Dissertation

Trees, Shrubs, and Land-use Change: The Future of Carbon Storage in an African Savanna

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Preface

Originally, I had aspired to become a teacher and have studied biology, history, and educational sciences at University of Cologne for many years, not least because I always felt there was so much more knowledge still to gain. For a while, I have been working as a research assistant at the Historical Institute for Prof. Norbert Finzsch and Dr. Katharina Loeber within the interdisciplinary project *Resilience, Collapse and Reorganization* at the intersection of history and ecology. This was the first time I ever encountered the concept of social-ecological systems, and I was excited to learn, that history and biology can integrate their findings in such ways. For months, I sieved through depressing files of the South African apartheid regime and caught a glimpse of how pseudo-scientific and twisted ecological reasoning were utilized to support a deeply racist social order and the suppression of black South Africans. This experience may have shaped my view on the world quite a bit. Only much later, I was encouraged to begin a dissertation project myself, and was thrilled to get the chance for interdisciplinary research in Africa. Honestly: I would not have left teaching for a lab experiment.

This doctoral thesis and the research connected to it were conducted as part of Collaborative Research Centre *Future Rural Africa – Future-making and social-ecological transformation* funded by DFG (funding codes TRR-228/1 and TRR-228/2). This international research centre emphatically cultivates an interdisciplinary orientation with its member researchers rooted in the natural sciences, geography, economy, social anthropology, and health sciences. Within this large interdisciplinary research consortium, I became a doctoral student in project *Future Carbon Storage (A01)* that in itself has a strong interdisciplinary component as it integrates plant ecology with soil sciences and agricultural economics and is jointly headed by principal investigators from all three disciplines. From the onset, research was designed to be interdisciplinary and data acquisition was jointly planned and deliberately conducted to allow for cross-disciplinary analysis. This approach was time-consuming and required many agreements, joint workshops, detailed planning and, after all, also compromises. However, I am deeply grateful for the experience including the innumerable discussions, learning opportunities and insights that I gained in the course of this project and hope to continue in my future research.

I am determined to share knowledge and data as openly and widely as possible so that local communities and research can benefit from it.

Acknowledgements / Danksagungen

Over the course of this thesis, I was allowed to learn innumerable things from, with and through the people around me, whom I am immensely grateful for.

First of all, I need to thank my supervisor Anja Linstädter, who has given me the opportunity for this adventure and this thesis project. She asked me if I was interested to become a doctoral student with her while we both sat in a dripping wet piece of meadow in search of plants, and there she caught me totally unprepared. Ever since then she has always treated me at eye level, given me every opportunity to learn and grow in my research, has encouraged me to be proud of my interdisciplinary background instead of fearing the gaps in my statistics background, has granted me the liberty to develop my own ideas, and has supported me in every way possible, no matter how difficult it was. Thank you for being the best supervisor I could have wished for.

Besonders dankbar bin ich meinen Eltern, Inge und Hans Herbert, die mir ein Studium überhaupt ermöglicht haben, mich in einem Haus voller Bücher und Wissen aufwachsen ließen und mir eine Kindheit voller Natur geschenkt haben. Ohne euch hätte ich diesen Weg nie eingeschlagen.

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Preface

Preface

Summary

The global drylands cover nearly half of the terrestrial surface and are home to more than two billion people. In many drylands, ongoing land-use change transforms near-natural savanna vegetation to agricultural land to increase food production. In Southern Africa, these heterogenous savanna ecosystems are also recognized as habitats of many protected animal species, such as elephant, lion and large herds of diverse herbivores, which are of great value for the tourism industry. Here, subsistence farmers and livestock herder communities often live in close proximity to nature conservation areas. Although these land-use transformations are different regarding the future they aspire to, both processes, nature conservation with large herbivores and agricultural intensification, have in common, that they change the vegetation structure of savanna ecosystems, usually leading to destruction of trees, shrubs and the woody biomass they consist of.

Such changes in woody vegetation cover and biomass are often regarded as forms of land degradation and forest loss. Global forest conservation approaches and international programs aim to stop degradation processes, also to conserve the carbon bound within wood from volatilization into earth's atmosphere. In search for mitigation options against global climate change savannas are increasingly discussed as potential carbon sinks. Savannas, however, are not forests, in that they are naturally shaped by and adapted to disturbances, such as wildfires and herbivory. Unlike in forests, disturbances are necessary for stable, functioning savanna ecosystems and prevent these ecosystems from forming closed forest stands. Their consequently lower levels of carbon storage in woody vegetation have long been the reason for savannas to be overlooked as a potential carbon sink but recently the question was raised if carbon sequestration programs (such as REDD+) could also be applied to savanna ecosystems. However, heterogenous vegetation structure and chronic disturbances hamper the quantification of carbon stocks in savannas, and current procedures of carbon storage estimation entail high uncertainties due to methodological obstacles. It is therefore challenging to assess how future land-use changes such as agricultural intensification or increasing wildlife densities will impact the carbon storage balance of African drylands.

In this thesis, I address the research gap of accurately quantifying carbon storage in vegetation and soils of disturbance-prone savanna ecosystems. I further analyse relevant drivers for both ecosystem compartments and their implications for future carbon storage under land-use change. Moreover, I show that in savannas different carbon storage pools vary in their persistence to disturbance, causing carbon bound in shrub vegetation to be most likely to experience severe losses under land-use change while soil organic carbon stored in subsoils is least likely to be impacted by land-use change in the future.

Preface

I start with summarizing conventional approaches to carbon storage assessment and where and for which reasons they fail to accurately estimated savanna ecosystem carbon storage. Furthermore, I outline which future-making processes drive land-use change in Southern Africa along two pathways of land-use transformation and how these are likely to influence carbon storage. In the following chapters, I propose a new method of carbon storage estimation which is adapted to the specific conditions of disturbance-prone ecosystems and demonstrate the advantages of this approach in relation to existing forestry methods. Specifically, I highlight sources for previous over- and underestimation of savanna carbon stocks which the proposed methodology resolves. In the following chapters, I apply the new method to analyse impacts of land-use change on carbon storage in woody vegetation in conjunction with the soil compartment. With this interdisciplinary approach, I can demonstrate that indeed both, agricultural intensification and nature conservation with large herbivores, reduce woody carbon storage above- and belowground, but partly sequesters this carbon into the soil organic carbon stock. I then quantify whole-ecosystem carbon storage in different ecosystem compartments (above- and belowground woody carbon in shrubs and trees, respectively, as well as topsoil and subsoil organic carbon) of two savanna vegetation types (scrub savanna and savanna woodland). Moreover, in a space-for-time substitution I analyse how land-use changes impact carbon storage in each compartment and in the whole ecosystem. Carbon storage compartments are found to differ in their persistence to land-use change with carbon bound in shrub biomass being least persistent to future changes and subsoil organic carbon being most stable under changing land-use. I then explore which individual land-use change effects act as drivers of carbon storage through Generalized Additive Models (GAMs) and uncover non-linear effects, especially of elephant browsing, with implications for future carbon storage. In the last chapter, I discuss my findings in the larger context of this thesis and discuss relevant implications for land-use change and future-making decisions in rural Africa.

Zusammenfassung

Weltweit bedecken Trockengebiete fast die Hälfte der Erdoberfläche und sind die Heimat von mehr als zwei Milliarden Menschen. In vielen Regionen wird durch den fortschreitenden Landnutzungswandel die naturnahe Savannenvegetation in landwirtschaftliche Flächen umgewandelt, um die Nahrungsmittelproduktion zu steigern. Im südlichen Afrika sind diese diversen Savannenökosysteme auch als Lebensraum für viele geschützte Tierarten wie Elefanten, Löwen und große Herden vielfältiger Pflanzenfresser bekannt, die großen Wert für die Tourismusbranche haben. Im Umfeld vieler großer Schutzgebiete leben Kleinbauern und Viehhirten

oft in unmittelbarer Nachbarschaft zu diesen – oft gefährlichen – Tieren. Obwohl sich beide Landnutzungen im Hinblick darauf unterscheiden welche Zukunftsvision verfolgt wird, haben sie doch beide gemeinsam, dass sowohl Schutzgebiete mit großen Pflanzenfressern wie Elefanten als auch die Landwirtschaft, die Vegetationsstruktur von Savannenökosystemen verändern. In der Regel reduzieren beide Prozesse die holzige Biomasse im Ökosystem, indem Bäume und Sträucher entfernt, zerstört oder durch Fraßverhalten und Holzeinschlag geschädigt werden.

Solche Veränderungen der holzigen Vegetationsschicht samt Einflüssen auf die Biomasse werden oft als Formen von Umweltzerstörung oder Waldverlust betrachtet. Globale Waldschutzkonzepte und internationale Programme zielen darauf ab, solche Degradationsprozesse zu stoppen und den im Holz gebundenen Kohlenstoff vor der Verflüchtigung in die Erdatmosphäre zu bewahren. Auf der Suche nach Möglichkeiten zur Eindämmung des globalen Klimawandels werden Savannen zunehmend als potenzielle Kohlenstoffsenken diskutiert. Savannen sind von Wäldern jedoch fundamental verschieden, da sie von Natur aus durch starke Störungen, wie z. B. Elefantenfraß und Buschfeuer, geprägt und an diese evolutionär angepasst sind. Anders als in Wäldern sind hier Störungen für Funktion und Stabilität von offenen Savannenökosysteme notwendig und verhindern, dass sie sich zu geschlossenen Waldbeständen oder undurchdringlichen Gestrüppen entwickeln. Folglich ist die Kohlenstoffspeicherung in der holzigen Vegetation in Savannen geringer als in Wäldern und dies war lange Zeit der Grund dafür, dass Savannen keine Beachtung als potenzielle Kohlenstoffsenke fanden. In letzter Zeit wurde jedoch zunehmend die Frage aufgeworfen, ob Programme zur Kohlenstoffbindung (wie REDD+) auch auf Savannenökosysteme angewendet werden könnten. Die heterogene Vegetationsstruktur und chronischen Störungen erschweren jedoch erheblich die Quantifizierung der Kohlenstoffvorräte in Savannen, so dass die derzeitigen Verfahren zur Schätzung der Kohlenstoffspeicherung aufgrund methodischer Hindernisse mit großen Unsicherheiten verbunden sind. Daher ist es auch schwierig abzuschätzen, wie sich künftige Landnutzungsänderungen wie die Intensivierung der Landwirtschaft oder die Erhöhung von Wildtierdichten auf die Kohlenstoffspeicher der afrikanischen Trockengebiete auswirken werden.

In dieser Arbeit fasse ich zunächst die konventionellen Ansätze zur Quantifizierung von Kohlenstoffspeichern zusammen und zeige auf, wo und aus welchen Gründen sie in Savannenökosystemen versagen. Darüber hinaus skizziere ich entlang zweier Pfade der Landnutzungsänderung, welche Zukunftsvorstellungen den Landnutzungswandel im südlichen Afrika vorantreiben und wie diese voraussichtlich die Kohlenstoffspeicherung beeinflussen werden. In den folgenden Kapiteln entwickele ich eine neue Methode zur Schätzung der Kohlenstoffspeicherung, die an die spezifischen Bedingungen störungsanfälliger Ökosysteme angepasst ist, und zeige die Vorteile dieses Ansatzes gegenüber den bisherigen forstwirtschaftlichen Methoden auf. In den beiden daran anschließenden Kapiteln wende ich die neue Methode an, um

die Auswirkungen von Landnutzungsänderungen auf die Kohlenstoffspeicherung zu analysieren und berücksichtige dabei auch das Verhältnis von holziger Biomasse zu im Boden gespeichertem Kohlenstoff. Mit diesem interdisziplinären Ansatz kann ich zeigen, dass sowohl die Intensivierung der Landwirtschaft als auch der Naturschutz mit großen Pflanzenfressern die ober- und unterirdische Kohlenstoffspeicherung in Büschen und Bäumen verringern, dieser Kohlenstoff jedoch nicht verloren geht, sondern teilweise in den organischen Kohlenstoffbestand des Bodens eingelagert wird. Anschließend quantifiziere ich die Kohlenstoffspeicherung im gesamten Ökosystem sowie in verschiedenen Ökosystemkompartimenten (ober- und unterirdischer Holzkohlenstoff in Sträuchern bzw. Bäumen sowie organischer Kohlenstoff im Ober- und Unterboden) von zwei verschiedenen Vegetationstypen der Studienregion. Darüber hinaus analysiere ich in einer Raum-Zeit-Substitution, wie sich zukünftige Landnutzungsänderungen auf die Kohlenstoffspeicherung in jedem Kompartiment und im gesamten Ökosystem auswirken. Die hier untersuchten Kohlenstoffspeicher unterscheiden sich in ihrer Beständigkeit gegenüber Landnutzungsänderungen, wobei jener Kohlenstoff, der in der Strauchbiomasse gebunden ist sich als am wenigsten beständig gegenüber künftigen Änderungen herausgestellt hat; demgegenüber ist der organische Kohlenstoff im Unterboden bei veränderter Landnutzung am stabilsten. Anschließend untersuche ich mit Hilfe von statistischen Modellen (*Generalized Additive Models*, GAMs), welche individuellen Landnutzungsfaktoren die Kohlenstoffspeicherung beeinflussen, und decke nichtlineare Effekte auf. Insbesondere Elefantenfraß kann zunächst positive Auswirkungen auf die Kohlenstoffspeicherung haben, die sich bei weiterer Intensivierung jedoch ins Gegenteil verkehrt. Dies muss bei zukünftigen Planungen berücksichtigt werden. Im letzten Kapitel diskutiere ich meine Ergebnisse im größeren Kontext dieser Arbeit und erörtere relevante Implikationen für Landnutzungsänderungen und zukünftige Entscheidungen.

Contents, Boxes and Figures

Table of Contents

Boxes

Figures

Glossary

Adult: Life stage at which a woody plant reaches reproductive maturity but may not have reached its maximum size yet (Swemmer and Ward 2020); but see Chapter 2 and Chapter 3 for growth class definitions used in this thesis.

Afforestation: Conversion to forest of land that historically has not contained forests (IPCC 2021).

AGB: aboveground woody biomass of a tree, shrub or stand; where individual plants are quantified it is usually given in [kg], but in case of stands is usually expressed on a unit per areas basis as [t ha^{-1}].

AGC: aboveground carbon storage: carbon stored in aboveground woody biomass; AGB of an individual tree or shrub multiplied by the species' mean wood carbon content; where individual plants are quantified it is usually given in [kg], but in case of stands is usually expressed on a unit per areas basis as [t ha^{-1}].

Agroforestry: the deliberate integration and management of trees on farms and in landscapes (Minang et al. 2014).

Allometric equations: Mathematical equations that draw on the physical, mechanical and hydraulic relations between certain size parameters of a tree or shrub and the biomass needed to build those structures (Chave et al. 2009, Loubota Panzou et al. 2021); are derived by first measuring certain size proxies such as height or stem diameter in trees or shrubs of different sizes, and then cutting them and weighing their biomass; this ultimately allows to non-destructively estimate other trees' or shrubs' biomass from measuring the same size proxies (Chave et al. 2005, Meyer et al. 2014).

Anthropogenic: Resulting from or produced by human activities (IPCC 2021).

BGB: belowground woody biomass, i.e. roots and belowground storage organs, of a tree, shrub or stand; where individual plants are quantified it is usually given in [kg], but in case of stands is usually expressed on a unit per areas basis as [t ha^{-1}].

BGC: belowground carbon storage: carbon stored in belowground woody biomass; BGB of an individual tree or shrub multiplied by the species' mean wood carbon content; where individual plants are quantified it is usually given in [kg], but in case of stands is usually expressed on a unit per areas basis as [t ha^{-1}].

Biochar: Charcoal produced from slowly burning organic material under limited oxygen supply so that little CO_2 is volatilized into the atmosphere and instead fixed in inert charcoal particles which in turn can be used for soil improvements in agriculture (IPCC 2022).

Biomass: The mass of living tissues in either an individual or cumulatively across organisms in a population or ecosystem (Millennium Ecosystem Assessment 2005); organic material or mass of organic matter in a specific area (IPCC 2021).

Browsers: Herbivore species which predominantly feed on leaves, shoots and bark of woody plants.

Glossary

Carbon dynamics: "Carbon store and flux dynamics are physical changes to an ecosystem's structures and processes, resulting in changes in the bundle of services flowing from an ecosystem and the benefits that humans derive from interactions with that ecosystem" (Stringer et al. 2012).

Carbon inventory: The estimation of stocks and fluxes of carbon from different land-use systems in a given area (Ciais et al. 2011).

Carbon persistence: The inverse likelihood of a carbon pool to suffer severe losses to major disturbances, such as wildfires or drought (Kristensen et al. 2022).

Carbon pool: A reservoir in the earth system in which carbon resides for a period of time (IPCC 2021).

Carbon storage: amount of carbon present in one or more carbon pools of an ecosystem at a specific time; also: a proxy which is often used to simplify the estimation of the ecosystem service of global climate regulation. There are four major terrestrial carbon pools: aboveground biomass (AGB), belowground biomass (i.e. roots, BGB), dead organic matter (DOM), soil organic carbon (SOC) (Bartholomée et al. 2018).

Carbon sequestration: The process of storing carbon in a carbon pool (IPCC 2021).

CBNRM: Community-based natural resource management as promoted by Namibian and other state's conservation programs in which inhabitants of a communal conservancy have to participate in nature conservation efforts and in turn are allowed to sell and benefit from their wildlife resources (Jones et al. 2013, Khumalo and Yung 2015, Meyer et al. 2021), see **Box 5**; also called 'community-based conservation' (Drake et al. 2020).

Climate change: A change in the state of the climate that can be identified (e.g., by using statistical tests) by changes in the mean and/or the variability of its properties and that persists for an extended period, typically decades or longer (IPCC 2021).

Communal Conservancy: see CBNRM.

DBH (Diameter at breast height): A tree's stem diameter at 130 cm above the ground; a standard measure from forestry research, serving as a common proxy for tree age and important variable in allometric equations for tree biomass estimations (Chave et al. 2014).

Decomposition: The ecological process carried out primarily by microbes that leads to a transformation of dead organic matter into inorganic mater; the converse of biological production. For example, the transformation of dead plant material, such as leaf litter and dead wood, into carbon dioxide, nitrogen gas, and ammonium and nitrates. (Millennium Ecosystem Assessment 2005).

Deforestation: reduction in wooded area (i.e. clearing, mostly due to agricultural expansion) (McNicol et al. 2018b).

Degradation: reduction of woody density within areas that remain a woodland (i.e. selective cutting for timber harvest or fuel wood) (McNicol et al. 2018b); ecosystems become degraded when anthropogenic factors adversely affect ecosystem health, functions and services (Osborne et al.

2018); savannas are different from forests, in that degradation can mean both, the total loss of tree cover or bush encroachment (Osborne et al. 2018).

Disturbance: "The mechanisms which limit the plant biomass by causing its partial or total destruction" (Grime 1979); Disturbances are events which occur in time intervals that are longer than the recovery time of the system; hence, after a disturbance event the measured system characteristic changes, but can recover to pre-disturbance level before the next disturbance event occurs (Borics et al. 2013).

Disturbance event: a "relatively abrupt change in resource availability or ecological structure or function, often associated with the conversion of live to dead biomass; is discrete in time, unlike stress" (Burton et al. 2020); "any relatively discrete event in time that disrupts ecosystems, community, or population structure and changes resources, substrate availability, or the physical environment" (White & Pickett 1985, cited from Newman (2019)).

Driver: Any natural or human-induced factor that directly or indirectly causes a change in an ecosystem. (Millennium Ecosystem Assessment 2005).

Drylands: Regions that are characterized by an overall climatic water deficit, i.e. Aridity Index (AI) of <0.65 mm mean annual precipitation per mm mean annual potential evapotranspiration (Safriel et al. 2005).

Ecosystem: An ecosystem is a dynamic complex of plant, animal, and microorganism communities and the nonliving environment interacting as a functional unit. Humans are an integral part of ecosystems. Ecosystems vary enormously in size (Millennium Ecosystem Assessment 2005); A functional unit consisting of living organisms, their non-living environment and the interactions within and between them (IPCC 2021).

Ecosystem functioning: A widely used but hard to define term subsuming the overall processes that sustain an ecological system; refers to the supposedly correct way the ecosystem is meant to function and as such has quite normative meanings (Jax 2005; also see further remarks on concepts and terminology there).

Ecosystem functions: An intrinsic ecosystem characteristic related to the set of conditions and processes whereby an ecosystem maintains its integrity (such as primary productivity, food chain, biogeochemical cycles). Ecosystem functions include such processes as decomposition, production, nutrient cycling, and fluxes of nutrients and energy (Millennium Ecosystem Assessment 2005); a widely used descriptive category that alternatively refers to the habitat, biological or system properties or processes of ecosystems (Jax 2005; also see further remarks on concepts and terminology there).

Ecosystem services: benefits that humans obtain from ecosystems (Millennium Ecosystem Assessment 2005); benefits that people derive from biodiversity and ecosystem function (Wu 2014); very different things are subsumed under this term such as direct local benefits such as food and firewood, economic benefits such as tourism income, but also global benefits such as carbon storage and biodiversity conservation. There also exists distinct criticism to the ecosystem service

approach as it often goes hand-in-hand with neoliberal approaches to conservation and commodification of nature (Lele 2021).

Ecosystem stability: A description of the dynamic properties of an ecosystem. An ecosystem is considered stable if it returns to its original state shortly after a perturbation (resilience), exhibits low temporal variability (constancy), or does not change dramatically in the face of a perturbation (resistance). (Millennium Ecosystem Assessment 2005).

Elephant impact: habitat modification through elephant activity i.e. mechanically changing the structure and composition of canopy trees; includes the 'wasteful feeding' of elephants which remove more biomass than they actually consume (Balfour et al. 2007).

Escape heights: Fire and browsing both create demographic bottlenecks for tree recruitment; only individuals which can out-grow the escape heights make it out of the **browsing trap**, or **fire trap**, respectively (Osborne et al. 2018).

Fire regime: The temporal and spatial patterns of burning that characterize an ecosystem, averaged over many fires over a long period of time (Miller and Safford 2020).

