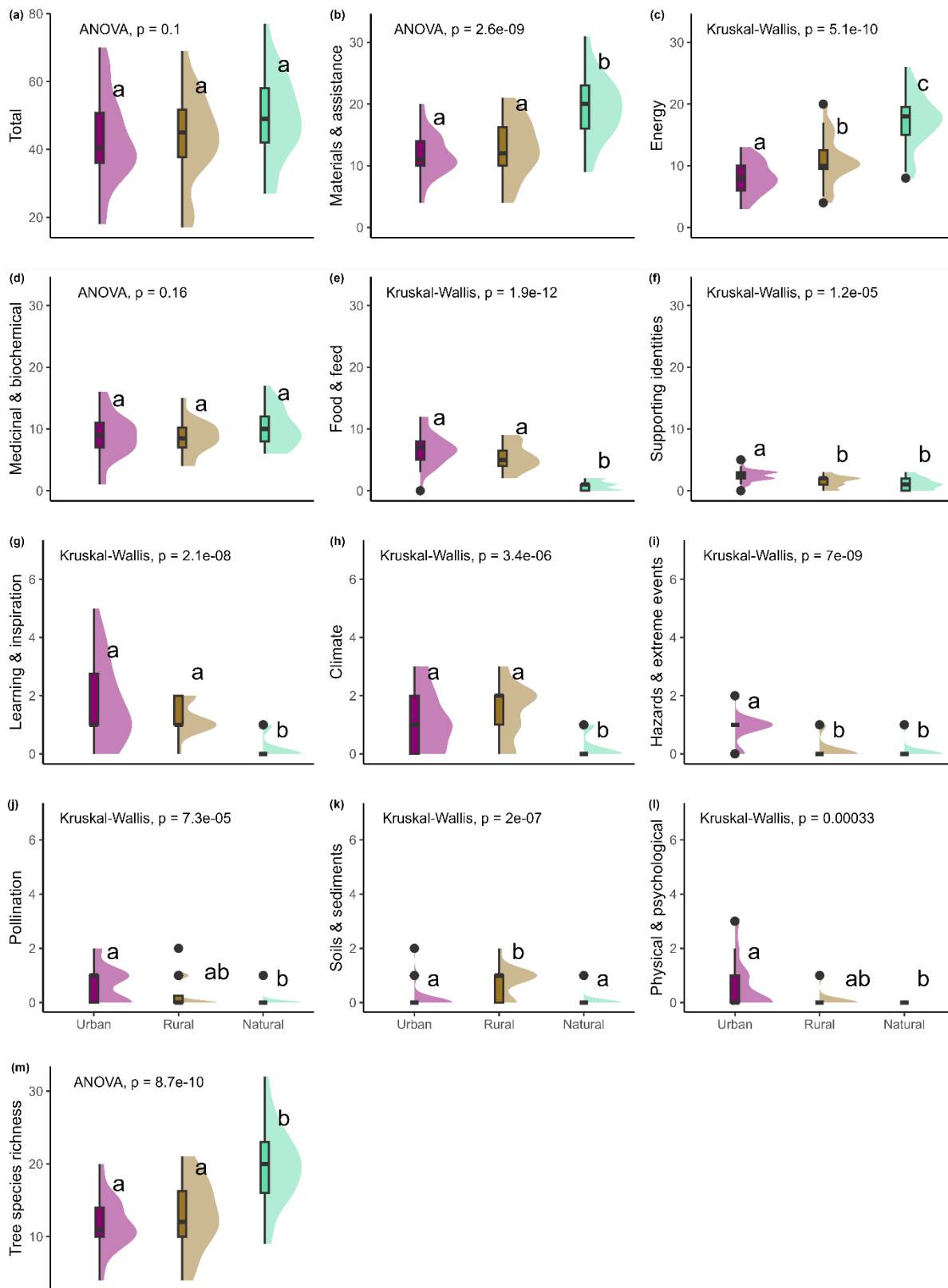
Title: Native and introduced trees are recognised for different Nature's Contributions to People across an island anthropogenic gradient



App. C.1. Number of species (left) and individuals (right) of trees recognised for supporting total contributions, broad groups, and reporting categories according to the Nature's Contribution to People conceptual framework, based on expert opinions, along 81 transects on São Tomé Island. Label colours: blue = material contributions; olive = non-material contributions; violet = regulating contributions. Note changes in the scale of the X axis.

