

Master's Thesis – Master Sustainable Development

Linking faunal seed dispersal to
tree dispersal traits and carbon storage in
southern African woodlands

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Abstract

Within climate change mitigation, forests play an important role as natural carbon pools. Human-induced defaunation, however, threatens carbon storage by putting successful seed dispersal by faunal activity at risk. Furthermore, in previous studies, the loss of large-bodied seed dispersers has been linked to a decrease of carbon storage in tropical forests. It remains unclear whether the same applies for savanna woodlands, in which a large share of carbon is stored by small number of fruit-producing tree species with large seeds, relying on large-bodied faunal seed dispersers. Savannas have largely been misunderstood as degraded forests and targeted by reforestation projects, threatening biodiversity, and affecting ecosystem processes such as fire regimes. To find synergies between climate change mitigation and biodiversity, this research aims to detangle the relationship between faunal seed dispersal, tree dispersal traits, and carbon storage in southern African woodlands. Subsequently, it investigated the effect of human disturbance on this relationship. Five new SEOSAW plots were set-up and sampled in Madagascar. Subsequently, tree inventory, carbon, and tree dispersal traits of the four southern African countries Angola, Madagascar, Mozambique, and South Africa were analyzed and compared. The analysis included a description of dispersal modes and fruit characteristics on country level and a statistical analysis including Spearman rank correlations, principal component analysis and linear regressions on species- and plot-level using community-weighted means. Results showed significant positive relationships between above-ground biomass, seed size and fruit size in tree communities. The effect of human disturbance on carbon storage and seed dispersal traits was negative. Finally, no distinct patterns between carbon storage and seed dispersal traits of faunal dispersed species on species level were found, while large gaps in trait data and dispersal mechanisms highlight the importance of further research.

Keywords: Carbon storage, above-ground biomass, wood density, faunal seed dispersal, savanna woodlands, tree traits

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Abbreviations

SEOSAW	Socio-Economic Observatory for Studying African Woodlands
FACA	Faunal Activities for Climate Action
MAS	Madagascar
ZAF	South Africa
AGO	Angola
MOZ	Mozambique
Agb	Above-ground biomass
DBH	Diameter at breast height

1. Introduction

Human-induced climate change poses risks to nature and humans and is causing adverse impacts and damages that can lead to irreversible outcomes (IPCC, 2021). Consequences of climate change include droughts, fires, rising sea levels, extreme weather events, and a decline in biodiversity (IPCC, 2021). Estimations of the rate of biodiversity loss suggest up to 1000-times background levels, with about 100 extinctions per million species-years (E/MSY) (Pimm et al., 2014). It is found that population sizes of mammals, birds, fish, reptiles, and amphibians, have dropped by an average of 69% since 1970, with the largest biodiversity losses in Latin America and the Caribbean with 94% and Africa with 66% (WWF, 2022).

The loss of biodiversity risks the alteration of ecosystem processes and ecosystem collapse. This will ultimately backfire on humans, such as through the loss of ecosystem services supporting livelihoods like the production of food, fresh water, and climate regulation (Cardinale et al., 2012). With the large threats and pressures on the environment and human livelihoods posed by climate change, actions for climate change mitigation are urgently needed.

Climate change mitigation: Carbon storage in forests

According to the IUCN, forests are one of the main solutions in climate change mitigation, highlighting the potential for restoration of degraded forests across the world to address the effects of climate change (IUCN, 2021). Climate change mitigation focuses on reducing climate change through lowering the amount of greenhouse gasses released into the atmosphere (e.g. carbon dioxide) and on increasing the uptake of such gasses by sinks like forests, oceans, and soil (Fawzy et al., 2020). Plants turn carbon dioxide into energy and sugar using light and water through photosynthesis (Eberhard et al., 2008). This process of taking up atmospheric carbon and storing it for longer periods of time makes ecosystems such as forests function as natural carbon pools (Lal, 2007).

Problem definition: Reforestation of savannas

Based on the role of forests in carbon sequestration and storage, tree-for-carbon projects are an important part of the work of climate change mitigation programs. One focus of climate mitigation is reforestation and afforestation in Africa (Bond et al., 2019; Parr et al., 2014). For instance, in the context of the Bonn challenge, which is a global goal to restore 350 million

hectares of degraded and deforested landscapes by 2030, 31 out of the 74 global pledges aim to restore African landscapes (IUCN, 2020).

Although reforestation plays an important role in climate change mitigation, the reforestation projects planned in Africa can become a threat to African ecosystems. A significant share of forestation projects is planned in ecosystems that are dominated by savanna, because those ecosystems are mistaken for degraded forests (Bond et al., 2019; Veldman et al., 2015). The areas selected for forestation are based on global deforestation and degradation maps, which assume that in climates that can support forests, areas with low tree cover, such as savanna ecosystems, are deforested and degraded (Bond et al., 2019). *Savannas*, however, are defined as an ecosystem with continuous grass cover that is occasionally interrupted by woody trees and shrubs (Scholes & Archer, 1997). The tree density in savannas can range from 5 – 10% in open savanna towards 80% in closed savanna woodlands depending on the savanna type (Scholes & Archer, 1997). Recent work by Solofondranohatra et al. (2018), suggested that for example Malagasy woodlands dominated by the endemic tree species *Uapaca bojeri* are likely to be native savanna ecosystems rather than degraded forests.

About 60% of the African continent is covered by savanna ecosystems (Foxcroft et al., 2010). As a result of the frequently made incorrect assumption that savannas are degraded forests, a large majority of biomes targeted for reforestation in Africa are grassy biomes. Afforesting savanna ecosystems can introduce severe threats to biodiversity associated with savannas and livelihood services that are provided by those ecosystems (Bond et al., 2019; Veldman et al., 2015). Grassy biomes such as African savannas are habitat to many fauna species that do not occur in forests, including many species of (large) mammals, as well as birds and reptile species. For this reason, savanna forestation programs are a concern for biodiversity conservation (Bond et al., 2019).

In the past, African woodlands have been described as a battleground between climate change and biodiversity conservation goals, because those goals are often played against each other (Andela et al., 2017). Instead, a focus on synergies which promote climate goals and biodiversity goals simultaneously should be the focus. Several researchers have argued that fully functioning grassy biomes are more efficient in carbon storage than if those biomes would be forested as part of an afforestation program, for example due to the high vulnerability of afforested plantations to fires (Bond et al., 2019; Dass et al., 2018). Instead of reforesting grassy biomes, restoration and conservation efforts can also benefit climate change goals by maximizing the carbon storage capacity of those ecosystems (Dass et al., 2018).

The link between faunal diversity and carbon storage in savannas

In savanna ecosystems, a small number of large trees is responsible for the largest share of above-ground carbon that is stored (Amara et al., 2019; McNicol et al., 2018). Of this small group of tree species many produce fruits which are consumed by large fauna such as birds, bats, and primates who eventually disperse the seeds (*endozoochory*) (Namah et al., 2019).

Many animal seed disperser species that play a role in tree dispersal strategies are threatened due to hunting, illegal trade, and habitat loss (Bello et al., 2015). Changes in plant-animal interactions due to the loss of large seed dispersers affects the ecosystem functioning and can be linked to a decrease of carbon storage in many tropical forests (Albert-Davinaud et al., 2018; Bello et al., 2015; Kurten et al., 2015; Osuri et al., 2016; Peres et al., 2016). Although studied for tropical forests, this strong connection between carbon storage and faunal diversity is largely unstudied for savanna ecosystems. Previous research of savanna ecosystems include the role of vertebrates for the seed dispersal of individual tree species, such as the sausage tree (*Kigelia Africana*) and the marula tree (*Sclerocarya birrea*), which both share a relatively high wood densities (about 0.6 g/cm³). For most of the species however, the role of vertebrates in seed dispersal is still unknown (Midgley et al., 2012; Namah et al., 2019). Understanding the connection between faunal diversity and carbon storage is of fundamental importance for restoring full functionality of savanna ecosystems and ensuring ecosystem services continue to contribute to local livelihoods and carbon storage. Thus, instead of merely focusing on above-ground carbon storage in the form of afforestation, this research aims to contribute to filling the knowledge gap of the intertwined relationship between faunal seed dispersal, carbon storage and tree dispersal traits in savanna woodlands.

Human disturbance

Human disturbance has led to a decrease in functioning ecosystems worldwide, for instance through biodiversity loss and increased ecosystem vulnerability (Hannah et al., 1994; MacDougall et al., 2013). Increased vulnerability can make ecosystems more prone to species invasions, which can have direct and indirect negative effects (Levine et al., 2003; Rajaonarivelo et al., 2022). Species invasions can directly influence plant communities through competition and exclusion of native species, and indirectly through alteration of ecosystem processes such as fire regimes (Levine et al., 2003). In addition to biodiversity loss and ecosystem vulnerability, anthropogenic pressures threaten seed dispersers, affecting ecosystem functioning and carbon storage (Bello et al., 2015). Those threats of human

disturbance to ecosystems lead to the overall objective of this research to investigate the effect of human disturbance on the relationship between tree dispersal traits, faunal seed dispersal and carbon storage.

Savannas and open-canopy woodlands face large pressures from anthropogenic activities such as human-induced environmental change (Parr et al., 2014, Veldman et al., 2015). For African savannas, four anthropogenic drivers that are causing rapid vegetation changes were identified by Osborne et al., (2018) in the form of land clearance, altered human disturbance (affecting fire regimes and herbivory) climate change, and rising of atmospheric carbon dioxide. In a study comparing the disturbance effect of humans and elephants on savanna woodlands in Zambia, Tripathi et al. (2019) have shown that the replacement of elephants by humans as dominant disturbance agents is leading to changes in woodland structure, sustainability, and ecosystem functioning.

Tapia woodlands in Madagascar

Madagascar is an island state off the Eastern shore of Africa. It is the fourth largest island in the world and a biodiversity hotspot with high biodiversity and endemism, meaning that many species only exist in Madagascar and nowhere else (Mittermeier et al., 1998; Whitehurst et al., 2009; Wright, 1999). At the same time, many species are critically endangered and the share of primary vegetation remaining is very low, which makes Madagascar a high conservation priority (Myers et al., 2000).

example of endemic tree species in Madagascar is *Upaca bojeri* (called tapia), which is the dominant species within tapia woodlands and associated to many other species such as edible mushrooms, mycorrhizal fungi, and the silk moth *Borocera madagascariensis* (Andriamanohera et al., 2020). *Upaca* populations currently face limitations and constraints of *recruitment*, which is the number of saplings that reach a specific height or diameter at breast height (DBH) in a given time (Lexerød, 2005). Reasons for the recruitment difficulties of *Upaca* populations remain poorly understood. As tapia woodlands are endemic to Madagascar, monitoring and conservation of these ecosystems is of high importance. One aim of this research is to add Madagascar to the southern African vegetation-monitoring network SEOSAW (Socio-Economic Observatory for Studying African Woodlands, Box 1) for future vegetation monitoring and research projects. Therefore, one part of this research focuses on setting up and sampling the first five SEOSAW plots in Madagascar.

Societal relevance of research

Studies found that ecosystem services provided by woodlands in Southern Africa contribute to the livelihood of more than 100 million people living in rural areas and play an important role in poverty mitigation (Ryan et al., 2016). Important ecosystem services of savannas include not only carbon storage and nutrient cycling, but also providing rural households with wood used for purposes such as fire and construction, charcoal, food, and medicine (Deweese et al., 2010; Ryan et al., 2016). In the case of tapia woodlands in Madagascar for instance, the silk moth associated to *Uapaca bojeri* plays a key role in the local silk production. Not only is the silk of cultural importance because it is used to make burial shrouds, but it is also important for local economies as it is used to produce clothes for locals and to be sold to tourists (Kull, 2002). Fully functional savanna woodlands are therefore of great importance for the livelihood of large parts of the local population of Southern Africa.

1.1 Research aim & research question

The aim of this study is to assess the relationship between faunal seed dispersal, tree dispersal traits (e.g. seed size), and carbon storage in southern African woodlands. Such knowledge can be used for the conservation and restoration of faunal diversity and thereby help to promote seed dispersal and pollination of tree species essential for ecosystem services. For this I used tree inventory data from 4 countries in the SEOSAW network: Angola, Madagascar, Mozambique, and South Africa. Additionally, as part of a team of local researchers, I conducted fieldwork in Madagascar with the aim to add the island country to the SEOSAW network and to collect tree inventory data in Malagasy savanna woodlands for further projects and vegetation monitoring.

My thesis is constructed in two parts. The first part focuses on the addition of Madagascar to the SEOSAW network through the set-up of the first SEOSAW plots in the country and sampling of the tree inventory. The analysis of this part solely dives into Madagascar plot data. The second part investigates tree trait data and compares Madagascar data with data from Angola, Mozambique, and South Africa on country-level. For the analysis I used plot-based tree inventory data along a human disturbance gradient, country-scale biodiversity data, and tree dispersal trait data. This research is part of a bigger collaborative effort of an international team of researchers based in Sweden, The Netherlands, Madagascar, Angola, Mozambique, South Africa, and the United Kingdom (see Box 1 in Chapter 2.2.1). Parts of the data used for this research have therefore already been collected during previous

work and are provided by the FACA research team, such as tree trait data and community tree data from Mozambique, Angola and South Africa.

My main research question was “*What is the relationship between faunal seed dispersal, tree dispersal traits and carbon storage in southern African woodlands and how is this affected by human disturbance?*” To answer the main research question, five sub-questions were formulated:

Part 1: Madagascar tree inventory

SQ1 - What are the seed dispersal modes and fruit characteristics of tree species in Madagascar?

SQ2 - What is the above ground biomass in the plots set up in Madagascar and how does it relate to human disturbance?

Part 2: Comparison of southern African woodlands

SQ3 - What are the seed dispersal modes and fruit characteristics of tree species in the four countries?

SQ4 - What is the relationship between tree dispersal traits and wood density in southern African woodlands?

SQ5 - What is the relationship between tree dispersal traits, above ground biomass and human disturbance?

In the following, a brief overview of the underlying theory and the relevant concepts is given, followed by a method section outlining the planned research activities including field work and statistical analyses. Then, following the division of the research, results and discussion chapters are both divided into a first part diving into the Madagascar data (SQ1 & SQ2), followed by a second part focusing on the country-scale analysis (SQ3-5). In the last step, combined conclusions are drawn from both chapters.

1.2 Theory

The main concepts and theory that I will discuss below are wood density and above ground biomass related to carbon storage, tree dispersal traits, and seed dispersal. After introducing the defaunation theory by Bello et al. (2015) upon which my research is based, I will present my main hypotheses.

Carbon storage in forests

Forests are important carbon sinks because trees can accumulate carbon as they grow over time, referred to as *carbon storage* (McPherson, 1998). Linked to carbon storage are two closely related carbon traits *above ground biomass* (agb), and *wood density*. Agb is the living vegetation above the soil and is related to wood density, which is the carbon storage per unit volume of stem that varies with species (Chave et al., 2009). Previous studies in Amazonian plots have shown that wood density accounts for a large a large share of agb (and therefore carbon content). This highlights the importance of wood density to accurately calculate agb (Baker et al., 2004; Chave et al., 2009).

Tree dispersal traits and seed dispersal

In general, plants show specific *plant traits*, which are defined as a set of characteristics that “determine how plants respond to environmental factors, affect other trophic levels, and influence ecosystem properties and their benefits and detriments to people” (Kattge et al., 2020, p.1). For instance, trees express *tree dispersal traits*, such as seed mass and seed size, which influence seed dispersal and their respective seed dispersal strategy. (Tuthill et al., 2023). *Tree dispersal* is the horizontal movement of seeds away from their parent plants by different mechanisms, such as abiotic dispersal by wind or faunal dispersal by animals (*zoochory*). Different types of zoochory include the dispersal outside of animals (*epizoochory*), and inside of animals after ingestion (*endozoochory*) (Iluz, 2010).

Broad suits of fruit or seed characteristics are documented as *dispersal syndromes*, which reflect on agents most likely to disperse those seeds (Howe, 2016; Van der Pijl, 1982). When seeds are dispersed by animals, the seed dispersal syndrome is a reflection of the adaptation of a species to its primary seed disperser (Albert-Daviaud et al. 2018).

Defaunation theory by Bello et al. (2015)

Defaunation is a human induced process defined as the “decline in abundance and occurrence of animals in a community”, and disproportionately affects large-bodied species (Galetti & Dirzo, 2013; Kurten, 2013, p. 24). Defaunation diminishes key ecosystem services and functions such as effects on nutrient cycling, pollination, and seed dispersal (Dirzo et al., 2014; Kurten, 2013).

Local or functional extinctions of large-bodied seed dispersers through defaunation can largely affect composition and population dynamics, which has been shown in tropical forest ecosystems by Bello et al. (2015). The research has focused on the disappearance of large-bodied frugivores, which have unique ecological roles like fruit removal and dispersal of large-seeded plants (Bello et al., 2015; Galetti et al., 2013; Nuñez-Iturri et al., 2007; Poulsen et al., 2013; Terborgh et al., 2008). The successful seed dispersal of large-seeded plants is limited by the seed size, because the dispersal is restricted to dispersers that can ingest whole fruits and seeds of that size (Galetti et al., 2013). If such large-bodied dispersers are lost, they cannot be replaced by smaller species as the tree species continue to express the original dispersal syndromes, and smaller species cannot ingest their fruits and seeds (Albert-Daviaud et al., 2018). One example of the effect of defaunation on seed dispersal is the dispersal species *Archaeoindris fontoynontii*. This species of endemic lemur in Madagascar is thought to have been one of the largest primates that ever evolved. After their extinction, this group of large-bodied seed dispersers could not be replaced by smaller lemur species due to their exceptional size (Jungers et al., 2008).

Bello et al. (2015) based their work on the theory that the defaunation of large frugivores leads to the extinction of large-seeded tree species. Subsequently, the loss of large frugivores affects the carbon storage capacity of tropical forests because carbon storage capacity of tree species is positively related to tree traits like wood density and tree height, and large hardwood tree species tend to produce large fruits and seeds that require large-bodied dispersers (Figure 1) (Chave et al., 2005; Diaz et al., 2004; Thompson & Rabinowitz, 1989; Wright et al., 2007). The evidence of current research showing the dependence of tropical forests on large frugivores for seed dispersal and the decrease of carbon storage capacity in tropical forests as a result raises the question whether the relationship between seed dispersal, plant traits and carbon storage might be similar in ecosystems like savanna woodlands.

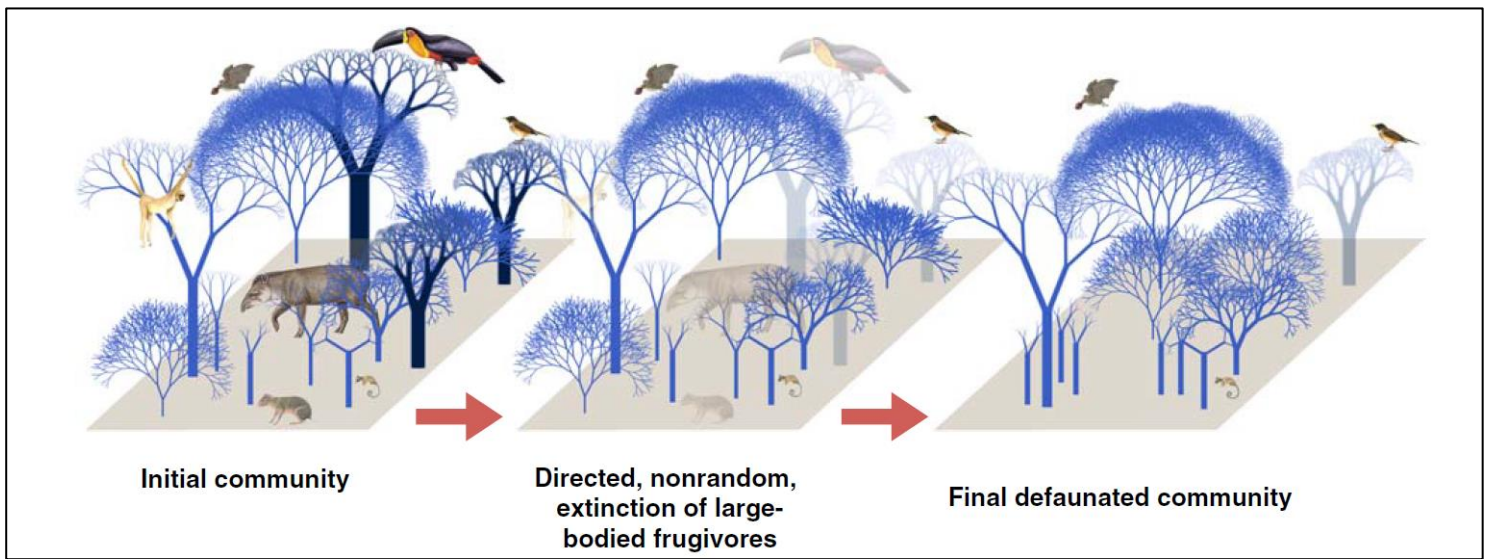


Figure 1. Simulation pathway of frugivore defaunation on carbon storage. Dark blue representing tree individuals of hard-wood species with seeds sized ≥ 12.0 mm. Light blue representing other tree species. The illustration shows the simulation of the extinction of large-seeded species resulting from defaunation of large-bodied frugivores, followed by the replacement by other tree species remaining in the tree community (Figure from Bello et al., 2015).

1.3 Hypotheses

Based on the scientific background and the defaunation theory by Bello et al. (2015), I hypothesized a positive relationship between wood density and tree dispersal traits such as seed size and seed mass in the analysis of SQ2. In addition, I expected a negative effect of human disturbance on agb in Malagasy plots for SQ1, as well as a negative effect on the agb of tree communities and the mean seed size and seed mass on country level for SQ5.

2. Methods

The research approach visualizes how the five sub-questions relate to the introduced concepts and levels of analysis (Figure 2). Sub-questions 1 and 3 are analyzed on country-level, looking into the seed dispersal modes and fruit characteristics of trees in Madagascar (SQ1), and comparing those to trees in Angola, South Africa, and Mozambique (SQ3). On species-level, the relationship between wood density and tree dispersal traits is analyzed for all tree species found in the plots in all four countries (SQ4). Finally, the relationship between tree dispersal traits and agb in a selection of plots in Madagascar, Angola, and South Africa is investigated, as well as the effect of human disturbance on this relationship (SQ2 & SQ5).

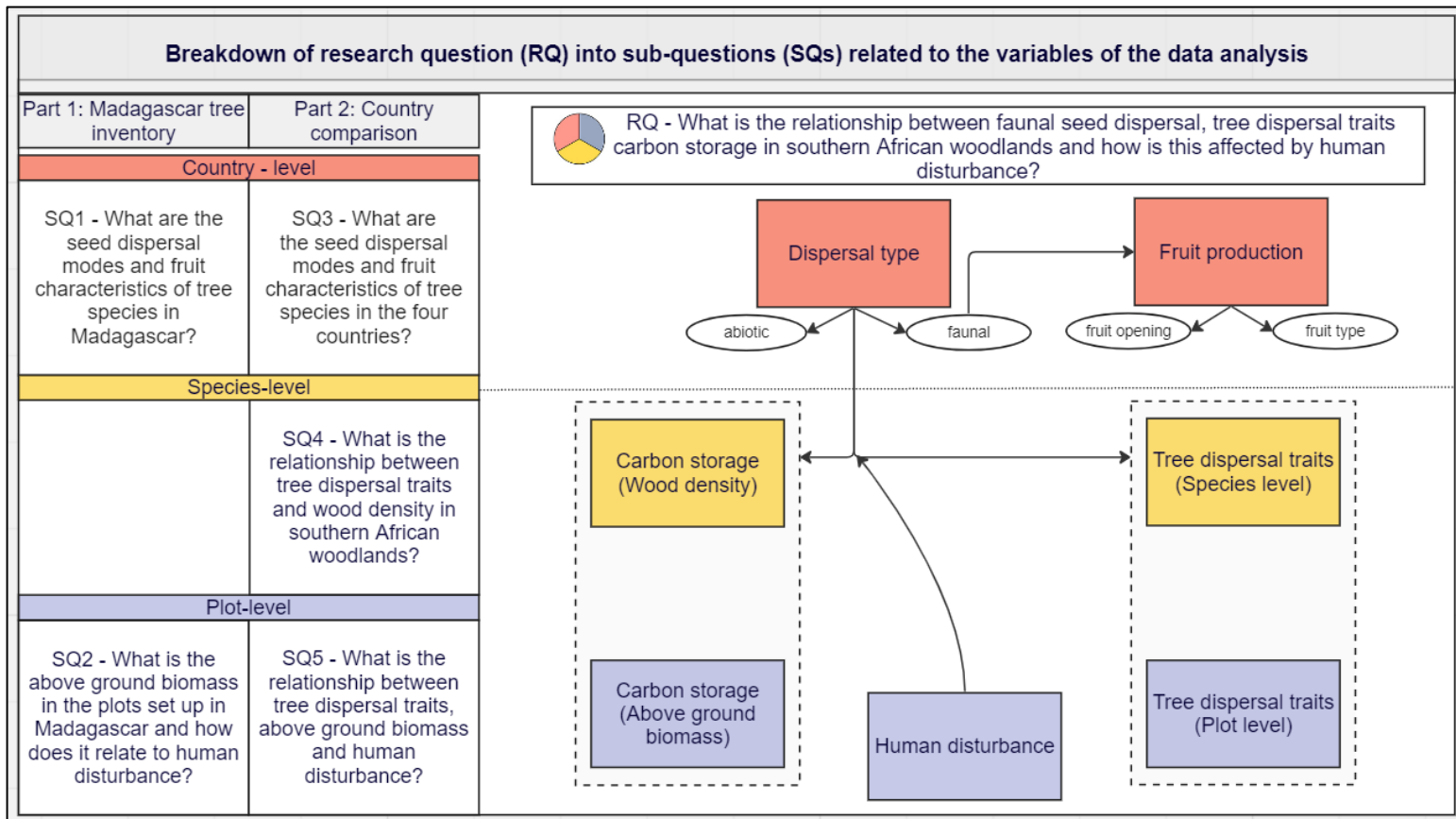


Figure 2. Research framework breaking down the research question (RQ) into five sub-questions (SQs) allocated to two parts (left) and relating them to the variables that are included in the data analysis. The colors indicate the level of the analysis, with SQ1 and SQ3 (red) being at the country level, SQ4 (yellow) being at the species level, and SQ2 and SQ5 (blue) being at the plot level.

2.1 Types of data

The thesis research is based on quantitative research methods and uses tree trait, tree inventory and seed dispersal data of four countries (Figures 2 & 3). Community tree data for Madagascar was collected through plot-based sampling in the field as part of this research. Community tree data of the other countries, tree trait data and dispersal data used was based on previous work of the FACA research team, work of C. Schröcker (Schröcker, 20xx, unpublished), publications of Kindermann et al. (2022), Vargas et al. (2023), and Lososova et al. (2023). Furthermore, the databases African Wood Density Database (World Agroforestry Centre, 2012), Global Wood Density Database (Zanne et al., 2009), TRY database (TBA), Seed Information Database (ER, INSR, RBGK, 2023), and open-source information of the South African National Biodiversity Institute were used when gathering wood density and seed dispersal data. The wood density data of *Uapaca bojeri*, *Pinus kinesiya* and *Eucalyptus robusta* were determined after wood core sampling in the field in Madagascar. In Angola, Mozambique, and South Africa, plots were sampled per country by researchers of the SEOSAW team (Box 1). The process steps of the methodology include data collection, data manipulation and imputation, and data analysis (figure 3) and will be discussed in the following parts of the chapter.

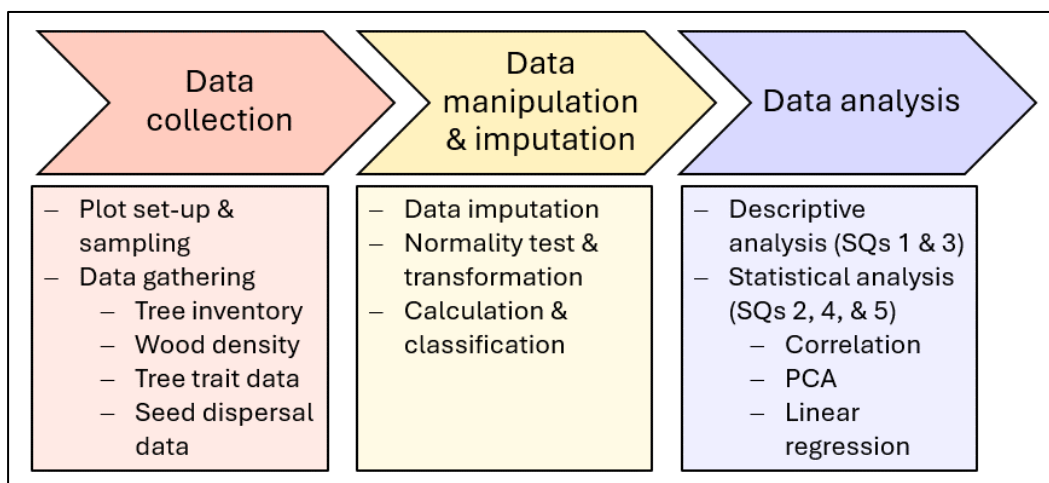


Figure 3. Three-step research process with 1) data collection, 2) data manipulation & imputation, and 3) data analysis, including a descriptive (SQ1 & 3) and statistical analysis (SQ2, 4 & 5).

2.2 Data collection

2.2.1 Plot set up and sampling in Madagascar

During four weeks of fieldwork, in collaboration with local master's student T. Nandrasanjafy and local guides we set up five new permanent plots in Madagascar and sampled tree inventory data. The field work was supervised by Dr. S. Holmes from Sveriges lantsbruksuniversitet and Dr. S. Andriantsaralaza from Université d'Antananarivo-Département de Biologie et Ecologie Végétale, both part of the FACA project (Box 1). The plot establishment and data sampling followed standard SEOSAW sampling protocols to ensure reliability and compatibility with other sampling sites in southern Africa and globally (SEOSAW partnership, 2021). Each plot was a 100 x 100m square of the size of 1ha with varying slopes. The plots were set up following a gradient of human disturbance, defined by the distance of the southwest corner to the main road RN1 (see Table 3 in section 3.1). The location of the plots can be found on the map (Figure 4), plot photos can be found in figure 6.

Box 1. The FACA project

This research is part of the research project “Faunal Activities of Climate Action: A southern Africa network to find synergies between biodiversity and carbon storage in woodlands” (FACA). As stated in the FACA funding proposal, the project is based on a newly developed partnership between scientists from Africa and Europe, aiming to investigate the hypothesis that the restoration of animal diversity will promote successful dispersal and pollination of a broad tree diversity, essential for ecosystem services such as carbon storage. The partnership expands the southern African vegetation-monitoring network SEOSAW (Socio-Ecological Observatory for Studying African Woodlands) by using passive acoustic sensors for animal diversity monitoring and adding Madagascar to the SEOSAW network. Further analyses of the FACA research project will include plot-based audio data on faunal activity and aim to involve all southern African countries that are currently included in SEOSAW in the future (Holmes et al., 2021).