Forest: Areas with woody canopy area index >70% and upper tree layer (with DBH>10 cm) with >12 m mean height (Torello-Raventos et al. 2013); but see much broader definitions that would also include savanna and savanna woodland into forest category listed by Chazdon et al. (2016).

Forest restauration: transition from <25 % tree cover to >25 % tree cover in areas where forests historically occurred (Cook-Patton et al. 2020).

Global warming: Global warming, also called 'global climate change' refers to the increase in global surface temperature relative to a baseline reference period, averaging over a period sufficient to remove interannual variations (e.g., 20 or 30 years). A common choice for the baseline is 1850–1900 (IPCC 2021).

Grazers: Herbivore species which predominantly feed on non-woody plants like grasses and forbs in the herbaceous vegetation layer.

Gulliver: A woody plant that through repeated topkill events has been prevented to progress to larger size classes (Higgins et al. 2012); throughout this research gullivers are defined to have suffered extensive aboveground biomass losses >30 % and/or have lost entire adult-sized stems (>5 cm basal stem diameter); also see Chapter 2 and Chapter 3 for growth class definitions used in this thesis.

Human-Wildlife Conflict (HWC): "Human Wildlife Conflict occurs when wild animals injure, destroy or damage human life or property and are killed, injured, captured or otherwise harmed as a result - i.e. both humans and animals suffer from the interaction with each other. (WWF 2008)" (Khumalo and Yung 2015)

Juvenile: Young woody plants, often not more than a few years old; most vulnerable to drought stress, disturbances, and competition (Swemmer and Ward 2020); also sometimes called 'seedling' (but see Chapter 2 and Chapter 3 for growth class definitions used in this thesis).

Glossary

KAZA-TFCA: Kavango-Zambezi Transfrontier Conservation Area: an international cross-border conservation area between Angola, Namibia, Botswana, Zimbabwe and Zambia (Pinter-Wollman 2012, Munthali et al. 2018).

Land-use: The human utilization of a piece of land for a certain purpose. Influenced by but not synonymous with land cover (Millennium Ecosystem Assessment 2005); The total of arrangements, activities and inputs applied to a parcel of land. The term land use is also used in the sense of the social and economic purposes for which land is managed (e.g., grazing, timber extraction, conservation) (IPCC 2021); as a categorial variable mostly referred to as 'land-use type'.

Land-use change: The change from one land use category to another (IPCC 2021).

Material legacies: individuals or matter present in an ecosystem after disturbance (survivors, seeds, dead trees etc); they emerge on short temporal and local spatial scale (Johnstone et al. 2016).

Megafauna: An animal species with adult body mass beyond a certain threshold (can be >45 kg or >1000 kg for herbivores) (Malhi et al. 2022).

Methusalem tree: A particularly large and old tree individual which has apparently long ago reached the necessary escape heights (see glossary) to outgrow the fire and browser trap that characterize savanna ecosystems (Sankaran et al. 2013, Staver and Bond 2014, Ouédraogo et al. 2015). We defined them to have a DBH >60 cm, a size beyond which elephants can no longer topple or break stems (Caughley 1976, Moncrieff et al. 2011, Stevens 2021). Moreover, farmers often reported stems of such sizes to be "too big to cut them" (own communication, Namibia 2019-2022).

Mitigation (of climate change): A human intervention to reduce emissions or enhance the sinks of greenhouse gases (IPCC 2021).

Mixed-feeders: Herbivore species which partly browse and partly graze, i.e. feed both on leaves, shoots and bark of woody plants as well as on non-woody plants like grasses and forbs in the herbaceous vegetation layer.

Non-linearity: A process is called non-linear when there is no simple proportional relation between cause and effect (IPCC 2021).

Pathways: The temporal evolution of natural and/or human systems towards a future state. Pathway concepts range from sets of quantitative and qualitative scenarios or narratives of potential futures to solution-oriented decision-making processes to achieve desirable societal goals. Pathway approaches typically focus on biophysical, techno-economic, and/or socio-behavioural trajectories and involve various dynamics, goals, and actors across different scales.(IPCC 2021).

Primary production: The synthesis of organic compounds by plants and microbes, primarily by photosynthesis using light and carbon dioxide (CO_2) as sources of energy and carbon respectively (IPCC 2021).

Protected area: According to the widely used definition of the International Union for Conservation of Nature (IUCN) it is "a clearly defined geographical space, recognized, dedicated, and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values" (IUCN, cited after Kabra (2019)).

Glossary

Rangeland: An area where the main land-use is related to the support of grazing or browsing mammals, such as cattle, sheep or goats (Millennium Ecosystem Assessment 2005).

REDD (Reducing Emissions from Deforestation and Degradation): "The REDD concept is—at its core—a proposal to provide financial incentives to help developing countries voluntarily reduce national deforestation rates and associated carbon emissions below a baseline (based either on a historical reference case or future projection). Countries that demonstrate emissions reductions may be able to sell those carbon credits on the international carbon market or elsewhere. These emissions reductions could simultaneously combat climate change, conserve biodiversity and protect other ecosystem goods and services." (Gibbs et al. 2007).

REDD+: REDD with the additional aim to increase carbon sequestration through forest restoration, agroforestry, and other restoration interventions (Reiner et al. 2023).

Reforestation: Conversion to forest of land that has previously contained forests but that has been converted to some other use. (IPCC 2021).

Resilience: The capacity of a system to tolerate impacts of drivers without irreversible change in its outputs or structure. (Millennium Ecosystem Assessment 2005).

Restoration: "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (Gann et al. 2019).

Rewilding: "restoration to promote self-regulating complex ecosystems through restoring non-human ecological factors and processes while reducing human control and pressures" (Svenning 2020).

Root-to-shoot (RS) ratio: Ratio between woody belowground biomass (i.e. roots) to woody aboveground biomass (i.e. stems, branches, crown); can be calculated for each individual shrub or tree but is also often estimated and expressed on stand level, i.e. all trees' and shrubs' estimated belowground biomass in relation to their collective aboveground biomass (Mokany et al. 2006).

Sapling (life stage): Life stage of woody plants after the seedling stage; older and larger than seedling, but not yet reproductive; not yet large enough to avoid herbivory or fire, but able to produce defence mechanisms and storage organs (Swemmer and Ward 2020) (but see Chapter 2 and Chapter 3 for growth class definitions used in this thesis).

Savanna: Vegetation unit with a continuous ground cover of C4 grasses and a discontinuous tree cover (Osborne et al. 2018); also called "Wooded grassland": continuous grass layer with woody plants covering 10-40 % which can also be secondary through intense fires and anthropogenic influence, typically with trees or shrubs in groups and on deep sandy soils in flat areas with up to 500 mm rainfall per year (White 1983).

Savanna woodland / forest type savanna: canopy cover up to 50%, height 9 m, 3000 trees per hectare (Grace et al. 2006); open stand of trees >8 m tall with 40 % or more canopy cover (White 1983); herbaceous cover >10% & canopy area index of woody vegetation 30-70% & mean height of upper tree layer (with DBH>10 cm) is 6-12 m (Torello-Raventos et al. 2013).

Scrub savanna: Vegetation type with herbaceous cover >10% & canopy area index of woody vegetation 30-70% & mean height of upper tree layer (with DBH>10 cm) is <6 m (Torello-Raventos et al. 2013).

Seedling: Life stage of recently germinated woody plants, 1-2 years old; most vulnerable to drought stress, disturbances, and competition (Swemmer and Ward 2020); also sometimes called 'juvenile' (but see Chapter 2 and Chapter 3 for growth class definitions used in this thesis).

Shifting cultivation: "a land use system that employs a natural or improved fallow phase, which is longer than the cultivation phase of annual crops, sufficiently long to be dominated by woody vegetation, and cleared by means of fire" (Mertz et al. 2021); also called 'shifting agriculture' or 'slash-and-burn' (Nath et al. 2022); it is a traditional subsistence farming and an old practice that nonetheless is ecologically and economically efficient despite being maligned as a practice that generates low productivity and environmental degradation (Nath et al. 2022).

Shrub: A "woody, non-climbing plant with multiple stems and/or small size that do not meet the tree definition criteria" (Conti et al. 2019); woody plant >0.5 m but <3.0 m height or < 6 cm basal stem diameter (Walker 1976); small woody plants <3 m with many stems, a dense and relatively wide crown, reproductive at small height, and vigorously resprouting after topkill (Zizka et al. 2014).

Shrubs which can sometimes grow to small trees (SST): medium-sized woody plants, with variable architecture from multi-stemmed to single-stemmed, reproductive at small heights, low resprouting vigour; was defined by (Zizka et al. 2014) to cope with the phenomenon, that not all woody individuals clearly fall into the definitions for "Shrub" or "Tree".

SOC: soil organic carbon, either as a fraction of soil volume or as a carbon stock expressed on a unit per areas basis as [t ha^{-1}].

Sprouting: also 're-sprouting'; adaptive trait which enables survival after considerable damage from fire or physical disturbance by initiating new vegetative growth from roots or stems (Wigley et al. 2009).

Stresses: Events which occur in time intervals that are shorter than the recovery time of the system; therefore, after a stress event the measured system characteristic changes, and cannot recover to pre-event level before the next stress event occurs and sets it back again (Borics et al. 2013).

Sustainability: A characteristic or state whereby the needs of the present and local population can be met without compromising the ability of future generations or populations in other locations to meet their needs (Millennium Ecosystem Assessment 2005); environmental, social and economic goals, such as conservation of natural resources, viability of economic activities and reduction of poverty and inequality, are achieved (Eriksen and Watson 2009).

Sustainable land management: "the stewardship and use land resources, including soils, water, animals and plants, to meet changing human needs, while simultaneously ensuring the long-term productive potential of these resources and the maintenance of their environmental functions" (e.g. conservation agriculture or agroforestry) (IPCC 2022).

Tipping point: the point or threshold at which small quantitative changes in the system trigger a non-linear change process that is driven by system-internal feedback mechanisms and inevitably

leads to a qualitatively different state of the system, which is often irreversible. This new state can be distinguished from the original by its fundamentally altered (positive and negative) state-stabilizing feedbacks (Milkoreit et al. 2018).

Threshold: A point or level at which new properties emerge in an ecological, economic, or other system, invalidating predictions based on mathematical relationships that apply at lower levels. For example, species diversity of a landscape may decline steadily with increasing habitat degradation to a certain point, then fall sharply after a critical threshold of degradation is reached. (Millennium Ecosystem Assessment 2005).

Topkill: partial or total mortality of above-ground biomass (but not death of the tree individual) (Higgins et al. 2012).

Tree: A potentially large woody plants, either single stemmed or with few stems, distinct but rather sparse crown well above ground-level, delayed reproduction, focused investment in height growth of a major stem (Zizka et al. 2014); "perennial woody plant with many secondary branches supported by a single main stem or trunk with clear apical dominance" (Conti et al. 2019); woody plant >3 m height and >6 cm basal stem diameter (Walker 1976).

Upscaling: The process of aggregating or extrapolating information collected at a fine resolution to a coarser resolution at greater extent. (Millennium Ecosystem Assessment 2005).

Introduction

Global climate change & the biodiversity crisis

Mitigation of climate change is probably the most important challenge of this century because man-made global warming is posing threats to billions of livelihoods and to ecosystems worldwide (IPCC 2018). The detrimental effects are all the more severe in global drylands which cover 45% of the terrestrial surface and are inhabited by more than two billion people (Safriel et al. 2005, Prăvălie 2016, IPCC 2022). In these regions in particular, safeguarding food supply and food security under future climate conditions and at growing population densities is a major political, social, and developmental challenge (IPCC 2022).

The second major global challenge is the ongoing biodiversity crisis that is threatening many species with extinction and can cause unforeseeable negative consequences for humanity at large (Svenning 2020, Dannenberg et al. 2024). These dual crises are often weighed against each other, but only addressing them both at the same time and realizing that they are coupled problems can bring the much-needed change (Svenning 2020, Allen et al. 2024, Dannenberg et al. 2024). The coupling and trade-offs between climate change mitigation, biodiversity conservation and safeguarding food security under climate change are central elements in landscape planning for rural Africa. Here, many people still depend on subsistence farming and livestock keeping for their daily needs (IPCC 2022). At the same time, many near-natural landscapes in Southern Africa still contain mega-fauna assemblages including protected wildlife species like elephant and lion and are therefore important biodiversity hotspots and ecotourism areas (Arbieu et al. 2017). Future-making scenarios for one and the same region can therefore often be found to alternatively promote agricultural intensification or nature conservation and ecotourism (see **Box 1**).

Box 1: Future-making perspective: Land-use change along pathways

Two common pathways of land-use change currently drive changes in coupled social-ecological systems, especially in rural Africa: agricultural intensification versus nature conservation (Folke et al. 2002, Lambin et al. 2003). They form two economic developmental pillars also in Namibia's 5th National Development Plan and are a recurring theme in political narratives, in which they are portrayed as parallel pathways (Hulke et al. 2021). Especially in the context of KAZA (see **Box 6**) the conservation pathway also represents a strong political paradigm (Dittmann and Müller-Mahn 2023). While the two pathways are seemingly unrelated their implementation on a common territory leads to interrelations and conflicts (Hulke et al. 2021, Lele 2021). These conflicting visions for the future of the social-ecological system create trade-offs between the anticipated ecosystem services, namely food and feed production in the case of agricultural intensification versus ecotourism income and biodiversity protection in case of conservation efforts (Eriksen and Watson 2009). However, attempting to maximize agricultural production and livestock husbandry next to free-roaming elephants and large carnivores is bound to generate human-wildlife-conflicts (Stoldt et al. 2020). In addition, both pathways of land-use change have unintended consequences for other ecosystem services, such as carbon storage.

In project *A01 Future Carbon Storage* of the collaborative research centre *Future Rural Africa* I aim to quantify changes in vegetation and soil (and ultimately ecosystem service delivery of both) along the two pathways and trade-offs between them. To this aim, I use a future-oriented space-for-time substitution (STS, see Pickett 1989) (**Figure 1**).
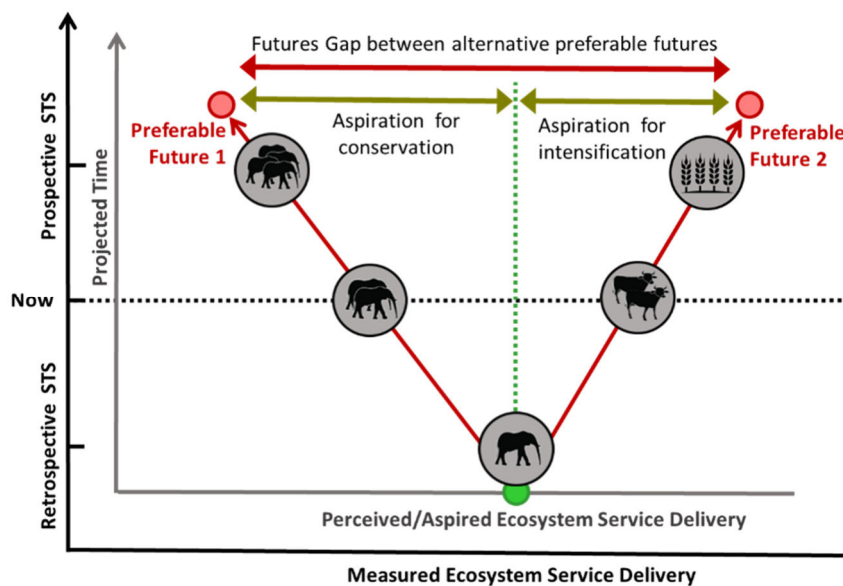
Figure 1: Conceptual graph of the future-oriented space-for-time-substitution (STS); grey icons stand for the five land-use types that I sampled to represent a common reference state and the two diverging future-making pathways: conservation pathway (left) and intensification pathway (right).

In this STS, we compare areas which are already subjected to one of the pathways with reference sites reflecting assumed conditions in the past. This reference state is characterized by low wildlife density and few human impacts, as a representation of the social-ecological system in the past when future-making towards the alternative preferable futures began. The endpoints of the pathways are intensively used agricultural fields and national parks with high wildlife density. Today, many areas in the region are at intermediary states between the reference state and the respective endpoints, i.e. extensive rangelands and areas with intermediate wildlife densities. The basic assumption of our STS is that we can grasp large-scale future-making impacts by studying exemplary areas with small-scale impacts along the pathways where the alternative futures are played out already. Taking the intermediary stages as a starting point, we assess the system state before land-use change along pathways started in the retrospective STS while we assess further system changes to be expected in the future in a prospective STS.

It is general consensus that carbon dioxide (CO_2) concentration in earth's atmosphere exceeds save limits and its ongoing increase needs to be stopped (IPCC 2018) but we are far from a consensus on how to most effectively remove excess CO_2 from the atmosphere (Bond et al. 2019). While new technical approaches such as direct air capture are currently being developed, analysed and their effectiveness is being debated (Chatterjee and Huang 2020, IPCC 2021), other actors have suggested that the only practicable way to remove carbon from the atmosphere in the short term is to increase carbon uptake by plants (Trumper et al. 2008). Among these less technical and rather nature-based approaches especially two methods are broadly discussed and funded: reforestation of degraded landscapes and afforestation of hitherto unforested landscapes. Their unifying idea is easy to convey to laypersons, as it is common knowledge that plants take up CO_2 and return oxygen to the atmosphere. As such, more plants will conduct even more of that exchange. Especially in trees, we can understand how carbon is used to build up wood biomass over the entire decades-long lifetime of a tree, hence no wonder that trees and forests became the epitome of materialized action against climate change. Conserving large, forested areas like the Amazonian rainforest and preventing the trees therein from destruction has been at the heart of global conservation efforts, initially for protecting them from land-use transformation and to preserve them as biodiversity hotspots (Palomo et al. 2014).

Carbon storage as a key concept

After becoming famous harbours of biodiversity, especially tropical forests also gained recognition as important carbon sinks that sequester CO_2 from the atmosphere and are critical to global climate stabilization in the future (Gibbs et al. 2007). Still, forest destructions continued and led the United Nations Framework Convention on Climate Change (UNFCCC) to recognize that especially in developing countries other incentives may be needed to effectively reduce carbon emissions from deforestation and forest degradation (Gibbs et al. 2007); see also **Box 2**. Carbon stored in woody vegetation thereafter became an economic value and preventing the carbon bound in trees from volatilization into the atmosphere can now be monetized in the form of carbon credits (Gibbs et al. 2007).

> **Box 2: REDD+**
>
> Carbon storage is a global ecosystem service (see glossary) in that humanity at large profits if CO_2 is removed from the atmosphere or retained in existing vegetation (Ryan et al. 2016). However, on a local level and especially in developing countries it is often contrasted with and trading off against very basic needs like firewood (Dewees et al. 2010, Ryan et al. 2016). The remaining intact tropical forests which comprise high carbon stocks, and are therefore often targeted by conservation initiatives, are often situated in developing countries. Setting such forests aside for conservation or carbon storage purposes and thereby hindering the local use of forest resources raises fundamental ethical concerns, as a greater global good is placed above direct local needs, especially as subsistence communities have neither driven nor benefitted from the industrial lifestyle that caused the global climate crisis (Lele 2021). Mainly targeting the economic imbalance between the global ecosystem service of carbon storage and the local ecosystem service needs, the program Reducing Emissions from Deforestation and Degradation (REDD) entails the idea that the global ecosystem service should be monetized in the form of 'payments for ecosystem services' to locally provide financial incentives for reduced deforestation (Gibbs et al. 2007, Calvet-Mir et al. 2015). Countries that reduce deforestation may be able to sell those 'carbon credits' on the international carbon market in the hope that this could simultaneously combat climate change, conserve forest areas, and protect other ecosystem goods and services (Gibbs et al. 2007, Newton et al. 2016). The REDD concept is often envisioned to work well within CBNRM schemes because they follow a similar management logic (Newton et al. 2016). An extension of REDD is called REDD+ and aims to incentivize further, additional carbon sequestration approaches, such as afforestation or biochar production (IPCC 2022). However, the real-world effectiveness of REDD projects is difficult to assess because the projected carbon storage gains are claimed in relation to 'unobservable' theoretical baseline values (West et al. 2023).

Carbon in soils

Even when being spared from active destruction trees are not immortal, and carbon bound within can be released to the atmosphere again once wood decays or burns. Focussing on trees alone is therefore short-sighted and the entire carbon cycle has to be regarded (Janzen 2006, Erb et al. 2018, Gaitán et al. 2019). Carbon captured through photosynthesis, including carbon stored in wood, often enters the soil compartment in the form of decaying dead organic material, thereby enriching the soils with soil organic carbon (SOC) (Janzen 2006, Kristensen et al. 2022). However, there is no a priori reason for assuming that low woody cover leads to lower inputs to the soil carbon pool (Ryan et al. 2011) , as I will demonstrate in Chapter 4 and Chapter 5. In contrast to living trees, SOC pools, especially in the deeper subsoil layers, are known to be more stable to decomposition and to persist for longer time spans (Shi et al. 2020, Sitters et al. 2020, Button et al. 2022, Kristensen et al. 2022). Consequently, SOC stocks build up over time and often account for a much larger fraction of total carbon storage in a given ecosystem compared to wood carbon stocks (Zhou et al. 2022b). The soil ecosystem compartment therefore became of increasing interest to national carbon accounting and greenhouse gas emission reduction aims (IPCC 2019a). Furthermore, increased soil carbon sequestration can provide co-benefits such as improved soil quality and water-holding capacity

(Stringer et al. 2012, IPCC 2018, 2022) rendering it especially interesting in the context of food security under climate change. However, the benefits of SOC can often only be realized when SOC is being depleted, e.g. soil fertilization through decomposition of soil organic material, which therefore is a trade-off against CO_2 sequestration; this is the so-called 'hoard it or use it conundrum' (Janzen 2006).