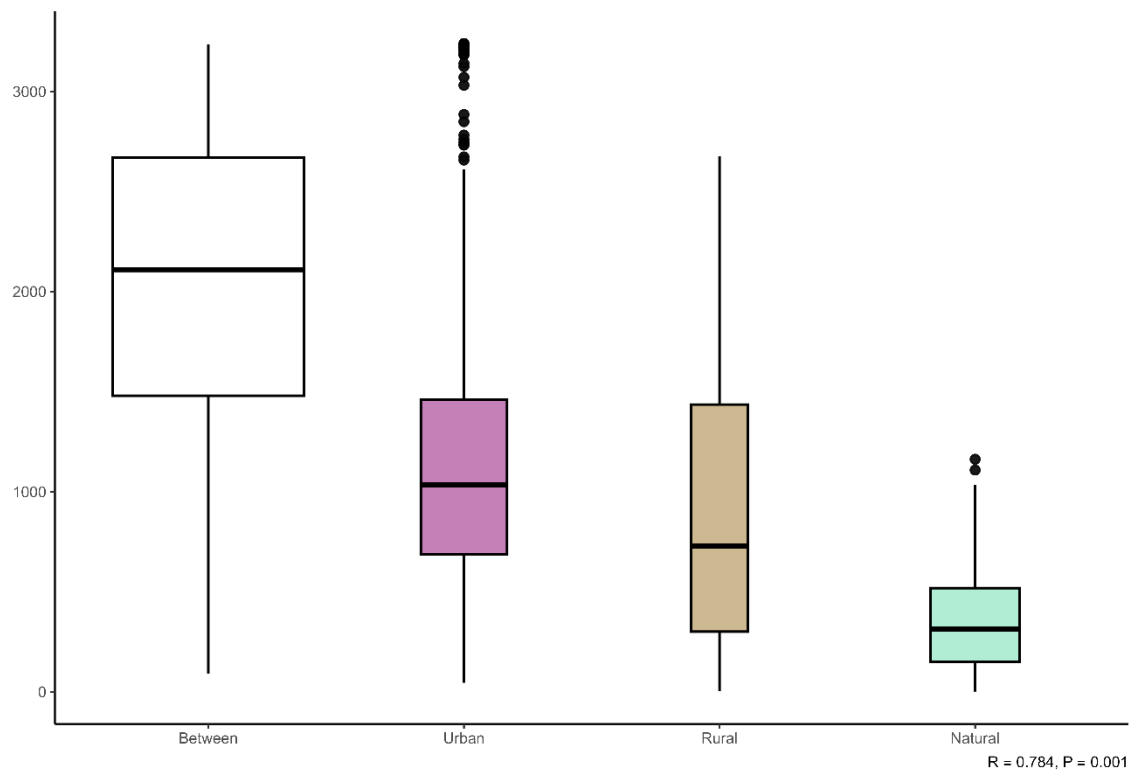


App. C.2. Inverted Bray-Curtis dissimilarities ($1 - \text{distance}$) of presence/absence of tree species identified with supporting different reporting categories of Nature's Contributions to People, with 1 equalling high similarity and 0 equalling high dissimilarity. Label colours: violet = regulating contributions; blue = material contributions; olive = non-material contributions.