To set up a new plot, we first determined the corners. We recorded the coordinates using a handheld GPS unit and measured the slope in all four corners and the middle of the plot, using a clinometer. The corners were marked with cement and rebar (Figure 7). Pink string was used to string the plot at the 20m, 40m, 60m, and 80m mark and white string was used to string along the 0m and the 100m mark (Figure 5). All stems of all trees with more than 50% of the base inside the plot and with a diameter above the minimum diameter of 5cm at the point of measurement (DBH – diameter at breast height) were identified, tagged, and the height and diameter measured and recorded, following the SEOSAW protocol (SEOSAW partnership, 2021).



Figure 4. Map of the locations of the five newly set-up SEOSAW plots (called MAS01 to MAS05, further referred to as plot 1 - 5) set up in the Malagasy highlands, as well as road RN1, which was used to measure the distance to the southwest corner of each plot, functioning as indicator of human disturbance

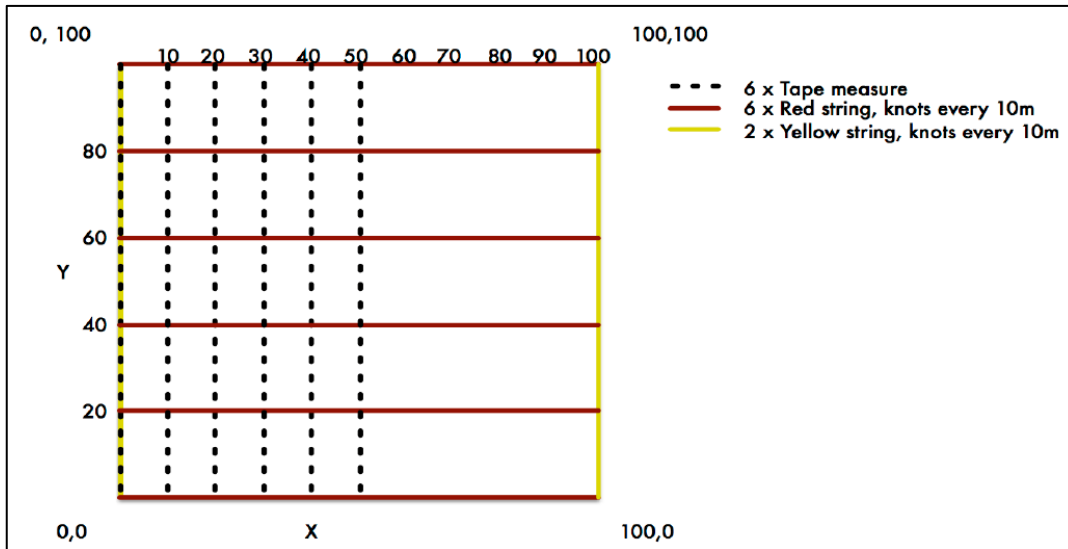


Figure 5. Layout for stringing a plot to assist with stem mapping as suggested in SEOSAW protocol (SEOSAW partnership, 2021). In the fieldwork, white and pink string were used.

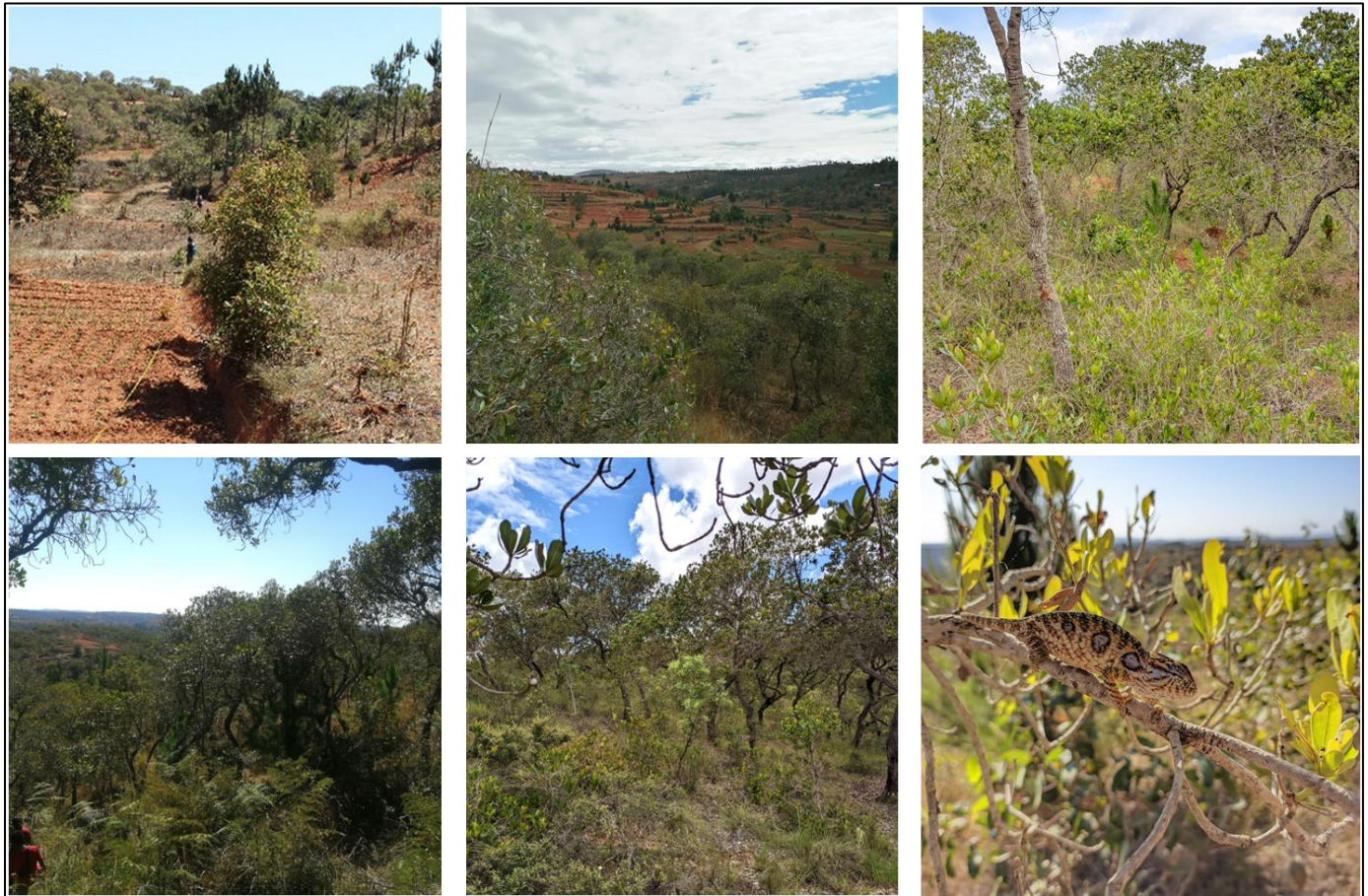


Figure 6. SEOSAW plots set up in Madagascar. From upper left to bottom right, plots 1 to 5, and a *Uapaca bojeri* tree with a chameleon on one of its branches. Photos taken by T. Nandrasanjafy, Dr. S. Holmes, and me. September and October 2023.

The data collection in the SEOSAW forms was done using the KoboToolBox smartphone application as well as a backup version on paper. In addition, to collect additional data on the smaller stems, the ground layer as well as the coarse woody debris, the SEOSAW protocols for coarse woody debris, small stems and ground layer biomass were followed (SEOSAW partnership, 2021).

For three out of the four identified tree species we collected wood cores from 5 individuals each. The collected wood cores were used to determine the wood density of *Uapaca bojeri*, *Pinus kesiya*, and *Eucalyptus robusta*. Wood cores of the fourth identified species *Syzygium cumini* could not be sampled because the stem diameter of the present individuals was below the needed threshold of 10 cm.



Figure 7. Photos of plot sampling, rebar mark of plot corners, and the fieldwork team. Photos taken by T. Nandrasanjy, Dr. S. Holmes, and me. September and October 2023.

2.2.2 Data gathering for country comparison of southern African woodlands

2.2.2.1 Country-level tree data

Tree species from Angola, Mozambique and South Africa were retrieved from raw SEOSAW data. Additionally, data from plots in South Africa that were not yet included in the SEOSAW database were provided by D. Tye. Tree species from Madagascar were added after the fieldwork.

2.2.2.2 Wood density

Species present in the SEOSAW plots were matched with wood density databases Global Wood Density Database (GWDD) and African Wood Density Database (AWDD). Furthermore, unpublished data on wood density for South Africa from the MSc thesis of C. Schröcker, provided by Dr. M. te Beest (Schröcker, 20xx) was included, as well as open-source data from Kindermann et al. (2022) and unpublished data from the tree traits database provided by N. Stevens, C. Lehmann & R. Maritz. Species that were not found in wood density databases were checked for synonyms and typos on the websites of Global Biodiversity Information Facility (GBIF), World Flora Online (WFO), and Plants of the World Online. Typos were corrected, species that were not found were removed, and synonyms were either kept if the accepted name was not on the list, or they were replaced with the accepted name to avoid double counting. Species only identified to genus level were left out, as well as species that were not trees (Supplementary data).

The GWDD included data from Africa as well as other continents. If several values were listed for a species, the average was calculated, using only the values from Africa. If no data from Africa was available, data from other continents was used. For some species entries in the AWDD, a wood density range was given instead of a single value. For those tree species, the midrange was calculated. If there were several entries for a tree species in the AWDD, the average of the range of the newest entry was used. In the case of *Eucalyptus robusta*, two entries were found in the AWDD. One entry included one newer source, the other entry included both an older source and the newer source. In this case, the entry with both sources was used. If a species was present in more than one data base, the average wood density was calculated. Furthermore, wood cores of three tree species (*Uapaca bojeri*, *Pinus kesiya* and *Eucalyptus robusta*) were sampled during fieldwork in Madagascar and the wood density determined by T. Nandrasanjafy. For those species, the average of the sampled wood density was used for the analysis. The full table of wood density per species can be found in the supplementary data.

2.2.2.3 Species-level dispersal trait data

The tree species on the species list were matched with a tree traits database kindly provided by N. Stevens, C. Lehmann & R. Maritz. An overview of the tree trait selection included in the analysis can be found in table 1. The average was calculated for tree height, fruit length and width, and seed length and width.

2.2.2.4 Species-level dispersal type data

Dispersal data was compiled from the Seed Information Database (SID), Lososova et al. (2023), Vargas et al. (2023) and the South African National Biodiversity Institute (exact sources for each species found in supplementary data). In addition, data on dispersal types was retrieved from the TRY database (TraitID 28 = Dispersal Syndrome) (Kattge et al. 2020).

Table 1. Variables in research analysis, relation to sub-questions, analysis level and data source.

Tree trait	SQ	Level	Source
Wood density	4	Species	GWDD, AWDD, Schröcker, Kindermann et al. (2022), fieldwork sampling
Agb	5	Plot	SEOSAW data & calculations
Max. & min. height	4 & 5	Species	Stevens, Lehmann & Maritz
Max. stem diameter	4 & 5	Species	Stevens, Lehmann & Maritz
Max. & min. fruit length & width	4 & 5	Species	Stevens, Lehmann & Maritz
Max. & min. seed length & width	4 & 5	Species	Stevens, Lehmann & Maritz
Seed mass and avg. 1000 seed mass	4 & 5	Species	Stevens, Lehmann & Maritz
Max. number of locules	4	Species	Stevens, Lehmann & Maritz
Max. number of carpels	4	Species	Stevens, Lehmann & Maritz
Species richness	1 & 3	Plot	SEOSAW data & fieldwork sampling
Number of stems	4	Species	Stevens, Lehmann & Maritz
Faunal/abiotic seed dispersal	1 & 3, 4	Species & country	Open-source data, TRY database
Fruit classification	1 & 3	Species & country	Stevens, Lehmann & Maritz
Level of human disturbance	2 & 5	Plot	Tye & own classification

2.3 Data manipulation & imputation

For the analysis in R Studio, raw tree traits data was loaded and then filtered down to the species and traits of interest. Averages were calculated for tree height, seed length and width, and fruit length and width. Wood density of the tree traits raw data and wood density compiled beforehand from databases were loaded, and the average was calculated. Dispersal data was compiled beforehand and fruit data was filtered from tree traits raw data. The loaded and manipulated data was joined into a new data frame for the subsequent analyses. Species lists for each country were prepared beforehand using raw SEOSAW stem data, which were loaded and matched with trait data in R Studio.

2.3.1 Data imputation

The tree trait data comprised through the previously mentioned steps showed a large percentage of missing values (table 2). Therefore, the data has been imputed based on the assumption of a missing-at-random mechanism, using the multivariate imputations by chained equations (MICE) with 10 iterations. All numerical variables were imputed using the “pmm” method, all categorical variables except dispersal type were imputed using the “polyreg” method. This technique has been used in a similar analysis of Albert-Daviaud et al. (2018) and has been performing well for both continuous and categorical data. In the analysis of Albert-Daviaud et al. (2018), the dispersal syndrome was excluded from the imputation because no data was missing. In this analysis, the dispersal type was excluded as well, because the assumption of missing-at-random mechanism would not be a good fit. I tested this with one round of imputation where I included dispersal type using the “logreg” method. As expected, the test run resulted in a combination of many tree species with a fleshy fruit type and an abiotic dispersal type, which is not a reliable representation of real-world seed dispersal processes. Therefore, the dispersal type was excluded from the imputation process.

Table 2. Full list of variables used, percentage of missing data, data type, and MICE imputation method used.

Variable	Missing data [%]	Data type	MICE imputation method
Wood density	57.57	Numeric continuous	pmm
Max. stem diameter	77.54	Numeric continuous	pmm
Max. height	24.46	Numeric continuous	pmm
Min. height	36.12	Numeric continuous	pmm
Average height	24.46	Numeric continuous	pmm
Fruit max. length	28.45	Numeric continuous	pmm
Fruit min. length	36.94	Numeric continuous	pmm
Fruit average length	28.45	Numeric continuous	pmm
Fruit max. width	28.79	Numeric continuous	pmm
Fruit min. width	38.60	Numeric continuous	pmm
Fruit average width	28.79	Numeric continuous	pmm
Seed max. length	70.72	Numeric continuous	pmm
Seed min. length	80.20	Numeric continuous	pmm
Seed average length	70.72	Numeric continuous	pmm
Seed max. width	71.71	Numeric continuous	pmm
Seed min. width	81.36	Numeric continuous	pmm
Seed average width	71.71	Numeric continuous	pmm
Seed mass	60.07	Numeric continuous	pmm
Average 1000 seed mass	53.25	Numeric continuous	pmm
Number of stems	49.09	Numeric discrete	pmm
Max. number of carpels	69.55	Numeric discrete	pmm
Max. number of locules	76.54	Numeric discrete	pmm
Fruit type	23.79	Categorical nominal	polyreg
Fruit opening	24.29	Categorical nominal	polyreg
Dispersal type	71.55	Categorical nominal binary	-

2.3.2 Normality test & data transformation

Due to the large sample size, the Kolmogorov-Smirnov normality test was chosen to test distribution. The results of the normality test showed that the data did not follow a normal distribution ($p = < 2.2e-16$). The Kolmogorov-Smirnov test results can be found in the appendix (Tables S 1 & 2).

Following the normality test, a log transformation was performed, following the example of a similar analysis done by Bello et al. (2015). Due to very small numbers of most variables, the variables in question were log transformed using a constant of 1 to avoid negative values. The variables tested in the Kolmogorov-Smirnov normality test, histograms, boxplots, and Q-Q-plots of before and after log transformation can be found in the appendix (Figures S1 – 4, Tables S 1 & 2).

2.3.3 Calculation & classification

2.3.3.1 Community-weighted mean calculation

One specific dataset in each country was selected for the plot-level analysis. The selection of datasets was based on the plots in which AudioMoths are deployed for faunal monitoring as part of the FACA project. In Angola, the faunal monitoring is done in the ABG dataset, which was in the SEOSAW database. The data from the plots in South Africa was received from D. Tye. The AudioMoths in the new plots in Madagascar were deployed after the set-up and sampling.

The community-weighted mean (CWM) was calculated for the plots in the selected datasets. The calculations were done in R Studio, using the R packages “tidyr” and “dplyr”. For each plot the community weighted means for average wood density, average height, average seed length and width, average fruit length and width, average seed mass and mass of 1000 seeds, and maximum stem diameter were calculated. Since disturbance and agb were added subsequently, the country column was used as a grouping factor.

2.3.3.2 Above ground biomass calculation

The agb was calculated using a standardized allometric equation to calculate the tree volume:

$$V = \pi \times r^2 \times H$$

With r being the radius of the stem (cm) and H the tree height (cm). For multi-stemmed individuals, the volume of each recorded stem was calculated. The agb was calculated by multiplying the tree volume with the wood density values that were previously comprised (g/cm^3).

The agb calculations for the Madagascar plots are based on the stem data sampled during fieldwork in the new SEOSAW plots (Diameter at breast height (DBH) > 5cm). For agb calculations in Angola, data from the SEOSAW plots in the ABG dataset were used. Since the newest census of the ABG did not include height measurements, old census data including diameter and height were used. Calculations for ABG1 – ABG4 were sampled in 2018, with the remaining plots ABG5 – ABG15 sampled in 2019. ABG16 – ABG19 miss height data, which is why those plots were left out of the analysis.

For the analysis of South Africa data, six plots where the AudioMoths for the FACA project were deployed were used for this sub-question: AE_T1 and AE_T3, WW_T1 and WW_B3, and WE_B2 and WE_T3. Here the first two letters indicate the location of the plots along the human use gradient (either AE = *anth edge*, WW = *wild*, or WE = *wild edge*) and

the third letter and number indicate the plot. The setup of these plots followed different protocols than the standard SOESAW monitoring protocol (supplementary material). The shape of the AE plots is circular and for this analysis only the inner nested plot with a radius of $r = 5.64\text{m}$ was used for comparison with the SEOSAW plots. In this inner section of the plot all individual trees were measured, whereas in the outer section of the plot only individuals above 6m height were measured. The other four plots are square, with a size of 50 x 50m. For this analysis, data from the middle line up to 10m to each side were included, because between the 10m and 25m line on each side only individuals above 5m height were measured. In the SEOSAW plots only trees with height of 1.3m or more as well as a DBH of at least 5cm were included, which is why the South Africa and Angola data was then filtered for only trees within these thresholds. Based on the plot area, the agb calculations were scaled to t/ha to be comparable.

For the agb calculation in the ABG plots in Angola, the wood density given in the SEOSAW dataset was used. For the Madagascar data, the average wood density sampled during the fieldwork was used for three out of the four species. For the last species, the wood density was retrieved from the mean wood density included in the analysis of SQ3, similar to the agb calculations of the South Africa plots.

2.3.3.3 Disturbance classification

Similarly to the human use classification of the South Africa data provided by D. Tye, the level of disturbance of the remaining plots of the other countries was defined based on the proximity of the plots to human infrastructure. For the Madagascar plots, the distance of the plots to the main road RN1 was measured. For the AGO plots, the reference road was the main road EN280. The distance was translated into wild, anthropogenic and edge areas on a disturbance scale of 1 – 3, 3 being the highest.

2.4 Data analysis

The analyses included data from the four southern African countries Angola, Mozambique, Madagascar and South Africa. Figure 2 shows the type of data used, and the link to the research questions through answering the five sub-questions. The analysis to answer the first two sub-questions of chapter 1 included exploration and description of the data sampled in the plots set up during the fieldwork (SQ1) and a linear regression model of the effect of disturbance on agb, and tree and stem densities (SQ2).

The data analysis of part 2 considered a multiplication approach that is obtained through plot-based sampling. After testing the distribution of the residuals on normality, the analysis included exploration of categorical variables to understand the relative contribution of faunal seed dispersal and fruit production within dispersal traits in the plots (SQ3). To understand the relationship between tree dispersal traits and carbon storage (wood density & agb), spearman rank correlations were performed on species level and on plot level using community-weighted means. On species-level the Spearman rank correlation test was performed for the full numerical set of variables and repeated using averages of seed length and width, fruit length and width, and height (grouped dataset). The reason for grouping the dataset was to reduce complexity and increase readability through avoidance of clusters of correlations between averages, minimum and maximum values. Following the Spearman rank correlations, principal component analyses (PCA) were performed. The PCA was chosen to reduce the dimensions of the large dataset. This technique captures the directions in which the variation of the data is maximal into principal components, of which the first two explain the largest share of variance (Ringnér, 2008)

In addition, human disturbance on a scale from 1 to 3 (3 being the highest) was included as a factor in the analysis of the last sub-question to understand whether disturbance influences tree dispersal traits and agb (SQ5). To dive deeper into the relationship of wood density, agb, tree dispersal traits and human disturbance, scatterplots of linear regression models were added for sub-questions 4 and 5.

The tree traits included in the analyses can be found in table 2. All statistical analyses were performed in R Studio[®] (R version 4.2.3, RStudio version 2023.12.1+402). The results of the statistical analyses were interpreted and discussed, and ultimately used to answer the sub-questions and the main research question.

3. Results

3.1 Results part 1: Madagascar tree inventory

Overall, the species richness was low and without strong pattern in the Madagascar plots (Table 3). *Uapaca bojeri* was by far the most common species (Table 4), and the only native species in the plots (Table 5).

Table 3. Overview of novel SEOSAW plots in Madagascar, including plot length and width, longitude and latitude of the southwest corner, area, slope, agb of stems of at least 5 cm DBH, and species richness.

Plot	Plot length [m]	Plot width [m]	Plot slope	longitude	latitude	Distance [km]	agb [t/ha]	Area [m ²]	Species richness
MAS01	100	100	15.98	-19.009039	47.142806	0.120	16.55791	10000	4
MAS02	100	100	11.36	-19.006789	47.152481	0.420	22.87208	10000	2
MAS03	100	100	12.12	-19.004128	47.150200	0.665	24.48456	10000	2
MAS04	100	100	16.06	-18.998861	47.146828	1.180	54.30642	10000	2
MAS05	100	100	12.38	-19.000547	47.144097	0.910	25.92515	10000	3

Table 4. Share of tree species per plot in Madagascar.

Plot	<i>Uapaca bojeri</i> [%]	<i>Pinus kesiya</i> [%]	<i>Eucalyptus robusta</i> [%]	<i>Syzygium cumini</i> [%]
MAS01	85.18	14.56	0.54	0.54
MAS02	99.52	0	0.24	0
MAS03	98.71	1.29	0	0
MAS04	94.63	5.38	0	0
MAS05	99.56	0.22	0.44	0

Seed dispersal modes and fruit characteristics in Madagascar (SQ1)

The share of fruiting trees ranged from about 85% in plot 1 up to 100% in plot 2 (Table 6). The large majority of fruits were fleshy and indehiscent. In all plots, the dispersal mechanism of the majority of trees (between 85 and almost 100%) was faunal. Between 0% of trees in plot 4 and almost 15% of trees in plot 1 were dispersed by fauna, and minor share between 0% and 0.5% was dispersed abiotically (Table 6).

Table 5. Trait characteristics and status of species found in novel SEOSAW plots in Madagascar. *Uapaca bojeri* is marked (*), indicating that the seed dispersal mechanism was not found in any database. Based on fruit traits and dispersal of other *Uapaca* species, dispersal is likely to be faunal with an unknown seed disperser. *U. bojeri* is the only native species, *P. kesiya*, *E. robusta*, and *S. cumini* are alien.

Species	Native/alien status	Fruit type	Fruit opening	Seed dispersal
<i>Uapaca bojeri</i>	Native	Fleshy	Indehiscent	Unclear*
<i>Pinus kesiya</i>	Alien	-	-	Faunal
<i>Eucalyptus robusta</i>	Alien	Dry	Dehiscent	Abiotic
<i>Syzygium cumini</i>	Alien	Fleshy	Indehiscent	Faunal

Table 6. Overview table of share of fruiting trees, fruit and dispersal details of the tree communities in the novel SEOSAW plots in Madagascar.

Plot	Fruiting trees [%]	Fruit fleshy [%]	Fruit dry [%]	Faunal Dispersal [%]	Abiotic Dispersal [%]	Unknown Dispersal [%]	Fruit Dehiscent [%]	Fruit Indehiscent [%]
MAS01	85.56	99.38	0.63	14.97	0.53	84.49	1	99
MAS02	100	99.76	0.24	0.00	0.24	99.76	0	100
MAS03	98.71	100	0.00	1.29	0	98.71	0	100
MAS04	94.63	100	0.00	5.37	0	94.63	0	100
MAS05	99.78	99.56	0.44	0.22	0.44	99.34	0	100

Above ground biomass and human disturbance in Madagascar (SQ2)

Agb ranged from 16.6 t/ha in plot 1 to 54.3 t/ha in plot 4 (Table 3). The agb increased with distance from the main road. A similar pattern can be found when plotting the tree and stem counts against the distance from the main road. Most *Uapaca bojeri* individuals in the Malagasy plots were multi-stemmed, with 5 or 6 stems per tree at times. Both tree and stem counts increased with larger distances (Figure 8).

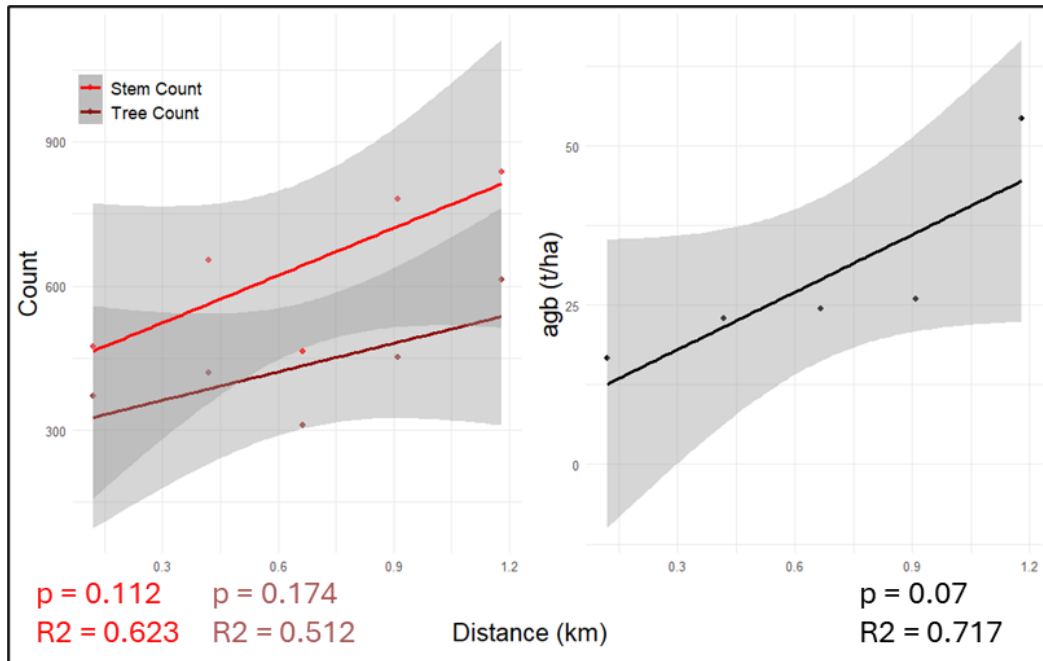


Figure 8. Linear regression of tree counts ($r^2 = 0.512$, $p = 0.174$, $n = 5$), stem counts ($r^2 = 0.623$, $p = 0.112$, $n = 5$), and agb ($r^2 = 0.717$, $p = 0.07$, $n = 5$) against distance from the main road (km), with linear regression fit and confidence intervals (envelopes). Tree counts depicted in dark red, stem counts depicted in red, agb depicted in black.

3.2 Results part 2: Comparison of southern African woodlands

Seed dispersal modes and fruit characteristics across countries (SQ3)

Species richness varied with total plot area per country (Figure 9, Figure S5). Overall, Madagascar stood out with the smallest area, the smallest overall species richness as well as the lowest species richness per hectare per plot (Figure 9, Figure S6).

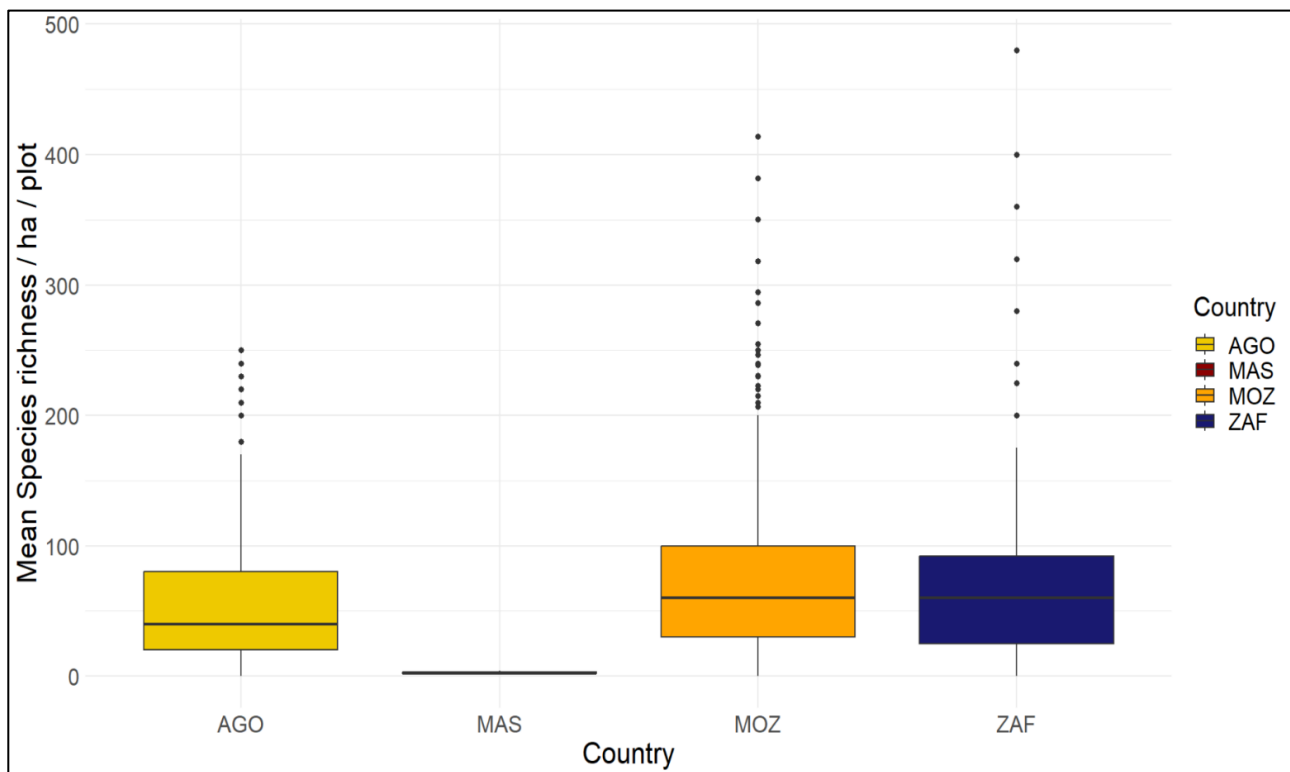


Figure 9. Mean number of species per hectare per country, including median, interquartile range, and outliers. Angola (AGO) depicted in yellow, Madagascar (MAS) in dark red, Mozambique (MOZ) in orange, and South Africa (ZAF) in dark blue.