Chapter 1

Carbon storage in savannas

The savanna biome

Savannas and savanna woodlands cover more than 20% of the global terrestrial surface and are the dominant vegetation type in Africa spanning more than 4 million km² (Godlee et al. 2021). Savannas constitute the most spatially extensive ecozone in southern Africa and are home to most people in the region (Eriksen and Watson 2009). The savanna biome is defined by sparse and open tree cover with continuous grass cover underneath, often with a layer of shrub vegetation in between (Torello-Raventos et al. 2013, Osborne et al. 2018, Pennington et al. 2018), see **Figure 2**. However, some authors suggest to refrain from using the term 'savanna' for classification as it has been used broadly and for quite different vegetation units (White 1983). Depending on relative cover of trees, shrubs and herbaceous vegetation, several different savanna types can be distinguished, such as open grassland savanna with few trees or shrubs, scrub savanna with more shrubs and small trees, or woodland savanna with shrubs being overshadowed by taller trees (Torello-Raventos et al. 2013). Savannas occur in a wide range of climates (Pennington et al. 2018), although they typically prevail in drylands where, at least seasonally, water availability limits plant growth (Sankaran et al. 2005). Interestingly, they are often also found in climatic conditions that potentially allow for closed forest formations where the typical characteristic that prevented them from forest formation in the past are the intense natural disturbances at play, i.e. they are disturbance-prone ecosystems (Sankaran et al. 2005, Eriksen and Watson 2009, Charles-Dominique et al. 2016, Werner and Peacock 2019). To plants, disturbances are all factors that suddenly destroy plant biomass (Grime 1979) in discrete events which can also cause mortality of some plant individual, and change resource availability for the remaining (White & Pickett 1985, cited from Newman 2019), such as feeding herbivores, wildfires, pests, or various engagements of humans with their environment. Savannas are typically shaped by disturbance through recurring wildfires and diverse herbivores of various body sizes and feeding types (Archibald and Hempson 2016, Charles-Dominique et al. 2016, Buisson et al. 2021). As human populations grew and expanded, disturbances such as woodcutting, tree clearing for and

ploughing of fields, and intentionally managed fires were added to the mix and have since shaped savannas for thousands of years (Ouédraogo et al. 2015, Twine 2020). These manifold disturbances often interact and have complex repercussions with each other, which means that each change of probability, extent, or severity in one disturbance factor potentially alters co-occurring and future disturbance impacts (Shannon et al. 2011, Burton et al. 2020), see also **Figure 3**. The combination of all disturbance agents and disturbance attributes which jointly act on a particular landscape are referred to as the 'disturbance regime' (Burton et al. 2020).

Figure 2: *Typical, heterogenous savanna vegetation comprising large, scattered trees in the overstorey, diverse shrubs in understorey and continuous grass cover on the ground; browsing by large herbivores alters growth form and often reduces tree species to shrub-like growth forms; Mudumu National Park 2019; source: own photo.*

Importantly, ecosystem functioning and biodiversity in savannas are fostered by and depend on disturbances (Eriksen and Watson 2009, Newman 2019, Buisson et al. 2021). In that regard, savannas are different from other ecosystems, in which high disturbance levels usually imply ecosystem degradation and would be interpreted as a negative sign for the functioning of the overall ecosystem (Eriksen and Watson 2009). This has important implications for sustainable savanna management in the future, e.g. the need to restore historical disturbance regimes (Newman 2019,

Buisson et al. 2021). Finally, disturbance regimes make savannas a profoundly interesting area of study for ecologists.

Quantifying carbon storage in savannas

While forest protection from deforestation and carbon credits for rainforests became known and applied widely, other wooded ecosystems such as savannas and dry woodlands have so far received little attention for their potential to store carbon even though they are important, and increasingly will be, if climate change increases their coverage (Conti et al. 2019). It has been argued that this disregard may partly be a result of terminology and misinterpretation. With the onset of national carbon accounting and forest resource reporting as required under the Kyoto Protocol and UNFCCC, international environmental and forestry organizations laid down definitions for broad land-cover classes such as 'forest' (Chazdon et al. 2016, FAO 2019). To aid reporting, the Intergovernmental Panel on Climate Change (IPCC) provided default biomass estimates per land-cover class because more detailed and country-specific biomass equations were, and often still are, scarce or missing (IPCC 2006a, b, Henry et al. 2011, IPCC 2019a, b). The IPCC guidelines include chapters for forests and grasslands, with savannas being covered to some extend in both, but not treated separately (IPCC 2006b, 2019b). Therefore, those default values and land-cover classes are often too inaccurate as they do not properly account for differences in biomes, climate, soil types, patchy distribution of trees and herbaceous vegetation, or disturbances in savannas (Ciais et al. 2011, Cook-Patton et al. 2020, Reiner et al. 2023).

Vegetation types with variable, sparse and scattered tree layer are challenging to define and classify into broader land-cover classes (Reiner et al. 2023, Scogings 2023) and vegetation types (Torello-Raventos et al. 2013). When vegetation types do not qualify as a forest (also see definitions in glossary) they are often labelled as 'degraded forest', 'fragmented forest', 'secondary forest', 'fallow land', 'transitional forest', 'forest type savanna' or very generally as 'other wooded land' (Grace et al. 2006, IPCC 2006a, Keenan et al. 2015, Mertz et al. 2021, Nath et al. 2022, Reiner et al. 2023). Moreover, they are often described as an unwanted and 'degraded rather than regrowing' forest category with low commercial value (Keenan et al. 2015, Mertz et al. 2021). All of these terms reflect attempts to somehow fit heterogeneous, disturbance-shaped savanna vegetation types into forest and forest degradation classifications, although many of these areas are in fact fully functioning and vital ecosystems in their naturally or semi-naturally disturbed states (Scogings 2023). This obstructs carbon pool reporting and greenhouse gas emission monitoring, but has also led to false estimates on degradation, forest loss, and even potential regenerations and their carbon gains (Keenan et al. 2015, Rozendaal et al. 2022, Reiner et al. 2023, Scogings 2023). For instance, more than a quarter of Africa's tree cover consists of scattered trees and is overlooked by many mapping and remote

sensing approaches because these trees grow outside areas classified as 'forest' (Reiner et al. 2023, Scogings 2023). Global analyses of forest cover dynamics over time entail high uncertainties in savannas due to 'forest' definition problems and land-cover classification differences between assessments (Keenan et al. 2015). Furthermore, the default estimates of wood biomass per continent and biome, as provided by the IPCC, often reflect intact old-growth forests (instead of open and disturbance-prone savanna or woodland vegetation types) and thereby led to substantial overestimation of carbon storage (Rozendaal et al. 2022).

On a smaller level, disturbances not only change woody cover and average stand-level biomass in general but may also heavily impact an individual tree's shape or growth form (Moncrieff et al. 2011, Stevens 2021); see **Figures 3-7**. This phenomenon has implications especially for individual-based inventories and estimation approaches, as those rely on allometric equations (see glossary) in which measured size parameters are used to non-destructively estimate the biomass of a tree. Usual forestry methods primarily rely on single, easy-to-measure size proxies like stem diameter at breast height (DBH, measured at 130 cm height above the ground) to estimate tree biomass (Mugasha et al. 2013). However, allometries which are derived from healthy trees, may not fit disturbed ones (Paul et al. 2016). Moreover, under chronic disturbances which episodically remove biomass, as is typically the case in savannas, these allometric relationships are altered in comparison to non-disturbed trees (Moncrieff et al. 2011, Stevens 2021). This is relevant for remote sensing applications as those typically draw conclusion about biomass only from canopy shapes and crown dimensions (Colgan et al. 2013, Jucker et al. 2017, Reiner et al. 2023). When disturbances alter the shape of a tree or shrub to such an extent that measuring the usual size proxies becomes impossible (e.g. if stems are broken or cut off below 130 cm or grow in irregular shape, see **Figures 3 & 6**), suitable workarounds can be used to reconstruct missing or unmeasurable size proxies from those that are accessible (Mugasha et al. 2013). Yet, some size proxies may not be changed at all, even though a disturbance event essentially removes larger fractions of the individual biomass (**Figure 6**). For instance, elephants may break tree stems of up to 60 cm in diameter (Stevens 2021) and consequently remove the entire crown of such a tree, while the stem diameter at 130 cm or basal stem circumference may be left unchanged. Employing allometric equations that are built on more than one measured size proxy may therefore be advisable (Mugasha et al. 2013); see Chapter 2 & Chapter 3. Additionally, the visible biomass losses should be accounted for via a damage assessment if possible and be deducted from raw biomass estimates to reflect actual post-disturbance tree biomass and carbon storage more precisely (see Chapter 2 & Chapter 3).

Figure 3: Large and old but severely damaged tree (Guibourtia coleosperma) in Bwabwata National Park. From green leaves in the crown, it is apparent that this tree is still alive, although repeated and additive disturbances have removed considerable portions of its aboveground biomass. Detailed damage assessment revealed extensive elephant damages to the bark of the stem which consequently rendered the tree more vulnerable to repeated fires. Still, survival at such severe disturbance highlights how evolutionarily adapted many savanna species are to disturbances. Doctoral student for scale; source: own photo, Bwabwata National Park, Namibia 2018.

Thus, using forest baselines and forestry methods in disturbed savanna ecosystems are problematic because they may lead to overestimation of carbon stocks, but intriguingly the opposite is true at the same time: Carbon storage in savannas has often been underestimated and the two major reasons are again closely linked to savannas' characteristic disturbed-ness. The first source of potential underestimation of savanna carbon storage lies in their particular vegetation structure. Aside from scattered trees in the overstorey, extensive herbaceous vegetation in the grass layer and commonly an intermediate shrub layer are the other two defining vegetation structures in savannas (Torello-Raventos et al. 2013, February et al. 2020). Recent studies highlight that the grass layer plays an important role in savannas' carbon storage (Zhou et al. 2022a). Unfortunately, grass-derived carbon storage could not be integrated in my study because sampling campaigns partly fell into drought years and therefore herbaceous biomass estimates were not comparable throughout the dataset.

The shrub layer however was recorded with great care, and I specifically amended existing methods and developed new protocols (see Chapter 2 & Chapter 3) to ensure that this vegetation layer was properly included in our data. At a closer look, the shrub layer by no means consists of only shrubs

(see glossary). In fact, it also comprises young individuals (like juveniles, see glossary) and many severely damaged, i.e. disturbance-shaped tree and shrub individuals (gullivers; see **Box 3** & **Box 4**). Such individuals often tend to be excluded from other inventories through a size threshold e.g., by a minimum stem diameter at breast height (DBH) of 5-10 cm (Mitchard et al. 2011, McNicol et al. 2018a, Sichone et al. 2018) because their contribution to stand-level aboveground woody biomass (AGB) is implicitly assumed to be negligible (Chave et al. 2014). However, in savannas the shrub vegetation is known to hold large fractions of overall biomass and has been found to contribute more than 75% of the biomass that is contained in large trees (Brown 2002) or even 84% of overall wood biomass (Colgan et al. 2013). Ignoring savannas' shrub biomass therefore results in a significant underestimation of the total woody biomass (Kouamé et al. 2022) and consequently carbon storage.

Figure 4: Elephants browsing on stunted Terminalia sericea, which usually grow as single-stemmed trees, but cope well with chronic disturbance and then exhibit unusual growth forms ('gullivers'); Mudumu National Park, Namibia 2018; source: own photo.

> **Box 3: Growth classes**
>
> The growth classes in this thesis were specifically created to categorize recorded tree and shrub individuals in such a way that for each growth class a standardized procedure of biomass estimation and biomass loss quantification could be formulated. Undeniably, there had been extensive literature on life stages and age classes and growth forms in woody vegetation before, which all attempted to categorize individual woody plants. However, none of the classifications in the literature was fully applicable to my recorded dataset. Taxonomic literature usually describes species as typically growing as either a tree or a shrub but I, like others, found no clear distinction and encountered many species which, depending on circumstances, either grew as shrubs or trees (Kouamé et al. 2022). Many classifications work on the basis of size thresholds such as height and stem diameters or stem circumferences to distinguish a tree from a shrub (Zizka et al. 2014, Conti et al. 2019). Others draw on elements such as reproductivity (Higgins et al. 2012, Swemmer and Ward 2020). Many growth form classifications depend on number of stems, maximum height, and crown architecture, but often struggle with forms that are intermediate between trees and shrubs (e.g. multi-stemmed trees) (Ben-Shahar 1993, Zizka et al. 2014). Disturbances, and the effects they may have on growth form and plant architecture, are only rarely regarded in classification attempts (Fairman et al. 2019).
>
> Size classes are problematic in disturbance-prone ecosystems as intense disturbance events can remove so much biomass that an individual may revert into previous size classes (Sankaran et al. 2013), which has been dubbed 'size class reversion' (Das et al. 2022). Age classes are often posing problems, as very different things can be implied by them such as a biological, ontogenetic or physiological age (Gatsuk et al. 1980). Also individuals that on first glance appear to be, e.g., young seedlings are in fact older and resprouting upon closer inspection (Fairman et al. 2019). Furthermore, 'age' implies a calendric number of years, whereas for assessing individuals' ecological properties rather their resource use in space and time and hence their stage of development is important (Gatsuk et al. 1980). Still, age is relevant in so far as growth rates and root-to-shoot ratios in savannas are age-dependent and change non-linearly over the lifetime of trees (which was comprehensively visualized by Swemmer and Ward 2020, Figure 12.1). In disturbance-adapted ecosystems, a woody plant's small size can therefore either reflect a young age, a severe damage, or a combination of both (see Chapter 2 & Chapter 3).
>
> I first distinguished between three life history stages, i.e. juveniles, saplings, and adult woody individuals (Werner and Prior 2013, Werner and Peacock 2019, Swemmer and Ward 2020). For each life history stage, I defined a non-damaged and a severely damaged growth class ('gullivers', see **Box 4**), resulting in six growth classes. For reasons of biomass and biomass loss calculation procedures a few sub-classes exist (see Chapters 2 & 3).

Figure 5: *Torn and broken branches as clear signs of recent elephant browsing damage on a stunted-growing individual of Terminalia sericea; Bwabwata National Park 2019; source: photo by team member of research group.*

As an additional methodological constraint, the allometric models that are used for trees are usually based on stem predictors. However, small individuals are not well represented by such stem-based allometries (Ryan et al. 2011). Moreover, measurements of shrub stem diameters or basal areas can be demanding or introduce further inaccuracies when species are spiny, dense, or have many stems (Conti et al. 2019), as again is typically the case in African savannas, since woody plants there are evolutionarily adapted to defend themselves against disturbances from browsing herbivores (Charles-Dominique et al. 2016). Hence, canopy dimensions are better predictors for shrub-like growth forms (Meyer et al. 2014) which require additional field measurements and a second allometric model for estimation. Assumedly, the additional effort of such a second measurement routine for small woody plants is often avoided for practical reasons.
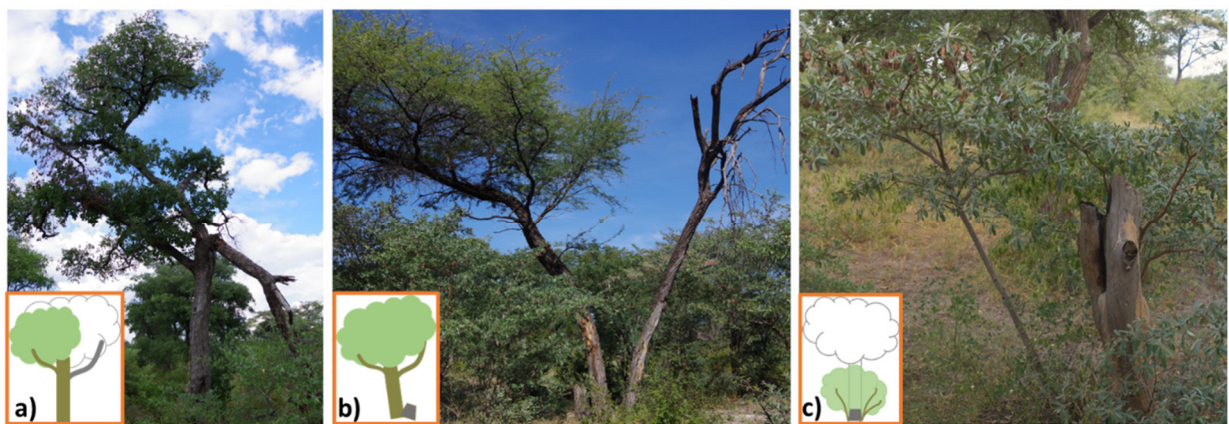
Figure 6: Three of the gulliver growth classes identified in adult tree individuals when recording woody vegetation of all size-, age- and damage-levels. All individuals pictured here had been fully grown adult trees when disturbance impacts from elephant browsing, wildfire or storm destroyed larger fractions of their aboveground biomass; sketches in the lower left corner represent growth class according to classification in Chapter 2; a) biggest branch of the tree crown broken-off by storm thereby reducing canopy dimensions without stem loss; b) a large multi-stemmed tree lost one entire stem to a combination of elephant bark removal and severe fire damages at the stem base, and therefore lost half of its canopy, yet the other half grows on, likely benefitting from a root system that is larger than its living aboveground dimensions would suggest; c) single-stemmed adult tree was entirely topkilled from elephant damage and subsequent burning, but is vigorously resprouting now as multi-stemmed shrub, which appears to be much younger than it actually is. [Figure adapted from Chapter 2 and Chapter 3]

Box 4: Gullivers

The earliest reference to the term 'gulliver' is likely by Bond and van Wilgen (1996), in which the authors use it as a special category for juvenile woody plants which were intensely damaged by fires and caught in the fire trap. They were still small enough to be classified as juveniles although they were in fact much older than a typical juvenile and older than their current size would suggest (Bond and van Wilgen 1996, Wigley et al. 2009, Higgins et al. 2012). Although the term is not very popular, many publications have, without naming it such, reported on and dealt with phenomena that I subsume under the term 'gulliver' (Walker 1976, Lévesque et al. 2011, Bond and Midgley 2012, Sankaran et al. 2013, Levick et al. 2015, Swemmer and Ward 2020, Mertz et al. 2021, Wilson et al. 2021, Zhou et al. 2022b). In these publications, they are called 'converted trees' (Walker 1976, Wilson et al. 2021), 'coppicing' (Lévesque et al. 2011), 'curtailed', 'severely damaged', experiencing 'retarded or negative growth' (Swemmer and Ward 2020), or 'small plants that persist for decades suffering repeated topkill' (Bond and Midgley 2012) from being 'frequently burned' (Zhou et al. 2022b). In 2007 the term seems to have been revived as the 'gulliver syndrome' by Higgins et al. (2007).

Gullivers need to be regarded as a separate category because of their very high growth rates and their ability to reoccupy their very own canopy gap before new seedlings do (Lévesque et al. 2011). Extensive research has been conducted on the ability of savanna trees and shrubs to grow coppice shoots after topkill which is an important adaptation to disturbance-prone ecosystems (Lévesque et al. 2011, Morrison et al. 2016, Das et al. 2022). These resprouting individuals are exploiting the already well-developed root system thereby obtaining more resources than a newly growing seedling could, which allows them to grow more rapidly and perform better (Stokes 2002, Neke et al. 2006, Wigley et al. 2009, Lévesque et al. 2011, Hermann et al. 2012). Trees may even seem dead after total topkill, but can be found to have in fact survived and are resprouting if follow-up inventories are conducted a few years later; this was for instance the case for 17-18 % of all recorded trees after 3-year intervals in a study by Das et al. (2022) and for a fifth of all trees during a 6-year period in a study by Morrison et al. (2016). Importantly, gullivers can leave the gulliver state behind if they are permitted to grow un-disturbed for some years and finally gain adult size (Higgins et al. 2012). This was dubbed the 'gulliver syndrome' by Higgins et al. (2007) emphasizing the potential of a damaged tree to become a giant once it escapes the disturbance trap. Gullivers that are released from the fire trap after disturbance regime changes may drive bush encroachment and ecosystems can be altered substantially (tipping points) (Skowno et al. 1999).

Several gulliver growth classes are proposed here, mainly because they differ much in regard to the balance between living and dead structures (see **Box 3**) and in the balance between actively-growing and fully-formed, passive structures (Gatsuk et al. 1980). Importantly, I extended the definition of 'gullivers' so that it encompasses not only seemingly juvenile trees but instead all individuals that are in fact older than their size may suggest at first glance. This is important for carbon storage estimation, as the root biomass of gullivers and their belowground organs are likely also much larger than their current aboveground dimensions suggest; also see **Figure 6**.

Another routine that requires additional efforts when amending inventory protocols to disturbance-prone ecosystems is accounting for disturbed growth forms. As was mentioned above, the shrub layer also comprises individuals which, considering their age, could be, or in fact had been, fully grown trees but were reduced to shrub height and often to a shrub-like growth form despite belonging to tree species (gullivers; see **Box 3** and **Box 4**). The distinction between tree and shrub

species is often difficult as many species in savannas can either grow as single-stemmed trees or multi-stemmed shrubs and also as various forms in between (Mannheimer and Curtis 2009, Zizka et al. 2014, Kouamé et al. 2022). Often, tree species initially grow as a single-stemmed tree before being severely damaged or topkilled. Afterwards they resprout from the base and regrow as a multi-stemmed small tree or a shrub (Zida et al. 2009, Levick et al. 2015, Morrison et al. 2016, Das et al. 2022)(see **Figure 6c**). Which allometric equation is to be employed should therefore be determined along suitable growth classes (see **Box 3**), not species. Additionally, visible biomass losses should be accounted for via a damage assessment and visible remains of dead stems on living individuals should be regarded, as they are important indicators of belowground dimensions (see **Box 4**, Chapter 5, and next section).