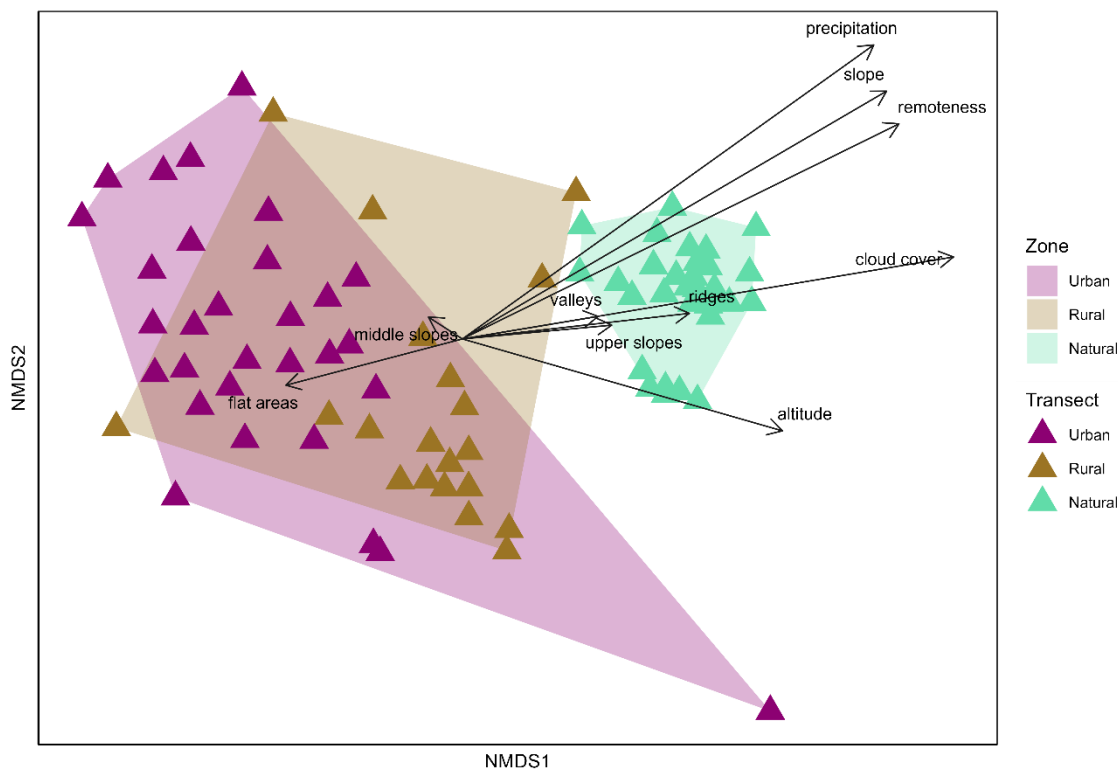


App. C.3. Violin box plots on transect level according to zones for the number of tree species identified with supporting different reporting categories of Nature's Contributions to People, (a) in total and (b-l) individually, versus (m) tree species richness. P-values ($df = 2$) of one-way ANOVA, (a) $F = 2.325$, (b) $F = 25.720$, (d) $F = 1.861$, and (m) $F = 27.590$, or Kruskal-Wallis rank sum tests, (c) $\chi^2 = 42.787$, (e) $\chi^2 =$

53.939, (f) $\chi^2 = 22.720$, (g) $\chi^2 = 35.346$, (h) $\chi^2 = 25.168$, (i) $\chi^2 = 37.556$, (j) $\chi^2 = 19.062$, (k) $\chi^2 = 30.838$, and (l) $\chi^2 = 16.021$, at the top of each graph. Significant differences from Tukey HSD or pairwise Wilcoxon rank sum tests (following Bonferroni correction) indicated by different superscript letters. Maximum violin width is scaled to 1. Graphs b-l were ordered according to total richness of each graph. Note changes in the scale of the Y axes.



App. C.4. Analysis of similarities in assemblages of trees recognised for supporting subcategories of Nature's Contributions to People based on dissimilarity ranks between zones ("Between") and within zones ("Urban", "Rural", "Natural"), with associated R- and p-value. The R-value can range between 1 (high dissimilarities between zones) and close to 0 (equal dissimilarities between and within zones).