The majority of species had an unknown dispersal vector (429 species), followed by faunal seed dispersal (155 species). Only the seeds of a minority of the species (16 species) present in the plots were dispersed through abiotic mechanisms (Figure 11). Angola and Mozambique had a similar distribution of dispersal types. The distribution of dispersal types in South Africa looked not much different, except that the number of species dispersed by fauna was almost as high with 48.2% as by an unclear mechanism with 48.6%. In the Malagasy plots, the majority of tree species (50%, 2 species) were dispersed by fauna, while the dispersal type of one species was abiotic and one species unknown (25% respectively) (Figure 11).

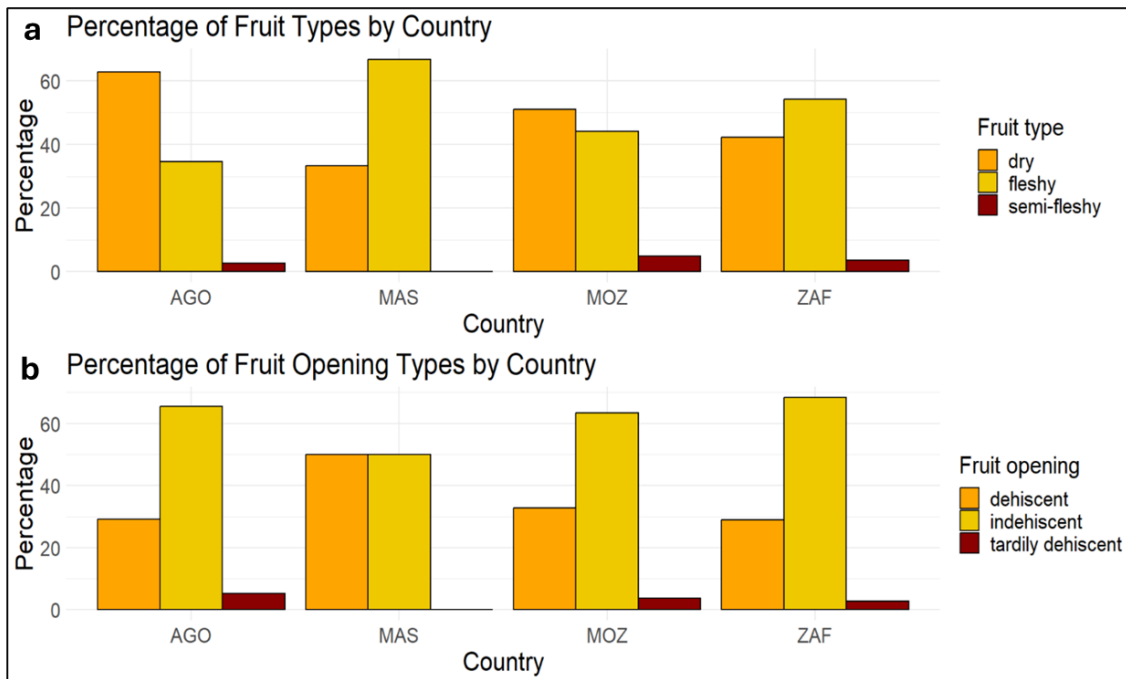


Figure 10. Percentage of dry (orange), fleshy (yellow) and semi-fleshy (dark red) fruit types (a), and dehiscent (orange), indehiscent (yellow) and tardily dehiscent (dark red) fruit opening types (b) per country.

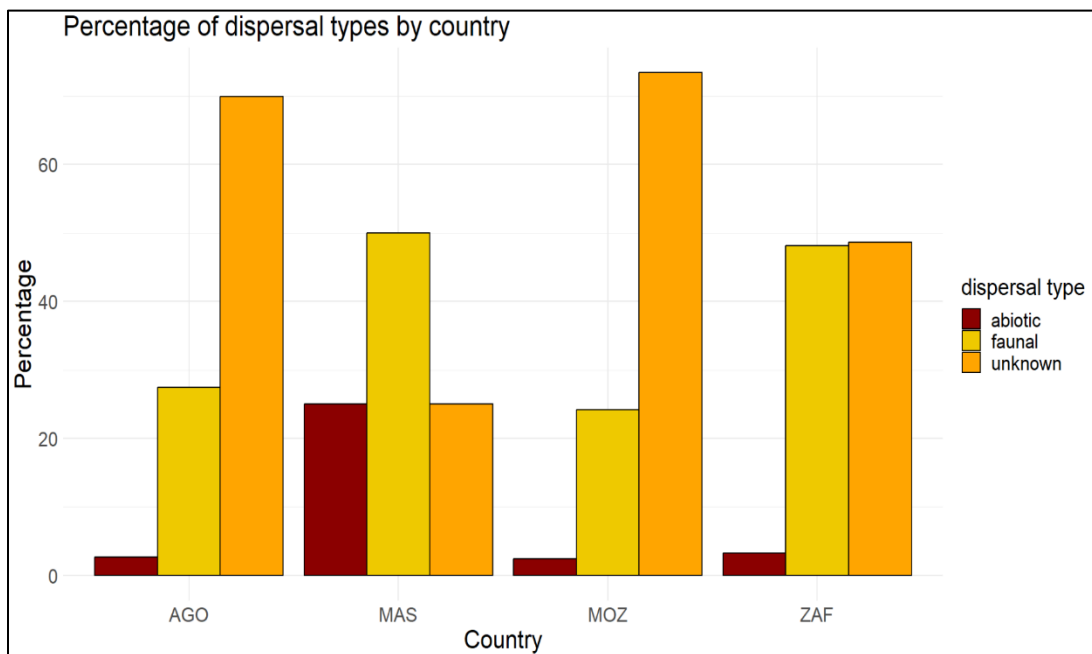


Figure 11. Percentage of dispersal types in each country, with abiotic dispersal in dark red, faunal dispersal in yellow and unknown dispersal in orange.

The proportion of dry and fleshy fruit-producing tree species was similar in Madagascar, Mozambique, and South Africa, while there was a greater proportion of dry fruit-producing species in Angola. Semi-fleshy fruits were produced by few species, if any (Figure 10 a). The pattern of fruit opening types was similar in Angola, Mozambique, and South Africa with the largest share of fruit being indehiscent, whereas in Madagascar again 50% were dehiscent and 50% indehiscent (Figure 10 b).

The relationship between tree dispersal traits and wood density across countries (SQ4)

The heatmaps of both the full ungrouped dataset and the full grouped dataset using averages showed similar patterns for both sets of variables, so I continued the analysis with a reduced number of variables by using averages instead of maximum and minimum values (referred to as full grouped dataset) (Figure 12). The heatmap and correlation matrix of the full dataset can be found in the appendix (Figure S7).

The results of the Spearman rank correlation were interpreted based on an adaptation of Schober et al. (2018). The absolute observed correlation coefficient of the full grouped dataset showed two moderate correlations. Trees with longer fruits tended to have wider fruits (0.544), and trees with heavier seeds tended to have a larger mass of 1000 seeds (0.489) (Figure 12). All other correlations were either weak or negligible (Table S4).

Faunally dispersed trees showed stronger correlations between fruit and seed characteristics than trees in the full dataset. Some correlations changed from negative to positive or vice versa, all of them being negligible (0.00 – 0.10 observed correlation coefficient). The two moderate correlations observed in the full grouped dataset grew in strength from 0.544 to 0.881 (strong correlation) and from 0.489 to 0.533 (moderate correlation). In addition, taller faunally dispersed trees tended to have fewer stems (-0.447), and greater maximum stem diameters (0.486), and faunally dispersed trees with longer fruits and wider fruits tended to have a larger average mass of 1000 seed (0.440 and 0.403, respectively) (Figure 12, Table S5).

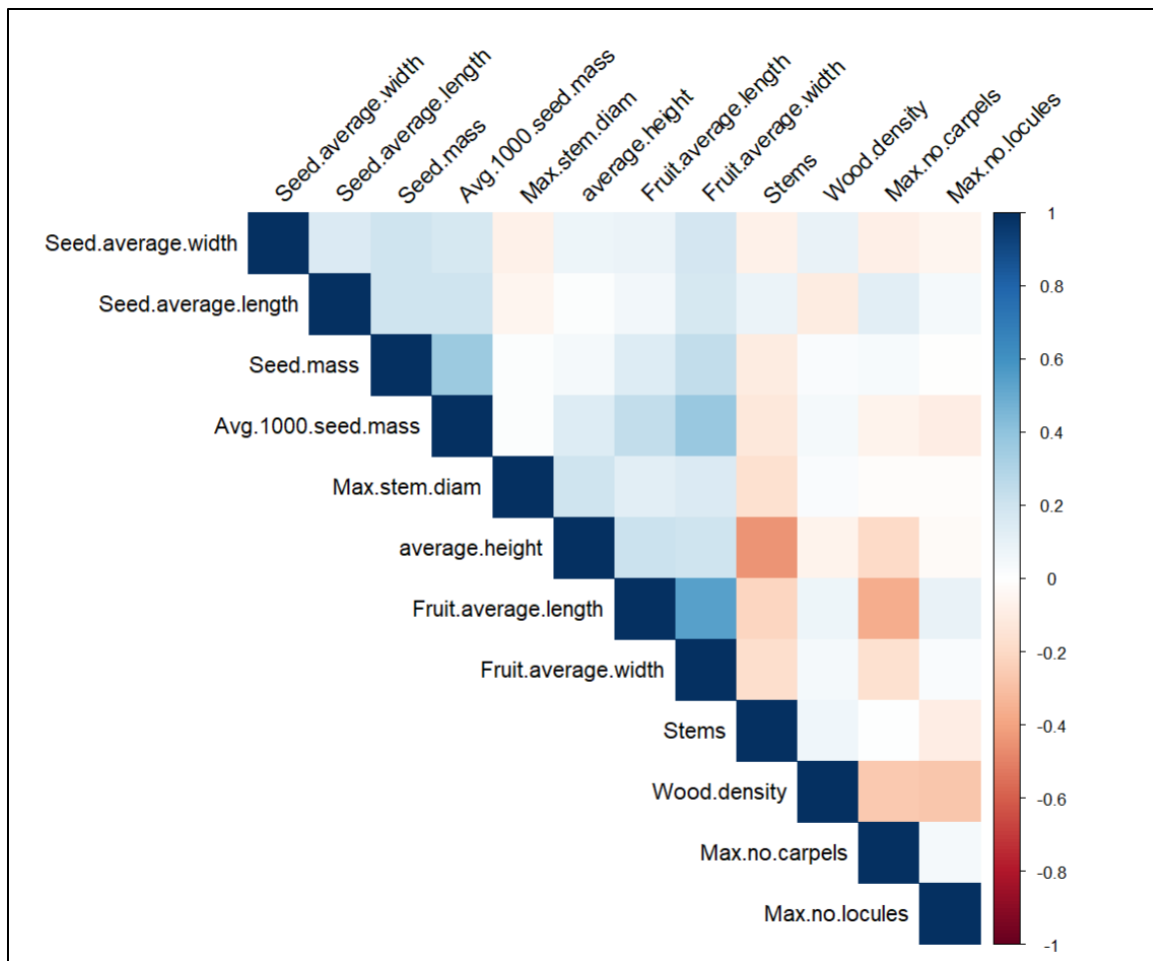


Figure 12. Heatmap of Spearman rank correlation results of grouped dataset (using averages) after MICE pmm imputation and log transformation. Positive correlations are depicted in a blue, negative correlations are depicted in red. The correlation matrix and results of the Spearman rank correlation before grouping data to averages can be found in the appendix (Table S4).

Wood density showed weak positive correlations with seed traits, weak negative correlations with maximum number of carpels and locules, and maximum stem diameter. No correlations were found with height and fruit traits. In the faunal dispersed subset, wood density showed overall positive correlations with seed and fruit traits, and negative correlations with average height and maximum number of locules. In addition to the moderate correlations, several patterns were observed among the weak correlations. Overall, fruit traits and seed traits were weakly positively correlated, meaning that trees with longer and wider fruits tended to also have longer, wider, and heavier seeds. Maximum number of carpels and locules showed contrasting patterns in the correlations with fruit traits and seed traits. Another noticeable correlation was found for average height. Taller faunally dispersed trees tended to have lighter seeds, but a larger average mass of 1000 seeds, which was not the case in the full dataset (Figure 13).

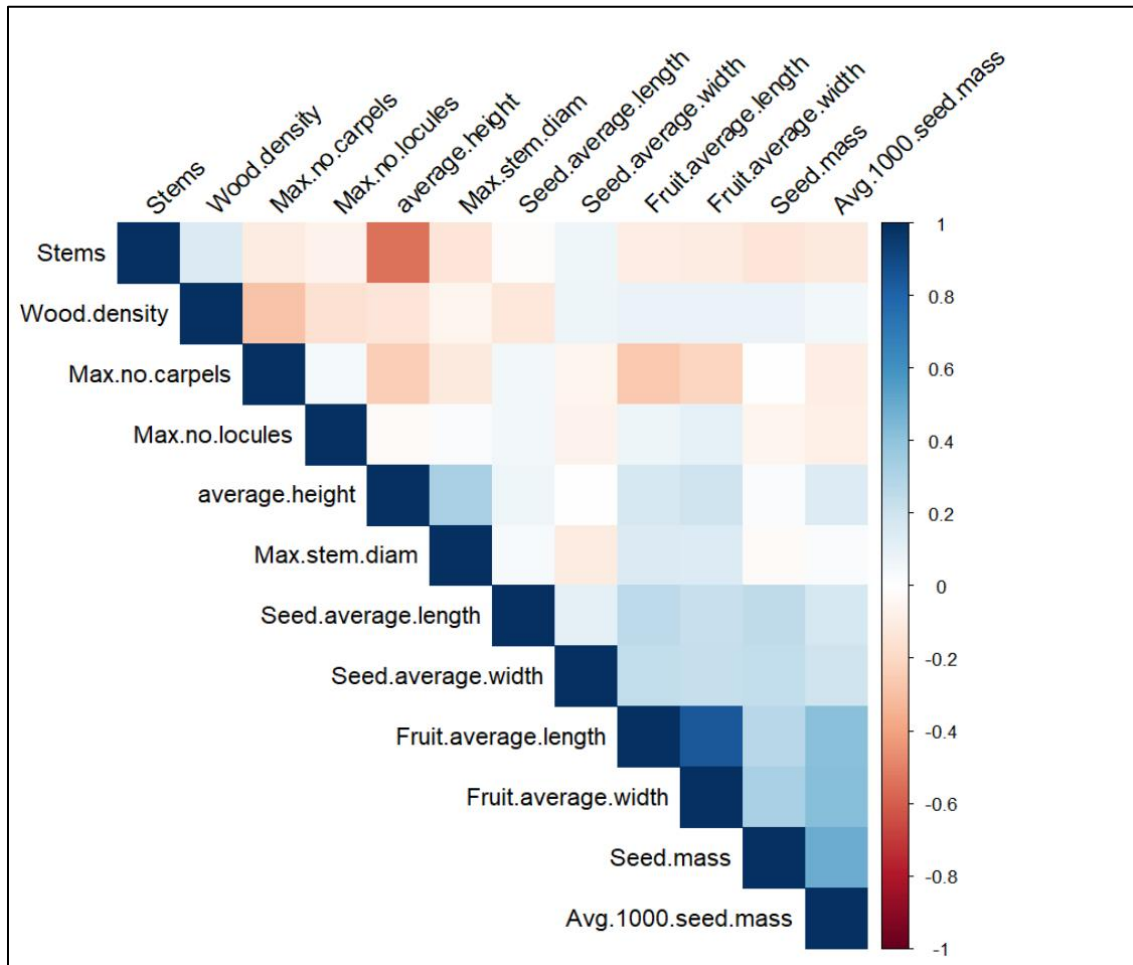


Figure 13. Heatmap of Spearman rank correlation results of faunal dispersed subset after MICE pmm imputation and log transformation. Positive correlations are depicted in a blue, negative correlations are depicted in red. The correlation matrix can be found in the appendix. (Table S5)

Relationship between wood density and tree dispersal traits

Trends between wood density and tree dispersal traits were similar in the full dataset and the faunal dispersed subset (Figure 14 and 15). In the full dataset, log average wood density was positively correlated with log average seed width and negatively correlated with log average seed length (Figure 14). The faunal dispersed subset did not show significant linear relationships (Figure 15).

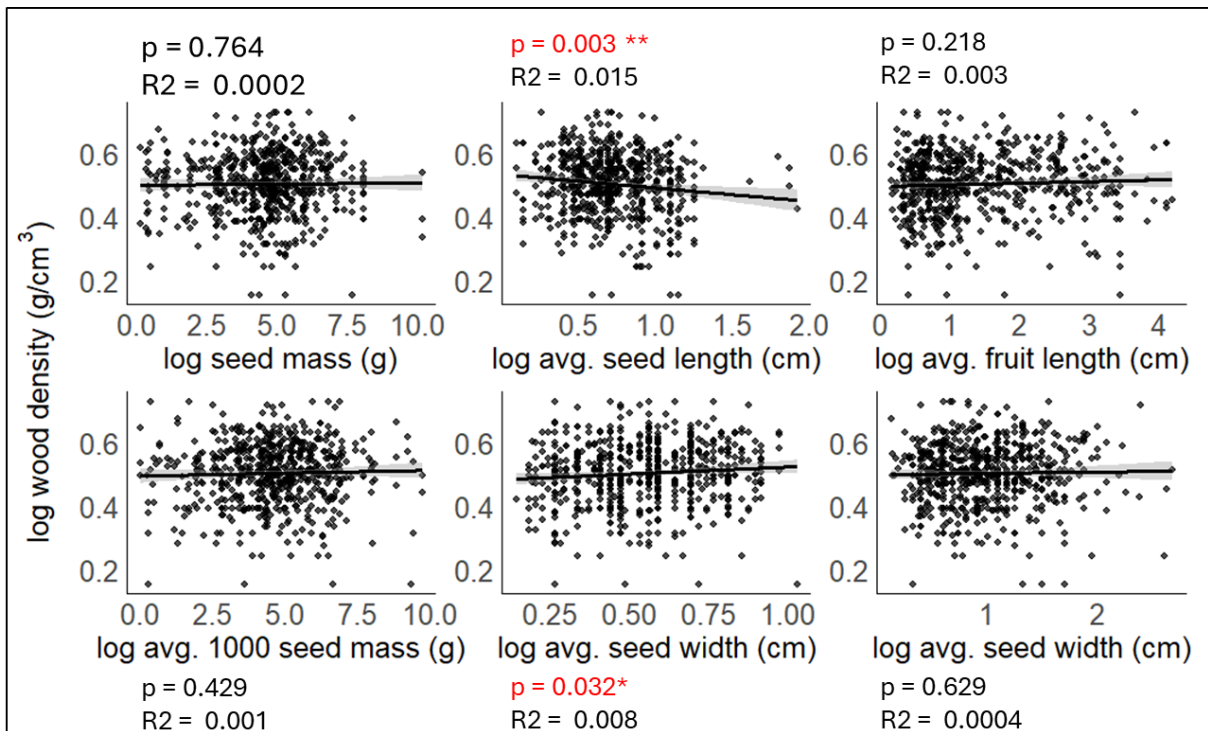


Figure 14. Linear regression results for full dataset with log wood density (g/cm^3) as dependent variable and tree dispersal traits as independent variables ($n = 600$). Significant linear relationships indicated in red.

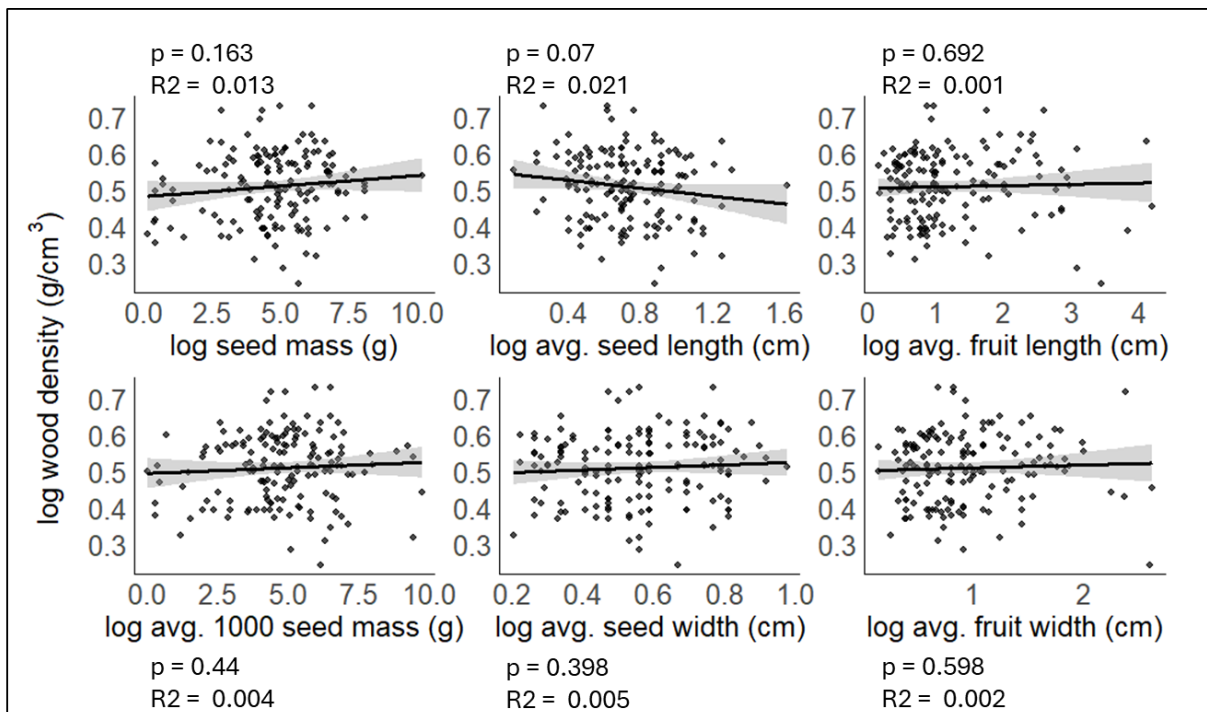


Figure 15. Linear regression results for faunal dispersed subset with log wood density (g/cm^3) as dependent variable and tree dispersal traits as independent variables ($n = 155$). Significant linear relationships indicated in red.

Relationship between average height, maximum stem diameter and tree dispersal traits

The linear regressions with additional carbon traits showed overall positive relationships between log average height and tree dispersal traits, with significant results for log average mass of 1000 seeds, log average fruit width and length (Figures 16 & 17). In addition, relationships between log maximum stem diameter and seed mass and fruit size were positive. Relationships between log maximum stem diameter and seed size were negative (Figures 18 & 19).

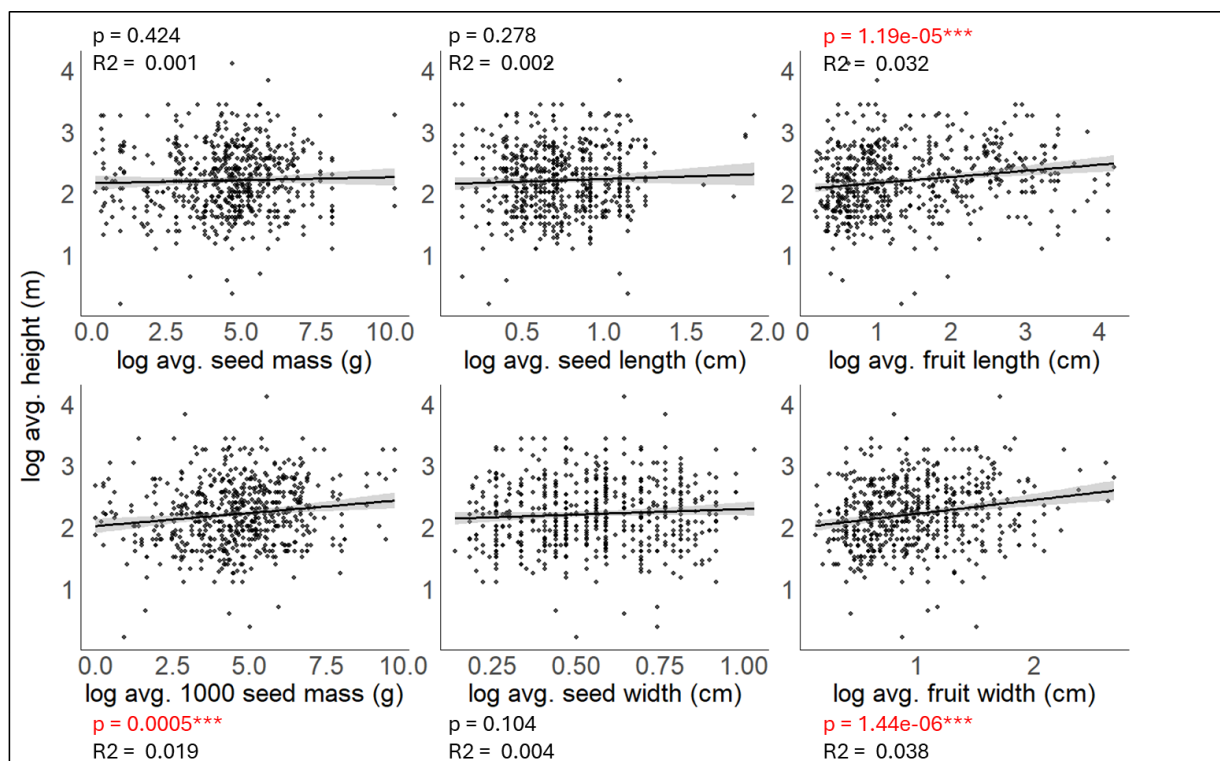


Figure 16. Relationship between log average height (m) as dependent variable and tree dispersal traits of full dataset (n = 600). Significant linear relationships indicated in red.

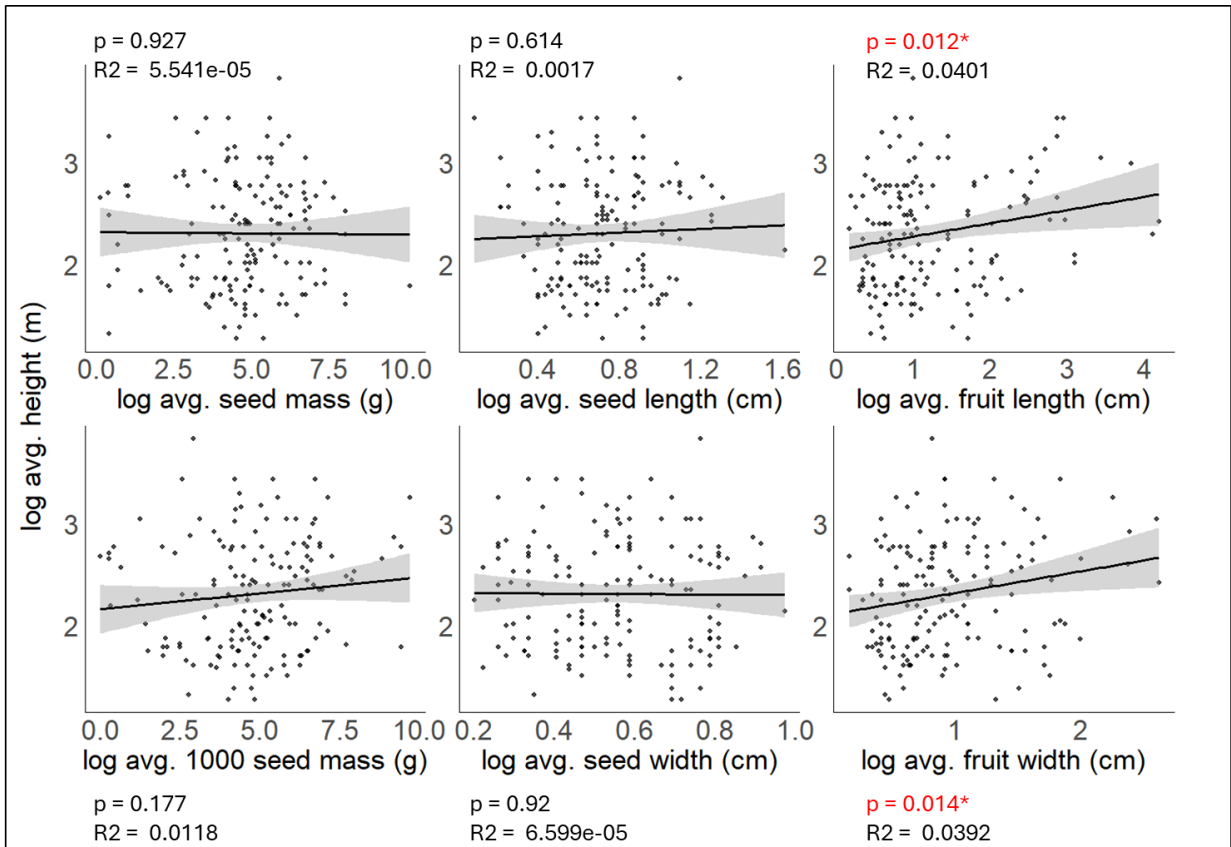


Figure 17. Relationship between log average height (m) as dependent variable and tree dispersal traits of faunal dispersed subset (n = 155). Significant linear relationships indicated in red.