The second source for underestimation of carbon storage in savannas lies hidden from plain sight in the belowground realms: Forests and trees typically hold less biomass in roots belowground than in the aboveground stem and crown parts. The ratio of root biomass to shoot biomass (i.e. the root-to-shoot (RS) ratio) in temperate and moist forests typically ranges between 0.2–0.5 (Mokany et al. 2006, Kachamba et al. 2016), meaning that root biomass is less than half as big as aboveground parts. The actual ratio is dependent on stand age and structure, but also on individuals' age. Because trees accumulate more stem biomass than root biomass over the course of their lifetime, their RS ratio decreases the older they get (Ryan et al. 2011, Mugasha et al. 2013, Kachamba et al. 2016, Ledo et al. 2018, Swemmer and Ward 2020, Kouamé et al. 2022). In forests, the most widely adopted approach to estimate the invisible root biomass is applying one default RS ratio across the entire stand, landscape, or biome in question, sometimes accounting for additional factors like stand age or aboveground biomass in broad classes (Mokany et al. 2006, IPCC 2019b). For drylands and savannas, however, estimating belowground biomass accurately is both more difficult to achieve and more important for several reasons: Firstly, the RS ratio depends not only on age, but also on climatic water deficits with trees having larger roots in drier climates because they invest more biomass to acquire scarce soil water resources (Ledo et al. 2018). Secondly, the shrubs that often occur in savannas (see above), on average have much larger RS ratios than trees, and usually even more root biomass than aboveground biomass (i.e. RS ratios >1)(Kouamé et al. 2022). Thirdly, heavily damaged individuals (gullivers; see **Box 4**) likely retain large fractions of their root biomass after losing aboveground biomass to disturbances (Morrison et al. 2016, Das et al. 2022) and will therefore have even larger RS ratios. In consequence, current methodologies, such as default RS ratios as suggested in IPCC protocols, are very likely underestimating carbon storage in savanna ecosystems in general, with deviations that have been found to be enormous in some cases (here 160%; Kouamé et al. 2022).

Land-use change & disturbance regimes

To complicate matters even further, savannas, like most other biomes, are increasingly transformed by the people inhabiting them (see **Box 1**), e.g. by agricultural conversion or deforestation (Ciais et al. 2011), and population growth will even accelerate this process (Buisson et al. 2021). Land-use change has been highlighted as a most concerning driver of further carbon emissions, biodiversity loss, and ecosystem degradation, especially in synergy with ongoing global climate change (Newbold et al. 2015, Pricope et al. 2015, Ryan et al. 2016, Archer et al. 2021, Asamoah et al. 2022, IPCC 2022). Separating human and climatic drivers of carbon storage requires sub-sampling of regions with similar climate but different human impacts (Stringer et al. 2012), e.g. various neighbouring land-use types. Ecosystems in climatically challenging environments display lower resistance to land-use change (Archer et al. 2021). African communities in savanna ecosystems are particularly threatened, for instance, by drought effects and food insecurity (Osborne et al. 2018, IPCC 2022). Land-cover conversion from near-natural states to agriculturally used land and altered land management are known to reduce vegetation biomass (Newbold et al. 2015) but for savannas the baseline data is scarce and estimates entail high uncertainties (Erb et al. 2018). Ultimately, land-use change will even impact how and if humans and wildlife can co-exist, especially where settlements, rangeland and agricultural fields are located in immediate neighbourhood to national parks (see **Figure 8**) and along major wildlife migration corridors (Guarnieri et al. 2024).

Figure 7: Common type of disturbance to trees in agricultural fields: tree species (in this case Colophospermum mopane) which are known to regrow after damages, are cut at a height of 80–110 cm thereby eliminating the shading crown; fresh coppicing shoots are cut yearly by farmers and piled-up in distance to the tree stump, then slowly burned to enrich the soil with nutrients and carbon particles; in this agricultural technique, trees are not killed, but deliberately kept alive in this gulliver state.
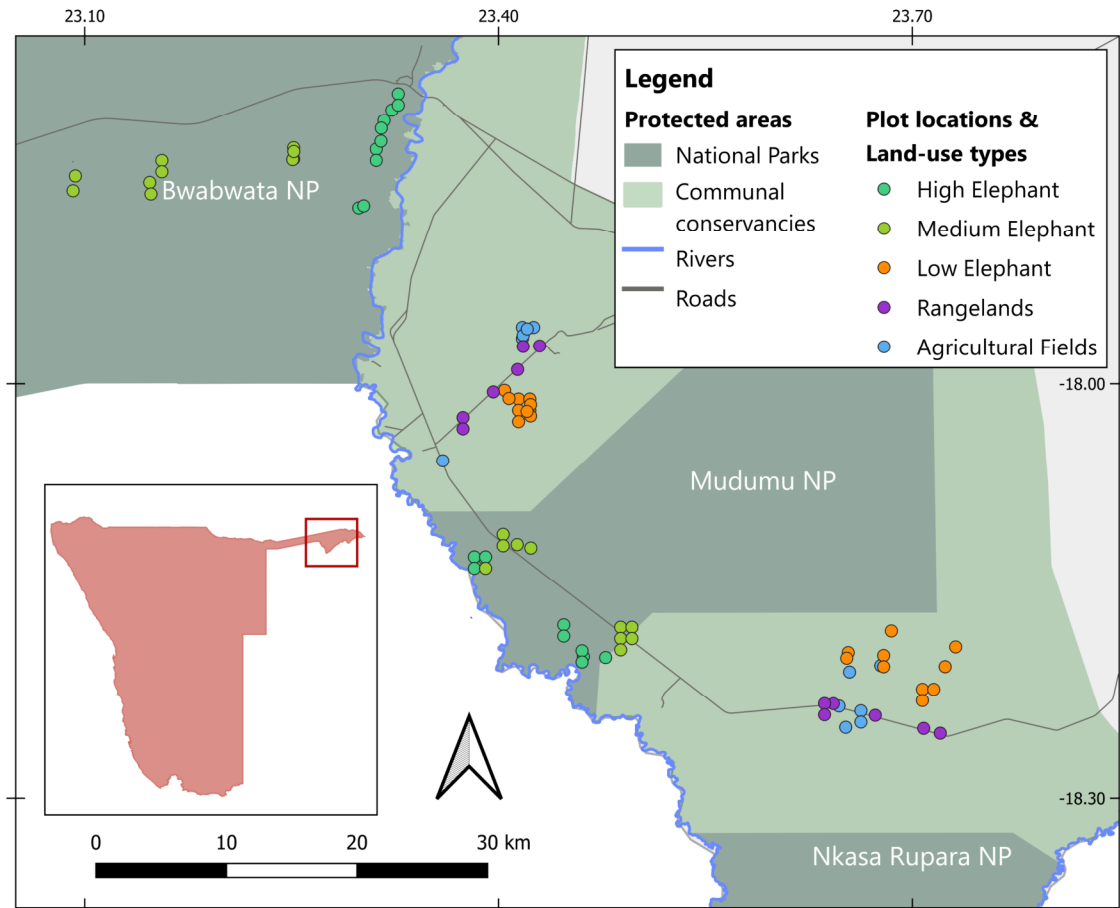
Figure 8: *Study area in North-Eastern Namibia (Zambezi Region) and plot locations of my study with land-use types as colour code. Figure taken from Supplementary material of Chapter 5. GIS layers kindly provided by Namibian Association of CBNRM Support Organizations (NACSO); the Environmental Information Service (EIS) of Namibia; Open Street Map project; and Hijmans (2015).*

Quantifying disturbance losses and ecosystem services

From an ecological point of view, land-use change means that a disturbance regime is altered (Newman 2019) which is particularly challenging in open savanna ecosystems. As these are essentially disturbance-driven, shifting the delicate balances in their complex disturbance regime can lead to manifold unintended consequences and drive ecosystem degradation (Newman 2019). For instance, savanna ecosystems can derail from a healthy state (i.e. degrade) in more than one direction: While too much disturbance can lead to a total loss of vegetation cover and ultimately to desertification, disturbance suppression has been proven to cause bush encroachment and thereby loss of essential ecosystem functions (Higgins et al. 2000, Trumper et al. 2008, Sankaran et al. 2013, Osborne et al. 2018, Venter et al. 2018, Davies et al. 2019). To understand ecosystem resilience in the face of shifting disturbance regimes and land-use change requires more knowledge on disturbance characteristics (Johnstone et al. 2016). For instance, the effects of multiple simultaneous disturbance factors need to be disentangled so that predictions can be made of likely

shifts in vegetation structure, biomass, or species composition under certain future land-use changes (also see **Box 1**). To this end more detailed and individual-level demographic data are required (Morrison et al. 2016), for instance on biomass losses caused by different disturbance agents such as woodcutting, wildlife browsing or wildfire (Stringer et al. 2012, Tripathi et al. 2019). This can also help to quantify disturbance levels for larger areas which is challenging but necessary, not least for better carbon accounting (Rozendaal et al. 2022); see Chapter 3.

Box 5: Nature Conservation and CBNRM in Namibia

Namibia is one of the countries with the largest percentage (more than a third) of its area subjected to conservation efforts (Benitez et al. 2022). However, most of this conservation area is in fact not exclusively used for nature conservation (i.e. the island approach to conservation (Palomo et al. 2014)) and instead inhabited not only by wildlife, but also by people. Since 1998 first the network idea, then the landscape approach, and recently the social-ecological approach to conservation (Palomo et al. 2014) led to the establishment of wildlife corridors, buffer zones and finally so-called communal conservancies all over the country (86 in total) which follow the concept of community-based natural resource management (CBNRM) (Jones et al. 2013, Khumalo and Yung 2015, Meyer et al. 2021). In these conservancies, attempts are being made to foster co-existence of wildlife with resident communities, and a wide variety of land-uses is permitted (but also prohibited) depending on designated zones, such as agriculture, livestock herding, tourism and even big game hunting (Drake et al. 2020). The concept therefore is a step towards recognition that protected areas are integrated into a coupled social-ecological system and that buffer zones need to be managed along with protected areas so that conservation objectives are not compromised (Palomo et al. 2014). In practice, CBNRM is based on the assumption that local communities can be motivated to take part in conservation efforts if they benefit financially from the protected wildlife so that it becomes an asset rather than a liability (Jones et al. 2013, Khumalo and Yung 2015, Drake et al. 2020). In that sense, it is a 'payments for ecosystem services' scheme (Naidoo et al. 2011, Calvet-Mir et al. 2015).

The income of Namibian conservancies is largely dependent on the tourism sector (Hulke et al. 2021), and especially on hunting tourism (Drake et al. 2020). Income from trophy hunting was a central element of the financial incentives to local communities as it is the most direct means to commercialize wildlife (Drake et al. 2020). In addition, being eligible to receive compensation payments or mitigation measures for wildlife damages to crops and property were another incentive to gazetting conservancies (Khumalo and Yung 2015). However, these economic benefits do not balance against the high losses in crops, livestock and even lives that locals experience from co-existence with wildlife (Khumalo and Yung 2015, Drake et al. 2020, Kalvelage et al. 2020, Hulke et al. 2021, Lele 2021), although cost/benefit ratios between conservancies can be highly variable (Benitez et al. 2022). Recently, more critical voices have been raising concerns about the inherent contradictions of the CBNRM model and the current approaches to conservation area planning which both expect to see a future with increased wildlife numbers and agricultural development in a common territory (Cassidy and Salerno 2020, Hulke et al. 2021). Further criticism also highlights ethical concerns regarding unfairness in negotiations over what is to be conserved (Lele 2021) as well as the hidden costs of continuous human-wildlife conflict such as uncertainty about the future and fear (Khumalo and Yung 2015).

Furthermore, we need to understand which effects such vegetation shifts may have for the social-ecological system at large and specifically the local communities and their daily resource and income

base. To quantify these local ecosystem services, which people derive from the natural resources around them, we need data on species composition and detailed understanding of which species are useful to locals (Dimobe et al. 2018). Therefore, species inventories are needed which are difficult to obtain via remote sensing approaches (Levick et al. 2015). And yet again, this is another argument for recording small woody growth forms as well, as ecosystem services such as medicinal products are by no means restricted to large trees and are instead often found in small species or young individuals (own communication, Namibia 2018-2022, and van Wyk and Gericke (2000)). Furthermore, species inventories and shifts in population structures can be early warning indicators of long-term effects (Tietema 1993).

Nature conservation, livelihoods and carbon storage

Where nature conservation and rural livelihoods based on agriculture and livestock keeping exist in close vicinity, these two visions for the future are mostly trading-off against each other and often directly clashing (Lele 2021)(also see **Box 1** and **Box 5**).

Box 6: KAZA & Transfrontier conservation

Decades of wildlife conservation efforts have caused increases in many wildlife populations in Southern Africa and Namibia itself (Naidoo et al. 2011), most notably elephants (Skarpe et al. 2004, MacFadyen et al. 2019, Stoldt et al. 2020, Bollig and Vehrs 2021, Craig et al. 2021). However, historical forms of nature conservation (often referred to as 'fortress conservation' or the 'island approach') dating back to colonial times had created conservation areas which restricted animal movements and granted only low connectivity between wildlife populations (Palomo et al. 2014, Stoldt et al. 2020). To overcome this, conservation projects since the 1990s started emphasizing the need of connectivity via wildlife corridors which often span international borders (Pinter-Wollman 2012, Palomo et al. 2014, Brennan et al. 2020, Dittmann and Müller-Mahn 2023). To this aim, existing national parks were integrated into transfrontier conservation concepts like the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA)(Pinter-Wollman 2012, Munthali et al. 2018).

KAZA was created by five neighbouring countries (Angola, Namibia, Botswana, Zambia and Zimbabwe) in 2012 and is the largest transfrontier conservation area in the world (520,000 km², i.e. larger than Spain; (Pinter-Wollman 2012, Dittmann and Müller-Mahn 2023)). Southern Africa now has more than 300,000 elephants, of which 75% belong to a population roaming in the larger KAZA area (Thouless et al. 2016). In this modern landscape and network approach to conservation (Palomo et al. 2014) the Namibian part of KAZA is an essential and central, element through which major wildlife herds migrate between Botswana and Angola or Zambia (Lindsay et al. 2017, Chibeya et al. 2021, Atlas-of-Namibia-Team 2022, Dittmann and Müller-Mahn 2023). The idea of KAZA is widely supported by national elites and development agencies, also for economic and political motivations because it promises economic growth by linking natural resources in border regions to the international tourism economy (Dittmann and Müller-Mahn 2023). In connection with CBNRM initiatives this conservation landscape approach aspires to integrate both nature conservation and rural development (Palomo et al. 2014, Munthali et al. 2018, Bollig and Vehrs 2021).

Aside from the methodological challenges outlined above other aims of my research centre around the question to what extent these two goals can be implemented together and if there are additional means by which to reconcile them e.g. through additional ecosystem services or income sources. One such income source may be found in payments for ecosystem services, in this case the ecosystem service of carbon storage (Jagger et al. 2022). This could be implemented through carbon certificates and programs such as REDD+ (Jagger et al. 2022)(see **Box 2**) which potentially open up a third source of revenue apart from farming and wildlife tourism. As was described above, savannas and drylands have been understudied in regard to their potential to store carbon under different land-use types, a research gap which I am addressing in Chapter 4 and Chapter 5 of my thesis. As an ecologist, I would by no means suggest to subject savannas to afforestation programs or establish monoculture plantations in the name of carbon sequestration, as those are problematic on many levels and therefore harshly criticized (Bond et al. 2019). Instead, I want to explore to what extent viable, existing modes of land-use could potentially be eligible for additional revenues from carbon certification.

For instance, it has been argued that protected areas should be considered as carbon sinks (Chidumayo et al. 2011) or that carbon storage programs should be located near conservation areas in order to increase income alongside ecotourism (Grace et al. 2006), but due to the methodological challenges addressed above it is very much uncertain to what extent they can indeed be considered carbon sinks and whether they will continue to be so, should wildlife densities increase further (Balfour et al. 2007, Shannon et al. 2011). An essential part of that question is connected to elephants, which because of their body size and their wasteful feeding behaviour exert heavy disturbance impacts on the woody vegetation in their habitat, earning them the nickname of 'ecosystem engineers' (Balfour et al. 2007, du Toit et al. 2014), see **Figures 3-5**. But also smaller herbivore species play an important role in structuring vegetation, especially where they act synergistically with elephants (Rutina and Moe 2014, Coetsee et al. 2023). Under these circumstances, more and more voices raise concerns about further increasing elephant densities, including when and how to control populations for avoiding negative effects on vegetation in general, potential resource depletion for other herbivores, and biodiversity decreases (Ben-Shahar 1993, Balfour et al. 2007, O'Connor and Page 2014, Sianga et al. 2017, Teren et al. 2018, Tripathi et al. 2019, Chibeya et al. 2021, Hyvarinen et al. 2021, Szangolies et al. 2023).

Traditional agricultural techniques with shifting cultivation modes (formerly often called 'slash-and-burn') were for a long time maligned as practices that generate low productivity but drive environmental degradation, while recent meta-analyses provide evidence that forest loss can not necessarily be attributed to shifting cultivators (Ziegler et al. 2012, Nath et al. 2022). Instead, many researchers have highlighted that shifting agriculture in fact is an ecologically and economically

efficient practice for drylands and can be highly sustainable depending on farmer knowledge and mode of shifting (Ziegler et al. 2012, Ryan et al. 2016, Lele 2021, Nath et al. 2022). However, REDD+ policy makers often tend to ban all forms of shifting agriculture, although too little is known about its actual effects on carbon cycling (Ziegler et al. 2012). Especially agroforestry and 'conservation agriculture' approaches building on indigenous knowledge and traditional cultivation practices aim to foster the retention of trees in agricultural fields hence basically encourage higher woody biomass for sustainable agricultural production increase (Garrity et al. 2010, Minang et al. 2014, IPCC 2022). Agroforestry (sometimes called 'evergreen agriculture') therefore is a good example of a multifunctional land-use type that, next to yield increases, simultaneously amplifies a whole range of ecosystem services, such as drought resilience, biodiversity conservation, soil fertility improvements, soil water holding capacity, medicinally used plants, livestock feed or fuelwood provision and can potentially be a way out of poverty (Garrity et al. 2010, Jagger et al. 2022).

What holds true for sustainable agriculture may even be easier to implement for extensively used rangelands as these commonly contain trees for shading (Brinkmann et al. 2023). Livestock herding often is the underlying cause of savanna degradation (Buisson et al. 2021, Brinkmann et al. 2023, Geißler et al. 2024). However, in coexistence with, or even in replacement of, native herbivores sustainably managed livestock herds can contribute to foster plant diversity, structural diversity, nutrient distribution and therefore help to retain relevant ecosystem functions (Buisson et al. 2021, Young et al. 2021, Szangolies et al. 2023, Geißler et al. 2024). Rangelands are now also increasingly valued as sources of woody biomass for production of biochar or bushfeed from shrubs removed in bush-encroached communal areas, opening-up an additional income source for rural households (Angombe et al. 2023, Brinkmann et al. 2023).

All of the ecosystem services mentioned above are directly linked to trees and shrubs and the carbon cycle they participate in. In my research, I aim to extend the data basis needed to assess to what extent such multifunctional fields, extensive rangelands, and neighbouring national parks could be supported through the additional function of carbon credit income or other schemes of payment for ecosystem services (Minang et al. 2014, Jagger et al. 2022). However, many of the potentially synergistic effects I describe above are difficult to predict because ecosystem responses to land-use are often not linear (Folke et al. 2002). Furthermore, the natural and the human systems are inherently interconnected, i.e. coupled social-ecological systems (Folke et al. 2002, Palomo et al. 2014, Sianga et al. 2017), especially in such integrated conservation landscape approaches like KAZA (Bollig and Vehrs 2021); also see **Boxes 1 & 5**. Understanding ecological shifts and future-making effects in social-ecological systems therefore requires research rationales spanning entire gradients of land-use change, methodologies that work well across several land-use types, and

statistical approaches which can incorporate non-linearity (Zuur et al. 2009, Messier et al. 2016, Barfuss et al. 2018), also see **Box 7**.

Box 7: Generalized Additive Models (GAMs)

GAMs are particular powerful for modelling non-linear relations between predictors and response variable and to decompose the additive effects of predictors on changes in the observed response variable. The nature and shape of these changes can best be understood through visualization. The visual GAM output consists of potentially curved smoother lines for each term, demonstrating the isolated 'partial effect', i.e. the impact each predictor has on the response variable in hypothetical conditions of holding all other variables at fixed values.
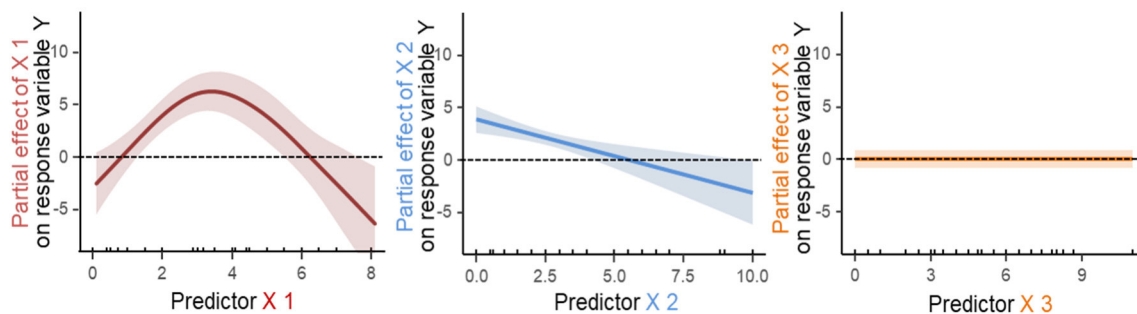

Figure 9: Example of what a GAM output typically looks like for three hypothetical predictors (X 1 to X 3), see further description below (adapted from Suppl. Material of Chapter 5).

In the example above the visual GAM outputs are interpreted in the following way:

➤ If hypothetically all other predictors in the model were fixed and only X 1 varies, the response variable would first increase at lower levels of X 1 but eventually tip over and undergo reduction where X 1 exceeds values of ~3.5. This predictor therefore is demonstrated to have an essentially non-linear, unimodal effect on the response variable.

➤ Holding all other predictors at fixed values and only varying X 2 would have a negative linear effect on the response; this also indicates that the GAM has detected no evidence of improved model performance by allowing X 2 to have a non-linear influence on the response variable and has therefore reduced its smoother to a linear model term.

➤ The smoother curve for predictor X 3 is identical with the horizontal mean zero line as the GAM has found this predictor to be non-significant for modelling the response variable; in such a case X 3's impact on the model is "set to zero" (i.e. the GAM assigns zero estimated degrees of freedom (edf) to X 3), meaning it is effectively selected out of the model.