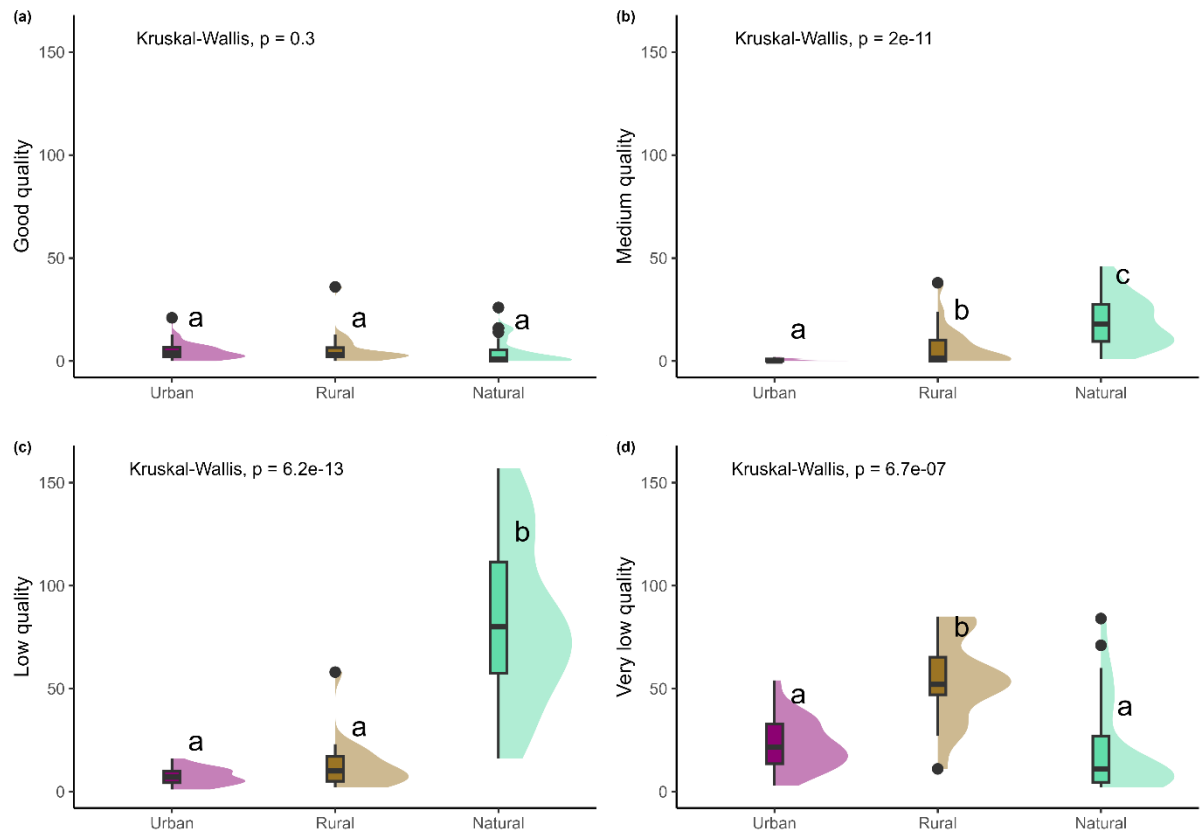


App. C.5. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities of the abundances of trees recognised for supporting 25 subcategories of Nature's Contributions to People per transect ($k = 2$, stress value = 0.125): Structural differences between 81 transects, with fitted vectors of six environmental variables ($R^2 = 0.249$ to 0.580 , $p = 0.001$); transects in each zone are united by the minimum convex polygon.