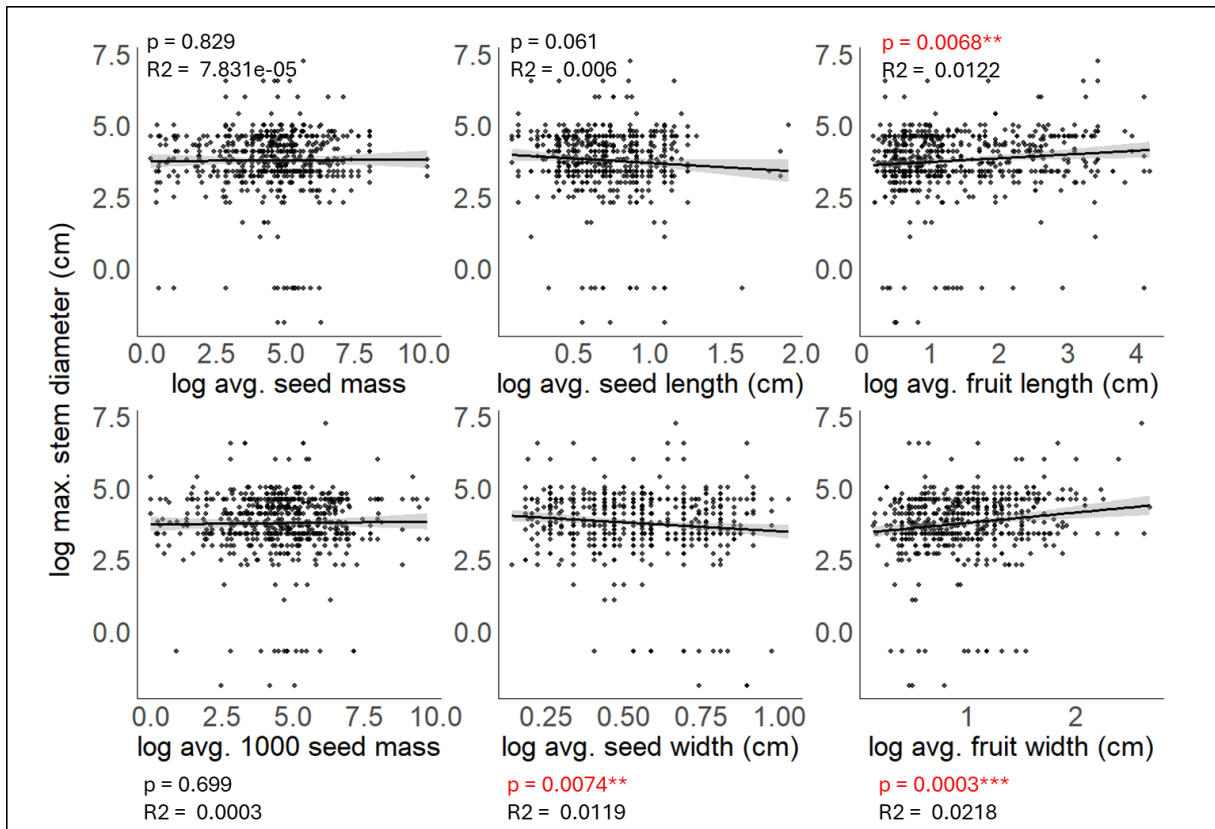


Figure 18. Relationship between log maximum stem diameter (cm) as dependent variable and tree dispersal traits of full dataset (n = 600). Significant linear relationships indicated in red.

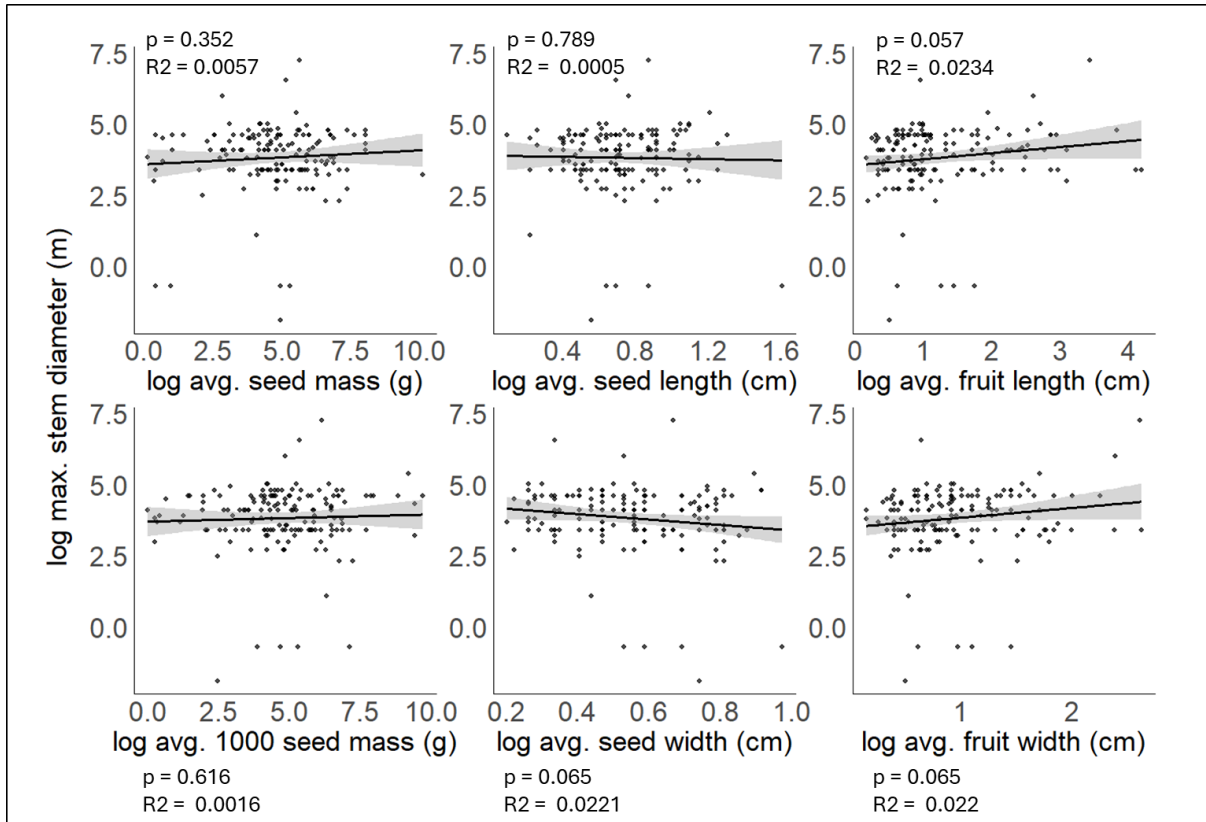


Figure 19. Relationship between log maximum stem diameter (cm) as dependent variable and tree dispersal traits of full dataset ($n = 600$). Significant linear relationships indicated in red.

Dimension reduction through summary indices on species-level (PCA)

The combination of the first two components of the PCA explains about 33% of the variance (Figure S9). An explanation of more than 80% of variance is only reached through combining the first eight components (Table S9). The log average mass of 1000 seeds contributed the most to the two principal components (PC1 and PC2), followed by log average fruit length and width, and log seed mass. The log average fruit length and width had the strongest influence on PC1, and log average seed mass had the strongest influence on PC2 (Table S6).

Relationship between tree dispersal traits, above ground biomass and human disturbance across countries (SQ5)

The Spearman rank correlation for the CWM dataset showed three strong correlations, and various moderate and weak correlations (Table S7). The strong correlations showed that trees in the plots with high agb tended to have wide seeds and long fruits, and communities with taller trees tended to have a larger CWM log average fruit length (Table S7, Figure 20).

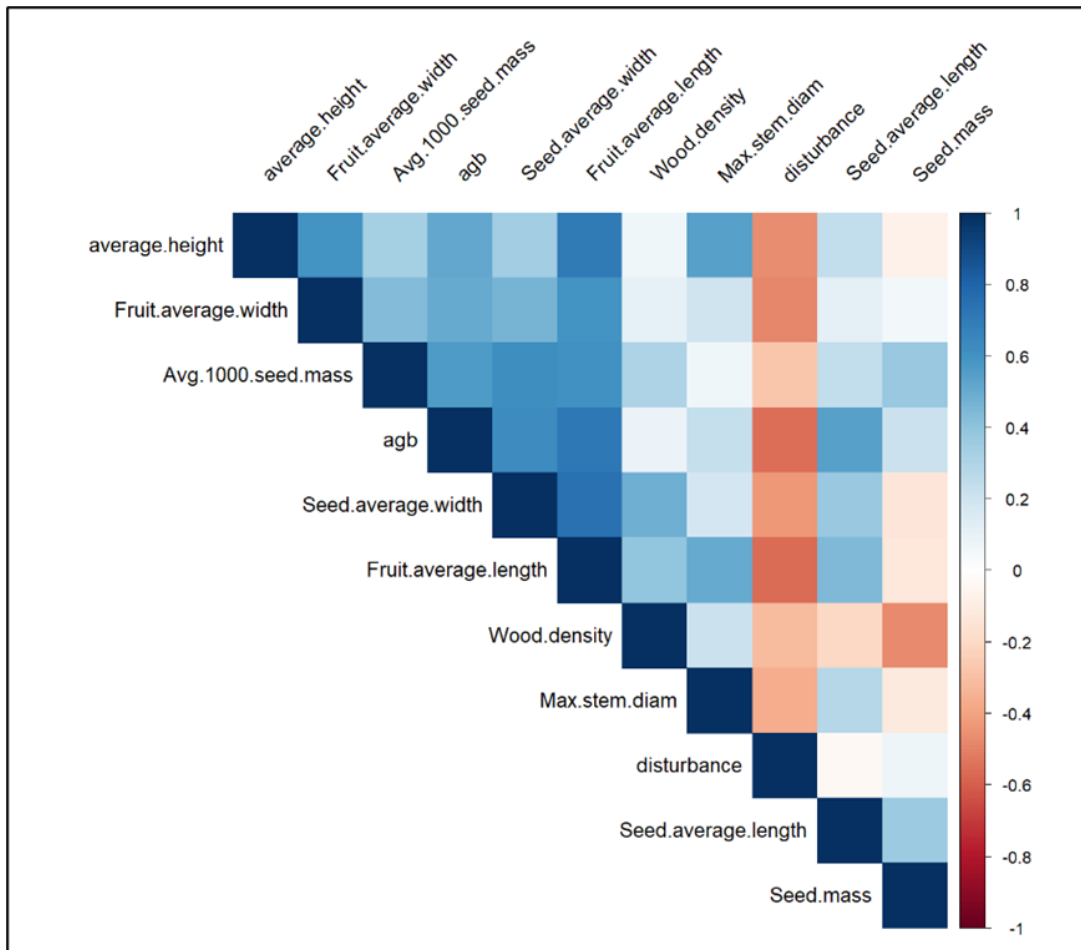


Figure 20. Heatmap of Spearman rank correlation results of CWM of the plots of the selected datasets, after MICE pmm imputation and log transformation. Positive correlations are depicted in blue, negative correlations are depicted in red. The correlation matrix can be found in the appendix (Table S7).

Overall seed mass was negatively correlated with all variables except for negligible positive correlations with agb. Fruit traits and all variables except seed traits were positively correlated with each other (Table S7, Figure 20). This means for instance that trees in communities with larger mean seed mass tended to have shorter and narrower fruits (Figure 20). Wood density showed weak or moderate correlations with all variables except average height, of which all correlations were positive except for average seed mass.

Dimension reduction through summary indices on plot-level (PCA)

On plot-level, the combination of the first two components of the PCA explains 54% of the variance (Table S8, Figure S17). An explanation of more than 80% of variance is only reached through combining the first five components (Table S8, Figure S17). Log average seed mass had the strongest influence on PC1, and log average height and log maximum stem diameter had the strongest influence on PC2 (Table S8).

Relationship between agb, tree dispersal traits and disturbance

The trend between agb and carbon traits was positive, with the only significant relationship being with CWM log average height (Figure 21). The relationship between agb and disturbance was negative, meaning that agb decreased with human disturbance (Figure 22). All correlations between tree dispersal traits and agb were positive (Figure 23). Trees in plots with greater agb tended to have longer and wider seeds and longer and wider fruits. The linear trend between agb and seed dispersal traits was significant for all dispersal traits except CWM log average seed mass (Figure 23). Trends differed between countries (Figure S 11). The only significant linear trend found on country level between disturbance and agb was in Madagascar (Figure S15).

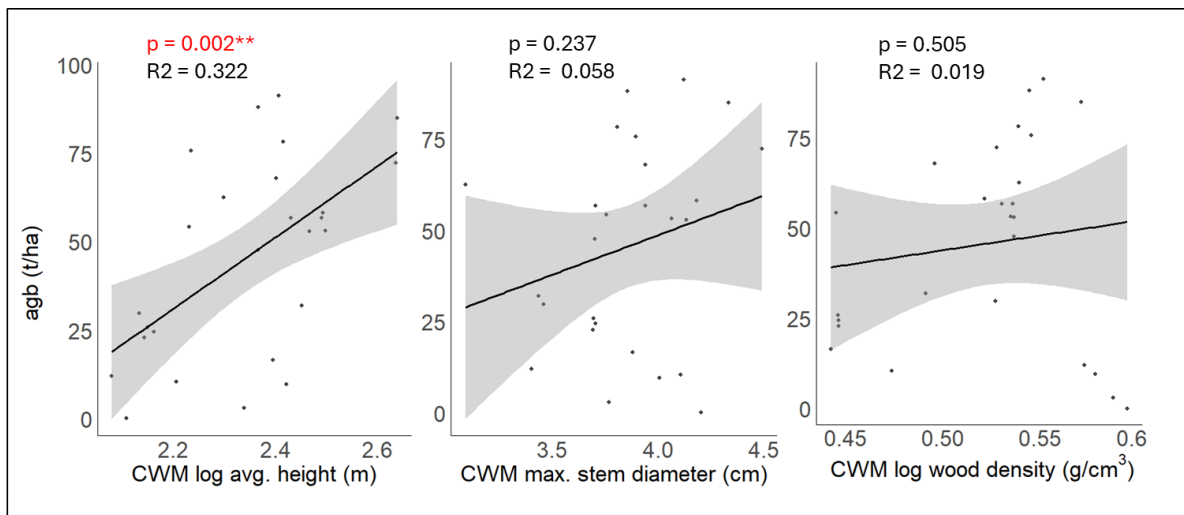


Figure 21. Relationships between agb (t/ha) as dependent variable and CWM carbon traits average height, maximum stem diameter and wood density on plot-level. Significant linear relationships indicated in red.

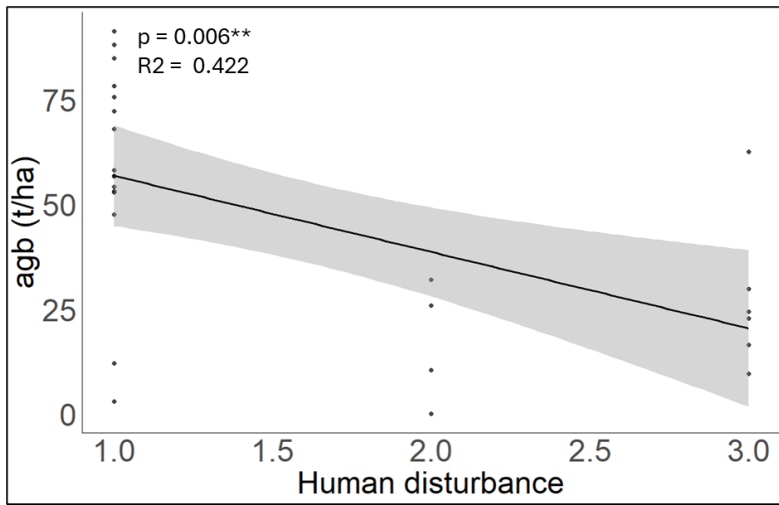


Figure 22. Relationship between agb (t/ha) as dependent variable and human disturbance as a factor between 1 and 3 for full dataset (n = 600).

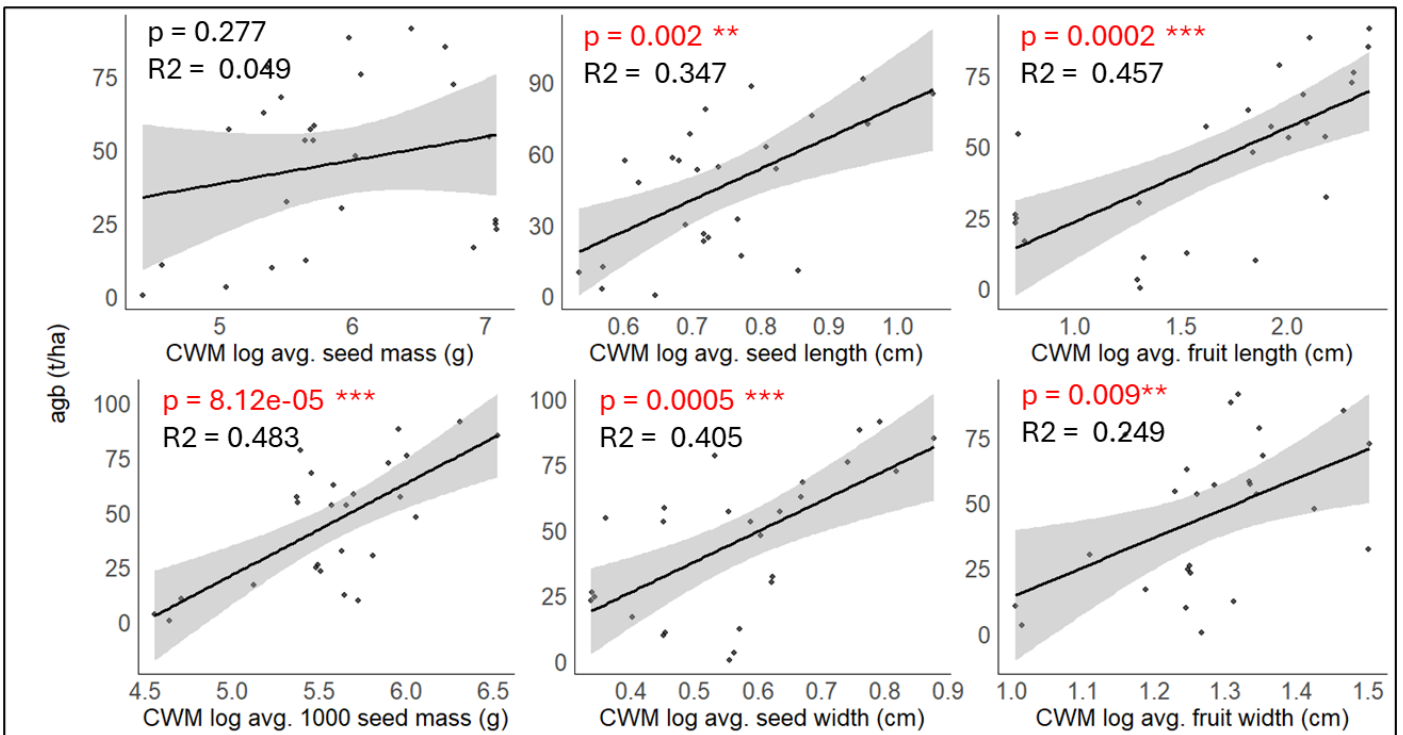


Figure 23. Relationships between agb (t/ha) as dependent variable and tree dispersal traits for the full dataset (n = 600). Significant linear relationships indicated in red.

Effect of disturbance on tree dispersal traits

Disturbance showed moderate and weak negative correlations with all variables except CWM log average seed mass, which was weakly positively correlated, meaning that trees in more disturbed communities tended to have smaller fruit traits, lower height, and stem diameters, but slightly heavier seeds (Figure 20). More highly disturbed plots tended to have a lower mean wood density and agb (Figure 20). In the full dataset, disturbance showed a significant negative trend with log average height, log average seed length and width, log average fruit length, and agb (Figure 24).

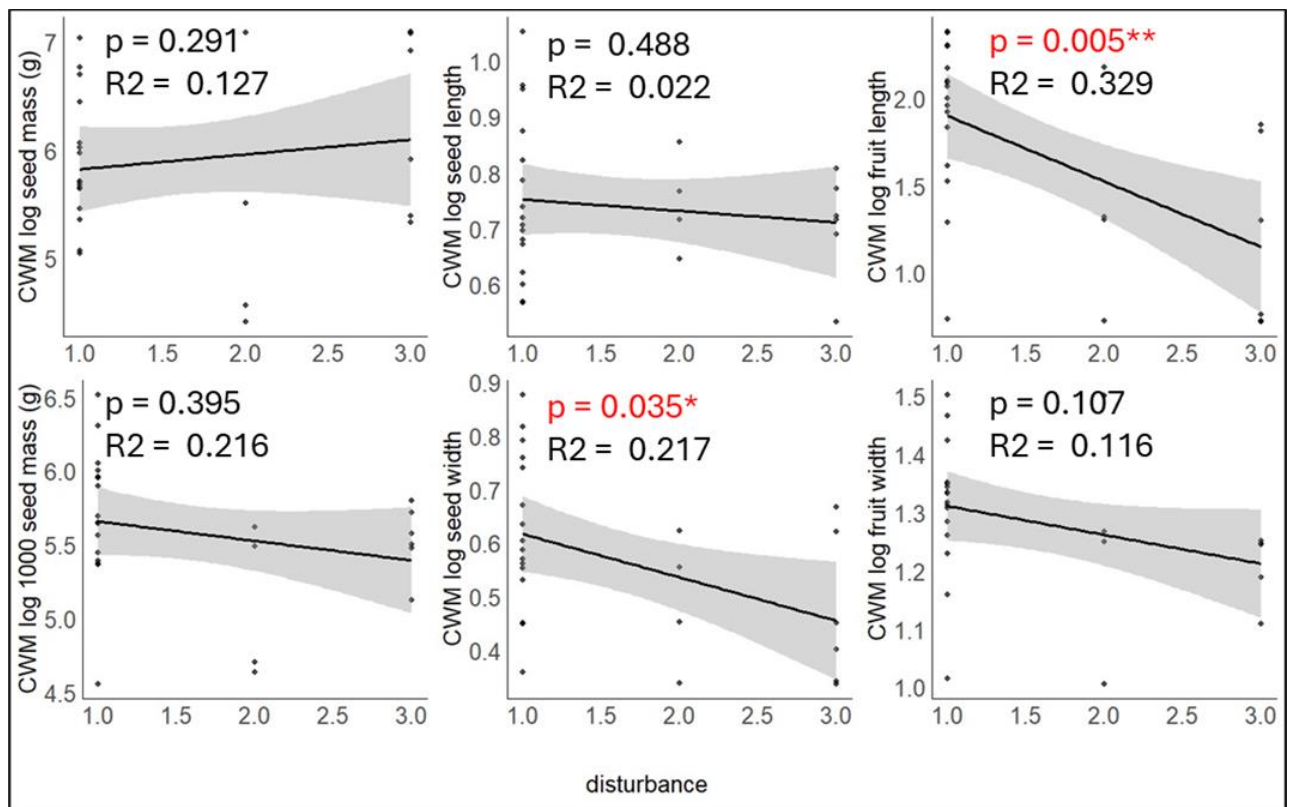


Figure 24. Relationship between human disturbance (factor between 1 and 3) and tree dispersal traits as dependent variables for the full dataset (n = 600). Significant linear relationships indicated in red.

4. Discussion

The following discussion is divided into two parts. The first part dives into the findings from the Madagascar tree inventory analysis, covering tree diversity, tree dispersal, species invasions and human pressures. The discussion of the second part dives into the comparison of Madagascar, Angola, Mozambique, and South Africa. This section compares seed dispersal types across countries, relationships between tree dispersal traits and carbon storage on species- and on plot-level, the effect of human disturbance, and finally compares the tree inventory across countries. The discussions of part 1 and 2 are followed by a section of joint findings and limitations of the research, before diving into answering the research question in the next chapter.

4.1 Discussion part 1: Madagascar tree inventory

Tree diversity

As Madagascar is well known for being a biodiversity hotspot with a large share of endemism, the overall low tree diversity and low share of endemic species within the plots was surprising at first. The SEOSAW stem protocol used for sampling the trees, however, puts the low tree diversity into perspective, because only trees of at least 1.3m height and DBH of 5 cm were sampled, excluding a large proportion of the smaller stems and ground cover vegetation. Therefore, the overall biodiversity including other vegetation layers might be much higher. Having a closer look at the small stems protocol of the fieldwork revealed at least 24 species, supporting this assumption (Table S3).

Seed dispersal types

With *Uapaca bojeri* being the most abundant tree species in the Malagasy plots, a large majority of trees had an unknown dispersal vector. There was no scientific evidence found in literature that made the dispersal type certain. However, Alvarado et al. (2014) suggested that although the ecology and reproductive biology of *Uapaca bojeri* is still largely unknown, it can be compared with other African species of the *Uapaca* genus such as *U. kirkiana*, *U. pilosa*, and *U. nitida* (Alvarado et al., 2014). Based on the fruit production and the dispersal type of other species of the *Uapaca* genus, it is therefore likely that the dispersal type of *Uapaca bojeri* is faunal. This assumption was supported by conversations with local guides involved in the fieldwork, who did not know the historic disperser species, but had observed bats feeding on the fruit of *Uapaca bojeri*. This observation aligns with the suggestion of

Alvarado et al. (2014) because bats are among the dispersal species of the faunal dispersed *Uapaca kirkiana* (Richter & Cumming, 2006). Andriamanohera et al. (2020) speculate whether the disperser species of *Uapaca bojeri* could be lost or extinct megafauna, such as giant tortoises or ground lemurs (Andriamanohera et al., 2020) which can be linked back to the defaunation theory of Bello et al. (2015).

Although bats might not be the original disperser group, they might have filled the gap as a replacement for the loss of historic dispersal species. This theory is supported by the conversations we had with locals during the fieldwork, who were unaware of a disperser species and further raised propagation and recruitment difficulties of *Uapaca bojeri*. Out in the field, one of the guides could point out a hand full of small *Uapaca bojeri* seedlings, which sprouted naturally. Those seedlings stood out because currently the large majority of seedlings are transferred from a tree nursery after they have grown bigger than the seedlings that were spotted by the guide.

Human pressures on U. bojeri populations

Seeds of *Uapaca bojeri* have no extended dormancy but are recalcitrant, meaning that *Uapaca* seeds lose their viability shortly after being dispersed related to a decrease in moisture content (Barbedo et al., 2013; Kull, 2002). Further, the species has a low dispersibility due to missing seed dispersers, and fruits are collected and consumed by humans, which might act as limiting factors on the population (Kull, 2002). There is also an ongoing discussion about a fungal disease that kills young shoots and further adds pressure on *Uapaca bojeri* populations (Andriamanohera et al., 2020). The propagation difficulties of *Uapaca bojeri* might be aggravated by ecosystem changes through anthropogenic pressures and species invasions, such as changes in pH and soil nutrient cycles (Baohanta et al., 2012, Rajaonarivelo et al., 2022).

When finding locations for the plot set-up, one challenge we faced was to find a continuous area of 1ha in the fragmented tapia woodlands. More than once we randomly selected the first corner and spun the rectangle, just to find our plots partially within the boundaries of a plantation. The difficulty of finding a continuous area highlights the anthropogenic pressure on tapia systems, the increased fragmentation, and the replacement by agricultural landscapes, that the area has faced for over 50 years (Kull, 1998; Jenkins, 2003).

One of the pressures on Tapia woodland is the introduction of exotic species, such as fast-growing *Eucalyptus* spp. and *Pinus* spp. Out of the four species present across the whole plot area, only *Uapaca bojeri* is native to Madagascar. The three other species were alien.

Syzygium cumini is an introduced species that is used for medicinal purposes in Madagascar. The seeds of *S. cumini* are used for the production of Madeglucyl, which is medication used by Malagasy patients for type 2 diabetes (Randriamampionona et al., 2007). However, *S. cumini* was only found in the first plot, which is located right next to a small plantation, and the location and low abundance make it likely that the tree species had been planted for harvesting its fruits. This plot located at the border of the small agricultural plantation had the shortest distance to the main road, which classified the plot as most highly disturbed. The plot also showed the highest species richness, not only with native *U. bojeri* and the medicinal *S. cumini*, but also an abundance of *Pinus kesiya* and *Eucalyptus robusta*. As argued by Andriamanohera et al. (2020), planting exotic species such as *Eucalyptus* spp. and *Pinus* spp. can reduce the pressure on *U. bojeri* because they are preferred for charcoal production and as building material. However, the authors have further warned that these tree species can lead to hotter and more intense fires. Savanna ecosystems burn regularly, and *U. bojeri* trees are adapted to those fires with thick, corky bark (Solofondranohatra et al., 2018). With a change in fire regime through exotic species, hotter and intensified fires can lead to damage of tapia trees and pose a major threat when planted within tapia woodlands, leading to a reduction in ecosystem health and resilience (Andriamanohera et al., 2020).

Both *P. kesiya* and *E. robusta* pose threats to *U. bojeri* and the health and resilience of Tapia woodlands. It is known that *Eucalyptus* spp. have a drastic effect on the vegetation development of an ecosystem through the accumulation of litter releasing allelochemicals (del Moral & Muller, 1970). The establishment of *E. robusta* in Tapia woodland could therefore limit the growth of *Uapaca* seedlings and the root system development, which in turn can lead to lower ectomycorrhiza establishment. Ectomycorrhizas are a form of mycorrhizal fungi, which are key factors in nutrient cycling and in sustaining vegetation cover (Ramanankierana et al., 2013). A lack of these fungi has been found to cause establishment and growth difficulties in a range of ecosystems (Ramanankierana et al., 2013). In Tapia woodland Baohanta et al. (2012) have shown that a lowered abundance and diversity of ectomycorrhizal propagules limits the seedling establishment of *U. bojeri*. Facilitation of ectomycorrhizal infection plays a particularly important role with increased abiotic stress for instance in the case of species invasion, as it increases nutrient uptake of *Uapaca* seedlings. In the same study, the authors have also shown the positive effect the ectomycorrhizal shrub species *Leptolena bojeriana* on ectomycorrhizal establishment and the mitigation potential of the negative effect of exotic tree species and facilitation of early growth of *U. bojeri* (Baohanta et al., 2012).

L. bojeriana is among the ectomycorrhizal shrub species associated with *U. bojeri* (Ramanankierana et al., 2013). From personal conversations with locals, we learned about ongoing experiments in nurseries looking into the benefits of associated shrub species for the growth of *Uapaca* seedlings. Although associated ectomycorrhizal shrub species were not sampled when following the sampling protocols during the fieldwork, observations of associated ectomycorrhizal species have been made in plot 5. The fifth plot was among the least disturbed plots with high tree and stem density, and the observations of associated ectomycorrhizal shrub species could be an indicator for the association benefits for ecosystem health and growth of *U. bojeri*. Therefore, the findings suggest that *Uapaca* populations in more highly disturbed plots might benefit from planting associated ectomycorrhizal species.