Smoothing curves are always centred around zero, which essentially shows the response variable mean as GAMs are based on mean-centred values. The closer a smoother curve is to this mean, the less explanatory power a given predictor has. Where the smoother falls above the zero line, the original response value is above average and vice versa. The most convenient implementations for using GAMs with the free and open-source software **R** (RCoreTeam 2020) are package **mgcv** (Wood 2017) for computing and packages **gratia** (Simpson and Singmann 2018) for analysis and visualization. [Box content adapted from Supplementary Material of Chapter 5]

Aims

Even though savanna ecosystems' carbon storage is probably lower than in most forests, they cover an area three times larger than forests in Africa (Ciais et al. 2011). Carbon estimation in drylands is challenging due to constant disturbances and land-use change, hence, applying average values for undisturbed old-growth forests and land-cover classes introduces the largest estimation errors (Rozendaal et al. 2022). Inventory data on African carbon storage is scarce and national assessments are often not standardized (Ciais et al. 2011, Keenan et al. 2015). We even cannot be sure yet whether the carbon balance of savanna ecosystems at large is rather a net carbon source or a net carbon sink, owing to the large variability in savanna types across climates, soil types and under diverse land-use regimes (Ciais et al. 2011). Some governments even refrain from surveying savannas owing to their allegedly low commercial value (Keenan et al. 2015). Without research that addresses the challenges above, however, it will remain impossible to ascertain to what extent savanna carbon storage could be supported through restoration projects without having to abandon all human land-use and we will also not know if these landscapes could be eligible for carbon certificates such as REDD+ (Ciais et al. 2011, Egoh et al. 2012, Buisson et al. 2021).

In summary, the methodological problems outlined above may lead to substantial errors in carbon estimation, especially in highly disturbed dryland ecosystems such as African savannas and woodlands. This is particularly problematic for dryland regions in developing countries which on the one hand could benefit considerably from tree conservation in more than one way, not limited to carbon finance instruments, but are on the other hand least likely to accurately capture woody biomass and thus true carbon storage because of poor data availability and less suitable, disturbance-adapted methodologies.

Summing up the above, multiple factors create challenges for carbon storage assessments of savanna ecosystems in particular:

i) woody vegetation structure is heterogenous and woody cover can be patchy which hinders application of forest methodologies and remote sensing;

ii) woody growth forms are very diverse and shaped by chronic disturbances, hence, they do not comply with widely used allometric equations;

iii) disturbances constantly impact vegetation structure and aboveground biomass and thereby hinder estimation of belowground biomass and soil carbon inputs;

iv) land-use change and management decisions subject savannas to a wide range of different land-use types, each one altering the disturbance regime that acts on woody vegetation and carbon cycling;

v) land-use types remain interlinked in a social-ecological system and can therefore not be evaluated separately.

Where most currently applied and existing methods simultaneously produce both, large over- and underestimations, the need for a revised methodology is evident. Especially the fact that the root cause for all these challenges lies in the distinct ecology of disturbance-prone savanna ecosystems calls for new or refined and most importantly disturbance-adapted methods as a pre-requisite to accurate carbon storage estimation. This challenge is addressed in Chapter 2 and Chapter 3 of my thesis. I aim to find ways of adjusting existing methods and protocols to the necessities outlined above, and at the same time want to design them in such a way that they can be easily applied with limited technological requirements to make them reproducible for as many researchers as possible who are working under constraints. More observation data, including disturbance history and land-use intensity, needs to be made freely available to foster accurate carbon accounting (Rozendaal et al. 2022). To facilitate the real-world application of my methodological work and give other researchers the chance to adapt my ideas further to their own and potentially different needs, I have published my data (and will continue to do so) in an openly accessible repository together with a detailed protocol of data creation and processing (see Chapter 3). Finally, applying the methods to the task at hand, in Chapter 4 and Chapter 5 of my thesis I analyse carbon storage in savanna vegetation and soils and aim to understand which land-use change impacts act on carbon storage in which way. Especially, I aim to understand what effects certain decisions for the future and consequent land-use changes will have on carbon storage and the ecosystem services linked to it.

Manuscripts

Overview of manuscripts in this thesis

As chapters of my thesis, I am herewith attaching the following four manuscripts based on field data which I gathered in Namibia between 2018-2022 with the help of my collaboration partners at University of Namibia, my first supervisor Prof. Anja Linstädter and other colleagues, many engaged students, local field assistants and national park rangers who all kindly supported my work.

CHAPTER 2: "A NEW PROTOCOL FOR ESTIMATION OF WOODY ABOVEGROUND BIOMASS IN DISTURBANCE-PRONE ECOSYSTEMS" – ECOLOGICAL INDICATORS (2022)

Published as first and corresponding author; this is a detailed protocol to overcome the methodological problems of biomass estimation in savannas ecosystems. Through a formal method comparison approach, it seeks to highlight how important disturbance-adjusted methods are by quantifying potential under- and overestimations of woody biomass through commonly used approaches. In this chapter, I conducted the formal method comparison by creating suitable subsets of my data and comparing subset results with results from my full dataset. I designed growth classes that more aptly capture the vegetation in an African savanna. I further developed the method of combining allometric field measurements, with existing allometric equations, and the data I derived from my detailed damage assessment on biomass losses thereby creating a methodological procedure adapted to a disturbance-prone savanna ecosystem. Furthermore, I conducted the formal method comparison, statistical analyses, and data visualization. Finally, I wrote the first manuscript draft, published a pre-print version, and re-wrote the manuscript according to reviewers' suggestions.

CHAPTER 3: "DATASET ON WOODY ABOVEGROUND BIOMASS, DISTURBANCE LOSSES, AND WOOD DENSITY FROM AN AFRICAN SAVANNA ECOSYSTEM" – DATA IN BRIEF (2022)

Published as first and corresponding author; The third chapter specifically aims to demonstrate how I gathered and processed my data following the methodology developed in Chapter 2. including the most detailed account possible on how to reproduce each methodological step necessary for generating own data by applying the adapted method from Chapter 2. To this aim, it contains a step-by-step protocol, many detailed graphical explanations and helpful illustrations, background information, advise on potential further adaptations. Furthermore, I conducted exemplary data analysis to demonstrate the benefits of the proposed methodology. In addition, this chapter seeks to make raw and processed data available to local stakeholders and researchers. Here, I wrote the manuscript, conducted the analyses, created all visualizations including the illustrated step-by-step guidelines for method adaptation. Finally, I prepared the dataset for publication and uploaded it into an openly accessible data repository.

CHAPTER 4: "CONSERVATION WITH ELEVATED ELEPHANT DENSITIES SEQUESTERS CARBON IN SOILS DESPITE LOSSES OF WOODY BIOMASS" – GLOBAL CHANGE BIOLOGY (2021)

Published as co-author; in this interdisciplinary publication between vegetation ecology and soil sciences I did not take the lead authorship but contributed essential data on carbon storage in woody biomass which was created according to methodology and procedures developed in Chapter 2 and Chapter 3, see Figure 2 and Figure 4. Furthermore, I contributed all data listed in Table 1 (woody biomass losses, recent elephant abundances, cover estimations for habitat types per plot) and the data on dung deposits by elephants, see Table 2a. In addition, I contributed all data shown in Table S1 and Table S2. I was substantially involved in manuscript writing and discussion of results. This analysis demonstrated how closely vegetation carbon storage and soil carbon storage in conservation areas are linked. Although conservation areas with elevated elephant densities suffer a loss of woody aboveground biomass in relation to reference states with low elephant density, a larger fraction of the carbon previously contained in shrubs and trees is sequestered again in the soil organic carbon pool.

CHAPTER 5: "NATURAL AND HUMAN DISTURBANCES HAVE NON-LINEAR EFFECTS ON WHOLE-ECOSYSTEM CARBON PERSISTENCE IN AN AFRICAN SAVANNA" – TO BE SUBMITTED TO GLOBAL CHANGE BIOLOGY

Published as first author; the fourth chapter analyses carbon storage as estimated with the procedure developed and tested in the first two chapters. Apart from my data on tree and shrub biomass, biomass losses and disturbance assessments, the analysis also encompasses soil carbon and soil fertility data, as well as a large set of environmental predictors that were gathered across three participating research disciplines. It discusses to what extent two common pathways of land-use change impact carbon stocks in woody vegetation, in soil organic carbon compartments, and in the whole-ecosystem carbon storage. Furthermore, it models the impacts of specific disturbances and other environmental drivers on carbon storage through Generalized Additive Models (GAMs) and puts some of the results of Chapter 4 into perspective. Here, I conducted the statistical data analysis for both vegetation and soil data and all gathered environmental predictors. I was involved in conceptualization and story-boarding, created all visualizations, conducted the literature research, wrote the first manuscript draft, and was strongly involved in editing and finalization of the manuscript after integrating comments and suggestions from all participating disciplines.

Overview of other manuscripts based on thesis data

As my thesis work was embedded within the interdisciplinary collaborative research centre *Future Rural Africa*, the integration of my own research results with neighbouring, but also further distant scientific disciplines from the social sciences was highly encouraged. In addition to the manuscripts included in this thesis, I have been involved as a first author or co-author the following publications:

1. **"CONSERVATION WITH ELEPHANTS AND AGRICULTURAL INTENSIFICATION: EFFECTS ON LIGNIN AND N-ALKANES IN SOILS OF SUB-SAHARAN AFRICA" – PUBLISHED IN GEODERMA (2022)**

   Published as co-author (Sandhage-Hofmann et al. 2022); my data on relative contribution of habitat types per plot (see Chapter 5) was also used within this analysis for upscaling (see Figure 2, Figure 4 and Table S1). Furthermore, my data on elephant dung deposition and woody biomass were used (see Table S1 and Figure S1). In addition, I was involved in manuscript writing. DOI: https://doi.org/10.1016/j.geoderma.2022.116009. Impact Factor: 6.1

2. **"UNDERSTANDING THE CONSEQUENCES OF REFAUNATION IN COEXISTENCE LANDSCAPES: INTEGRATING SOCIAL AND ECOLOGICAL DIMENSIONS" – SUBMITTED TO CONSERVATION BIOLOGY (IN REVIEW)**

   To be published as co-author; this interdisciplinary paper spans four disciplines (vegetation ecology, agricultural economics, social anthropology, and soil science) and draws on a subset of observations from my thesis work. In addition, I was involved in the conceptualization, story-boarding, analysis, and writing. The manuscript explores which far-reaching changes are triggered in the social-ecological system when future-making activities change the functional composition of the herbivore community in a savanna ecosystem. A preprint version of the paper was published as Bollig et al. (2024), DOI: https://dx.doi.org/10.5880/TRR228DB.19.

3. **"MOSQUITO-BORNE DISEASE RISKS IN AFRICAN SAVANNAS: A ONE-HEALTH PERSPECTIVE ON THE ROLE OF LAND-USE CHANGE" – IN PREPARATION**

   I am first author of this interdisciplinary study; from the very beginning of my PhD, I connected to a neighbouring project of the collaborative research centre (*B02 Future Infections*) and closely collaborated with the virology team under PI Prof Sandra Junglen (Charité Berlin). In this study, we adopted a "One Health" approach to examine the interconnections between abundances and diversities of tree communities, herbivore communities, and mosquito communities, and the transmission of vector-borne diseases. I took the lead in generating a joint and overlapping dataset that allowed us to integrate data on trees, herbivores and mosquito species. Apart from guiding conceptualization, data collection, harmonization of fieldwork, and data cleaning, I conducted all statistical analyses and visualizations presented in this paper.

4. **"UNRAVELLING THE RELATIONSHIP BETWEEN RURAL FARM HOUSEHOLD WEALTH, CARBON STORAGE, AND NATURAL RESOURCES IN NAMIBIA'S ZAMBEZI REGION" – IN PREPARATION**

   Participating as a co-author; In this publication we seek to understand to what extent ecological knowledge of farmers, or their wealth and education level have an impact on field management, especially soil resources, soil fertility, management of trees, and biodiversity. I contributed to study design and in formulating research questions and hypotheses. Here, I also contributed data on biodiversity of woody vegetation in agricultural fields and tree biomass and performed statistical analyses of said data.

Other manuscripts

Aside from the publications listed above I have co-authored several other publications (none of them yet published, one in press, three others currently accepted for review) which are not related to the data I gathered for my thesis.

a) GROSS, N., F.T. MAESTRE, P. LIANCOURT ET.AL.: *"UNFORESEEN PLANT PHENOTYPIC DIVERSITY IN A DRY AND GRAZED WORLD" – ACCEPTED BY NATURE (IN PRESS; ACCEPTED FOR PUBLICATION 2023-05-13) ATTENTION: PUBLICATION STATUS OF THIS MANUSCRIPT IS STILL UNDER NATURE'S MEDIA EMBARGO!*

This publication is based on a global network initiative to which I contributed data. While it also analyses land-use change in drylands it has a global scope and focusses on grazing herbivores, hence was not included as a chapter to my thesis.

b) KORELL, L., M. ANDRZEJAK, S. BERGER, ET.AL.: *"LAND USE MODULATES RESISTANCE OF GRASSLANDS AGAINST FUTURE CLIMATE AND INTER-ANNUAL CLIMATE VARIABILITY IN A LARGE FIELD EXPERIMENT" – (MINOR REVISIONS WITH GLOBAL CHANGE BIOLOGY)*

This publication is closely related to the topic of my State Examination thesis and analyses data from a climate change experiment (Global Change Experimental Facility, GCEF) in Germany, where impacts of future climate on Central European Grasslands simulated.

c) BIANCARI, L., M.R. AGUIAR, D.J. ELDRIDGE, ET.AL.: *"DRIVERS OF WOODY DOMINANCE ACROSS GLOBAL DRYLANDS" – (IN REVIEW WITH SCIENCE ADVANCES)*

This publication is based on a global network initiative to which I contributed data. It analyses relative shifts between woody vegetation and herbaceous vegetation in global drylands in relation to climate conditions and grazing herbivore species.

d) DIAZ MARTINEZ, P., F. MAESTRE, E. MORENO-JIMÉNEZ ET.AL.: *"VULNERABILITY OF MINERAL-PROTECTED SOIL ORGANIC CARBON TO CLIMATE IN GLOBAL DRYLANDS" – (IN REVIEW WITH NATURE CLIMATE CHANGE)*

This publication is based on a global network initiative to which I contributed data. It analyses the vulnerability of mineral-associated soil carbon and particulate organic soil carbon to increasing temperatures and reducing precipitation. Due to its global approach it is not included in my thesis.

Formal description –Author contributions

CHAPTER 2: "A NEW PROTOCOL FOR ESTIMATION OF WOODY ABOVEGROUND BIOMASS IN DISTURBANCE-PRONE ECOSYSTEMS" – ECOLOGICAL INDICATORS (2022)

Contributions Liana Kindermann: Paper idea and conceptualization (lead), obtaining permission from traditional authorities (lead), data acquisition (lead), data curation (sole responsibility), methodology (lead), data analysis (sole responsibility), writing – original draft (sole responsibility), writing – review & editing (lead).

CHAPTER 3: "DATASET ON WOODY ABOVEGROUND BIOMASS, DISTURBANCE LOSSES, AND WOOD DENSITY FROM AN AFRICAN SAVANNA ECOSYSTEM" – DATA IN BRIEF (2022)

Contributions Liana Kindermann: Paper idea and conceptualization (lead), obtaining permission from traditional authorities (lead), data acquisition (lead), data curation (sole responsibility), methodology (lead), data analysis (sole responsibility), writing – original draft ((sole responsibility), writing – review & editing (lead).

CHAPTER 4: "CONSERVATION WITH ELEVATED ELEPHANT DENSITIES SEQUESTERS CARBON IN SOILS DESPITE LOSSES OF WOODY BIOMASS" – GLOBAL CHANGE BIOLOGY (2021)

Contributions Liana Kindermann: Paper idea and conceptualization (contributing), obtaining permission from traditional authorities (lead), data acquisition (contributing), data curation (contributing), methodology (contributing), writing – review & editing (contributing).

CHAPTER 5: "NATURAL AND HUMAN DISTURBANCES HAVE NON-LINEAR EFFECTS ON WHOLE-ECOSYSTEM CARBON PERSISTENCE IN AN AFRICAN SAVANNA" – TO BE SUBMITTED TO GLOBAL CHANGE BIOLOGY

Contributions Liana Kindermann: Paper idea and conceptualization (co-lead with Anja Linstädter), obtaining permission from traditional authorities (lead), data acquisition (lead), data curation (lead), methodology (lead), data analysis (sole responsibility), writing – original draft (sole responsibility), writing – review & editing (lead).

Chapter 2

A new protocol for estimation of woody aboveground biomass in disturbance-prone ecosystems
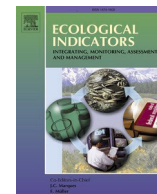
A new protocol for estimation of woody aboveground biomass in disturbance-prone ecosystems

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ABSTRACT

Almost one third of global drylands are open forests and savannas, which are typically shaped by frequent natural disturbances such as wildfire and herbivory. Studies on ecosystem functions and services of woody vegetation require robust estimates of aboveground biomass (AGB). However, most methods have been developed for comparatively undisturbed forest ecosystems. As they are not tailored to accurately quantify AGB of small and irregular growth forms, their application on these growth forms may lead to unreliable or even biased AGB estimates in disturbance-prone dryland ecosystems. Moreover, these methods cannot quantify AGB losses caused by disturbance agents. Here we propose a methodology to estimate individual- and stand-level woody AGB in disturbance-prone ecosystems. It consists of flexible field sampling routines and estimation workflows for six growth classes, delineated by size and damage criteria. It also comprises a detailed damage assessment, harnessing the ecological archive of woody growth for past disturbances.

Based on large inventories collected along steep gradients of elephant disturbances in African dryland ecosystems, we compared the AGB estimates generated with our proposed method against estimates from a less adapted forest inventory method. We evaluated the necessary stepwise procedures of method adaptation and analyzed each step's effect on stand-level AGB estimation. We further explored additional advantages of our proposed method with regard to disturbance impact quantification. Results indicate that a majority of growth forms and individuals in savanna vegetation could only be assessed if methods of AGB estimation were adapted to the conditions of a disturbance-prone ecosystem. Furthermore, our damage assessment demonstrated that one third to half of all woody AGB was lost to disturbances. Consequently, less adapted methods may be insufficient and are likely to render inaccurate AGB estimations.

Our proposed method has the potential to accurately quantify woody AGB in disturbance-prone ecosystems, as well as AGB losses. Our method is more time consuming than conventional allometric approaches, yet it can cover sufficient areas within reasonable timespans, and can also be easily adapted to alternative sampling schemes.

1. Introduction

1.1. Assessing woody biomass in drylands

Global drylands cover about 41% of earth's land surface and are inhabited by an estimated two billion people (Chidumayo et al., 2011; FAO, 2019). Almost one third of global drylands are under some form of tree canopy, often in the form of irregular, open stands (FAO, 2019). On the African continent, ca. 75% of its forested area is savanna woodland or dry forest, and thus characterized by comparatively low levels of aboveground biomass (AGB) (Saatchi et al., 2011). These areas play an important role in the global carbon cycle as they are a major carbon pool responsible for approximately 15% of global carbon storage (Swemmer and Ward, 2020). In southern Africa, ca. 5.5–11.6 Pg of carbon are

estimated to be stored in woody AGB (Baccini et al., 2012; McNicol et al., 2018b). Studies aiming to understand the functioning of these ecosystems or to assess ecosystem services provided by them all need to rely on robust estimates of AGB (Bartholomée et al., 2018; Ciais et al., 2011; Swemmer and Ward, 2020; Twine, 2020). Robust estimates are also essential for current efforts to quantify regional and global carbon stocks (Chidumayo et al., 2011; Gibbs et al., 2007). While substantial research has been carried out in the past decades to estimate carbon stocks in forests worldwide (Brown, 2002; Pan et al., 2011), savanna woodlands and dry forests have often been neglected (Ciais et al., 2011; Colgan et al., 2013). This has introduced major bias to global carbon estimates (Ciais et al., 2011; Keenan et al., 2015).

Unfortunately, measuring woody AGB in drylands is not an easy task. One of the main reasons is that dryland ecosystems are typically shaped by frequent natural disturbances such as wildfire and herbivory (Burton et al., 2020; Davies et al., 2018; Owen-Smith et al., 2020). In the past decades, they have also become severely impacted by human disturbances such as logging and deforestation (Dewees et al., 2010; McNicol et al., 2018b; Ouédraogo et al., 2015) and in the future will be increasingly shaped by simultaneous effects of multiple natural, anthropogenic, and climatic disturbances (Burton et al., 2020; Osborne et al., 2018; Twine, 2020). As disturbances and damages are an inherent characteristic of a healthy savanna the usual indicators for forest ecosystem health cannot be applied here (Osborne et al., 2018). However, disturbance thresholds of savanna degradation are not fully understood yet (Osborne et al., 2018; van Wilgen and Biggs, 2011), therefore new indicators for ecosystem health and disturbance impacts are needed.

Here we argue that current methodologies are not suitable to accurately quantify AGB of dryland woody vegetation. The most accurate approach would be to directly harvest and weigh species' AGB on large plots. However, this is not only highly labor-intensive, but also often unfeasible due to its destructiveness (Chabi et al., 2016; Chave et al., 2014; Cunliffe et al., 2020). Approaches based on remotely sensed data like LiDAR still need reliable ground-truthing data for calibration and validation (Anderson et al., 2018; Colgan et al., 2013; Villoslada Peciña et al., 2021). Moreover, these approaches do not deliver species- and individual-level data, which is a key desideratum in savanna disturbance ecology as species respond differentially to disturbances (Morrison et al., 2016; Osborne et al., 2018). Finally, allometric field-based estimations, which constitute a compromise with respect to workload and accuracy, have mainly been designed for undisturbed forest stands, limiting their applicability for severely disturbed ecosystems. This is even more problematic, as we currently lack suitable indicators and assessment procedures to quantify the impacts of simultaneous disturbance agents on woody vegetation.