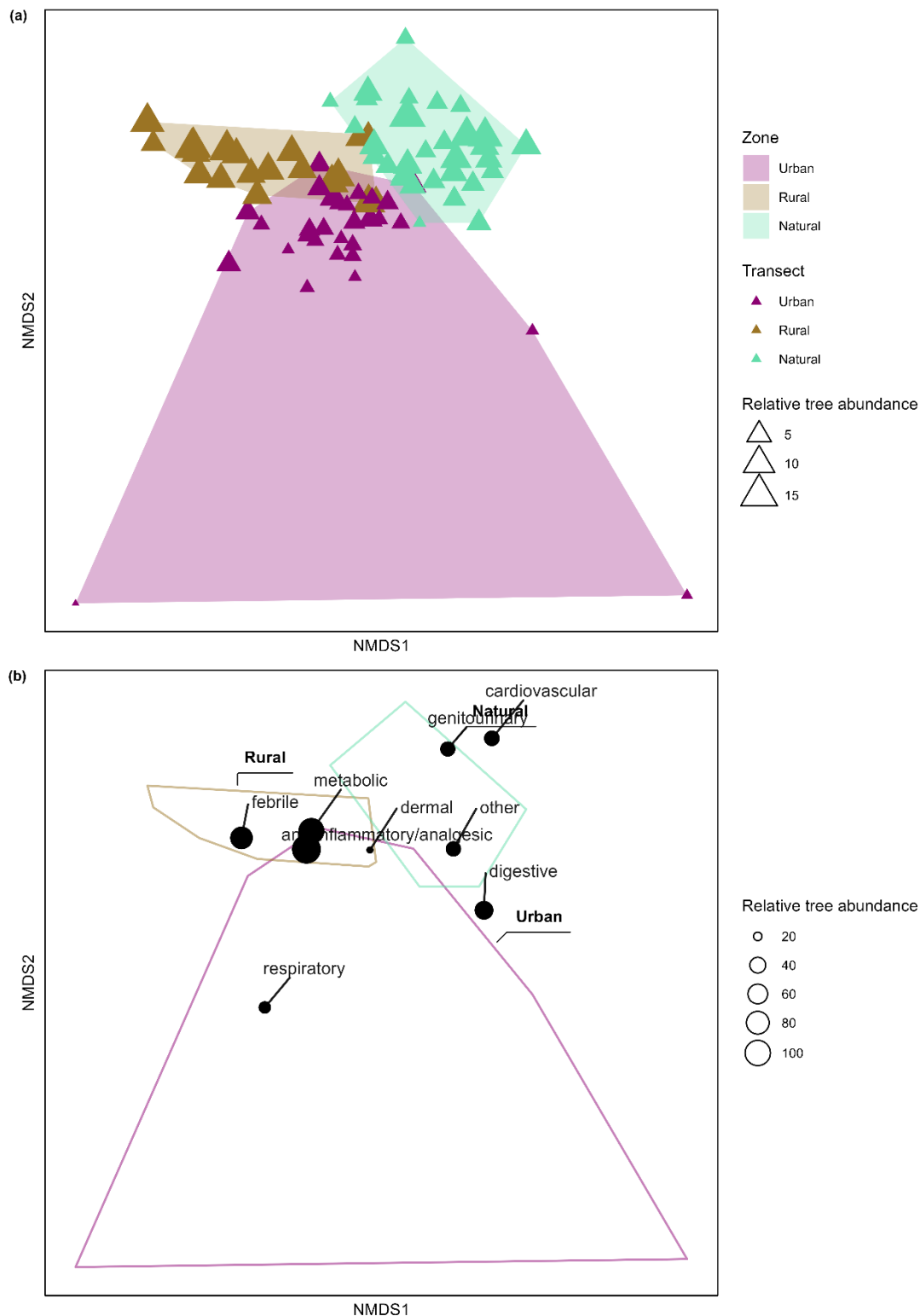
App. C.6. Significant indicator values (significance levels = *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$, ****: $p \leq 0.0001$) of subcategories of Nature's Contributions to People associated with trees for the urban, rural, and natural zone, as well as for combinations of them. The number in brackets refers to the number of tree species recognised for providing these subcategories.

Subcategory	Indicator value	Significance level
URBAN		
Social cohesion (n = 2)	0.887	**
Erosion prevention (n = 1)	0.810	**
Wood tools (n = 1)	0.750	**
Recreation (n = 5)	0.483	**
RURAL		
Manure (n = 1)	0.775	**
Soil fertility (n = 5)	0.732	**
URBAN and RURAL		
Crop food (n = 23)	0.977	**
Livestock fodder (n = 5)	0.975	**
Non-crop food (n = 17)	0.884	**
Aesthetic value (n = 17)	0.838	**

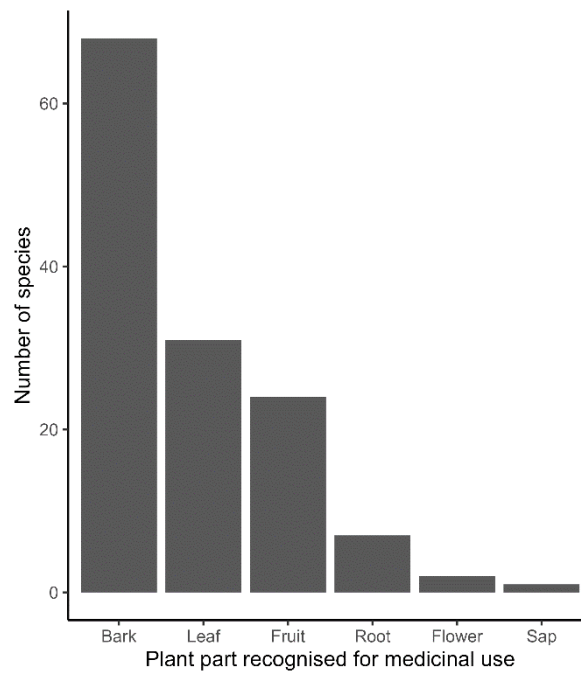
Microclimate (n = 9)	0.822	**
Ornamental products (n = 1)	0.705	**
Pollination (n = 4)	0.637	**