Eucalyptus spp. and *Pinus* spp. were historically planted to satisfy human needs for instance for fuelwood. *U. bojeri* trees are of light wood and irregular architecture, which limits the use for building and charcoal production and makes fast-growing exotic tree species preferable (Andriamanohera et al., 2020). One *Pinus* species, *Pinus kesiya*, was found in our plots. *P. kesiya* was planted around the Tapia woodlands and was subsequently found to invade the ecosystem (Kull, 2002). Even with the percentage of mature *P. kesiya* individuals being low, they were found to be an ongoing threat to species richness (Rajanoarivelo et al., 2022). Pine trees were found to decrease the pH in soil, which affects growth of tapia seedlings (Baohanta et al., 2012). This alteration might worsen the ongoing problems of the species' regeneration and propagation caused by limited dispersal capacity and the need to break strong seed dormancy (Kull, 2002; Rajaonarivelo et al., 2022). Seeds of *U. bojeri* belong to the group of recalcitrant seeds, which are sensitive to drying and need to maintain high water contents during the whole period of dormancy to stay alive (Obroucheva & Antipova, 2004). Seed germination is potentially linked to rainfall because one trigger of germination is water uptake. Correspondingly, dispersal of *U. bojeri* seeds takes place during rainy season when moisture levels are high and conditions are most favourable for seed germination (Alvarado et al., 2014).

As Kortz et al. (2018) have shown, even the establishment of one single sapling pine can reduce the tree species diversity, and in their study colonized plots showed a decrease in species richness with increasing pine abundance (Kortz et al., 2018). Thus, young pines can reduce species richness and especially affect *U. bojeri* in Tapia woodland, and even low *P. kesiya* abundance can pose a serious risk.

Studies have shown that the likelihood of seed establishment can increase with the quantity of seeds. In the case of *P. kesiya*, the risk is particularly high in Madagascar, because

for reasons that remain unclear, seed production of *P. kesiya* was found to be much higher compared to seed production in other countries. One mother tree in Madagascar can produce up to 20 000 seeds, which is almost double the number of seeds produced by the same species in Malawi (Missanjo & Matsumura, 2016). In addition, *P. kesiya* is wind dispersed, which can lead to an intense dispersal of seeds, especially in our study area. In their study, which was conducted in the same study area as our research, Rajaonarivelo et al. (2022) found pine seedlings as far as 1 km from the nearest seed source. The Tapia woodland in the Arivonimamo region is located in the flank of the valley and the vegetation patches are separated by rice fields, which can increase air circulation and affect seed dispersal distance for wind dispersed species such as *P. kesiya* (Rajaonarivelo et al., 2022).

In our study, only trees of 1.3 m height and with a minimum DBH of 5cm were included in the sampling. The share of *P. kesiya* already reached up to almost 15% in the first plot, without considering seedlings and saplings. We did, however, observe a number of younger pine individuals in the whole study area, and although the abundance of grown *P. kesiya* individuals was lower in less disturbed plots, especially in the fifth plot a large number of pine seeds were observed.

These observations support the claim of Marsico et al. (2010) and Rajaonarivelo et al. (2022), that the Tapia woodland in the Arivonimamo region might be undergoing the establishment phase of the invasion of *P. kesiya*. Considering the risk of high potential seed dispersal and propagule pressure, as well as the high adaptive capacity of pine trees (Moran et al., 2000) there is a risk of pine colonization of the Tapia woodlands if no actions are taken. Local guides have shared the plan to clear the mature pine trees in conversations, which is highly encouraged based on the results of this research. In addition, it is strongly recommended to pay special attention to pine saplings and seedlings as well.

Human disturbance increases ecosystem vulnerability

One objective for setting up the new SEOSAW plots in Madagascar was to set them up along a gradient of human disturbance. When selecting potential locations of the plots, this turned out to be more difficult than anticipated, because of the fragmentation of the remaining Tapia woodlands and the high human disturbance found across the area. With the help of local guides, the locations were selected on a gradient based on distance from the main road. During the sampling, one question focused on the share of damage that was caused by humans. Initially, I had planned to include this data in the plot disturbance classification. However, with humans being the cause in almost 100% of cases in all plots except the first

due to a sampling error, no difference has been found between the plots. The ubiquitous damage caused by humans shows that disturbance was high even in the plots classified as least disturbed. Although there has been no difference in the share or damage caused by humans compared to other causes such as wind or lightning, the plots showed a large difference across stem and tree counts, as well as agb with distance from the main road.

The cause for pine invasion is human activities and disturbance, for instance leading to a reduction of plant cover. It was found in numerous studies that invasion increases accordingly to the level of disturbance in study sites (Rajaonarivelo et al., 2022). The Tapia woodland consists largely of *U. bojeri* trees, which are relatively small and with a low basal area. Through disturbance and cutting down of Tapia trees, the light availability in the woodland changes and may lead to the ecosystem to become more vulnerable for invasion. This aligns with our finding of the most species richness and highest abundance of *P. kesiya*, *E. robusta*, and *S. cumini* in the most highly disturbed plot. Currently, the Tapia woodland in the study region is under temporary protection and cutting of Tapia trees is forbidden. However, enforcement of the regulations and punishment following a violation is not strict. For instance, during visits of the study area in the months after the plot set-up, felled Tapia trees have been spotted. A legal protected status of the area is currently being sought, and once the area is fully protected, it will be divided into zones where local communities will be allowed to harvest non-timber products such as fruits and mushrooms in a sustainable manner, and a core zone where use is strictly forbidden (personal conversation with T. Nandrasanjafy, March 27th, 2024). Whether a change in legal status will have an effect of the enforcement of laws and the abundance of such remains to be seen. In any case, stopping Tapia logging is required to limit pine invasion, and pine seedlings should be removed as soon as possible before maturing. In addition, it may be advisable to include ectotrophic shrub species such as *L. bojeriana* after invasion of species such as *Eucalyptus* spp. and *Pinus* spp. to increase ecosystem resilience in Tapia woodland.

4.2 Discussion part 2: Comparison of southern African woodlands

Country comparison of seed dispersal types

Across all countries, the majority of species had an unknown dispersal vector. The share of species with faunal and with unknown dispersal vector was only similar in the South Africa plots. In Madagascar, 50% of species were faunal dispersed - potentially 75% if *Uapaca bojeri* is considered faunal dispersed, although the overall low species richness and number of plots needs to be considered. In Mozambique and Angola, the large share of species with unknown dispersal vector could be based on the large number of species and diversity of plots. Although a number of different sources and databases were used to identify the dispersal types, still only a total of 131 species had a known dispersal mechanism in this analysis compared to 429 species with unknown dispersal vector. I would therefore argue that the large number of species with unknown dispersal vector is due to a lack of scientific data and a gap in research, which highlights the importance of the FACA project, and the monitoring of savanna ecosystems done by the SEOSAW network.

Relationship between wood density and tree dispersal traits on species level

On species level, the relationship between wood density and tree dispersal traits was positive for all traits except for average seed length. The significant relationship between wood density and average seed width and between average height and average mass of 1000 seeds are comparable to the positive links found by Bello et al. (2015). The results indicate that larger species tend to have larger and heavier seeds and higher wood density, supporting the theory that the loss of large seeded species may lead to a decline in carbon storage.

It might be worth mentioning that Bello et al. (2015) investigated seed diameter, while the results I found are based on seed mass, length, and width. Historically, seed size and seed mass have been used interchangeably, although seed size considers the volume and seed mass considers volume and density and therefore, they are different traits (Castro et al, 2006). However, seed dimensions and seed mass are closely linked and seed mass increases with an increase in seed length, size, or width (Rodrigues-Junior et al., 2018). Based on the close link between seed size and seed mass I would still argue that my results support the findings of Bello et al. (2015) and their defaunation theory.

The significant negative link between wood density and average seed length seems to be less clear. Although wind dispersed seeds tend to be long, narrow, and light, the abiotically dispersed subset was extremely small with 16 out of 600 species. In addition, a similar but not significant negative trend was found within the faunal subset, making wind dispersed seeds an

implausible explanation for this negative trend. The relationship between average seed length and other carbon traits was positive, and further research might be necessary to further investigate the relationship between seed length and carbon traits.

Relationship between agb, height and tree dispersal traits on plot level

Looking into the overall trend within the plot communities, strong and moderate correlations have been found between agb, average seed width, fruit length and width, supported by significant positive linear relationships. A similar pattern in seed and fruit size was found for average height, which was moderately correlated with agb. Since average height is used in the agb calculation, those two variables are closely linked together, and I found a significant increase in agb in communities with higher CWM height. Seed size and fruit size are also closely linked. It might seem obvious, but as already stated by Primack (1987), the fruit of a plant can never be smaller than the size of the seed it contains. Large fruits can either contain a large number of small seeds, or one large seed. Either way, naturally, the larger the seed, the larger the fruit needs to be (Primack, 1987). The findings for seed and fruit size suggest that in communities with larger CWM fruit size and seed size, agb and CWM height were higher, while both agb and average height were significantly lower in more highly disturbed communities. In turn, fruit and seed size were also negatively correlated with disturbance, and the more highly disturbed communities also showed a lower CWM seed and fruit size.

The effect of human disturbance

Overall, it is not surprising to find negative effects of disturbance on CWM tree dispersal traits. It has been found that worldwide human disturbance leads to a decrease in ecosystem functionality through a variety of mechanisms, such as increased ecosystem vulnerability and biodiversity loss. Madagascar stood out by showing the only significant negative relationship between disturbance and agb on plot level. As discussed in part 1, the results of Malagasy plots showed a larger number of alien species with increased disturbance. Through human disturbance, for example cutting down trees, the ecosystem becomes more vulnerable, which in turn increases the likelihood of species invasions, for instance by pine trees. It is further imaginable that the overall lower CWM seed size in more highly disturbed plots is related to biodiversity loss reducing faunal seed dispersal, which links to the theory that the recruitment difficulties *U. bojeri* populations are currently facing might stem from the loss of the original seed disperser through defaunation. There have been observations of bats feeding on the tapia fruits as well as that rodents might function as secondary dispersers. Further analyses of the

FACA team based on acoustic sampling in the same plots might help to shed some light on faunal seed dispersal.

Worth mentioning is a weak positive correlation between disturbance and average seed mass and average mass, showing that more highly disturbed communities tended to have a larger CWM seed mass. The linear regression trend was positive between disturbance and the average mass of 1000 seeds as well, but not significant. This trend was only present in the South African plots, which are located in the buffer zone and within the protected area of Sabi Sand Nature Reserve, adjacent to Kruger National Park. In the 20th century, the Sabi Sand Nature Reserve was still as number of cattle ranges that were privately owned, until they were sold as private hunting lodges and finally turned into a cooperative nature reserve in 1950 (Schmidt & Willott, 2012). The larger CWM seed mass found in the more highly disturbed plots could be based on the history of the area, when humans potentially altered tree communities by planting trees that held economic value, such as fruit trees. Studies have shown that fleshy fruits are associated with heavier seeds, which might link back to the larger share of fleshy fruit producing species found in the South Africa plots compared to plots in Angola and Mozambique (Bolmgren & Eriksson, 2010). The considerations of how the plot areas were previously used highlight the largely unstudied effect historic use might have on tree communities today.

Country comparison of tree inventory

In the country comparison, Madagascar stood out with the smallest total plot area, the lowest species richness, and the lowest species richness per hectare per plot. Compared to the other countries I expected to find overall fewer species in Madagascar, because the total sampling area in the five novel plots was considerably smaller compared to the sampling area in the other countries. The difference in species richness per hectare per plot can therefore at least be partially explained by the difference in sampling area. Although a difference in the species counted can reflect meaningful biological patterns, I would suggest refraining from drawing any conclusions from these results without increasing sampling size and sampling efforts in Madagascar.

4.3 Joint insights of parts 1 and 2

The lack of clear patterns within the faunal dispersed subset and the similarity of trends between wood density and tree dispersal traits in the full dataset and the faunal subset reflect the large share of species with unclear dispersal vector and the comparably small faunal subset (Table 7). The correlations found in the faunal dispersed subset were overall weak and uncertain, as they changed with the slight changes in the dataset coming from iterations of the MICE imputation. In combination with the small R^2 values of the linear regression models, this suggests a low explanatory power of the dataset. Additionally, the share of missing trait data was very high especially for seed traits and the carbon traits maximum stem diameter and wood density. This suggests that the correlations found between fruit traits were much more solid than the correlations with seed traits.

Table 7. Number of species in dataset per dispersal type.

Dispersal type	Number of species
Abiotic	16
Faunal	155
Unknown	429

While correlations between carbon traits and dispersal traits were weak on species level, interestingly, correlations among tree dispersal traits were stronger, especially positive correlations between seed size and fruit size. Since seed size is limited by fruit size, these correlations are to be expected. The same positive correlations were also found on plot level, and fruit size was positively linked to average height. Similar results were found in a study by Wright et al., 2007 in Neotropical forests. While the positive link between seed size and fruit size might be straightforward, the link between height and seed size remains not fully understood. One theory trying to explain the positive is the time a species requires to reach reproductive maturity. With the long juvenile period of large species, high juvenile survivorship is necessary, which may be associated with larger seed sizes (Moles et al., 2004).

Striking was that fruit size was the only tree dispersal trait that was significantly positively correlated on species level and plot level with agb and the additional carbon traits average height and maximum stem diameter, while only trends with wood density were not significant. The low explanatory power and the correlations between tree dispersal traits, and with additional carbon traits indicate that wood density may not be enough to explain these relationships. This assumption might be supported by the results of the PCA on species and

plot levels. With the first two principal components only describing about 30% of variance in the data, the axes could not explain enough of the variance to reduce the dimensions of the dataset and exclude variables. Therefore, there might be a higher complexity within relationships between carbon traits and dispersal traits, which require further research. In addition, more data on dispersal types is necessary to better understand the share, distribution, and characteristics of faunal dispersed and abiotically dispersed tree species in southern African woodlands, as well as the role of faunal seed dispersal.

Limitations of the research

Finally, I would like to emphasize that all findings and hypotheses discussed were results of the analysis of data with a high percentage of missing values. Not only was the dispersal vector unclear for more than half of the tree species that species-level analysis was based on, but the share of missing values in the trait data was very high. Leaving out species with missing traits was not an option because no species would have been left, which is why I chose to impute the missing values. The large share of missing data needs to be considered when drawing any conclusions from these results.

Furthermore, although I took differences in plot size and shape into account in my calculations, it is worth mentioning that not all plots included in the analysis were set up and sampled following the same protocols. The same goes for the human use classification: the original classification of the plots in South Africa were kept and used as an example for the classification of plots in Madagascar and Angola. However, I classified the plots in Angola solely based on the distance to the main road without having seen any of the plots. In the case of Madagascar, all plots were used by humans to some extent, and the difference in distance that the classification was based on was considerably smaller than in the other countries. The level of disturbance in highly disturbed plots in Madagascar might therefore be very different to high disturbance in South Africa or Angola, which I tried to factor in by grouping by country in the analysis of SQ5. Unfortunately, due to the lack of additional information, the plots in Mozambique could not be included in the country-level analysis. Hopefully, Mozambique can be included in the following analyses of the FACA team.

I previously mentioned a sampling error that was made during the fieldwork. Due to difficulties with the KoboToolBox smartphone, the first trees in the first plot needed to be resampled. During resampling, damage causes were not recorded, and this information is missing for some of the resampled trees. This is the reason why this data was not used for the human disturbance classification but did not jeopardize my results.

Lastly, since I found that the two principal components explained only 30% of variance instead of 80% as generally expected, the PCA turned out to be not ideal for data visualization and dimension reduction. While the low level of variance explained through the principal components may have indications for the complexity and interrelatedness of variables, future analyses may include additional dimension reduction techniques, such as multidimensional scaling (MDS) or t-distributed stochastic neighbor embedding (t-SNE). Due to the high complexity of this research, I did not have enough time to perform an alternative dimension reduction analysis.

5. Conclusion

The research question “*What is the relationship between faunal seed dispersal, tree dispersal traits and carbon storage in southern African woodlands?*” can be answered by bringing together the insights of the five sub-questions, specifically answered in the previous discussion sections. The results have shown a weak positive link between wood density and seed dimensions and mass, a positive link between agb and seed dimensions, seed mass, and fruit dimensions, and a negative overall effect of human disturbance on agb and tree dispersal traits (Figure 25). The large share of species with unclear dispersal vector highlights the need for further research on faunal activity and seed dispersal mechanisms. Furthermore, the results raise new questions for further investigations, such as the negative link between seed mass and seed length, and the ambivalent effect of human disturbance on CWM seed mass in the plots in South Africa. To shed light on these findings, further research is needed.

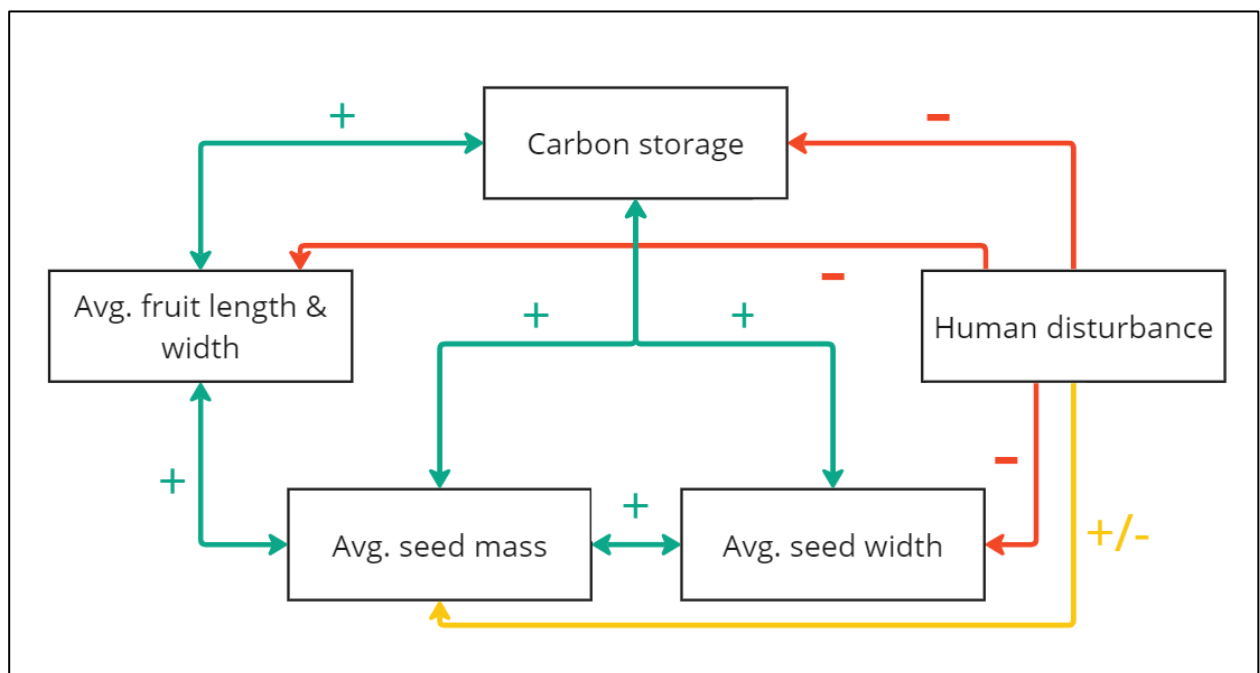


Figure 25. Relationship between seed dispersal traits, carbon storage and the effect of human disturbance, based on analysis results. Arrows indicating positive relationships in green (+), negative relationships in red (-), and ambivalent relationships in yellow (+/-).

Implications for climate action and biodiversity conservation

The research findings help to shed light on the intertwined relationship between faunal seed dispersal, tree dispersal traits and carbon storage in Southern African woodlands. Better understanding of this relationship helps to maximize carbon storage capacities in savanna

ecosystems instead of reforesting them for carbon storage, and to find synergies between carbon storage and biodiversity conservation goals. At the same time, promoting carbon storage through restoring full functionality of savannas prevents potential threats posed by projects aiming to reforest savannas, such as biodiversity loss and changes in fire regimes.

In addition to the scientific relevance of this study, restoration and conservation of savanna ecosystems further benefits local communities. Savannas support the livelihood of millions of households in Africa through providing ecosystem services such as timber and non-timber forest products. In Madagascar, for instance, local silk production depends on functional tapia woodlands and is not only important for the local economy, but the silk is used for burial shrouds, highlighting not only the economic but also the cultural importance of these ecosystems.

This research has given first insights in the relationship between faunal seed dispersal, tree dispersal traits and carbon storage in southern African woodlands. The results have pointed out interesting links to further investigate and paved the way for future research. Most of all, the findings of this research highlight the importance of exploring synergies between the climate action, biodiversity conservation, and the improvement of local livelihoods.

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Bibliography

- Albert-Daviaud, A., Perillo, S., & Stuppy, W. (2018). Seed dispersal syndromes in Madagascan flora: The unusual importance of primates. *Oryx*, 52(3), 418 – 426.
<https://doi.org/10.1017/S0030605317001600>
- Alvarado, S. T., Buisson, E., Rabarison, H., Rajeriarison, C., Birkinshaw, C., Lowry, P. P., & Morellato, L. P. C. (2014). Fire and the reproductive phenology of endangered Madagascar sclerophyllous tapia woodlands. *South African Journal of Botany*, 94, 79 – 87.
<https://doi.org/10.1016/j.sajb.2014.06.001>
- Amara, E., Heiskanen, J., Aynekulu, E., & Pellikka, P. K. E. (2019). Relationship between carbon stocks and tree species diversity in a humid Guinean savanna landscape in norther Sierra Leone. *Southern Forests: a Journal of Forest Science*, 81(3), 235 – 245.
<https://doi.org/10.2989/20702620.2018.1555947>
- Andela, N., Morton, D. C., Giglio, L., Chen, Y., van der Werf, G. R., Kasibhatla, P. S., DeFries, R. S., Collatz, G. J., Hantson, S., Kloster, S., Bachelet, D., Forrest, M., Lasslop, G., Li, F., Mangeon, S., Melton, J. R., Yue, C., & Randerson, J. T. (2017). A human-driven decline in global burned area. *Science*, 356(6345), 1356 – 1362. <https://doi.org/10.1126/science.aal4108>
- Andriamanohera, M. A., Rakotoarisoa, S. E., & Lehmann, C. E. R. (2020). 953. Uapaca Bojeri: Phyllanthaceae. *Curtis's Botanical Magazine*, 37(3), 313–323.
<https://doi.org/10.1111/curt.12345>
- Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T., J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Monteagudo, A., Neill, D. A., Núñez Vargas, P., Pitman, N. C. A., Silva, J. N. M., & Vásquez Martínez, R. (2004). Increasing biomass in Amazonien forest plots. *Philosophical Transactions of the Royal Society B*, 359(1443), 353 – 365. <https://doi.org/10.1098/rstb.2003.1422>
- Baohanta, R., Thioulouse, J., Ramanankierana, H., Prin, Y., Rasolomampianina, R., Baudoin, E., & Duponnois, R. (2012). Restoring native forest ecosystems after exotic tree plantation in Madagascar: Combination of the local ectotrophic species *Leptolena bojeriana* and *Uapaca bojeri* mitigates the negative influence of the exotic species *Eucalyptus camaldulensis* and *Pinus patula*. *Biol Invasions* 14(11), 2407–2421. <https://doi.org/10.1007/s10530-012-0238-5>
- Bello, C., Galetti, M., Pizo, M. A., Magnago, L. F. S., Rocha, M. F., Lima, R. A. F., Peres, C. A., Ovaskainen, O., & Jordano, R. (2015). Defaunation affects carbon storage in tropical forests. *Science Advances*, 1(11), e1501105. <https://doi.org/10.1126/sciadv.1501105>
- Bolmgren, K., & Eriksson, O. (2010). Seed mass and the evolution of fleshy fruits in angiosperms. *Oikos*, 119(4), 707 – 718. <https://doi.org/10.1111/j.1600-0706.2009.17944.x>

- Bond, W. J., Stevens, N., Midgley, G. F., & Lehmann, C. E. R. (2019). The trouble with trees: Afforestation plans for Africa. *Trends in Ecology & Evolution*, 34(11), <https://doi.org/10.1016/j.tree.2019.08.003>
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59 – 67. <https://doi.org/10.1038/nature11148>
- Castro, J., Hódar, J. A., & Gomez, J. M. (2006). Seed size. In A. S. Basra (Ed), Handbook of seed science and technology (pp. 397 – 428). Haworth Press.
- Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B. W., Ogawa, H., Puig, H., Riéra, B., & Yamakura, T. (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145, 87–99. <https://doi.org/10.1007/s00442-005-0100-x>
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12(4), 351 – 366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>
- Dass, P., Houlton, B. Z., Wang, Y., & Warlind, D. (2018). Grasslands may be more reliable carbon sinks than forests in California. *Environmental Research Letters*, 13(7), 074027. <https://doi.org/10.1088/1748-9326/aac339>
- De Moral, R., & Muller, C. H. (1970). The allelopathic effects of *Eucalyptus camaldulensis*. *The American Midland Naturalist*, 88(1), 254 – 282. <https://doi.org/10.2307/2424020>
- Deweese, P. A., Campbell, B. M., Katerere, Y., Siteo, A., Cunningham, A. B., Angelsen, A., & Wunder, S. (2010). Managing the miombo woodlands of southern Africa: Policies, incentives and options for the rural poor. *Journal of Natural Resources Policy Research*, 2(1), 57 – 73. <https://doi.org/10.1080/19390450903350846>
- Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Martí, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. C., Shirvany, F. A., Vendramini, F.,... Zak, M. R. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*. 15(3), 295–304. <https://doi.org/10.1111/j.1654-1103.2004.tb02266.x>
- Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345(6195), 401 – 406. <https://doi.org/10.1126/science.1251817>
- Eberhard, S., Finazzi, G., & Wollman, F. W. (2008). The dynamics of Photosynthesis. *Annual Review of Genetics*, 42, 463 – 515. <https://doi.org/10.1146/annurev.genet.42.110807.091452>

- Fawzy, S., Osman, A. I., Doran, J., & Rooney, D. W. (2020). Strategies for mitigation of climate change: A review. *Environmental Chemistry Letters*, 18, 2069 – 2084.
<https://doi.org/10.1007/s10311-020-01059-w>
- Foxcroft, L. C., Richardson, D. M., Rejmánek, M., & Pysěk, P. (2010). Alien plant invasions in tropical and sub-tropical savannas: patterns, processes and prospects. *Biological Invasions*, 12, 3913–3933. <https://doi.org/10.1007/s10530-010-9823-7>
- Galetti, M., & Dirzo, R. (2013). Ecological and evolutionary consequences of living in a defaunated world. *Biological Conservation*, 163, 1 – 6. <https://doi.org/10.1016/j.biocon.2013.04.020>
- Galetti, M., Guevara, R., Côrtes, M. C., Fadini, R., Von Matten, S., Leite, A. B., Labacca, F., Ribeiro, T., Carvalho, C. S., Collevatti, R. G., Pires, M. M., Guimarães, P. R., Jr, Brancalion, P. H., Ribeiro, M. C., & Jordano, P. (2013). Functional extinction of birds drives rapid evolutionary changes in seed size. *Science*, 340(6136), 1086 – 1090.
<https://doi.org/10.1126/science.1233774>
- Hannah, L., Lohse, D., Hutchinson, C., Carr, J. L., & Lanckerani, A. (1994). A preliminary inventory of human disturbance of World ecosystems. *Ambio*, 23(4/5), 246 – 250.
- Howe, H. F. (2016). Making dispersal syndrome sand networks useful in tropical conservation and restoration. *Global Ecology and Conservation*, 6, 152 – 178.
<https://doi.org/10.1016/j.gecco.2016.03.002>
- Iluz, D. (2010). Zoochory: The dispersal of plants by animals. In Z. Dubinsky, & J. Seckbach, (Eds.), *All flesh is grass* (pp. 199 – 214). Springer, Dordrecht.
https://doi.org/10.1007/978-90-481-9316-5_9
- IPCC. (2021). Summary for Policymakers. In Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (Eds.). *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 3 – 32). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- IUCN International Union for Conservation of Nature. (2020). *Restore our future: Bonn challenge*.
<https://www.bonnchallenge.org/about>
- IUCN International Union for Conservation of Nature. (2021). *Forests and climate change*.
<https://www.iucn.org/resources/issues-brief/forests-and-climate-change>
- Jenkins, P. (2003). Microgale, shrew tenrecs. In S. M. Goodman & J. P. Benstead (Eds.), *The natural history of Madagascar* (pp. 1273 – 1278). University of Chicago Press.
- Jungers, W. L., Demes, B., & Godfrey, L. R. (2008). How big were the “giant” extinct lemurs of Madagascar? In J. G. Fleagle, & C. C. Gilbert (Eds.), *Elwyn Simons: A Search for Origins* (pp. 343 -360). Springer, New York.

- Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar C, C., Aleixo, I., Ali, H., ... Wirth, C. (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, 26(1), 119 – 188. <https://doi.org/10.1111/gcb.14904>
- Kortz, A. R., Silva Matos, D. M., & Magurran, A. E. (2018). From individuals to communities: How singleton invasive pine saplings lead to biodiversity change in the Brazilian Cerrado hotspot. *Journal of Vegetation Science*, 29(5), 824–834. <https://doi.org/10.1111/jvs.12668>
- Kull, C. A. (1998). Leimavo Revisited: Agrarian land-use change in the highlands of Madagascar. *Professional Geographer*, 50(2), 163 – 176. <https://doi.org/10.1111/0033-0124.00112>
- Kull, C. A. (2002). The “degraded” Tapia woodlands of highland Madagascar: Rural economy, fire ecology, and forest conservation. *Journal of Cultural Geography*, 19(2), 95–128. <http://dx.doi.org/10.1080/08873630209478290>
- Kurten, E. L. (2013). Cascading effects of contemporaneous defaunation on tropical forest communities. *Biological Conservation*, 163, 22 – 32. <http://dx.doi.org/10.1016/j.biocon.2013.04.025>
- Kurten, E. L., Wright, S. J., & Carson, W. P. (2015). Hunting alters seedling functional trait composition in a Neotropical Forest. *Ecology*, 96(7), 1923–1932. <https://doi.org/10.1890/14-1735.1>
- Lal, R. (2007). Carbon sequestration. *Philosophical Transactions of the Royal Society B*, 363(1492), 815 – 830. <https://doi.org/10.1098/rstb.2007.2185>
- Levine, J. M., Vila, M., D'Antonio, C. M., Dukes, J. S., Grigulis, K., & Lavorel, S. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270, 775–781. <https://doi.org/10.1098/rspb.2003.2327>
- Lexerød, N. L. (2005). Recruitment models for different tree species in Norway. *Forest Ecology and Management*, 206(1-3), 91 – 108. <https://doi.org/10.1016/j.foreco.2004.11.001>
- MacDougall, A. S., McCann, K. S., Gellner, G., & Turkington, R. (2013). Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature*, 494, 86 - 89. <https://doi.org/10.1038/nature11869>
- Marsico, T. D., Burt, J. W., Espeland, E. K., Gilchrist, G. W., Jamieson, M. A., Lindstrom, L., Roderick, G. K., Swope, S., Szucs, M., & Tsutsui, N. D. (2010). Perspective: Underutilized resources for studying the evolution of invasive species during their introduction, establishment, and lag phases. *Evolutionary Applications*, 3(2), 203–217. <https://doi.org/10.1111/j.1752-4571.2009.00101.x>

- McNicol, I. M., Ryan, C. M., Dexter, K. G., Ball, S. M. J., & Williams, M. (2018). Aboveground carbon storage and its links to stand structure, tree diversity and floristic composition in South-Eastern Tanzania. *Ecosystems*, 21, 740 – 754. <https://doi.org/10.1007/s10021-017-0180-6>
- McPherson, E. G. (1998). Atmospheric carbon dioxide reduction by Sacramento's urban forest. *Journal of Arboriculture*, 24(4), 215 – 223.
- Midgley, J. J., Gallaher, K., & Kruger, L. M. (2012). The role of the elephant (*Loxodonta Africana*) and the tree squirrel (*Paraxerus cepapi*) in marula (*Sclerocarya birrea*) seed predation, dispersal and germination. *Journal of Tropical Ecology*, 28(2), 227 – 231. <https://doi.org/10.1017/S0266467411000654>
- Missanjo, E., & Matsumura, J. (2016) Wood density and mechanical properties of *Pinus kesiya roylei* ex Gordon in Malawi. *Forests* 7(7), 1–10. <https://doi.org/10.3390/f7070135>
- Mittermeier, R. A., Myers, N., Thomsen, J. B., Da Fonseca, G. A. B., & Olivieri, S. (1998). Biodiversity Hotspots and Major Tropical Wilderness Areas: Approaches to Setting Conservation Priorities. *Conservation Biology*, 12(3), 516–520. <https://doi.org/10.1046/j.1523-1739.1998.012003516.x>.
- Moles, A. T., Falster, D. S., Leishman, M. R., & Westoby, M. (2004). Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. *Journal of Ecology* 92(3), 384–396. <https://doi.org/10.1111/j.0022-0477.2004.00880.x>
- Moran, V. C., Hoffmann, J. H., Donnelly, D., Wilgen, B. W., Zimmermann, H. G., & Spencer, N. R. (2000). Biological control of alien, invasive pine trees (*Pinus* species) in South Africa. In N. R. Spencer (Ed.), *Proceedings of the Xth International Symposium on Biological Control of Weeds* (pp. 941–953). Mozeman: Montane State University.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858. <https://doi.org/10.1038/35002501>.
- Namah, J., Midgley, J. J., & Kruger, L. M. (2019). Reproductive biology of the sausage tree (*Kigelia africana*) in Kruger National Park, South Africa. *Koedoe*, 61(1), a1512. <https://doi.org/10.4102/koedoe.v61i1.1512>
- Núñez-Iturri, G., & Howe, H. F. (2007). Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in Western Amazonia. *Biotropica* 39, 348–354. <https://doi.org/10.1111/j.1744-7429.2007.00276.x>
- Obroucheva, N. V., & Antipova, O. V. (2004). The role of water uptake in the transition of recalcitrant seeds from dormancy to germination. *Russian Journal of Plant Physiology*, 51, 848 – 856. <https://doi.org/10.1023/B:RUPP.0000047835.84851.b1>
- Osborne, C. P., Charles-Dominique, T., Stevens, N., Bond, W. J., Midgley, G., & Lehmann, C. E. R. (2018). Human impacts in African savannas are mediated by plant functional traits. *New Phytologist*, 220(1), 10 – 24. <https://doi.org/10.1111/nph.15236>

- Osuri, A. M., Ratnam, J., Varma, V., Alvarez-Loayza, P., Astaiza, J. H., Bradford, M., Fletcher, C., Ndoundou-Hockemba, M., Jansen, P. A., Kenfack, D., Marshall, A. R., Ramesh, B. R., Rovero, F., & Sankaran, M. (2016). Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nature Communications*, *7*, 11351.
<https://doi.org/10.1038/ncomms11351>
- Parr, C. L., Lehmann, C. E. R., Bond, W. J., Hoffmann, W. A., & Andersen, A. N. (2014). Tropical grassy biomes: Misunderstood, neglected, and under threat. *Trends in Ecology & Evolution*, *29*(4), 205 – 213. <http://dx.doi.org/10.1016/j.tree.2014.02.004>
- Peres, C. A., Emilio, T., Schietti, J., Desmoulière, S. J. M., & Levi, T. (2016). Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *PNAS*, *113*, 892-897.
<https://doi.org/10.1073/pnas.1516525113>
- Pimm, A. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752.
<https://doi.org/10.1126/science.1246752>
- Poulsen, J. R., Clark, C. J., & Palmer, T. M. (2013). Ecological erosion of an Afrotropical forest and potential consequences for tree recruitment and forest biomass. *Biological Conservation*, *163*, 122–130. <https://doi.org/10.1016/j.biocon.2013.03.021>
- Primack, R. B. (1987). Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics*, *18*(1), 409 – 430.
- Rajaonarivelo, H. M., Flores, O., Rakotondrasoa, O. L., Rajemison, A. H., Ramamonjisoa, B., & Bouvet, J. – M. (2022). The interplay of disturbance, vegetation structure, and propagule pressure contributes to *Pinus kesiya* invasion in tapia woodland, Madagascar. *Biol Invasions*, *24*, 2997 – 3011. <https://doi.org/10.1007/s10530-022-02819-1>
- Ramanankierana, H., Baohanta, R., Thioulouse, J., Prin, Y., Randriambanona, H., Baudoin, E., Rakotoarimanga, N., Galiana, A., Rajaonarimamy, E., Lebrun, M., & Duponnois, R. (2013). Early growth improvement on endemic tree species by soil mycorrhizal management in Madagascar. In C.A. Busso (Ed.), *From seed germination to young plants: Ecology, growth and environmental influences* (pp. 1 - 30). Nova Science Publishers, Inc.
- Randriamampionona, D., Rafamantanana, M., Rabemanantsoa, C., Rakotoniriana, F., Cheuk, K., Corbisier, A.-M., Mahillon, J., Ratsimamanga, S., & El Jaziri, M. (2007). Ex situ conservation and clonal propagation of the Malagasy *Syzygium cuminii*, and antidiabetic plant. *Belgian Journal of Botany*, *141*(1), 14 – 20. <https://www.jstor.org/stable/20794648>
- Reqzena Suarez, D., Rozendaal, D. M. A., De Sy, V., Decuyper, M., Málaga, N., Durán Montesinos, P., Arana Olivos, A., De la Cruz Paiva, R., Martius, C., Herold, M. (2022). Forest disturbance and recovery in Peruvian Amazonia. *Global Change Biology*, *29*(13), 3601 – 3621.
<https://doi.org/10.1111/gcb.16695>

- Richter, H. V., & Cumming, G. S. (2006). Food availability and annual migration of the straw-colored fruit bat (*Eidolon helvum*). *Journal of Zoology*, 268(1), 35 – 44.
<https://doi.org/10.1111/j.1469-7998.2005.00020.x>
- Ringnér, M. (2008). What is principal component analysis?. *Nature Biotechnology*, 26, 303 – 304.
<https://doi.org/10.1038/nbt0308-303>
- Rodrigues-Junior, A., Mello, A. C. M. P., Baskin, C. C., Baskin, J. M., Oliveira, D. M. T., & Garcia, Q. S. (2018). Why large seeds with physical dormancy become nondormant earlier than small ones. *PLoS ONE*, 13(8), e0202038. <https://doi.org/10.1371/journal.pone.0202038>
- Ryan, C. M., Pritchard, R., McNicol, I., Owen, M., Fisher, J. A., & Lehmann, C. (2016). Ecosystem services from southern African woodlands and their future under global change. *Philosophical Transactions of the Royal Society B*, 371(1703), 20150312.
<http://dx.doi.org/10.1098/rstb.2015.0312>
- Schober, P., Boer, C., & Schwarte, L. A. (2018). Correlation Coefficients: Appropriate use and interpretation. *Anesthesia & Analgesia*, 126(5), 1763–1768.
<https://doi.org/10.1213/ane.0000000000002864>
- Schmidtz, D., & Willott, E. (2012). Private landowners cooperate to sustain wildlife habitat: The case of the Sabi Sand Game Reserve. *Journal of Applied Corporate Finance*, 24(2), 78 – 85.
<https://doi.org/10.1111/j.1745-6622.2012.00382.x>
- Scholes, R. J., & Archer, S. R. (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, 28, 517 – 544. <https://doi.org/10.1146/annurev.ecolsys.28.1.517>
- SEOSAW partnership. (2021). A network to understand the changing socio-ecology of the southern African woodlands (SEOSAW): Challenges, benefits, and methods. *Plants, People, Planet*, 3(3), 249-267. <https://doi.org/10.1002/ppp3.10168>
- Solofondranohatra, C. L., Vorontsova, M. S., Hackel, J., Besnard, G., Cable, S., Williams, J., Jeannoda, V., & Lehmann, C. E. R. (2018). Grass functional traits differentiate forest and savanna in the Madagascar central highlands. *Frontiers in Ecology and Evolution*, 6(184).
<https://doi.org/10.3389/fevo.2018.00184>
- Terborgh, J., Nuñez-Iturri, G., Pitman, N. C. A., Valverde, F. H. C., Alvarez, P., Swamy, V., Pringle, E. G., Paine, C. E. T. (2008). Tree recruitment in an empty forest. *Ecology*, 89(6), 1757–1768.
<https://doi.org/10.1890/07-0479.1>
- Thompson, K., & Rabinowitz, D. (1989). Do big plants have big seeds? *The American Naturalist*, 133, 722–728. <https://doi.org/10.1086/284947>
- Tripathi, H. G., Mzumara, T. I., Martin, R. O., Parr, C. L., Phiri, C., & Ryan, C. M. (2019). Dissimilar effects of human and elephant disturbance on woodland structure and functional bird diversity in the mopane woodlands of Zambia. *Landscape Ecology*, 34, 357–371.
<https://doi.org/10.1007/s10980-019-00774-2>

- Tuthill, J. E., Ortega, Y. K., & Pearson, D. E. (2023). Seed size, seed dispersal traits, and plant dispersion patterns for native and introduced grassland plants. *Plants*, 12(5), 1032. <https://doi.org/10.3390/plants12051032>
- Van der Pijl, L. (1982). *Principles of dispersal in higher plants* (3rd ed.). Berlin: Springer-Verlag.
- Veldman, J. W., Overbeck, G. E., Negreiros, D., Mahy, G., Le Stradic, S., Fernandes, G. W., Durigan, G., Buisson, E., Putz, F. E. & Bond, W. J. (2015). Where tree planting and forest expansion are bad for biodiversity and ecosystem services. *BioScience*, 65(10), 1011 – 1018. <https://doi.org/10.1093/biosci/biv118>
- Whitehurst, A. S., Sexton, J. O., & Dollar, L. (2009). Land cover change in western Madagascar's dry deciduous forests: a comparison of forest changes in and around Kirindy Mite National Park. *Oryx*, 43(2), 275–283. <https://doi.org/10.1017/S0030605309001756>.
- Wright, P. C. (1999). Lemur traits and Madagascar ecology: Coping with an island environment. *American Journal of Physical Anthropology, Suppl 29*, 31–72. [https://doi.org/10.1002/\(SICI\)1096-8644\(1999\)110:29+<31::AID-AJPA3>3.0.CO;2-0](https://doi.org/10.1002/(SICI)1096-8644(1999)110:29+<31::AID-AJPA3>3.0.CO;2-0)
- Wright, I. J., Ackerly, D. D., Bongers, F., Harms, K. E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Paz, H., Pitman, N. C. A., Poorter, L., Silman, M. R., Vriesendorp, C. F., Webb, C. O., Westoby, M., & Wright, S. J. (2007). Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany*, 99(5), 1003–1015. <https://doi.org/10.1093/aob/mcl066>
- WWF. (2022). *Living Planet Report 2022 – Building a nature-positive society*. Almond, R.E.A., Grooten, M., Juffe Bignoli, D. & Petersen, T. (Eds). WWF, Gland, Switzerland.

Appendix

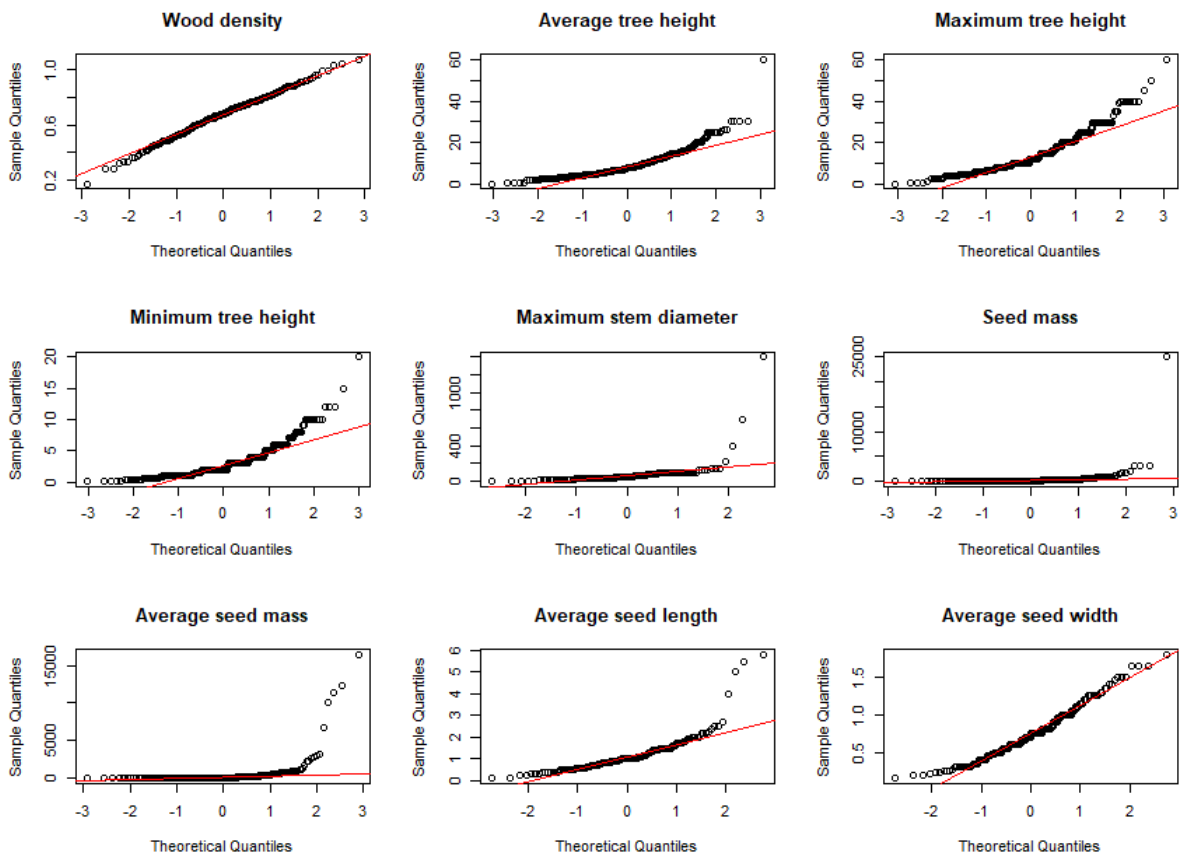
Methodology

Table S 1. Asymptotic one-sample Kolmogorov-Smirnov test results before MICE imputation and log transformation.

Variable	D	p-value
Stems	0.5	< 2.2e-16
Wood.density	0.61621	< 2.2e-16
average.height	0.96935	< 2.2e-16
Max.height	0.98754	< 2.2e-16
Min.height	0.75234	< 2.2e-16
Seed.average.length	0.59898	< 2.2e-16
Max.length.(seed)	0.61632	< 2.2e-16
Min.length.(seed)	0.6037	< 2.2e-16
Seed.average.width	0.57338	< 2.2e-16
Max.width.(seed)	0.58106	< 2.2e-16
Min.width.(seed)	0.57033	< 2.2e-16
Fruit.average.length	0.63229	< 2.2e-16
Fruit.max.length	0.66845	< 2.2e-16
Fruit.min.length	0.60128	< 2.2e-16
Fruit.average.width	0.62808	< 2.2e-16
Fruit.max.width	0.66002	< 2.2e-16
Fruit.min.width	0.59275	< 2.2e-16
Seed.mass	0.94515	< 2.2e-16
Avg.1000.seed.mass	0.94703	< 2.2e-16
Max.no.carpels	0.84134	< 2.2e-16
Max.no.locules	0.84134	< 2.2e-16
Max.stem.diam	0.97575	< 2.2e-16

Table S 2. Asymptotic one-sample Kolmogorov-Smirnov test results of faunal dispersed subset after MICE imputation and log transformation.

Variable	D	p-value
Stems	0.46921	< 2.2e-16
Wood.density	0.60489	< 2.2e-16
average.height	0.90141	< 2.2e-16
Seed.average.length	0.58672	< 2.2e-16
Seed.average.width	0.59666	< 2.2e-16
Fruit.average.length	0.60528	< 2.2e-16
Fruit.average.width	0.60565	< 2.2e-16
Seed.mass	0.90272	< 2.2e-16
Avg.1000.seed.mass	0.89647	< 2.2e-16
Max.no.carpels	0.49204	< 2.2e-16
Max.no.locules	0.4825	< 2.2e-16
Max.stem.diam	0.93771	< 2.2e-16



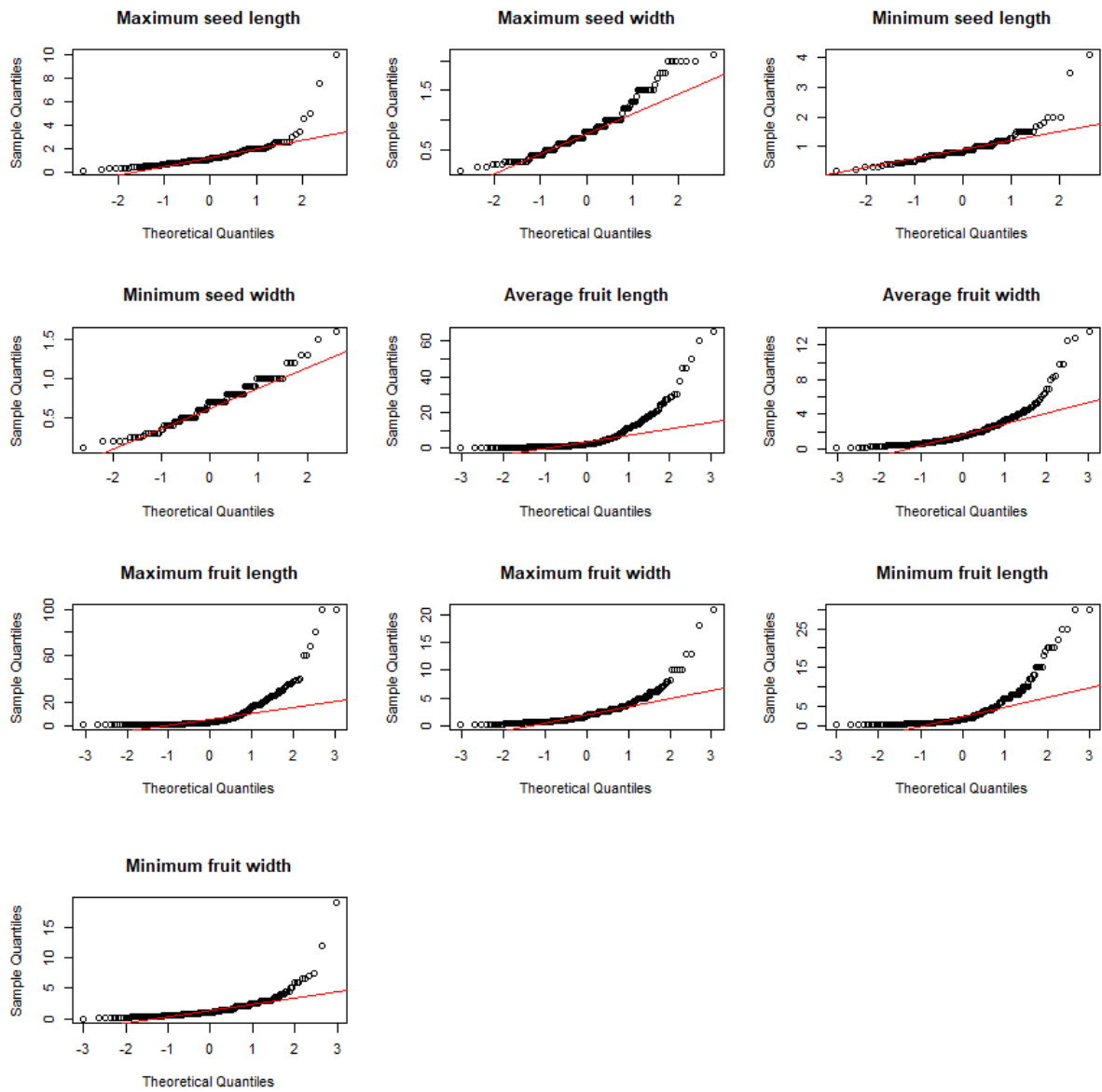


Figure S 1. Q-Q-plots before MICE imputation and log transformation.

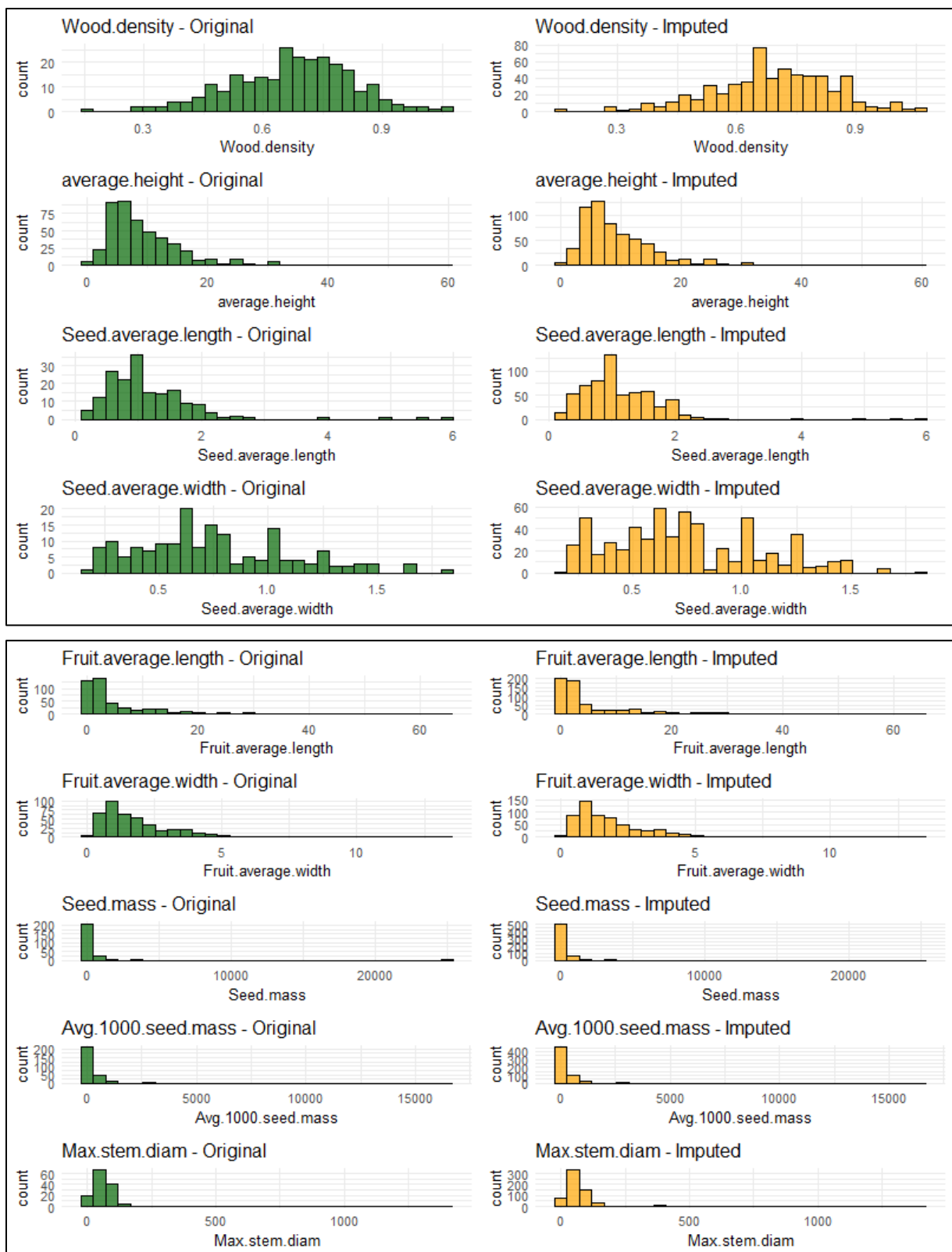


Figure S 2. Histograms before & after MICE imputation. Green plots visualizing data before MICE imputation, yellow plots visualizing data after MICE imputation.