1.2. Shortcomings of standard allometric approaches

A major shortcoming of current allometric approaches is that they mostly exclude shrubs and small trees. The main motivation for this is, besides practical considerations, that shrubs and small trees often have a high abundance on plots; their inclusion into allometric models would thus bias the equation towards small individuals. Excluding these individuals is usually done through a size threshold e.g., by a minimum stem diameter at breast height (DBH) of 2–10 cm (McNicol et al., 2018a; Mitchard et al., 2011; Sichone et al., 2018). This approach is statistically reasonable and can be regarded as a valid simplification for carbon estimations on regional or global scales (Chave et al., 2014; Jucker et al., 2017). However, it is problematic for local-scale ecological studies, because small individuals and species are a defining feature of savannas and may be ecologically highly important for ecosystem functioning and ecosystem service delivery (Linstädter et al., 2016; Osborne et al., 2018).

Another shortcoming of current methods is that they render false estimations when a high proportion of individual AGB is lost due to disturbances (Moncrieff et al., 2011). The reason for such false

estimations is that disturbances modify plant architecture and allometry and lead to irregular growth forms in tree species (Archibald and Bond, 2003; Hempson et al., 2020; Meyer et al., 2014). These irregular growth forms are rarely considered in allometric models (Moncrieff et al., 2011). In highly disturbed ecosystems such as African savannas, an individual's small size can either reflect a young age, a severe damage, or a combination of both (Ouédraogo et al., 2015; Wigley et al., 2009). In these systems, size thresholds may therefore be unsuitable for a meaningful classification of age groups. Still, demographic classifications are important to determine stand structure and potential regrowth, which has implications for management planning or future carbon storage potential (Archer et al., 2017; Osborne et al., 2018). Shortcomings of existing methods may also lead to false assignments of individuals to age groups, and to false estimations of individual-level and stand-level AGB. These errors are translated to incorrect estimations of carbon storage or other ecosystem services of woody vegetation (Bartholomée et al., 2018; Ciais et al., 2011; Colgan et al., 2013; Keenan et al., 2015).

1.3. The need to accurately quantify AGB losses

In disturbance-prone ecosystems such as drylands, there is not only a need to accurately quantify AGB itself, but also AGB losses caused by different disturbance agents. However, quantifying what has been lost requires different methodologies than estimating what is there (Stringer et al., 2012; Tripathi et al., 2019). Fortunately, trees are long-lived and hold ecological archives of many disturbances experienced over their lifetime (Moncrieff et al., 2011; Sander et al., 1998). The fact that they are stationary and consist of long-lasting tissue displaying scars from past biomass losses allows to reconstruct a tree's and its location's disturbance history far beyond time periods accessible through direct observation. Such an approach could also be a surrogate for repeated measurements on the same individuals, which are often not possible. Because of trees' archival function, the best observation unit for disturbance assessments and detailed quantification of AGB losses is the individual tree. Previous studies have demonstrated that it is indeed possible to estimate woody individuals' AGB losses from their remains (Morrison et al., 2016; Neke et al., 2006; O'Connor and Page, 2014). However, stand-level AGB losses are often estimated by comparing stands from disturbed sites to stands at less disturbed reference sites (Pellegrini et al., 2017; Singh et al., 2018). Another option is to compare stand-level data before and after disturbances. While these repeated measurements are indeed a valid approach, they are time-consuming and often not feasible due to resource constraints or because expected disturbance regime shifts are unprecedented and lack historical baselines (Anderegg et al., 2020). Moreover, only an individual-level assessment of AGB losses would allow assessing species' disturbance resistance and resilience.

1.4. Aims

Our main objective was to develop a methodology for individual-level and stand-level AGB estimation and AGB loss quantification in disturbance-prone ecosystems. The methodological challenges outlined above demonstrate an urgent need for a standardized field method with a structured sampling protocol and guidelines for data processing to incorporate woody individuals of all species, age classes, and damage levels. We thus specifically aimed to (a) develop an AGB sampling protocol, which also allows for the measurement of small and highly damaged individuals while keeping sampling effort in reasonable limits; (b) establish sampling routines and workflows for the estimation of individual AGB and AGB losses; and (c) perform a method evaluation with respect to conventional estimation approaches.

2

2. Materials and methods

2.1. Study area

Our study area is located in Namibia's Zambezi Region. Climate is semiarid, with mean annual precipitation between 500 and 600 mm, with a high spatio-temporal variability (Mendelsohn et al., 1997). Soils are mainly Arenosols with a sandy texture and poor soil fertility (Sandhage-Hofmann et al., 2021). Vegetation types range from open savannas over savanna woodland to dry open forest (White, 1983). On deep sandy soils, dominant overstorey trees (>15 m) are timber species such as *Baikiaea plurijuga*, *Burkea africana*, and *Vachellia erioloba*. The intermediate stratum (4–15 m) is dominated by tree species such as *Terminalia sericea*, *Combretum psidioides*, and *Philenoptera spp*. The lowest stratum (<4 m) consists of small tree and shrub species including *Dichrostachys cinerea*, *Baphia massaiensis*, and *Gymnosporia senegalensis*. The Zambezi Region hosts several national parks and community-based natural resource management schemes (so-called communal conservancies) in close vicinity to each other (Meyer et al., 2021). While the national parks provide important migration routes for large herds of wild herbivores such as elephants (*Loxodonta africana*), the communal conservancies with their concentration of human settlements rather deflect elephant and wildlife migration (Stoldt et al., 2020; Brennan et al., 2020).

2.2. Study design

We took advantage of steep disturbance gradients in our study area to develop and test our methodology. While we minimized local variation in soil conditions by focusing on deep sandy soils in non-flooded areas, we varied our sampling sites along a gradient of biotic disturbances. Specifically, we focused on elephant damage, as elephants are well-known to be major natural disturbance agents of the tree layer in Africa's savannas and savanna woodlands (Morrison et al., 2016; Owen-Smith et al., 2020; Staver and Bond, 2014), impacting trees through browsing, bark stripping and uprooting. We sampled woody vegetation in the national parks Mudumu and Bwabwata, and in the adjacent communal conservancies Wuparo and Mashi. While the Mudumu-Wuparo set represented more open, savanna-like vegetation (hereafter 'savanna'), the Bwabwata-Mashi set represented a more closed savanna woodland (hereafter 'woodland'), (see definitions for 'Wooded Grassland' vs 'Woodland' in Ratnam et al., 2011; White, 1983). In each vegetation type, we aimed to capture the full range of elephant disturbances, and sampled 30 independent observation plots (25 × 40 m = 1,000 m^2), which were evenly distributed over sites with low, medium, and high elephant densities (10 plots per elephant density level and vegetation type = 60 plots in total). The gradient from low to high elephant disturbance was achieved through sampling plots at different distances from permanent water sources, as elephant browsing impact is highest in closest proximity to water (Wilson et al., 2021). Plots had a minimum distance of 80 m to each other. Sampling took place in September to November 2018 and in April to June 2019.

2.3. Data acquisition

2.3.1. Growth classes and sampling strategy

One of the main aims of our study was to develop a flexible sampling protocol for a detailed assessment of all woody individuals within a stand, including small and highly damaged ones. To this end, we combined several size and damage criteria to define 'growth classes' as the basis for class-specific measurement protocols (Fig. 1). We first distinguished between three life-history stages i.e., juveniles, saplings, and adult woody individuals. Life-history stages were separated by ecologically meaningful thresholds of stem diameter and height. Juveniles were defined as being < 50 cm in height. Individuals in this size class can be easily topkilled in a groundfire or by other disturbances like elephant

damage (Higgins et al., 2012; Swemmer and Ward, 2020; Werner and Peacock, 2019). Saplings were defined to be taller (≥50 cm), while having a basal stem diameter (BD) < 5 cm. Hence, they are still susceptible to hot wildfires and elephant damage but are able to produce defense mechanisms and/or storage organs (Swemmer and Ward, 2020; Werner and Peacock, 2019). Finally, adults were defined to have at least one stem ≥ 5 cm BD, which usually means their crowns were (or once have been) above the fire trap and partly out of most browsers' reach; their stems were assumed to likely withstand individual future disturbance events such as wildfire (Staver and Bond, 2014; Swemmer and Ward, 2020; Werner and Peacock, 2019).

In a second step, each of the three life-history stages was further split into two damage classes i.e., a comparatively undamaged class, and a heavily damaged class exhibiting AGB losses ≥ 30%. This subdivision resulted in six major growth classes with one even needing subtypes (see Fig. 1 and details below). We termed the classes representing highly damaged individuals "gullivers". While the original definition of a gulliver only refers to heavily damaged individuals which are seemingly juvenile and not reproductive (Higgins et al., 2000; van Wilgen and Biggs, 2011), we extended this definition to encompass all heavily damaged individuals, irrespective of their true age or reproductive status. According to our definition, gullivers are heavily damaged woody individuals for which their height does neither reliably predict their age nor AGB. For these growth classes, we also considered the BD of dead stems to assign an individual to a life history stage, and the stem diameter rule takes precedence over the height rule (Werner and Peacock, 2019). This was most important for adult-sized gullivers, as they often consisted of a dead tree stump with small shrub-like regrowth from the root system after having been topkilled (AG3). The AGB losses of such individuals may be massive (compare 'converted trees' in Wilson et al. (2021)). Likewise, the resprouting capability of these individuals potentially facilitates a fast recovery, hence despite their current small height, they cannot be regarded to be juveniles or saplings (Bond and Midgley, 2001; Morrison et al., 2016).

On a plot level, we employed a flexible sampling strategy with a nested plot design to keep the sampling effort – particularly for small and damaged individuals – within reasonable limits. While the basic plot for our tree inventory had a size of 1,000 m^2, we adjusted plot size according to tree density. Moreover, we stratified our sampling within plots according to tree size distribution (Fig. 2) (Kershaw et al., 2016; Wilson et al., 2021). As young trees are usually much more abundant than old trees but represent smaller informative content regarding their archival function and their individual AGB contribution, we sampled the two juvenile growth classes (JJ, JG) on small subplots (usually 100 m^2) nested within plots. On subplots, each woody individual was identified to species level, recorded with allometric measures, and subjected to a damage assessment (see details below). Juveniles were only sampled in the subplot while saplings (SS, SG) and adults (AA, AG) were assessed on the remaining plot area, but only until a representative number of them (usually 15–20 individuals per species) had been recorded.

Depending on density of individuals in each growth class, its sampling area was thus flexibly decided (as suggested by Kershaw et al., 2016). We noted the sampling area for each growth class to allow upscaling from individual AGB to a unit per area basis.

2.3.2. Allometric measurements

We recorded separate sets of dendrometric proxies for adults and subadults. For subadults (including shrubs), we recorded a) height as well as b) widest canopy diameter of living tissue and a second measure orthogonal to the first. For adults, we recorded a) height of highest living tissue, and b) stem circumferences for all adult-sized stems (i.e. both at the base and at breast height (130 cm), if possible). For adult-sized gullivers, we also recorded basal circumference of adult-sized dead stems (if any were present) and noted them as "dead". For the special case that the living woody individual attached to such a dead stem contained no living adult-sized stems (growth class AG3; Fig. 1), we
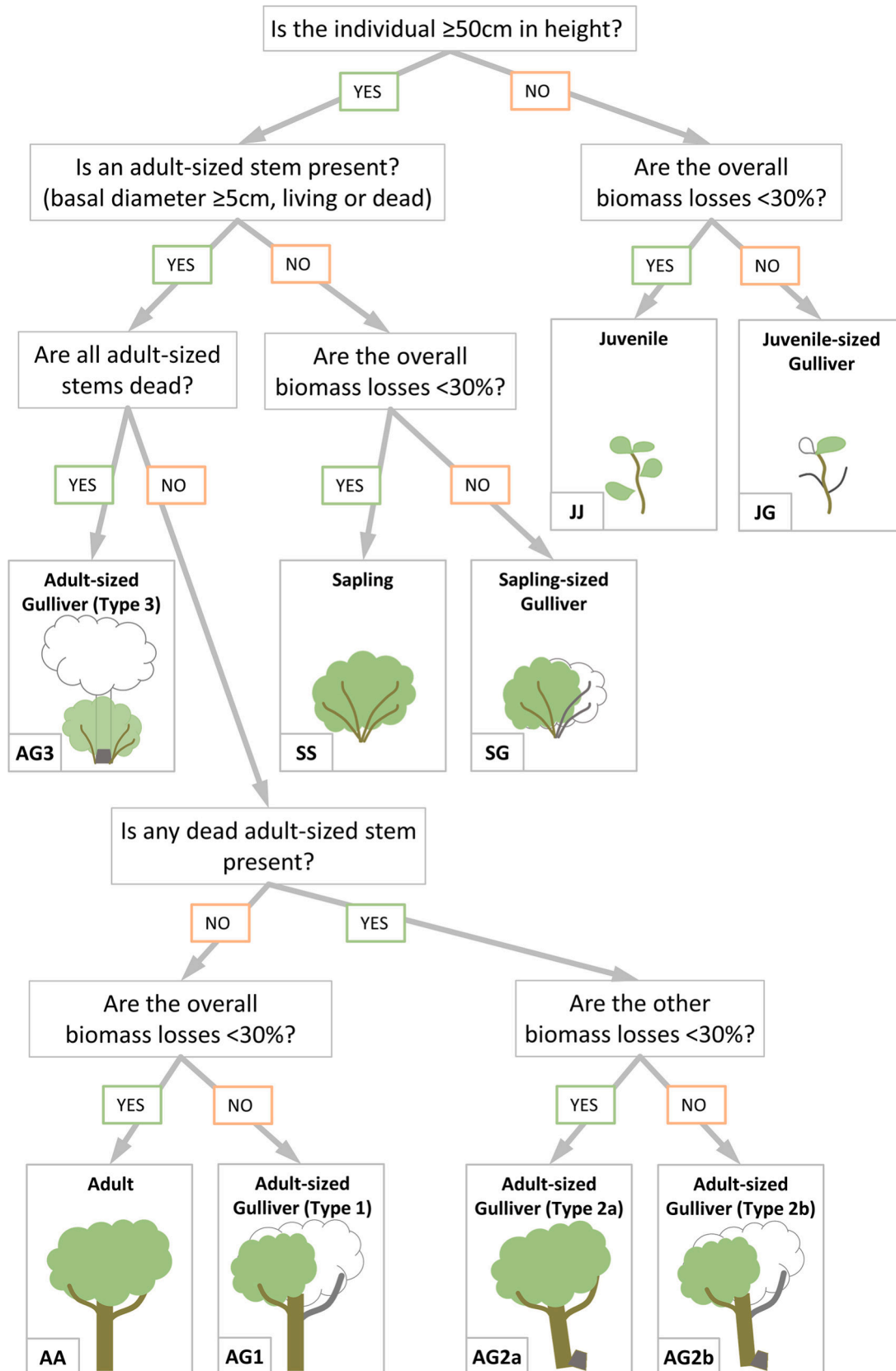
3

Fig. 1. Decision flowchart to differentiate growth classes and subtypes of our stratified sampling design in the field; for a detailed description see Table 1. Only woody individuals belonging to the cases displayed in the bottom row are recorded with stem-based allometric methods.
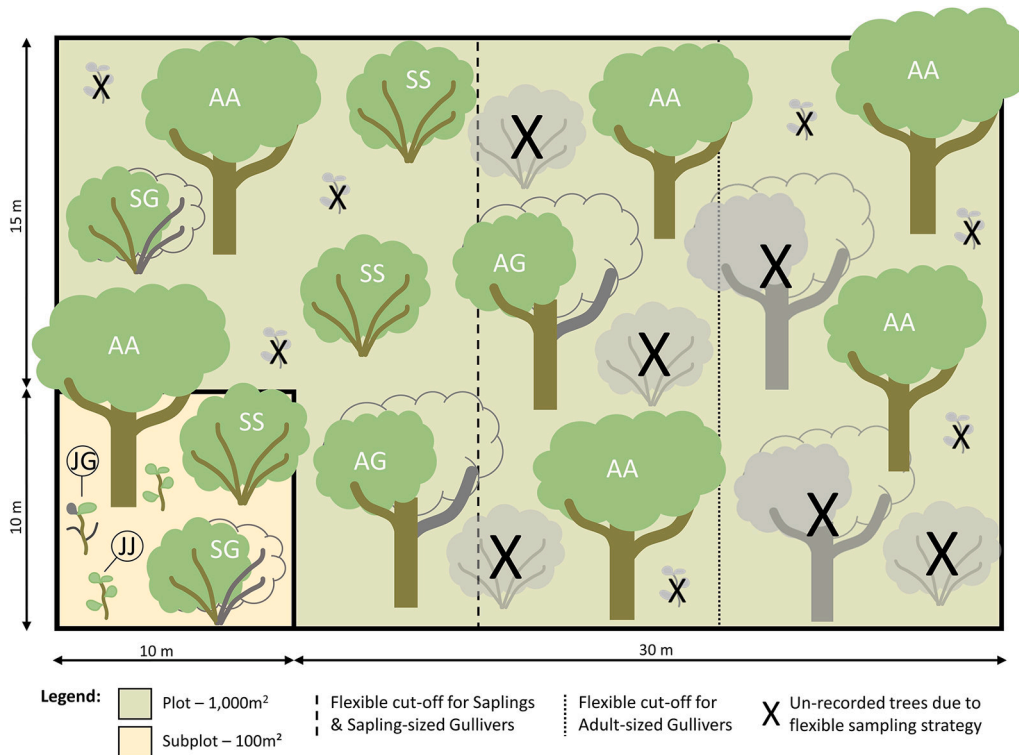
L. Kindermann et al.

Fig. 2. Plot layout and sampling strategy for the tree inventory. In the 100 m² subplot, all individuals are recorded (colored icons); beyond its area, first the juvenile growth classes (JJ and JG) are omitted (grey icons marked with an X). By a flexible delineation of sampling areas, further growth classes (saplings (SS and SG) and adult-sized gullivers (AG)) can be gradually excluded. Only adults with biomass losses < 30% (AA) are recorded on the total plot area. Depending on realized sampling area for each growth class, individual AGB was scaled to a unit per area basis before summing up per plot. See Table 1 for abbreviations and detailed description of growth classes.

Table 1
The six main growth classes and the criteria they are defined by.

Growth Class	Abbr	Size criteria	Explanation
Non-Gullivers (Damage criterion: biomass loss < 30%)			
Juvenile	JJ	- Height < 50 cm- BD < 5 cm	Very young woody plants
Sapling	SS	- Height ≥ 50 cm- BD < 5 cm	Young trees, but also most shrubs
Adult	AA	- BD ≥ 5 cm	Adult trees with a rather undisturbed life history; can also be individuals which have outgrown a severe damage event from the distant past and compensated major AGB losses since
Gullivers (Damage criterion: biomass loss ≥ 30%)			
Juvenile-sized Gulliver	JG	- Height < 50 cm- BD < 5 cm	Very small woody plants with a considerable loss of AGB
Sapling-sized Gulliver	SG	- Height ≥ 50 cm- BD < 5 cm	Small trees and shrubs with a considerable loss of AGB
Adult-sized Gulliver	AG	- BD ≥ 5 cm	Adult trees with a high loss of AGB, where AGB losses alternatively manifest …
		AG1	… entirely in crown and branches
		AG2a	… mainly as a dead adult-sized stem; additional losses in crown of living adult-sized stem < 30%
		AG2b	… as a dead adult-sized stem and additional losses in crown of living adult-sized stem ≥ 30%
		AG3	… as a dead adult-sized stem after total topkill, with no living adult-sized stems retained

Six growth classes and the criteria they are defined by; AGB = aboveground biomass, BD = basal stem diameter.

recorded canopy diameters as was done in subadults. For more details on data acquisition, see Supplementary Material and adjoining Data in Brief publication (Kindermann et al., in review).

2.3.3. Damage assessment

For each living individual, a detailed damage assessment was conducted. To this end, we visually estimated the percentage of AGB lost to different disturbance agents, as has been done before (Ben-Shahar, 1993; Morrison et al., 2016). We found that for common disturbance impacts like fire, woodcutting, or elephant browsing the damage signs were easily distinguishable by cutting or fire marks and breakage pattern (Ben-Shahar, 1993). Only where previously cut or broken branches were subsequently burned by fire the relative impact of disturbances was hard to tell apart. If this was the case, we assigned equal

damage proportions to both disturbance factors because previous disturbances likely caused woody growth to be more susceptible to fire damages (Hempson et al., 2020; Shannon et al., 2011). For adult-sized dead stems (≥5 cm BD) attached to a living gulliver, we additionally noted their topkill reason, but did not consider this dead biomass in the field estimation of lost AGB.

2.3.4. Measurement of specific wood density

Recently, specific wood density (SWD; the ratio of wood dry mass to wood fresh volume) has gained increasing importance in generic allometric equations for AGB estimation (Chabi et al., 2016; Chave et al., 2014; Kachamba et al., 2016). For AGB estimation with the allometric model of Chave et al. (2014), we measured species' specific wood density (SWD) following the 'wood specific gravity' protocol in Pérez-

L. Kindermann et al.

Harguindeguy et al. (2013). For details see Supplementary and adjoining Data in Brief publication (Kindermann et al., in review).

2.4. Workflow for the estimation of AGB and AGB losses

2.4.1. Estimation strategy

The six growth classes distinguished in the field (see Fig. 1 and Table 1) formed the basis for the assessment of individual AGB and AGB losses. During the course of developing a viable AGB estimation strategy for each growth class, we identified four main challenges: a) stems not suitable for DBH measurement; b) disturbed allometries, i.e. heights not matching stem circumference; c) shrub-like individuals not suitable for stem-based models, and d) extensive damages in shrub and tree canopies. Consequently, we identified four procedures through which a standard sampling design can be adapted to account for these challenges: a) DBH reconstruction, b) height correction, c) inclusion of shrubs and subadults through a second, canopy-based model, and d) a damage assessment; for details on each procedure, see next section. For each growth class a separate workflow was developed combining these four procedures as needed.

For the comparatively undamaged growth classes (AA, SS and JJ), our AGB estimation followed well-established routines i.e., we relied on few dendrometric proxies to estimate AGB with the aid of a stem-based model for adults (AA), and with a canopy-based model for subadults (SS and JJ). AGB losses were quantified via a visual estimation of the percentage of biomass lost to specific disturbance agents. For the growth classes with massive AGB losses (the gullivers), our methodology needed to accommodate the fact that severe disturbances considerably modify a tree's architecture. This implies that dendrometric measures no longer fit established allometric relationships between height and stem diameter (see Fig. 3A) (Moncrieff et al., 2011), and that established AGB estimation routines may not reflect irregular, damaged, and often composite growth forms. To this end, we developed a novel AGB estimation routine for gulliver growth classes which combines different allometric model types (see next section) to estimate individual AGB for plants with composite growth forms.