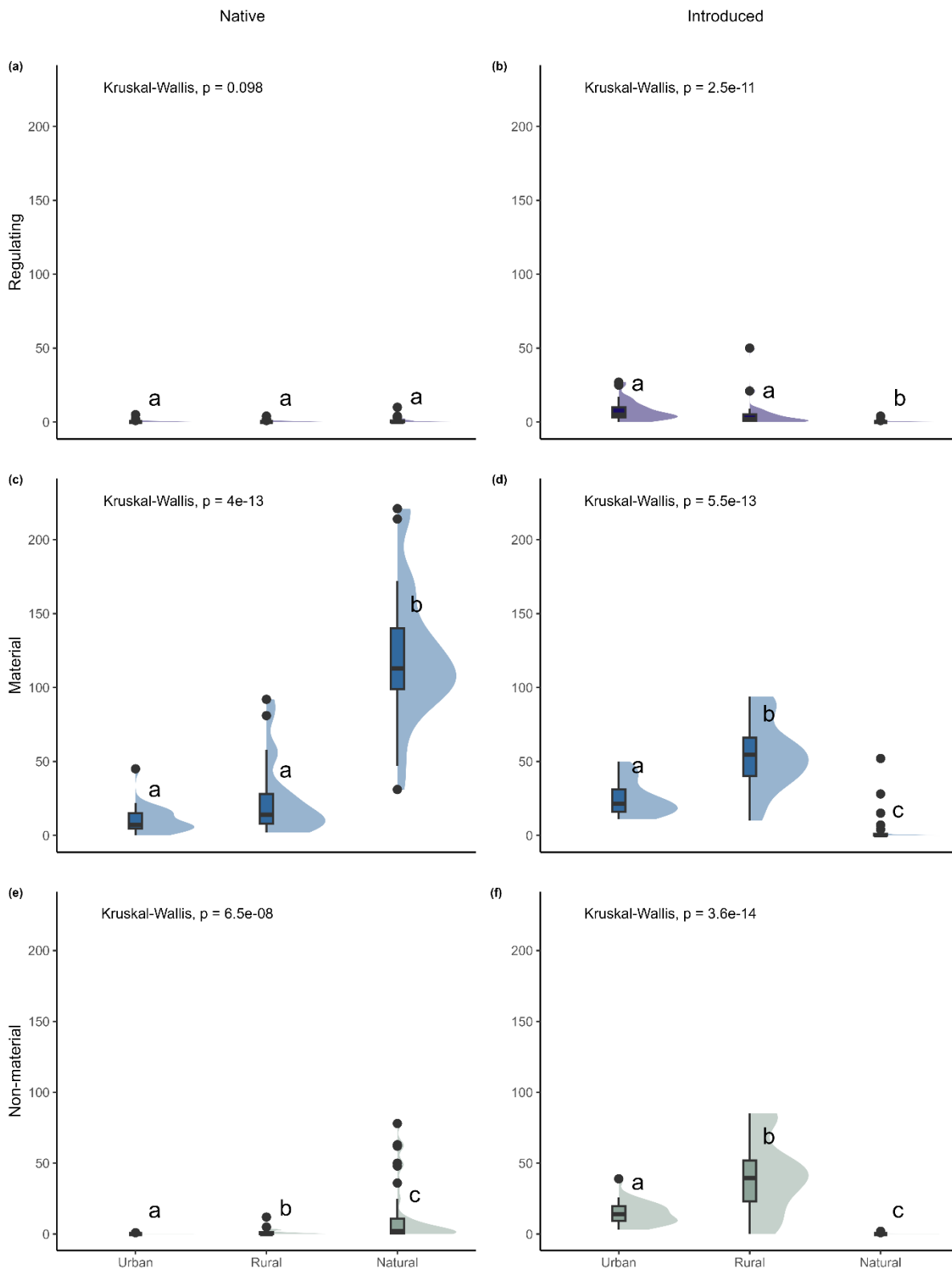
App. C.7. Violin box plots on transect level according to zones for the number of tree individuals identified with supporting four different qualities of timber (fuel wood, charcoal, building materials, wood tools, and ornamental products). P-values ($df = 2$) of Kruskal-Wallis rank sum tests, (a) $\chi^2 = 2.386$, (b) $\chi^2 = 49.306$, (c) $\chi^2 = 56.211$, and (d) $\chi^2 = 28.442$, at the top of each graph. Significant differences from pairwise Wilcoxon rank sum tests (following Bonferroni correction) indicated by different superscript letters. Maximum violin width is scaled to 1.