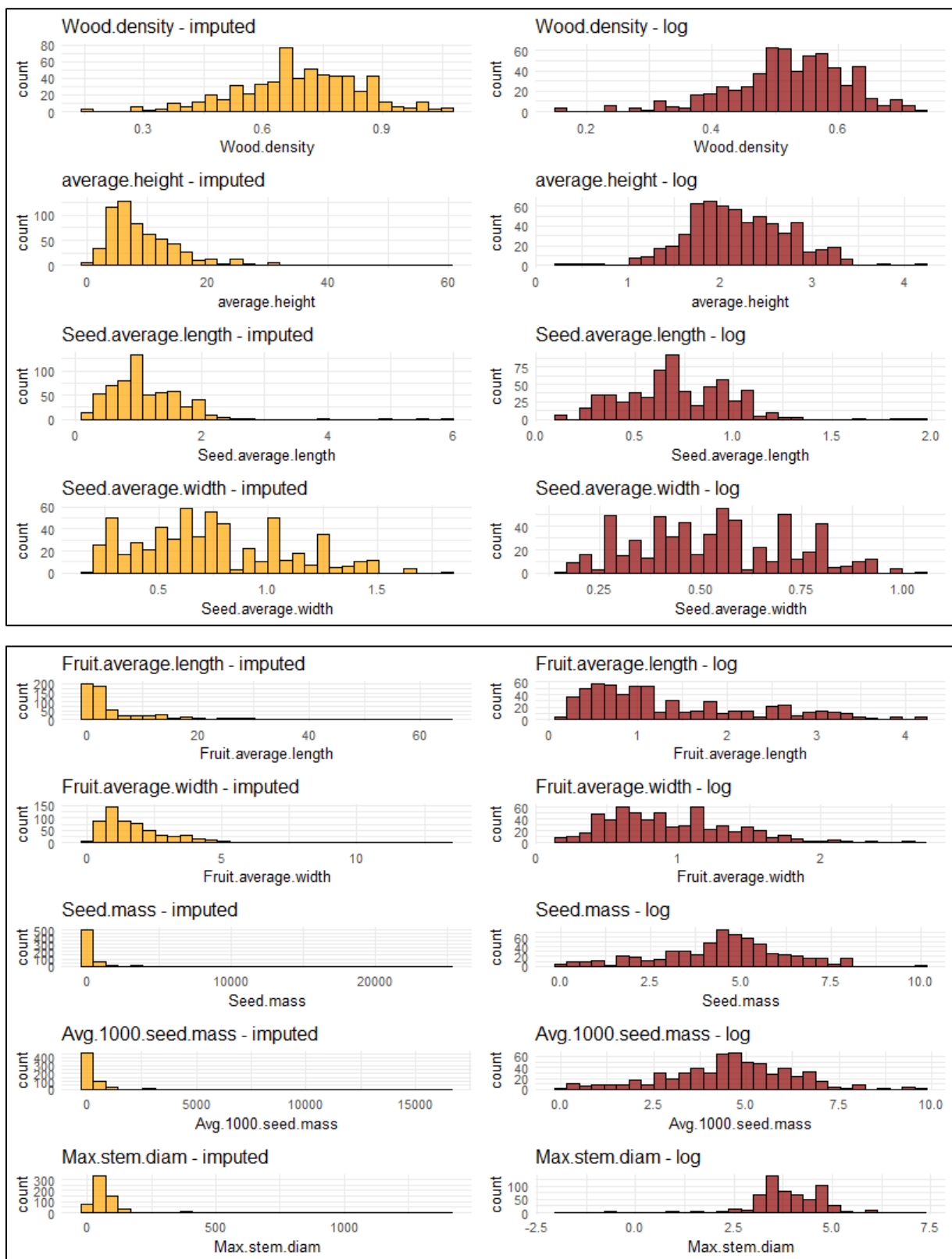
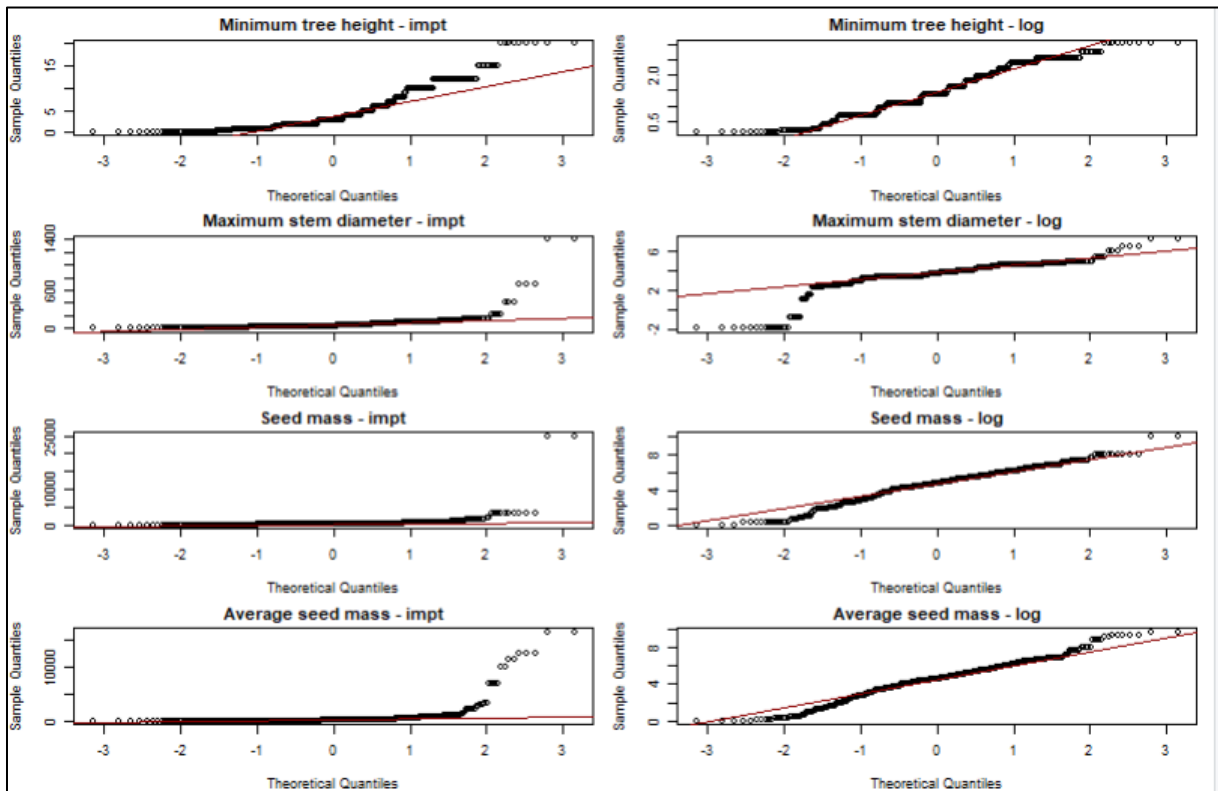
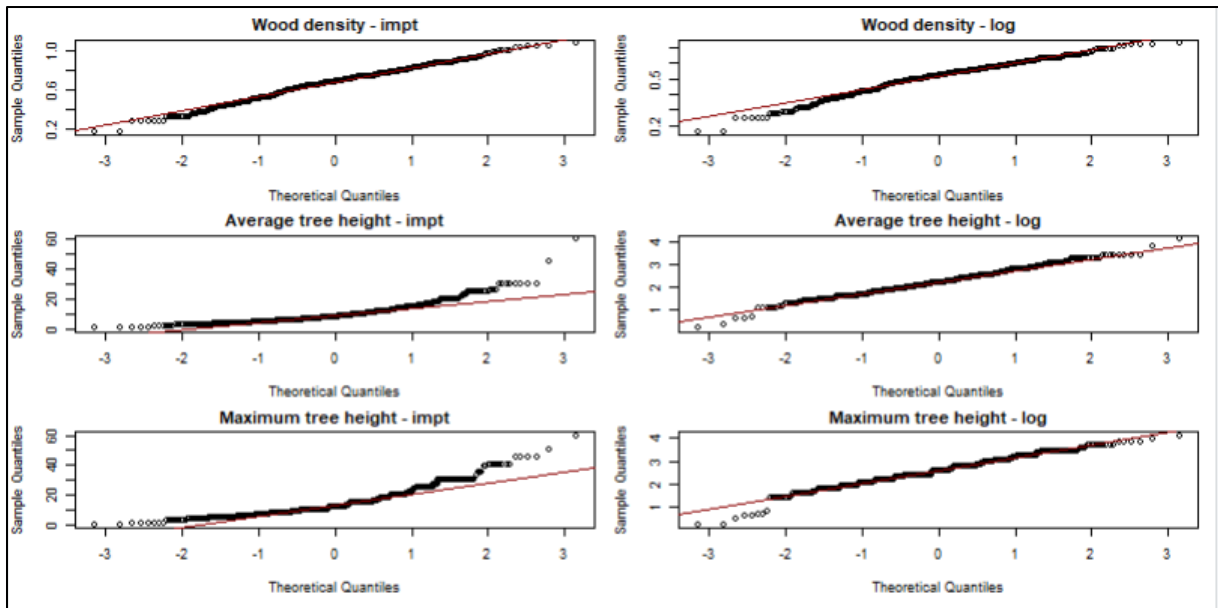
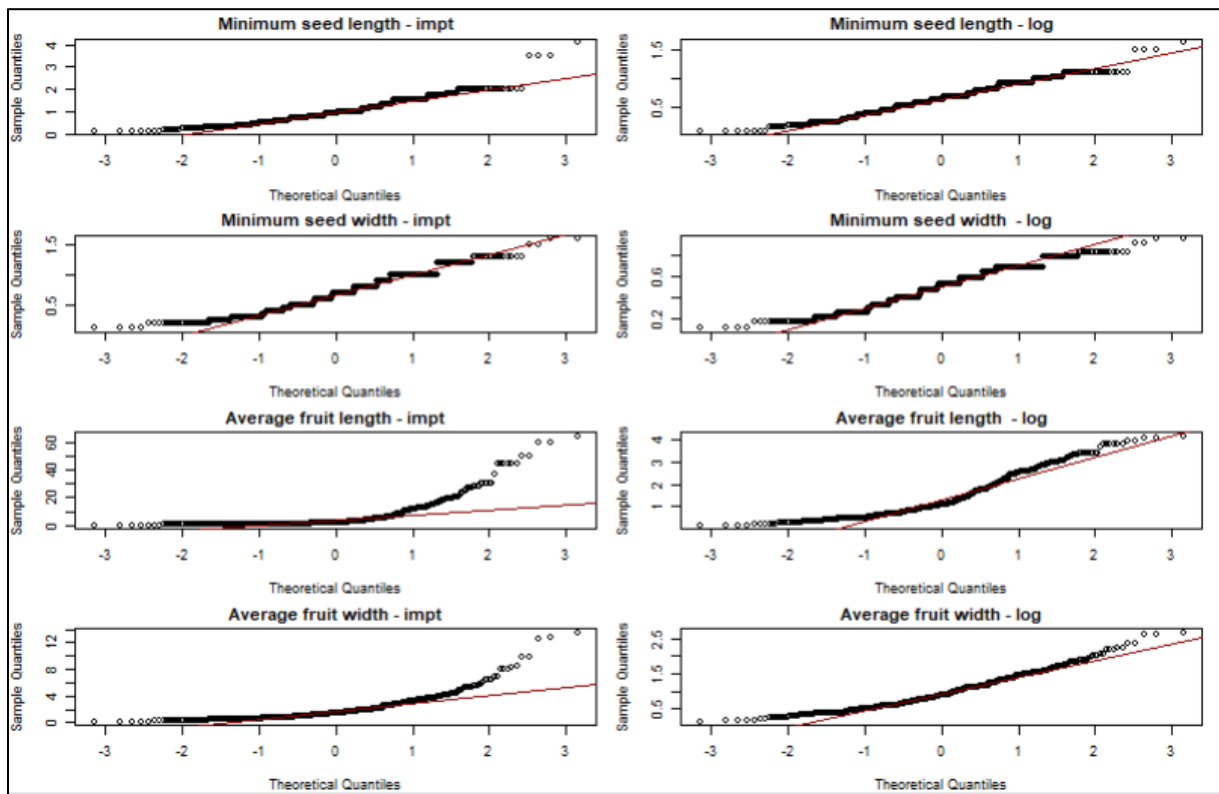
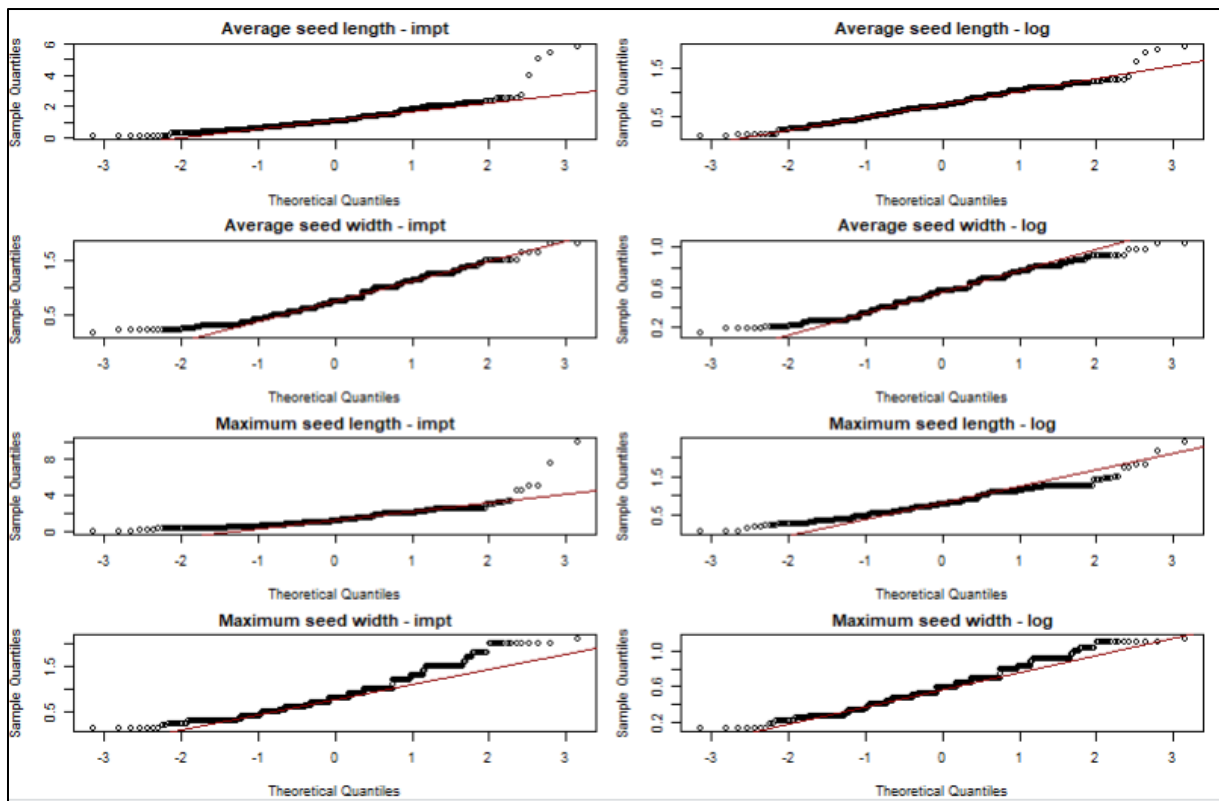


Figure S 3. Histograms before and after log transformation. Yellow plots visualizing data after MICE imputation but before log transformation, red plots visualizing data after MICE imputation and log transformation.





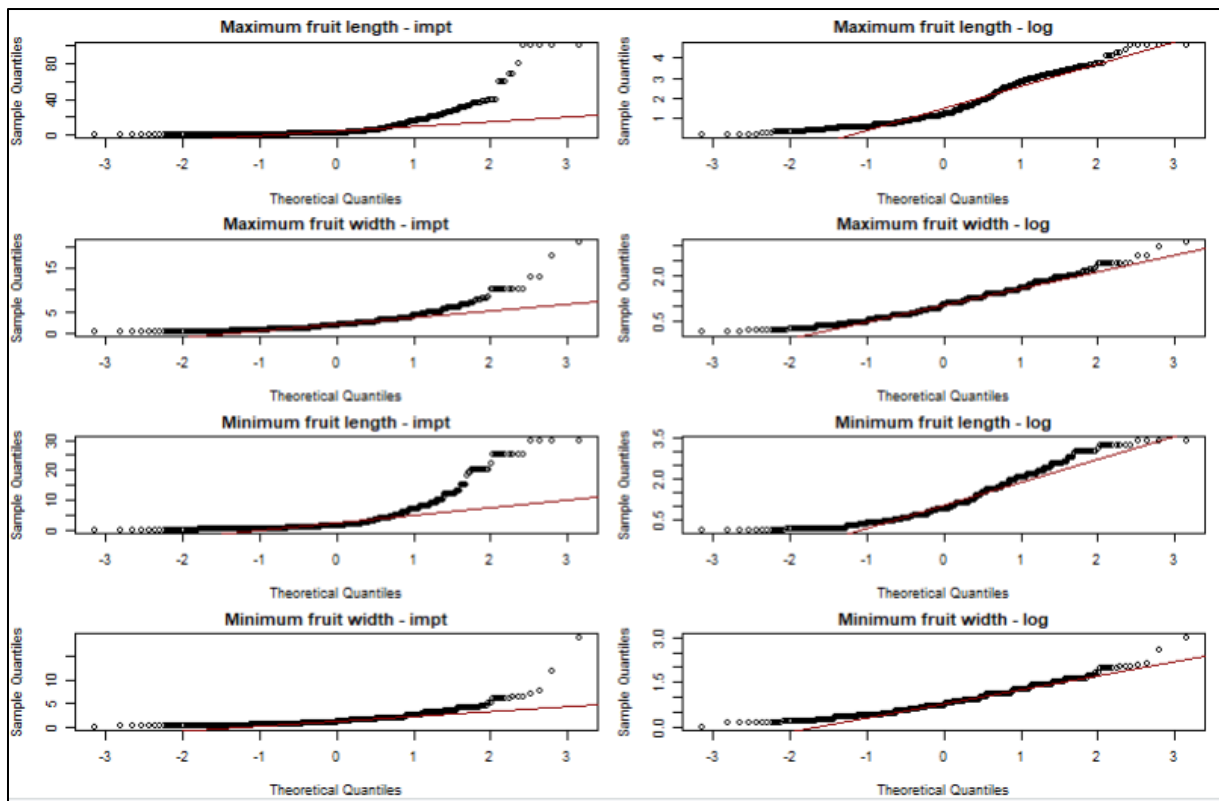


Figure S 4. Q-Q-plots before and after log transformation.

Part 1: Madagascar tree inventory

Table S 3. List of identified species identified in the five novel SEOSAW plots in Madagascar using the small stems protocol.

Species small stems protocol
Acacia sp
Aphloia theiformis
Buddleja madagascariensis
Cussonia bojeri
Desmodium sp
Eucalyptus robusta
Grewia sp
Kotschya strigosa
Lantana camara
Maesa lanceolata
Manihot esculenta
Mussaenda arcuata
Philippia sp
Pinus kesiya
Psiadia altissima
Psychotria retiphlebia
Pteridium sp
Rubus apetalus
Salix madagascariensis
Schefflera bojeri
Uapaca bojeri
Vernonia appendiculata
Vernonia glutinosa
Vernonia polygalifolia
Xerochlamys bojeriana

Part 2: Comparison of southern African woodlands

SQ3

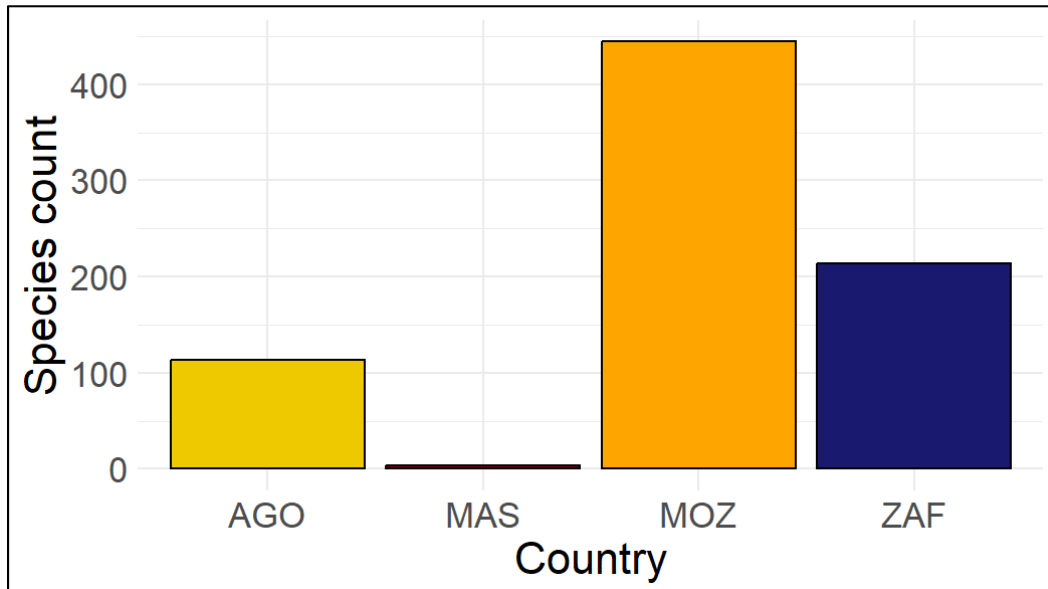


Figure S 5. Species richness per country. Angola (AGO) depicted in yellow, Madagascar (MAS) depicted in red, Mozambique (MOZ) depicted in orange, and South Africa (ZAF) depicted in blue.

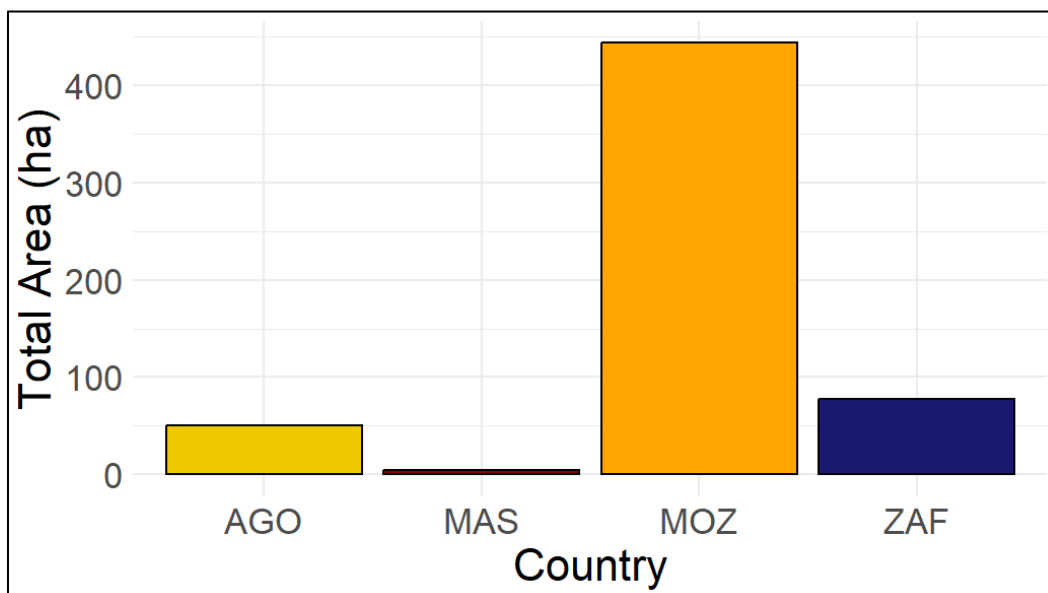


Figure S 6. Sampling area per country. Angola (AGO) depicted in yellow, Madagascar (MAS) depicted in red, Mozambique (MOZ) depicted in orange, and South Africa (ZAF) depicted in blue.

SQ4

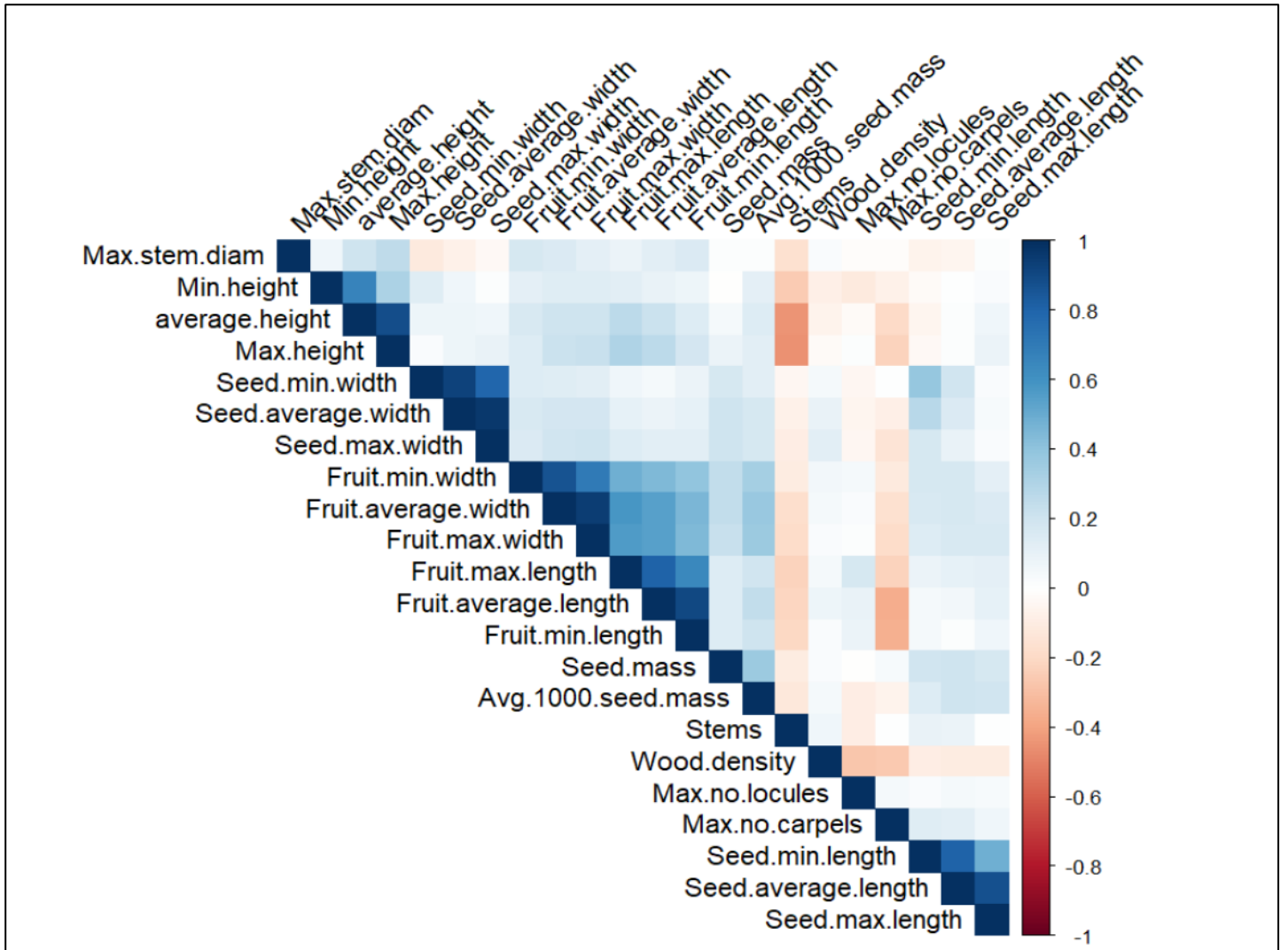


Figure S 7. Correlation heatmap before grouping. Positive correlations are depicted in a blue, negative correlations are depicted in red.

Table S 4. Correlation matrix of full grouped dataset. Weak correlations in italic, moderate correlation in bold.

	No. stems	Wood density	Avg. height	Avg. seed length	Avg. seed width	Avg. fruit length	Avg. fruit width	Avg. seed mass	Max.no. carpels	Max.no. locules	Avg. 1000 Seed mass	Max.stem diameter
No. stems	1	0.063893	-0.44585	0.083561	-0.07259	-0.21076	-0.17561	-0.10527	0.000116	-0.09606	-0.12213	-0.16127
Wood density	0.063893	1	-0.06804	-0.10284	0.091805	0.073307	0.045928	0.024984	-0.26564	-0.27126	0.043949	0.026162
Avg. height	-0.44585	-0.06804	1	0.014337	0.077925	0.217774	0.206362	0.047731	-0.19687	-0.02977	0.147946	0.202515
Avg. seed length	0.083561	<i>-0.10284</i>	0.014337	1	0.152784	0.058438	0.179723	0.20558	0.122759	0.045831	0.207914	-0.05165
Avg. seed width	-0.07259	0.091805	0.077925	<i>0.152784</i>	1	0.089269	0.183345	0.204426	-0.0857	-0.05277	0.171797	-0.07515
Avg. fruit length	<i>-0.21076</i>	0.073307	<i>0.217774</i>	0.058438	0.089269	1	0.546554	0.14853	-0.36278	0.093014	0.24834	0.123698
Avg. fruit width	<i>-0.17561</i>	0.045928	<i>0.206362</i>	<i>0.179723</i>	<i>0.183345</i>	0.546554	1	0.243685	-0.1603	0.025336	0.376422	0.155081
Avg. seed mass	<i>-0.10527</i>	0.024984	0.047731	<i>0.20558</i>	<i>0.204426</i>	<i>0.14853</i>	<i>0.243685</i>	1	0.031678	-0.00155	0.367369	0.016048
Max.no. carpels	0.000116	<i>-0.26564</i>	<i>-0.19687</i>	<i>0.122759</i>	-0.0857	<i>-0.36278</i>	<i>-0.1603</i>	<i>0.031678</i>	1	0.044335	-0.06654	-0.01698
Max.no. locules	-0.09606	<i>-0.27126</i>	-0.02977	0.045831	-0.05277	0.093014	0.025336	-0.00155	0.044335	1	-0.09534	-0.01563
Avg. 1000 Seed mass	<i>-0.12213</i>	0.043949	<i>0.147946</i>	<i>0.207914</i>	<i>0.171797</i>	<i>0.24834</i>	<i>0.376422</i>	<i>0.367369</i>	-0.06654	-0.09534	1	0.015136
Max.stem. diameter	<i>-0.16127</i>	0.026162	<i>0.202515</i>	-0.05165	-0.07515	<i>0.123698</i>	<i>0.155081</i>	0.016048	-0.01698	-0.01563	0.015136	1

Table S 5. Correlation matrix of faunal subset. Weak correlations in italic, moderate correlations in bold, strong correlations in bold italic.

	No. stems	Wood density	Avg. height	Avg. seed length	Avg. seed width	Avg. fruit length	Avg. fruit width	Avg. seed mass	Max.no. carpels	Max.no. locules	Avg. 1000 Seed mass	Max.stem diameter
No. stems	1	0.159115	-0.54841	-0.01418	0.069466	-0.09716	-0.10867	-0.13498	-0.10326	-0.06815	-0.11752	-0.13007
Wood density	<i>0.159115</i>	1	-0.13155	-0.12367	0.072889	0.083225	0.085676	0.087784	-0.28897	-0.15079	0.053513	-0.05118
Avg. height	-0.54841	<i>-0.13155</i>	1	0.064203	-0.00164	0.174471	0.206939	0.024341	-0.24983	-0.02764	0.145592	0.327045
Avg. seed length	-0.01418	<i>-0.12367</i>	0.064203	1	0.115249	0.262352	0.225603	0.257845	0.05129	0.056463	0.17761	0.03294
Avg. seed width	0.069466	0.072889	-0.00164	<i>0.115249</i>	1	0.240905	0.231925	0.240288	-0.05648	-0.06342	0.206644	-0.10988
Avg. fruit length	-0.09716	0.083225	<i>0.174471</i>	0.262352	<i>0.240905</i>	1	0.846006	0.27698	-0.26899	0.074714	0.411029	0.153899
Avg. fruit width	<i>-0.10867</i>	0.085676	<i>0.206939</i>	<i>0.225603</i>	<i>0.231925</i>	0.846006	1	0.329253	-0.21778	0.102734	0.428122	0.144048
Avg. seed mass	<i>-0.13498</i>	0.087784	0.024341	<i>0.257845</i>	<i>0.240288</i>	<i>0.27698</i>	<i>0.329253</i>	1	-0.00804	-0.05688	0.495047	-0.02155
Max.no. carpels	<i>-0.10326</i>	<i>-0.28897</i>	<i>-0.24983</i>	0.05129	-0.05648	<i>-0.26899</i>	<i>-0.21778</i>	-0.00804	1	0.040462	-0.09369	-0.1136
Max.no. locules	-0.06815	<i>-0.15079</i>	-0.02764	0.056463	-0.06342	0.074714	<i>0.102734</i>	-0.05688	0.040462	1	-0.08856	0.023758
Avg. 1000 seed mass	<i>-0.11752</i>	0.053513	<i>0.145592</i>	<i>0.17761</i>	<i>0.206644</i>	0.411029	0.428122	0.495047	-0.09369	-0.08856	1	0.025569
Max.stem. diameter	<i>-0.13007</i>	-0.05118	<i>0.327045</i>	0.03294	<i>-0.10988</i>	<i>0.153899</i>	<i>0.144048</i>	<i>-0.02155</i>	-0.1136	0.023758	0.025569	1

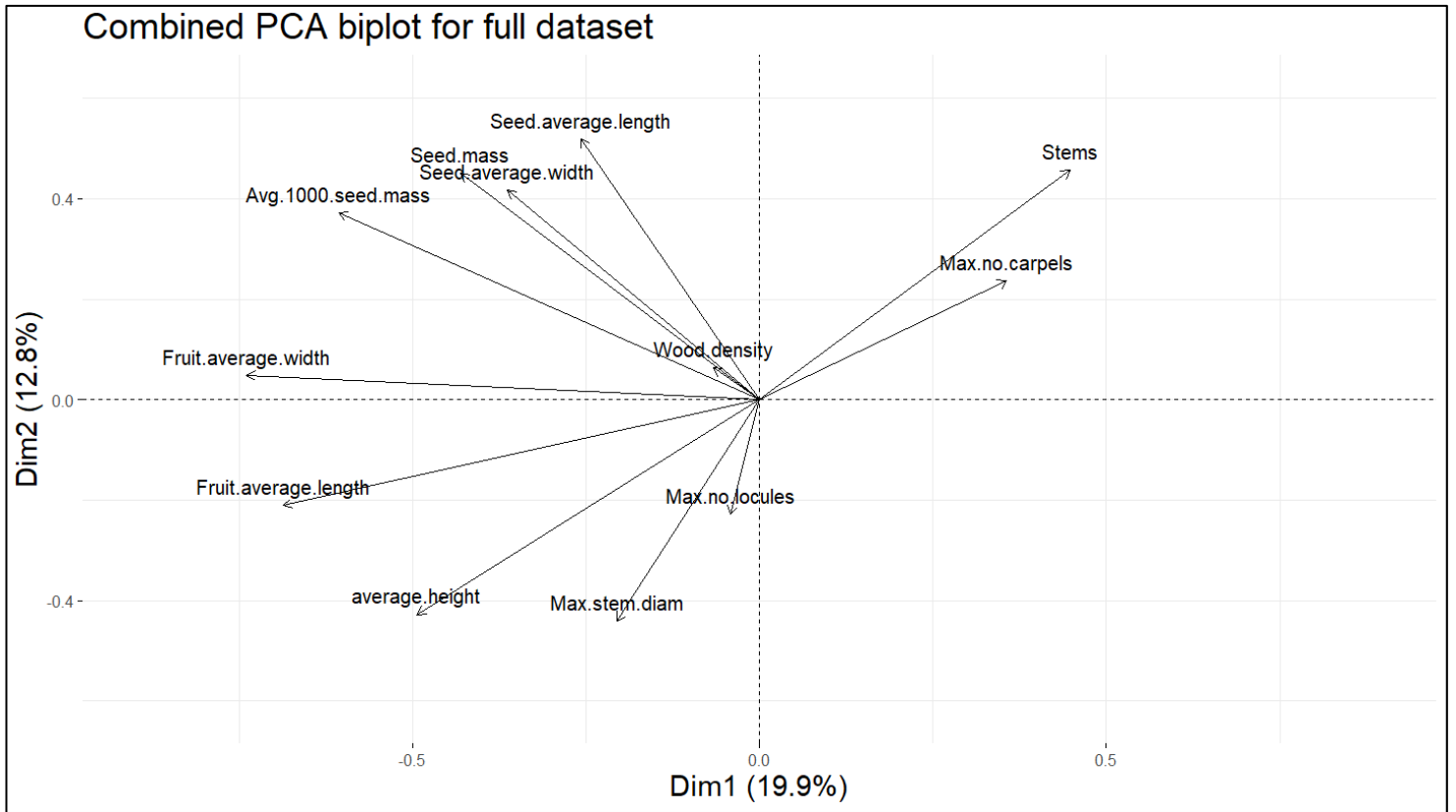


Figure S 8. PCA biplot of the full dataset. Dimension 1 on the y-axis explains about 20% of the trait variance, dimension 2 on the x-axis explains about 12% of trait variance.