Specifically, we established separate workflows for four subtypes of adult-sized gullivers (AG) to account for their distinct, irregular growth forms shaped by severe disturbances (see Fig. 1 and Table 1 and Supplementary Material). The first type (AG1) had more substantial biomass losses than non-gulliver adults (≥30%), but still a regular growth. Here we only added a height correction (Fig. 3) to the usual practice of estimating AGB with a stem-based model, as detailed below. The second type (AG2a) had both dead and living stems. As living stems bore comparatively undamaged crowns, a height correction was not necessary for them. Here, biomass losses were estimated for dead stems, based
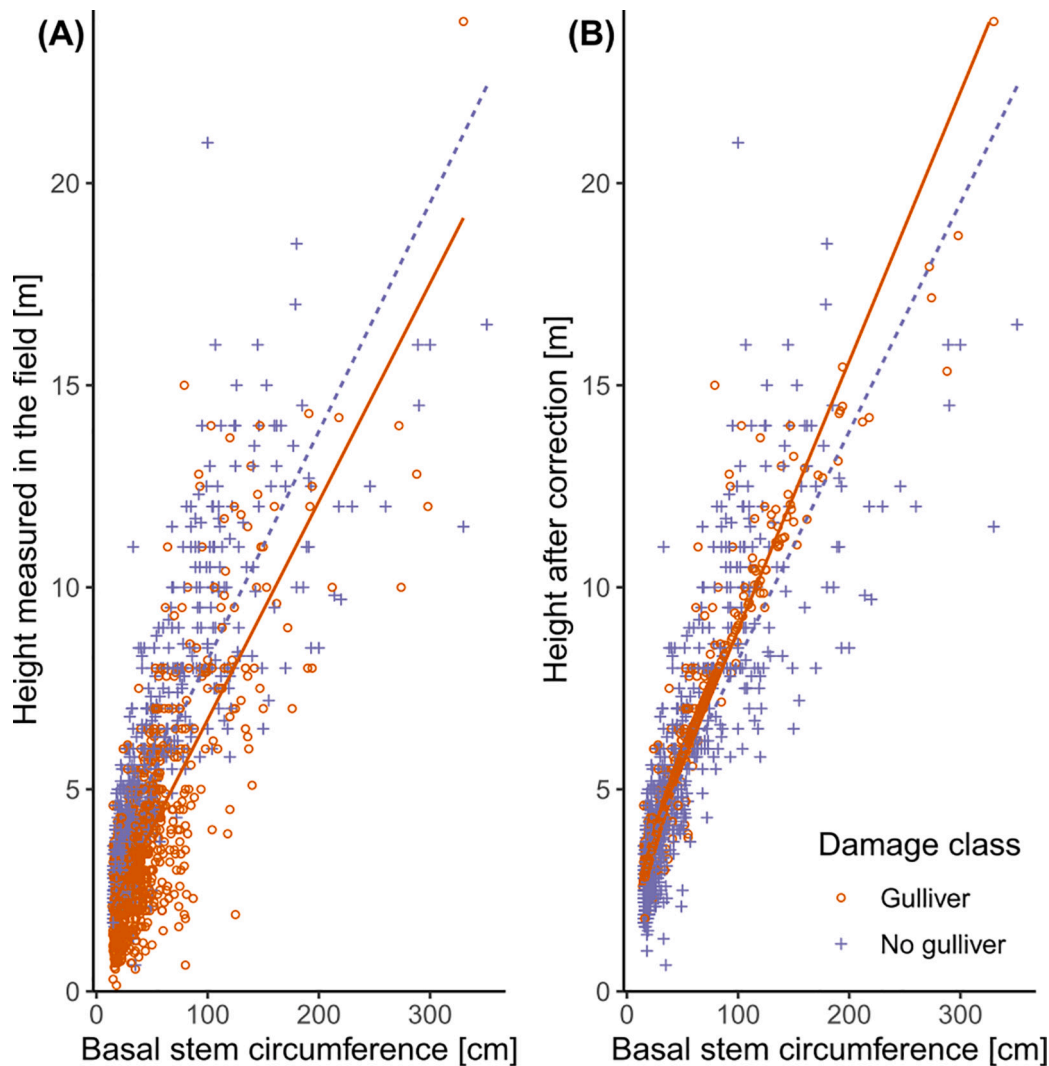

Fig. 3. Allometric relations before and after height correction, comparing gulliver trees (n = 971, orange circles) to non-gulliver trees (n = 781, purple crosses). A) Measured height of non-gulliver and gulliver trees in relation to their basal stem circumference; B) Corrected height in gullivers after estimation from stem size via Eq. (3).

on their basal diameter. Adult-sized gullivers of type AG2b showed a combination of damages seen in the former two subtypes i.e., they displayed both severe damages in living stems' canopy and had dead stems. We thus performed a height correction for living canopies (as done for AG1) and estimated dead stems' biomass (as done for AG2a).

Finally, AG3 gullivers had a shrub-like appearance after having experienced topkill, but also had at least one major dead stem. The living biomass was thus a regrowth from the root system. In this case, AGB losses were estimated as for dead stems in types AG2a and AG2b, while living AGB of the shrub-like part was estimated via the canopy-based allometric model also used for AGB estimation in subadults. For the specific formulas used in our case study, see next section. In general, the allometric models chosen in our example can be replaced by other stem-based and canopy-based models, as appropriate for the respective study region. The detailed workflows of AGB and AGB loss estimation in each growth class are provided in the Supplementary Material.

2.4.2. AGB calculation

For our exemplary workflow, we chose two allometric models which were derived from as many measurements as possible (i.e. generic models) and calibrated for our vegetation type. As stated above those who wish to adapt our workflow to their specific study regions, may exchange the allometric models used here by whatever stem- and canopy-based models fit best for the respective study region. For AGB estimation of subadult growth classes (JJ, JG, SS, SG), we used the canopy-based model developed by Conti et al. (2019) especially for shrub-like vegetation (Eq. (1)). It estimates AGB (in [kg]) from mean crown diameter (CD, in [m]) and height (h, in [cm]). The canopy-based model was also used to estimate living AGB fractions of adult-sized gullivers, if these fractions met the size criteria of subadults (AG3).

$$AGB = \exp(-0.370 + 1.903 Ln(CD) + 0.652 Ln(h)) * 1.403 \tag{1}$$

For adult trees, we used the generic, stem-based Model 4 by Chave et al. (2014) because it was derived from an exceptionally large dataset across all types of tropical forests, including African dry forests, and is widely adopted. It estimates AGB (in [kg]) from specific wood density (SWD, in [g cm^{-3}]), DBH (in [cm]) and the tree height h (in [m]), see (Eq. (2)).

$$AGB = 0.0673 * (SWD * DBH^2 * h)^{0.976} \tag{2}$$

Because heavily damaged trees cannot be expected to follow allometric relations established for comparatively undamaged trees (Moncrieff et al., 2011) and indeed exhibited disturbed allometries in our case study (Fig. 3A), we used indirect estimation procedures, as has been done before (Sullivan et al., 2018). For adult-sized gulliver trees (AG), we estimated their pre-disturbance height (h$_{est}$) from their DBH by using a regression developed from n = 625 adult trees in our dataset, see Eq. (3). To derive Eq. (3) a set of n = 781 trees was split 80/20 into a calibration dataset (n = 625) for model calibration and a validation dataset (n = 156) to evaluate the best fitting model on, see Supplementary Material. In cases where h$_{est}$ < h, we kept the initial height reading h.

$$h_{est[cm]} = \exp(4.72595 + 0.63385 * LN(DBH[cm]))(R^2 = 0.75) \tag{3}$$

For damaged and dead stems where a DBH reading was not possible, we took a basal circumference and estimated a pre-disturbance DBH (DBH$_{est}$) by a regression (Eq. (4)), again built from adult non-gulliver trees (AA, n = 375) in our own dataset (see Supplementary for details):

$$DBH_{est} = 0.7968 * \frac{basal\ circumference}{\pi}(R^2 = 0.9639) \tag{4}$$

This DBH$_{est}$ was used to estimate a former height h$_{est}$ (Eq. (3)) where necessary (living stems in AG1 and AG2b, or dead stems), and both proxies were used to calculate AGB according to Eq. (2). For trees with multiple adult-sized stems, we calculated individual stems' AGB with

their respective measured or estimated DBH. As done by Baraloto et al. (2013), we used the same height for all stems of an individual, because it was often not possible to measure individual stems' height in dense tree crowns. Multiple stems' AGB was then summed up per individual. As we had used different sampling areas per growth class, we used an upscaling factor (Eq. (5)) to express individual AGB on a per unit area basis (in kg ha^{-1}); see Kershaw et al. (2016). The plot-wise sum of upscaled individual values reflects stand-level AGB.

$$Upscaling\ factor = \frac{1ha}{area\ covered\ for\ respective\ growth\ class} \tag{5}$$

2.4.3. Calculation of AGB losses

On living stems and in crowns, AGB losses were calculated by a multiplication of AGB with the percent biomass losses estimated in the field. Please note that canopy-based models and stem-based models are fundamentally different with respect to the way how they incorporate AGB losses. Damages inflicted on shrub-like growth forms directly decrease the dendrometric proxy (canopy dimensions) which the allometric formula is based on, hence calculated AGB already represents the AGB *after* damages. On the other hand, moderate damages to a tree also decrease canopy dimensions, but the allometric formula is largely based on stem diameter, hence the AGB calculated rather represents a state *before* canopy losses. Therefore, estimated damages were subtracted from AGB calculated in a tree to obtain AGB *after* damages, while estimated damages in shrubs were conversely added onto calculated shrub AGB to obtain AGB *before* damages ('reverse damage assessment'). In dead stems, former AGB was quantified via the stem-based model by Chave et al. (2014) with the workaround of estimating an unmeasurable DBH from basal circumference (see above). A dead stem's former AGB was then added to the canopy AGB losses that were visually estimated for the respective disturbance which had caused topkill. Details on calculation workflows are presented in Supplementary Material. Where AGB losses were analyzed on a unit per area basis they have been multiplied by the upscaling factor (Eq. (5)), as was done for AGB.

2.5. Formal method evaluation

To address the challenges outlined above required adapting a standard stem-based method to a disturbance-prone ecosystem. To test and review our proposed methodology, we illustrate the pathway of its increasing complexity. We also analyzed the importance of each step for quantifying stand-level woody AGB (Task 1) and AGB losses (Task 2) in disturbance-prone ecosystems. We identified six steps of increasing method complexity (Fig. 4), each progressively including the method adaptation procedures described above.

As a baseline (Step 1), we used the results from the stem-based allometric model in combination with our DBH estimation procedure. The first step therefore comprised only the AGB of adult-sized trees, where AGB could be calculated with the stem-based Model 4 of Chave et al. (2014) from a measured or estimated DBH (Fig. 4A). In the next step (Step 2, Fig. 4A), we added the height correction procedure for severely damaged trees, but used the same set of trees as in Step 1. In Step 3 we added estimations with the canopy-based model of Conti et al. (2019) to also account for the shrubs and subadults. In Step 4 we acknowledged the fact that the two allometric models differ in the way how they reflect biomass losses: The canopy-based model estimates a post-disturbance AGB while the stem-based model reflects a pre-disturbance AGB (living plus lost AGB; see section 2.4 and Supplementary Material). We therefore incorporated the tree canopy damage assessment. Step 4 hence represents our best estimate on living AGB in woody vegetation. In our understanding, it reflects the level of complexity a method requires to accurately estimate post-disturbance AGB in a disturbance-prone ecosystem such as a savanna. When a study also seeks to quantify all AGB losses to estimate a pre-disturbance AGB, two more steps are needed (Task 2, Fig. 4B). In Step 5, trees' and
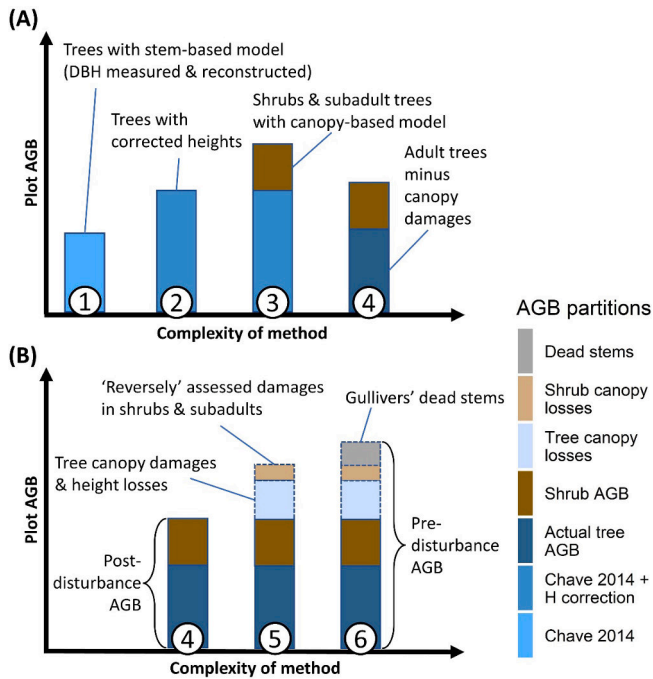
Fig. 4. Conceptual representation of stepwise increasing method complexity for AGB and AGB loss estimation. A) Estimation of living AGB (Task 1), with Step 1 = baseline AGB estimation with a stem-based model (Chave et al. (2014)), including estimations for unmeasurable DBHs (DBH$_{est}$); Step 2 = same trees and model as in Step 1, but with corrected heights in gullivers; Step 3 = adding AGB from shrubs and subadults, estimated with the canopy-based (Conti et al., 2019) model; Step 4 = subtraction of tree canopy losses to accurately quantify living AGB (proposed methodology). B) Reconstruction of AGB losses (Task 2), with Step 4 = living AGB as estimated with proposed methodology) for reference (see panel A); Step 5 = adding recorded tree canopy losses and reversely assessed shrubs' canopy losses; Step 6 = adding estimated former AGB of gulliver trees' dead stems, in total yielding pre-disturbance AGB levels in each plot; AGB = aboveground biomass, H = height.

shrubs' canopy losses were added to living AGB. For shrubs, this included the 'reverse damage assessment' described in section 2.4. In the final Step 6, we added AGB attributable to Gulliver trees' dead stems (Fig. 4B). For analyzing AGB partitions, we summed them up per plot and step, and compared results between steps. Mean AGB levels per step are presented as well.

2.6. Data analysis

Data analysis was conducted using the opensource programs R (R Core Team, 2020) and RStudio (R Studio Team, 2016) with packages dplyr (Wickham et al., 2020), magrittr (Bache and Wickham, 2014), rstatix (Kassambara, 2020b), reshape2 (Wickham, 2016b), and modelr (Wickham, 2020). For data visualization we used the R packages ggplot2 (Wickham, 2016a), scales (Wickham and Seidel, 2019), cowplot (Wilke, 2019), and ggpubr (Kassambara, 2020a). We tested for differences in pairs of each plot's AGB estimations between method complexity steps, respectively, by using paired T–tests from R package stats. We checked all data for normal distribution and used square root transformed values for T-tests throughout. Depending on steps tested against each other the T-tests were either one-tailed or two-tailed, but always paired. We visualized stepwise differences with scatterplots and stack bars. As an example for between-plot variability we selected the savanna vegetation site of our study region to present detailed stepwise data for each of the 30 plots. Where possible color-blind friendly palettes were used; otherwise, color information is supported by shapes and written labels.

3. Results

3.1. Number of recordable individuals

With our proposed methodology, we recorded 6,100 individuals of 65 species on 60 plots, with a total area of six hectares. Less than a quarter of them had at least one living adult-sized stem; a further 1.8% was only identified as adult because of an adult-sized dead stem being attached to a shrubby individual (AG3). We could measure DBH for just 14% of living stems, whereas the remaining 86% of stems required a reconstruction of DBH from basal stem diameter. Even among the least damaged trees (growth class AA), only 23% of stems were shaped in a way that DBH could be measured in the field. A further 4,624 individuals (76%) were assessed by implementing a second allometric model for canopy-based AGB estimation. In > 100 individuals (1.8%; growth form AG3), both stem- and canopy-based models were required to assess AGB. A total of 259 dead stems was attached to living gulliver trees, and their AGB before topkill was estimated by reconstructing former DBH and height from allometric relationships found in healthy trees.

3.2. Evaluation of AGB estimates (Task 1)

As expected, the procedure of height correction and the inclusion of shrubs and subadults (Steps 2 and 3, respectively) both increased stand-level AGB compared to the baseline method (Step 1, Fig. 5A-B and D). Stand-level AGB through height correction increased on average by 26% but could be up to 270%. When also including shrubs and subadults (Step 3), AGB was increased on average by 56% and could reach > 380% compared to the baseline method (Fig. 6). Non-surprisingly, accounting for tree damages (Step 4) decreased stand-level AGB again. Interestingly, AGB with our proposed method could be both, lower or higher than with the baseline method (Step 1), depending on plot (Fig. 5C). Though our proposed AGB estimation methodology (Step 4) only slightly increased mean AGB compared to the baseline (Fig. 5D), the effect was very heterogeneous (Fig. 6): In some plots our method increased AGB by > 260% while decreasing it in others by > 58%. By absolute numbers, deviation of stand-level AGB ranged from + 7.8 t ha^{-1} to − 23.8 t ha^{-1} (mean –2.2 t ha^{-1}). On average, with our proposed methodology, we found that woodland had a higher total plot AGB than savanna with mean AGB of 23 t ha^{-1} and 11 t ha^{-1}, respectively. Interestingly, absolute shrub AGB was nearly the same in both vegetation types (mean 2.8 t ha^{-1}, Fig. 5D). Hence, for the savanna site, a greater fraction of total AGB was accumulated in shrubs and subadults (mean 19% and 27% in woodland and savanna, respectively). Shrubs and subadults accounted for as much as 86% of total AGB in some plots (Fig. 6) and in one out of ten plots accounted for the majority (>50%) of total AGB.

Overall variability between plots along the steep gradient of elephant disturbance was high, even within one and the same vegetation type. Through adaptation of method though, coefficient of variation (CV) between plots decreased from 71% at reference baseline (Step 1) to 62% with our proposed method (Step 4, Fig. 6).

3.3. Reconstruction of AGB losses (Task 2)

By estimating AGB lost from living trees, shrubs and subadults, we were able to reconstruct pre-disturbance AGB levels. The inclusion of all canopy damages (Step 5) and of dead stems attached to gullivers (Step 6) allowed us to estimate minimum pre-disturbance AGB in our study region to be about 34 t ha^{-1} and 22 t ha^{-1} in woodland and savanna vegetation, respectively (Fig. 7D). Despite this general difference in pre-disturbance AGB, overall AGB losses were surprisingly similar between vegetation types: Actual AGB stocks (Step 4) were on average about 11 t ha^{-1} lower than the respective pre-disturbance AGB (Step 6, Fig. 7D). Woodland vegetation had lost about one third of its AGB, while savanna
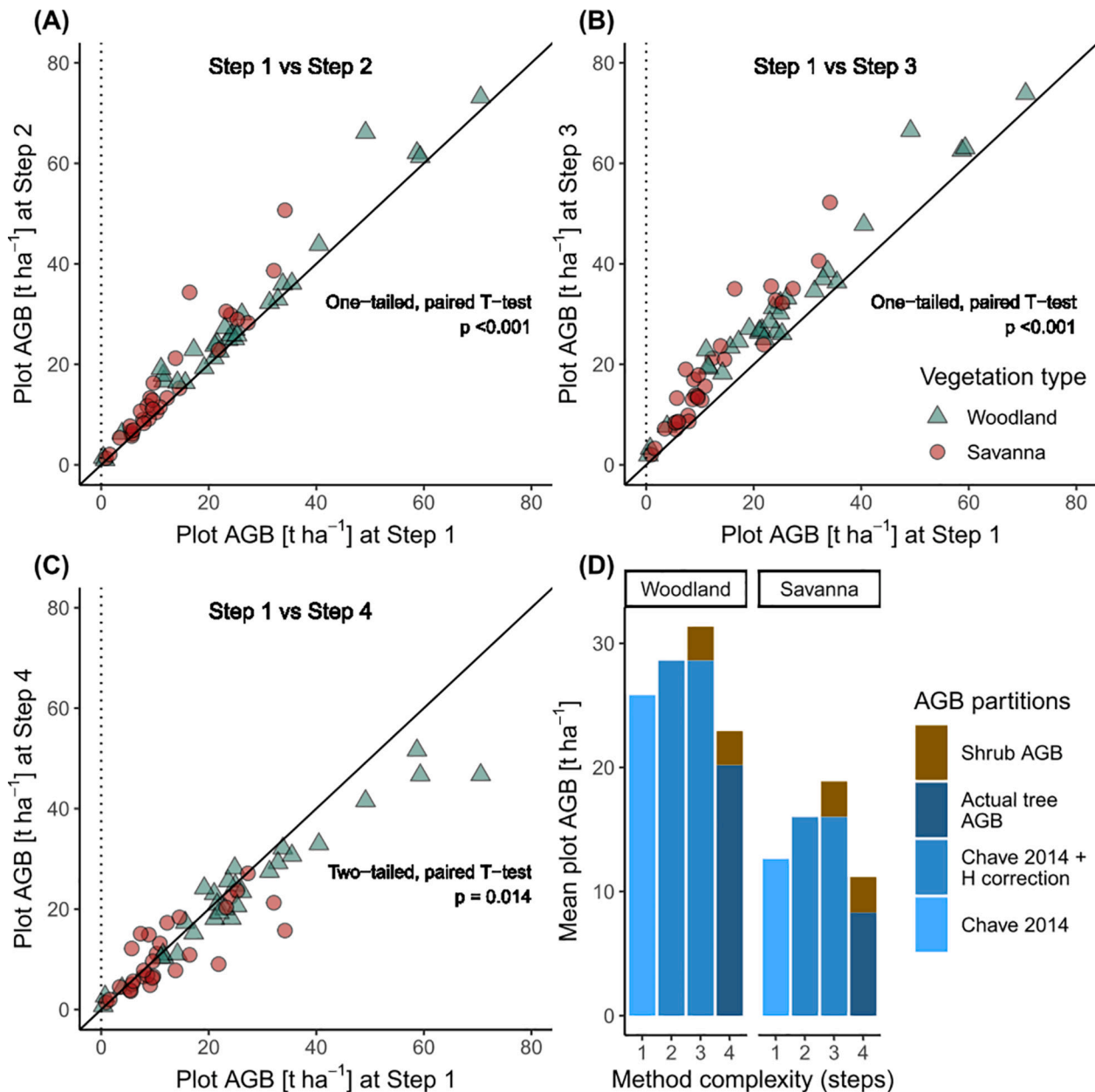
8

Fig. 5. Comparative plot-level AGB per methodological complexity step in task 1: Quantifying actual living AGB in trees and shrubs; A) – C) Pairwise comparison between reference baseline value (Step 1) and Steps 2–4 of increasing complexity, respectively; D) Mean AGB per step and vegetation type; Significances tested with pairwise T-tests; AGB = aboveground biomass, H = height.

vegetation even had lost half of it (Fig. 7D). Most of these losses were attributable to canopy losses in trees (with 74% in woodland and 72% in savanna), while dead stems in tree gullivers accounted for another 18–19%, and shrub canopy losses for only 9–10% of total losses (Fig. 8). Interestingly, these shares were found to be similar in both vegetation types. Damages recorded on living tree stems reduced plot tree AGB by a mean 39% but could be as high as 81% (Fig. 8). The reverse damage assessment in shrubs uncovered that canopy dimensions were on average reduced by 27% but losses could exceed > 40%.