App. C.8. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities of the abundances of trees recognised for supporting different medicinal treatment categories per transect ($k = 2$, stress value = 0.117): (a) Structural differences between 81 transects; transects in each zone are united by the minimum convex polygon. (b) Structural differences between nine medicinal treatment categories (indicated by dots representing accumulated numbers of sample relative tree abundances from 81 transects); convex hulls connect outer transects of each zone.

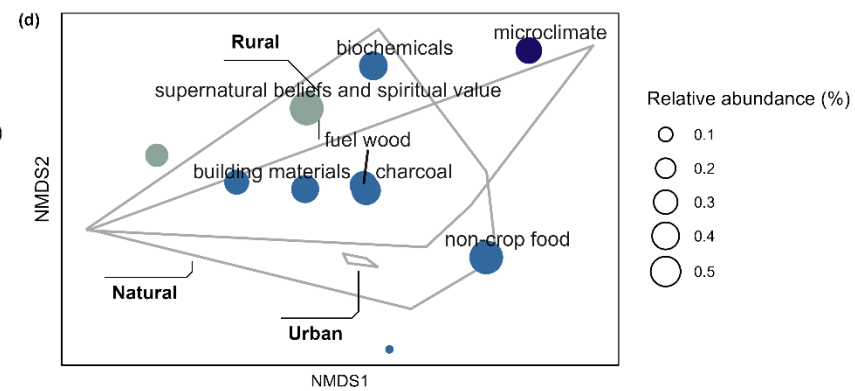
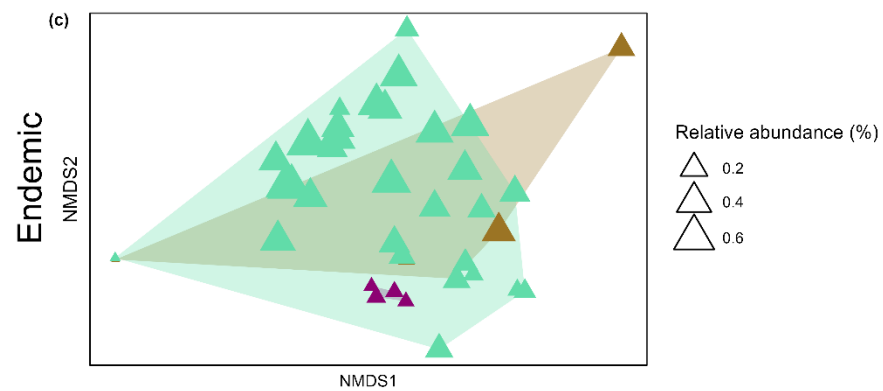
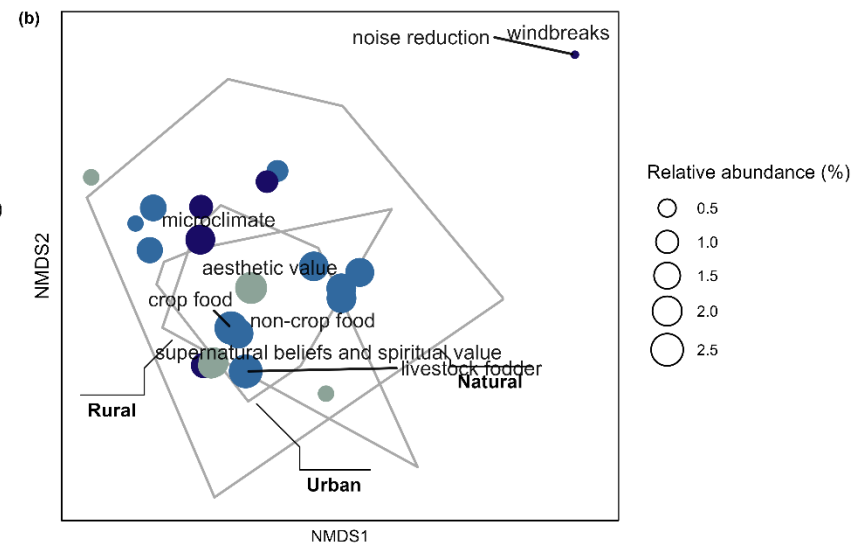
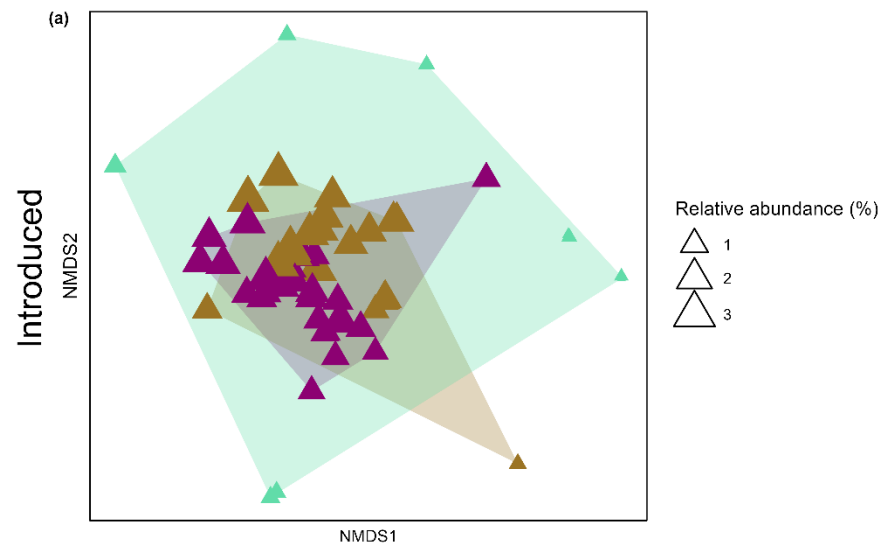