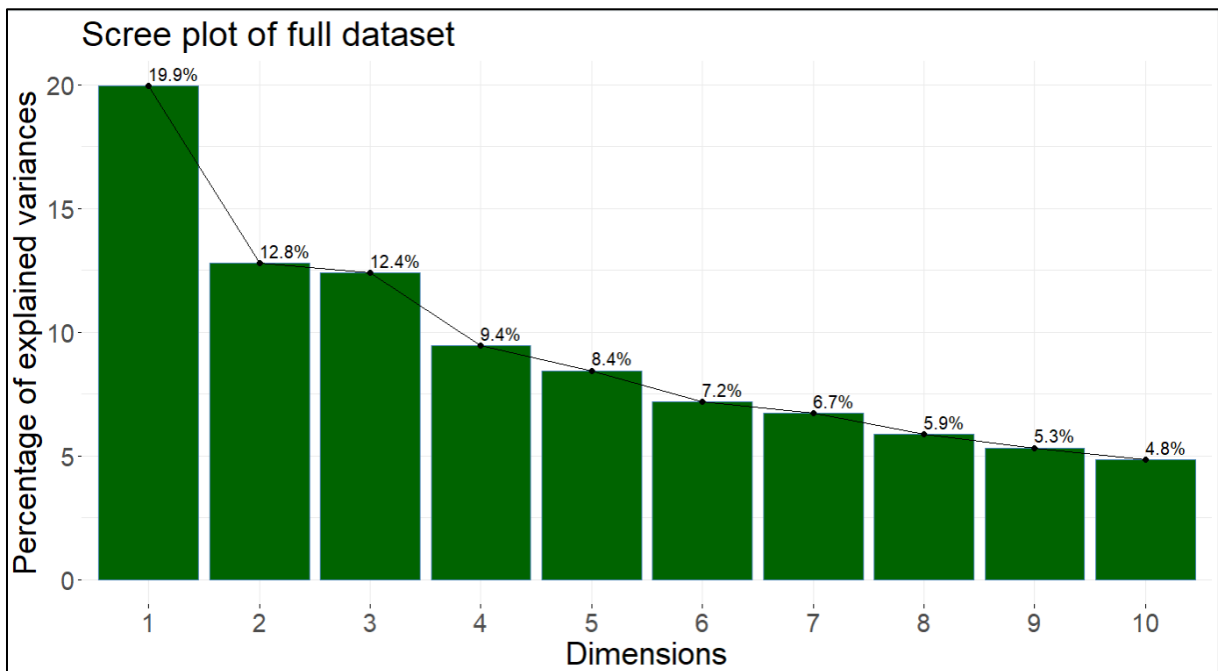


Figure S 9. Scree plot of PCA of the full dataset. The first two dimensions explain 32.7% of variance.

Table S 6. Loadings of principal component 1 and principal component 2 of the full dataset.

	Comp. 1	Comp. 2
Stems	0.28960354	0.36928298
Wood density	-0.04258768	0.05118207
Avg. height	-0.31933076	-0.34588852
Avg. seed length	-0.16678307	0.41938818
Avg. seed width	-0.23505860	0.33730292
Avg. fruit length	-0.44434898	-0.17053704
Avg. fruit width	-0.47808418	0.03915009
Seed mass	-0.27863180	0.36425632
Avg. 1000 seed mass	-0.39251454	0.30099103
Max. stem diameter	-0.13319446	-0.35648043
Max. number of carpels	0.23037613	0.19123688
Max. number of locules	-0.02733200	-0.18484640

SQ5

Table S 7. Correlation matrix of CWM data. Weak correlations in italic, moderate correlations in bold, strong correlations in bold italic.

	Wood density	average height	Seed avg. length	Seed avg. width	Fruit avg. length	Fruit avg. width	Seed mass	Avg.1000 seed.mass	Max.stem diameter	agb	disturbance
Wood density	1	0.06803419	0.208205128	0.486495726	0.397606838	0.103589744	-0.47829	0.303932	0.217778	0.088547	-0.31930869
Avg. height	0.068034	1	0.242393162	0.347692308	0.708034188	0.593846154	-0.0735	0.337436	0.546667	0.518632	-0.46516575
Seed.avg. length	-0.20821	0.24239316	1	0.377777778	0.445470085	0.116581197	0.366838	0.243761	0.281368	0.544615	-0.03547874
Seed.avg. width	0.486496	0.34769231	0.377777778	1	0.745641026	0.464615385	-0.13368	0.619829	0.180171	0.628034	-0.43362909
Fruit.avg. length	0.397607	0.70803419	0.445470085	0.745641026	1	0.595213675	-0.12479	0.609573	0.50906	0.713504	-0.56371782
Fruit.avg. width	0.10359	0.59384615	0.116581197	0.464615385	0.595213675	1	0.059829	0.435214	0.202051	0.500855	-0.48881825
Seed mass	-0.47829	0.07350427	0.366837607	0.133675214	0.124786325	0.05982906	1	0.373675	-0.11795	0.217094	0.078841653
Avg.1000 Seed mass	0.303932	0.3374359	0.243760684	0.61982906	0.60957265	0.435213675	0.373675	1	0.06188	0.563761	-0.27988787
Max. stem. diameter	0.217778	0.54666667	0.281367521	0.18017094	0.509059829	0.202051282	-0.11795	0.06188	1	0.232137	-0.3626716
agb	0.088547	0.51863248	0.544615385	0.628034188	0.713504274	0.500854701	0.217094	0.563761	0.232137	1	-0.55977573
disturbance	-0.31931	0.46516575	0.035478744	-0.43362909	0.563717818	0.488818247	0.078842	-0.279888	-0.36267	-0.55978	1

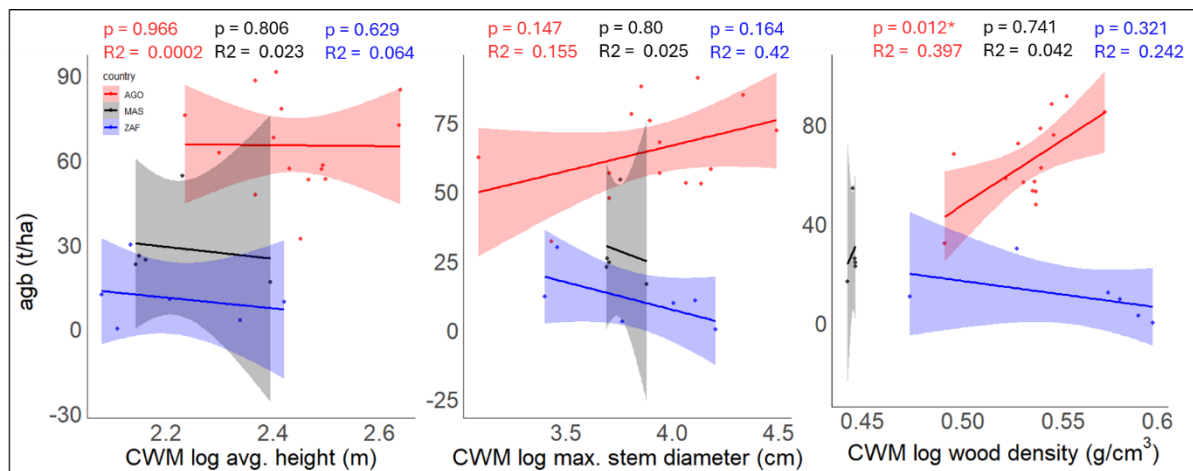


Figure S 10. Relationship between agb (t/ha) as dependent variable and carbon traits and CWM carbon traits average height, maximum stem diameter and wood density on plot-level, differentiated by countries. Angola (AGO) depicted in red, Madagascar (MAS) depicted in black, South Africa (ZAF) depicted in blue.

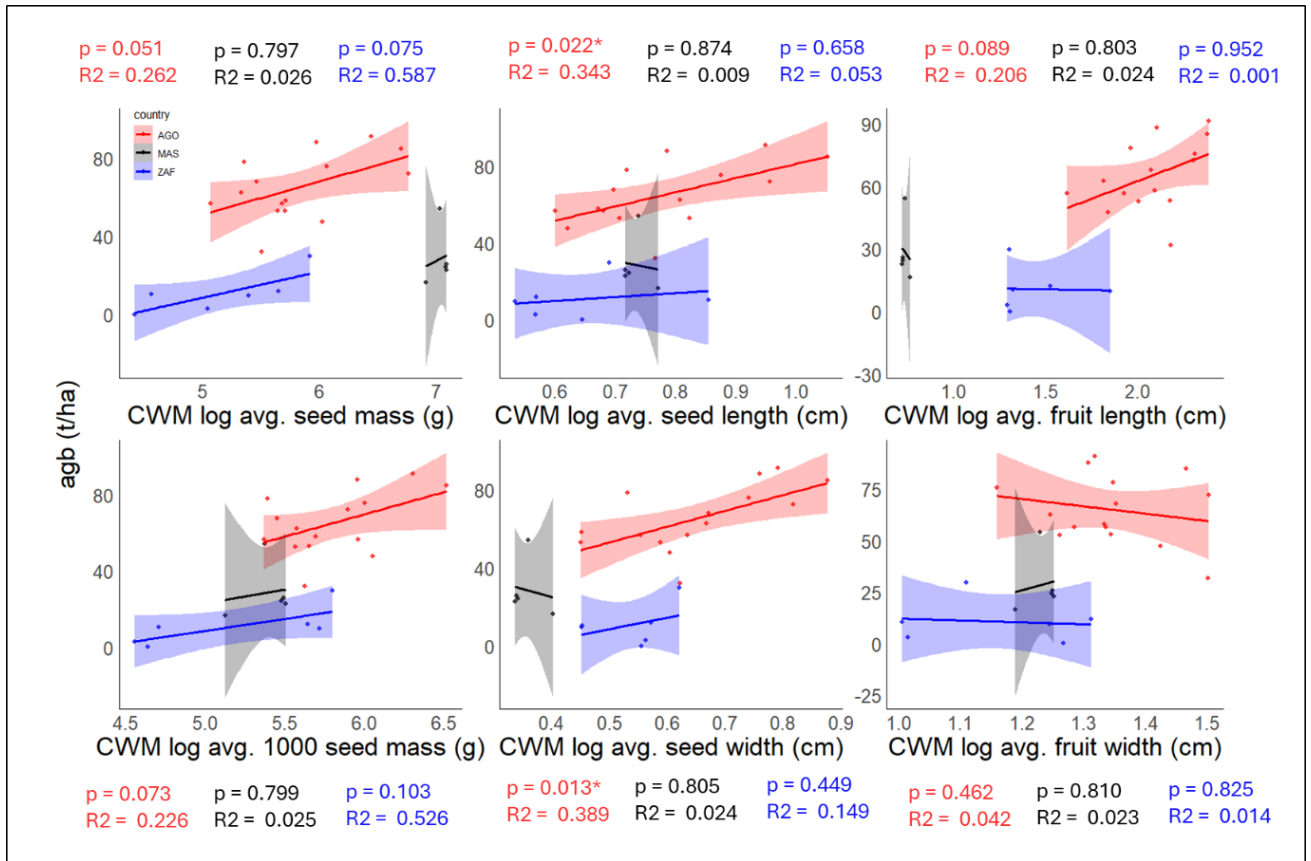


Figure S 11. Relationship between agb (t/ha) as dependent variable and CWM tree dispersal traits on plot-level, differentiated by countries. Angola (AGO) depicted in red, Madagascar (MAS) depicted in black, South Africa (ZAF) depicted in blue.

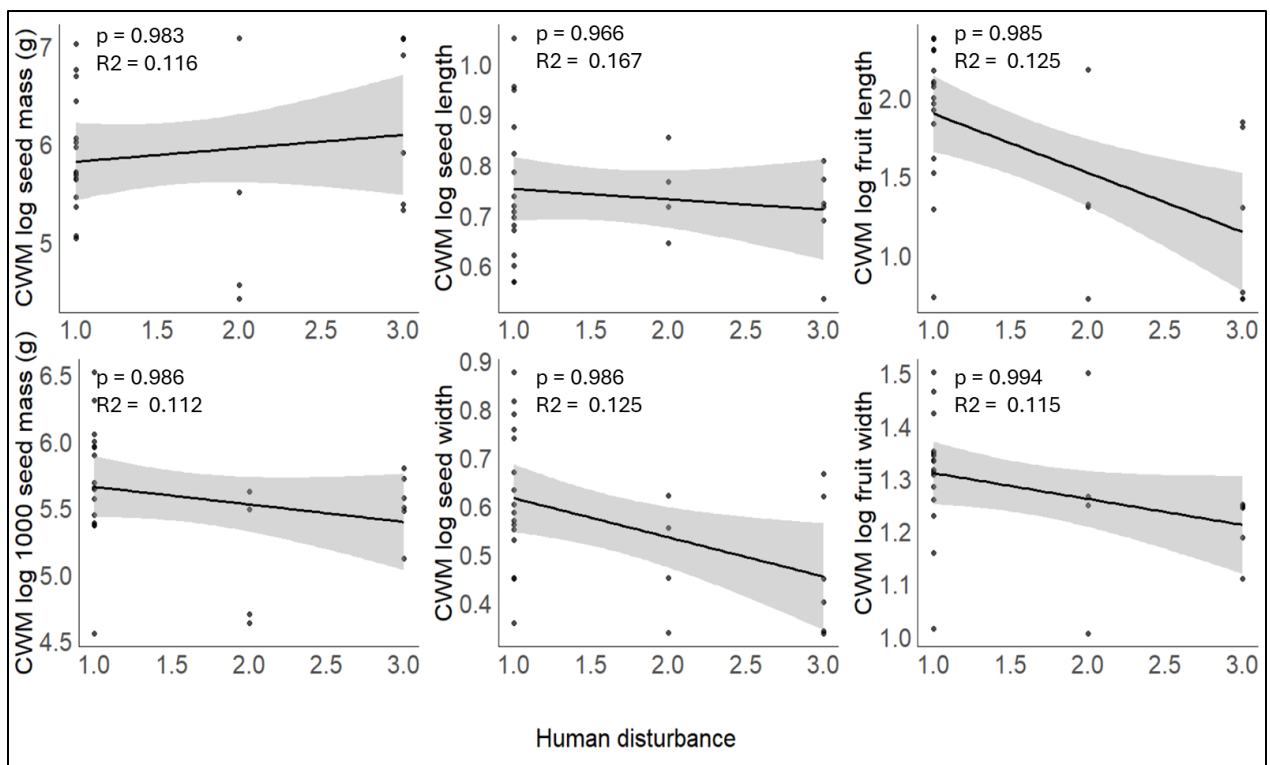


Figure S 12. Relationship between human disturbance (factor between 1 as low disturbance and 3 as high disturbance) and CWM tree dispersal traits as dependent variables on plot-level in Madagascar.

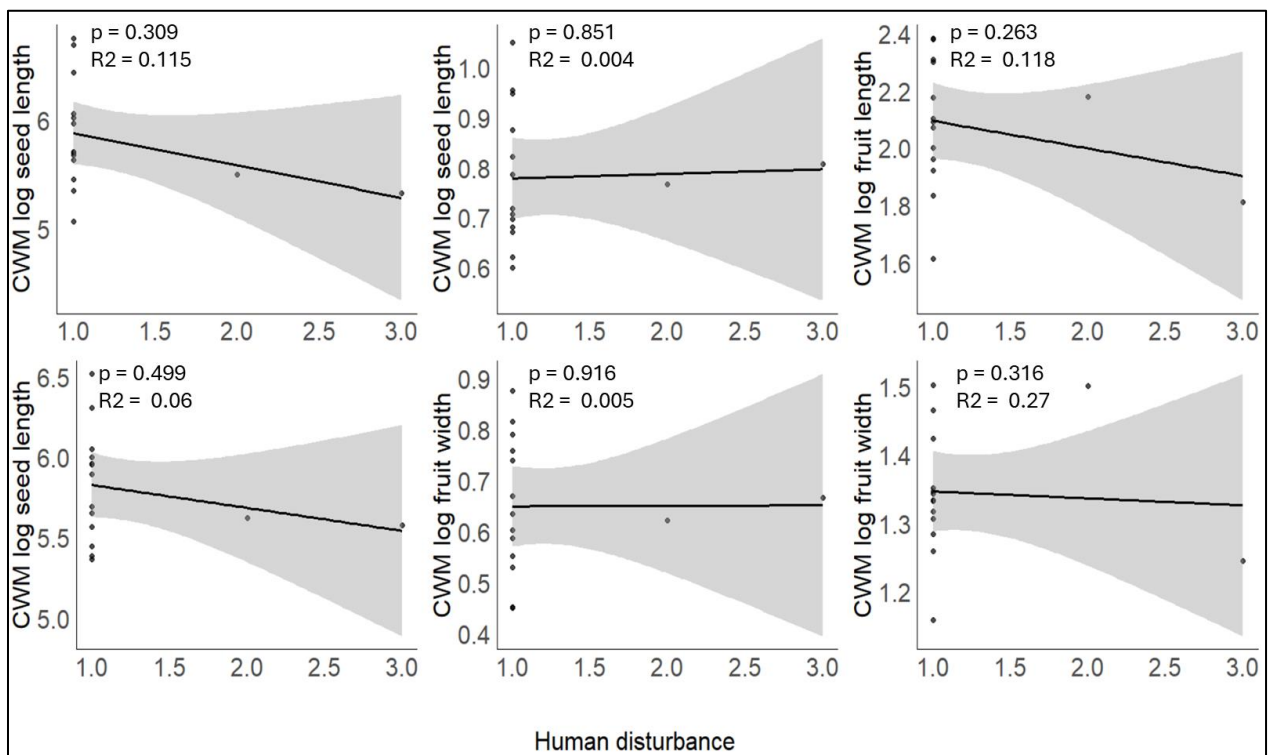


Figure S 13. Relationship between human disturbance (factor between 1 as low disturbance and 3 as high disturbance) and CWM tree dispersal traits as dependent variables on plot-level in Angola.

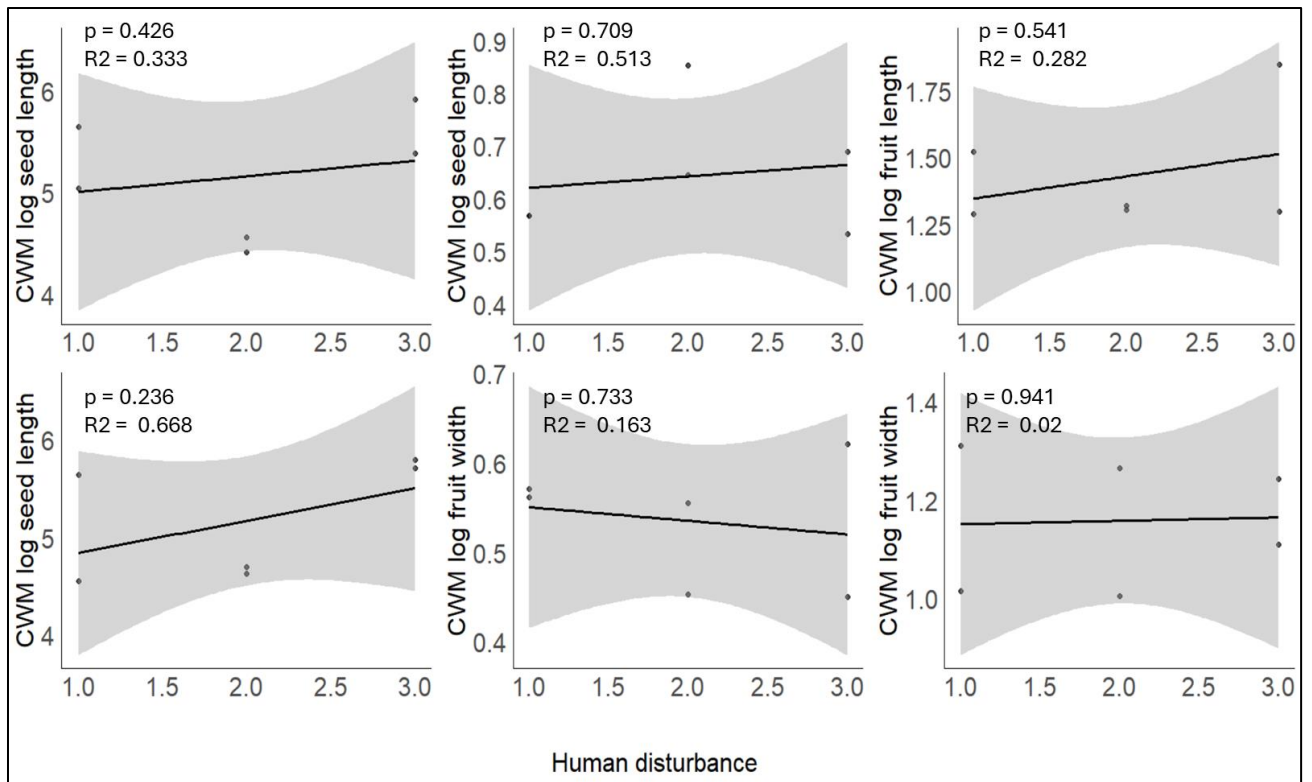


Figure S 14. Relationship between human disturbance (factor between 1 as low disturbance and 3 as high disturbance) and CWM tree dispersal traits as dependent variables on plot-level in South Africa.

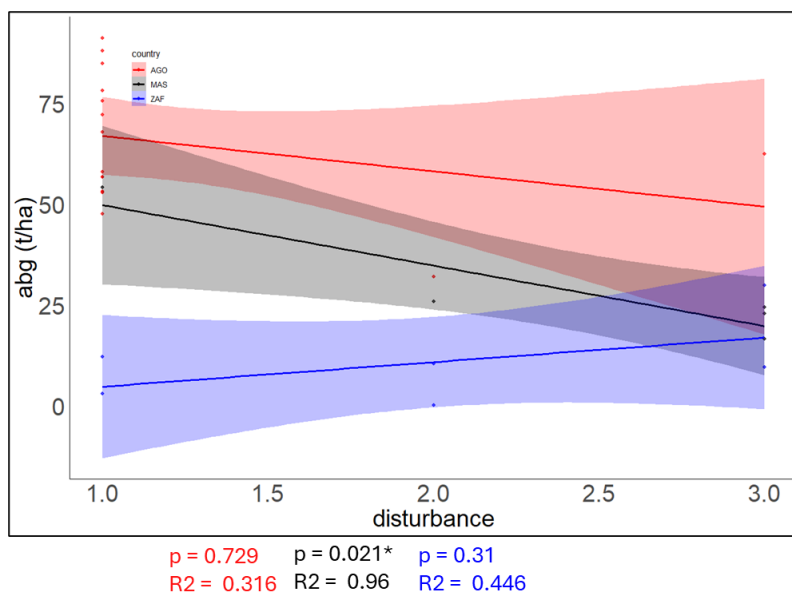


Figure S 15. Relationship between abg (t/ha) as dependent variable and human disturbance on plot-level, differentiated by countries. Angola (AGO) depicted in red, Madagascar (MAS) depicted in black, South Africa (ZAF) depicted in blue.

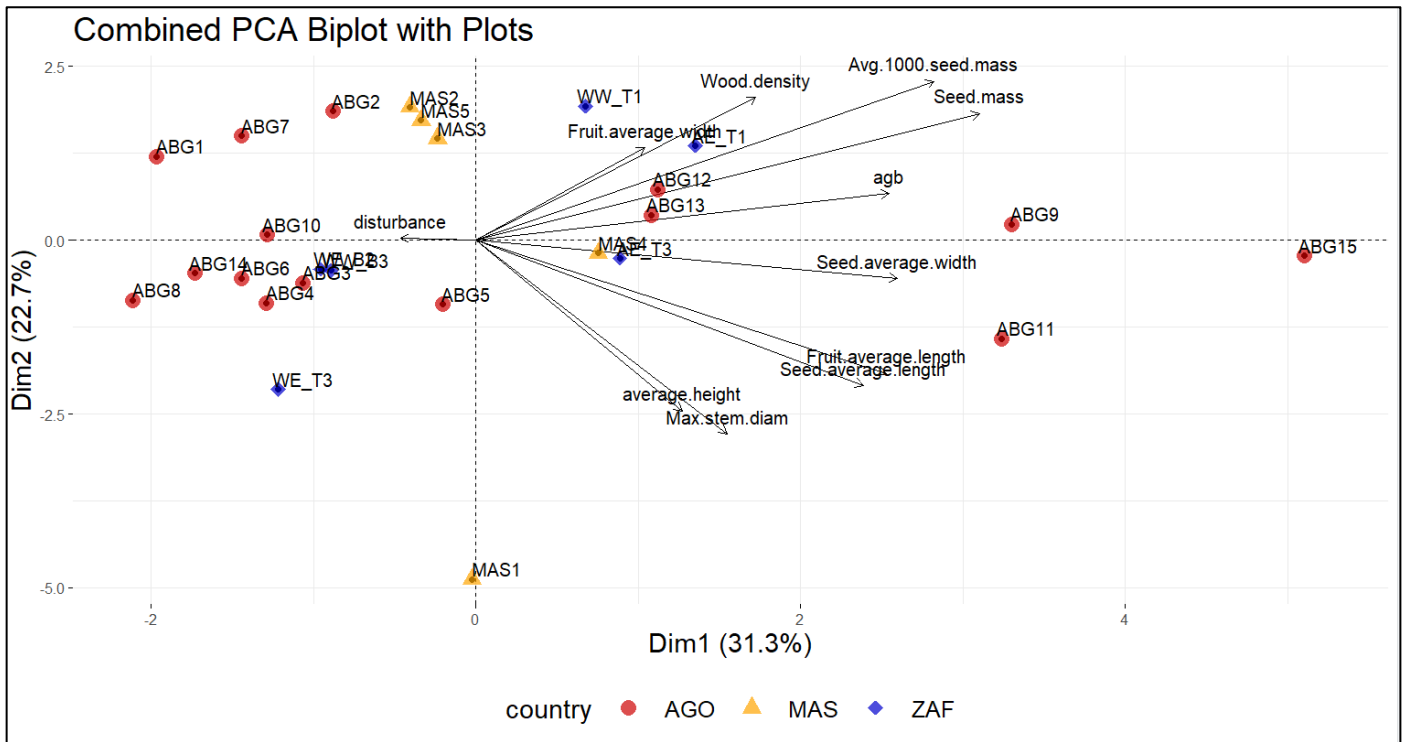


Figure S 16. PCA biplot of CWM dataset, including plots as observations. Plots in Angola (AGO) depicted in red, Malagasy (MAS) plots depicted in yellow, and South African (ZAF) plots depicted in blue. Dimension 1 on the y-axis explains about 27% of the trait variance, dimension 2 on the x-axis explains about 20% of the trait variance.

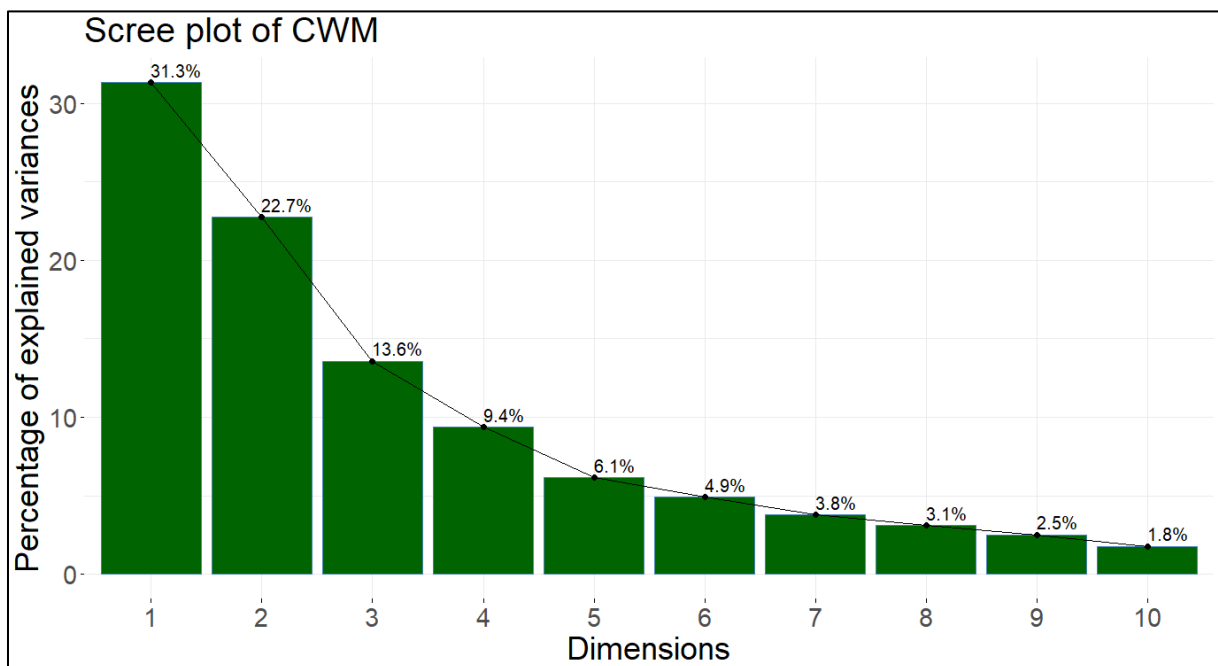


Figure S 17. Scree plot of PCA on plot-level. The first two dimensions explain 54% of variance.

Table S 8. Loadings of principal component 1 and principal component 2 of the data on plot-level.

	Comp. 1	Comp. 2
Wood density	0.24087650	0.336996493
Average height	0.17753992	-0.403101453
Average seed length	0.33337958	-0.343900673
Average seed width	0.36319876	-0.091057193
Average fruit length	0.35349744	-0.314396519
Average fruit width	0.14541220	0.217869596
Seed mass	0.43385349	0.299059902
Average 1000 seed mass	0.39448609	0.374484318
Maximum stem diameter	0.21595892	-0.457463819
agb	0.35584110	0.110026969
Disturbance	-0.06471774	0.004093436

Supplementary material

Analysis code: “MSc_Bodirsky_appendix.R”

Additional files to run the analysis:

- “SQ5_CWM.csv”
- “MAS_overview.csv”
- “agb.xlsx”
- “SQ5_plot_disturbance.xlsx”
- “plots.csv”
- “analysis_data_full.csv”
- “plots_area_richness.xlsx”
- “Country_vegetation_data.xlsx”
- “MAS_SEOSAW_-_plot_data_-_all_versions_-_labels_-_2023-11-08-15-10-22.xlsx”