App. C.9. The number of tree species identified with underpinning medicinal purposes per plant part (for some species, more than one plant part was mentioned).



App. C.10. Violin box plots on transect level according to zones for the abundances of native (left column) vs. introduced tree species (right column) identified with supporting different broad groups of Nature's Contributions to People. P-values ($df = 2$) of Kruskal-Wallis rank sum tests, (a) $\chi^2 = 4.646$, (b) $\chi^2 = 48.788$, (c) $\chi^2 = 57.111$, (d) $\chi^2 = 56.472$, (e) $\chi^2 = 33.103$, and (f) $\chi^2 = 61.918$, at the top of each

graph. Significant differences from pairwise Wilcoxon rank sum tests (following Bonferroni correction) indicated by different superscript letters. Maximum violin width is scaled to 1.



Zone Urban Rural Natural

Transect Urban Rural Natural

Broad Group Regulating Material Non-material

App. C.11. (a) and (b) Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities of the proportional abundances of introduced tree species recognised for supporting different subcategories of Nature's Contributions to People per transect ($k = 2$, stress value = 0.144): Structural differences between (a) 60 transects (urban: 30, rural: 20, natural: 10) and (b) 24 subcategories. (c) and (d) NMDS based on Bray-Curtis dissimilarities of the proportional abundances of endemic tree species recognised for supporting different subcategories of Nature's Contributions to People per transect ($k = 2$, stress value = 0.152): Structural differences between (c) 40 transects (urban: 4, rural: 5, natural: 31) and (d) 10 subcategories. (a) and (c) Transects in each zone are united by the minimum convex polygon. (b) and (d) Convex hulls connect outer transects of each zone. The names of the six subcategories with the highest sample relative proportional abundances averaged over transects and of those in distant positions are displayed.