Variability in pre-disturbance AGB was high between plots, and largely dependent on tree damages and gullivers' dead stems. Tree canopy damages were the most important damage category appearing in all plots, while not all plots exhibited dead stems in gulliver trees (Fig. 8).

4. Discussion

4.1. Feasibility and sampling effort of proposed field methods

We developed a flexible sampling protocol for estimating AGB and AGB losses in disturbance-prone ecosystems, including small and/or highly damaged individuals. In this way, we aimed to overcome two major shortcomings of current field methodologies based on allometric approaches i.e., that they mostly exclude shrubs and small trees (Baraloto et al., 2013), and that they render false estimations when a high proportion of individual AGB is lost due to disturbances (Moncrieff et al., 2011). The application of our field methods along a steep disturbance gradient in an African dryland showed huge differences with respect to the number of recordable individuals. With our proposed methodology, we recorded > 1,000 individuals per hectare. The majority of individuals and tree stems would not have been captured by a standard
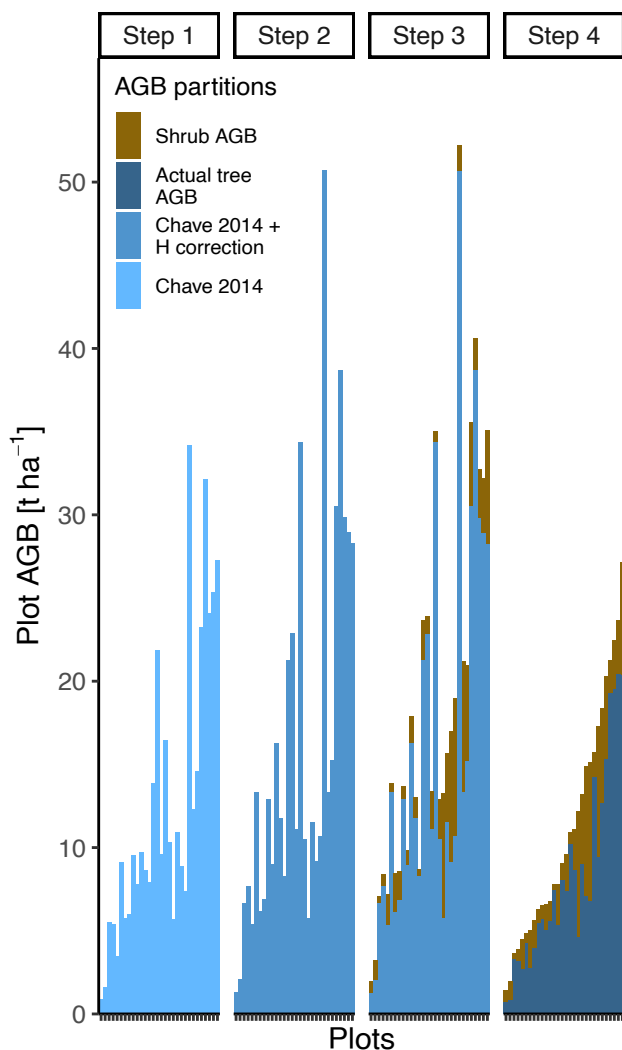
Fig. 6. Absolute plot-level AGB values at each method complexity step in Task 1: Accurate AGB estimation. Step 1 = baseline AGB estimation with Chave 2014 model, including estimations for unmeasurable DBHs; Step 2 = same trees and model as in Step 1, now using corrected heights in gullivers; Step 3 = adding AGB from shrubs and subadults, estimated with Conti 2019 model; Step 4 = subtracting recorded tree canopy losses to accurately quantify living post-disturbance AGB (proposed methodology); for demonstration purposes only showing site with savanna vegetation (n = 30 plots); AGB = aboveground biomass, H = height.

forest inventory method due to a DBH threshold. Applying such a stem size threshold in our case study would have caused three quarters of all individuals to be omitted for being small. Even when focusing on big trees with > 5 cm basal diameter, the vast majority of stems still had no measurable DBH. This underlines the necessity to properly record small and/or damaged individuals (Moncrieff et al., 2011); see discussion of stand-level AGB for further implications. Moreover, it shows that in heavily disturbed ecosystems, basal stem diameter should be recorded instead of, or in addition to, DBH (Fairman et al., 2019; Skowno et al., 1999).

Our method is not the first to propose flexible sampling strategies to more reliably cover woody individuals across size classes (Fairman et al., 2019). For example, Baraloto et al. (2013) suggested the use of modified Gentry plots (as defined by Baraloto et al. (2011)) for neotropical moist forests, and extended the 0.1 ha core plots to 0.5 ha plots for large trees (DBH ≥ 20 cm). However, this method requires establishing at least ten perpendicular subplots per plot and may be problematic due to the

extensive perimeter of such plots (Baraloto et al., 2011). While this might be a feasible approach in forest ecosystems, it is rather impractical in the often dense, spiny vegetation of African drylands. Nevertheless, our AGB estimation workflows could easily be adapted to differently shaped plot designs like Gentry plots.

With respect to sampling effort, our proposed field method including the damage assessment steps initially took about two person-days per 0.1 ha plot, as some training was required for the recognition of damages and growth classes. With a fully trained fieldwork staff, though, our method required on average one person-day per 0.1 ha plot including species identifications. This effort varied considerably across disturbance levels, with slightly disturbed plots requiring only a half person-day, and highly disturbed plots requiring up to two person-days. Despite taking small individuals into account, the sampling effort is thus about seven times smaller than for Whittaker plots of a similar size (0.1 ha) that are conventionally sampled in tropical forests. Here, sampling effort is about seven person-days, because non-stratified, full inventories are taken (Campbell et al., 2002) but a higher number of species might also contribute to that discrepancy.

For our study region, we estimate that our proposed methodology including the damage assessment, species identification and collection of wood samples took about 2–3 times longer than for inventories recorded with conventional methods. Our estimation is based on our field experience within the present study and within previous studies of or working group in African savannas and savanna woodlands (e.g. Ouédraogo et al., 2015). Therefore, while our proposed method may – in some ecosystems – be more laborious for plots of a similar size, it requires considerably smaller plot areas to adequately record species-specific woody AGB in highly disturbed ecosystems. Besides, from a statistical point of view, a larger number of smaller plots is superior to a smaller number of very large plots. Accordingly, Baraloto et al. (2013) also recommended a 'several small' (<1 ha) sampling strategy for neotropical forests, as this strategy led to a smaller coefficient of variation in AGB than a 'few large' strategy.

In summary, our flexible sampling strategy with variable plot areas sampled in a nested plot design kept the workload within reasonable limits and allowed for modifications according to tree density, damage intensity, and tree layer homogeneity.

4.2. Feasibility of calculation procedures

We differentiated our sampling routines and workflows for six growth classes, which we defined based on the two criteria 'size' and 'damage level'. This approach allowed us to estimate AGB and AGB losses for all woody individuals, irrespective of size, age, growth form, or damage level. A major advantage of our method was that we developed a workflow of combining two different model types for AGB estimation i. e., a stem-based model for adult growth classes, and a canopy-based model for shrub-like growth classes or gulliver individuals with shrub-like parts. While previous studies have often relied on a single, usually stem-based model (McNicol et al., 2018a; Mitchard et al., 2011; Sichone et al., 2018), shrub-like growth forms cannot be represented with such allometries (Ryan et al., 2011), and canopy dimensions are better predictors (Conti et al., 2019; Cunliffe et al., 2020; Meyer et al., 2014). For adopting our methodology to other research areas or vegetation types, stem- and canopy-based allometric models used in our case study can be replaced by whatever generic or local calibrations are preferred for trees and shrub-like growth, respectively. The general processes of integrating a stem- and a canopy-based model and how to adapt both to a disturbance-prone ecosystem as presented in this study should be transferable.

Our method also proposes novel routines for field sampling and AGB calculation of highly damaged individuals, so-called gullivers. Even though gullivers have already been described more than two decades ago (Bond and van Wilgen, 1996; Higgins et al., 2000; Skowno et al., 1999) and are well-known to play a key role in disturbance-prone
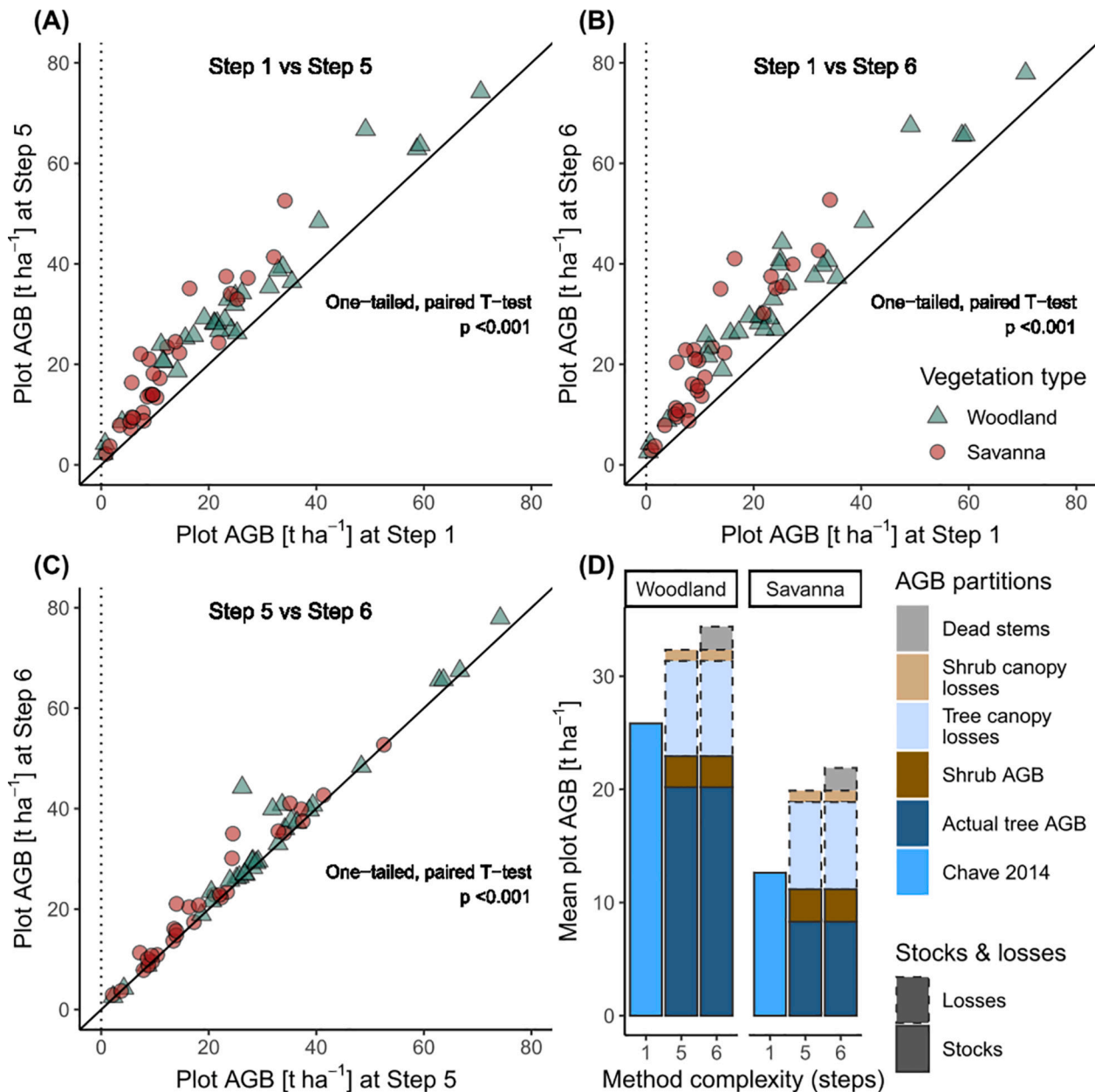
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Fig. 7. Comparative plot-level AGB per methodological complexity step in Task 2: Assessing AGB losses in trees and shrubs; A) – C) Pairwise comparison between method complexity steps; D) Mean AGB and AGB losses per step and vegetation type; Significances tested with pairwise T–tests; AGB = aboveground biomass.

dryland ecosystems due to their growth potential (Morrison et al., 2016), they have to our knowledge never been properly integrated in AGB sampling protocols. In this context, the distinction of four subtypes within the growth class of adult-sized gullivers (AG; Fig. 1) was a critical step for representing the variety of irregular growth forms of tree individuals shaped by severe disturbances. Moreover, the growth classes defined here may also be a valuable tool for better capturing demographic processes in disturbance-prone ecosystems (Anderegg et al., 2020; Swemmer and Ward, 2020).

4.3. Comparison of AGB estimates: Baseline versus proposed methodology

4.3.1. Evaluation of AGB estimates (Task 1)

The stepwise evaluation of our proposed methodology has demonstrated the necessity of adapting existing and well-established methodologies to yield robust AGB estimations in disturbance-prone ecosystems. We identified four necessary procedures: DBH

reconstruction, height correction, damage assessment, and inclusion of shrub-like and subadult woody growth forms. Because the exemplary stem-based allometric Model 4 by Chave et al. (2014) was not applicable to the majority (>85%) of recorded adult-sized stems as a result of non-measurable DBH, we reconstructed missing DBH readings from basal stem diameters. With this procedure we gained a simple AGB estimate that in our method evaluation represents a benchmark AGB which other stem-based models would likely approximate e.g., approaches that use stems' basal area as an AGB proxy instead of DBH (Henry et al., 2011). Nonetheless, we have presented this DBH reconstruction procedure as part of our method adaptation process, because DBH still is the most frequent predictor in published allometric models (Henry et al., 2011). Hence, it is likely that future studies will also need to reconstruct DBH before applying a generic allometric model. It should be noted that the necessity to reconstruct missing DBH readings could be due to two different reasons. First, the stem was branching below or at 130 cm preventing it from being measured. As described for other open dryland
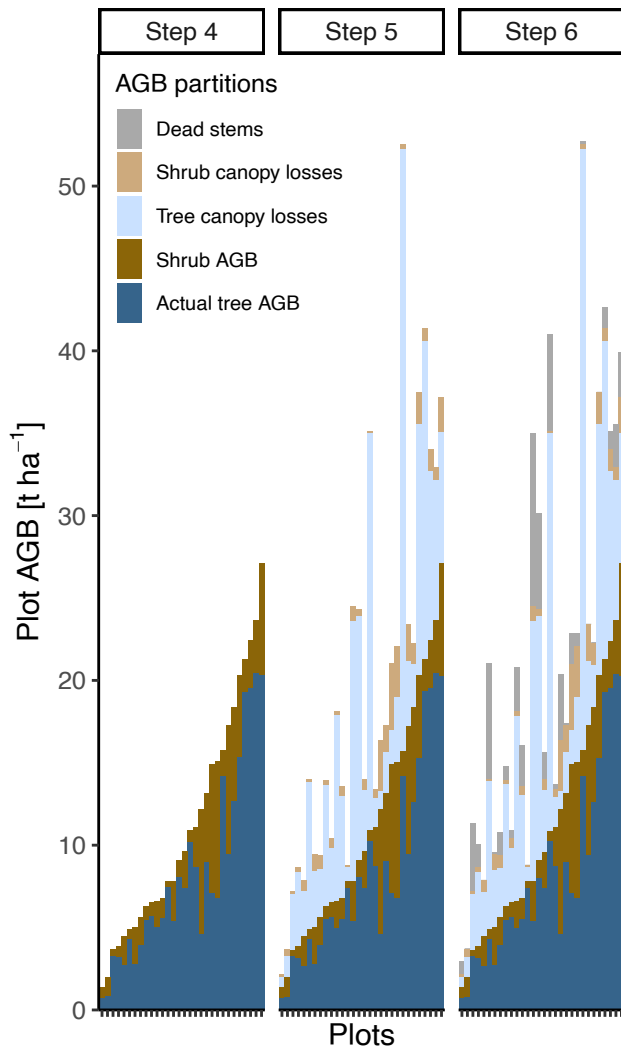
Fig. 8. Plot-level AGB and AGB losses for each methodological step of Task 2, illustrated for savanna vegetation (n = 30 plots). Step 4 = living AGB as estimated with our proposed methodology; Step 5 = adding recorded tree canopy losses and reversely assessed shrub canopy losses; Step 6 = adding estimated former AGB of gulliver trees' dead stems, yielding total pre-disturbance AGB per plot. Plots are sorted according to their total living AGB as captured in Step 4; AGB = aboveground biomass.

vegetation (Archibald and Bond, 2003; Sander et al., 1998), this was a common phenomenon in our case study, with<25% of non-gulliver trees having a field-recordable DBH. We assume that in open dryland vegetation where trees are generally smaller than in forests, branching height is generally closer to the ground, which makes it unfeasible to apply DBH-based models. Second, the tree could have been damaged so severely that its stem was only partly or non-existent at 130 cm. Hence, in the former case the reconstruction of a missing DBH value was merely a methodological detour to yield an approximate estimation of existing AGB, while in the latter case the same procedure caused the allometric model to quasi estimate AGB which in fact was no longer there.

Similarly, our height correction in severely damaged gulliver trees succeeded to restore the allometric proportions as assumed by baseline models (Sullivan et al., 2018), but at the same time further amplified an inevitable trade-off between increased accuracy in some trees opposing overcompensation in others. This overcompensation could only be addressed by conducting an individual-level damage assessment that allowed for subsequent deduction of visible canopy losses. In doing so, legitimately and falsely reconstructed AGB partitions were ultimately

differentiated into disturbed yet living biomass and lost biomass, respectively. This allowed for maximum method adaptation to variously disturbed trees along a steep disturbance gradient, which would not have been possible with a lower level of method complexity that simply records allometric proxies.

Our damage assessment for trees not only increased robustness of AGB estimates, as indicated by a decreased between-plot variability (Fig. 6), it was also key for a congruency of AGB loss estimations performed with the stem-based and the canopy-based model. To capture the vast number of shrub-like individuals and to integrate their considerable contribution to stand-level AGB (19–27%), a canopy-based model was needed, which unlike the stem-based model directly delivered a post-disturbance AGB estimate. With our proposed methodology, existing protocols have been aligned for different growth forms and damage levels, which allowed us to quantify the – often neglected – contribution of shrubs and subadults to stand-level woody AGB in dryland ecosystems. Our results corroborate previous findings from highly disturbed African drylands, where the smallest size classes were found to hold a large proportion (Baraloto et al., 2011; McNicol et al., 2018a; Ouédraogo et al., 2015) or even > 75% of stand-level AGB (Brown, 2002; Colgan et al., 2013). Our results also indicate that the relative importance of small size classes increases in more open and disturbed vegetation (Fig. 5D). Their omission in conventional forest-derived methods might thus be the main reason why stand-level AGB is more likely to be underestimated in highly disturbed ecosystems (Colgan et al., 2013), and why overall carbon storage potentials of savannas have high uncertainties (Erb et al., 2018). While we are not the first to integrate different allometric models for growth or size classes (Colgan et al., 2013; Ngoma et al., 2018), to our knowledge we are the first to have done so for individual-level estimates. Analyzing biomass fractions between growth classes and species could further illuminate underlying processes of ecosystem functioning and improve calibration for remote sensing approaches (Colgan et al., 2013; Erb et al., 2018; McNicol et al., 2018b).

We have demonstrated that non-adapted AGB estimation methods may considerably contribute to high uncertainties for AGB estimations in African savannas (Ciais et al., 2011; Stringer et al., 2012). Notably, the comparison between baseline AGB estimates and our proposed methods' estimates indicate that the deviation is non-directional: While high-AGB plots in woodland vegetation tended to be overestimated by the baseline method, most plots deviated from the baseline method in an unsystematic way (Fig. 5C). Consequently, the correction of standard method estimates via a conversion factor is hampered, and we therefore advocate more complex approaches for robustly quantifying AGB in disturbance-prone ecosystems. This is particularly desirable for dryland regions in Sub-Saharan Africa, which are not only highly threatened by global environmental change (Ferner et al., 2018; Guuroh et al., 2018), but are also shaped by severe disturbances (Ouédraogo et al., 2015; Sankaran et al., 2005). These regions could considerably benefit from forest conservation and carbon finance instruments (Stringer et al., 2012; Swemmer and Ward, 2020) but are less likely to correctly quantify their actual carbon stocks (Ciais et al., 2011; Sandhage-Hofmann et al., 2021), let alone the complex carbon loss dynamics.

4.3.2. Reconstruction of pre-disturbance AGB levels and AGB losses (Task 2)

Our second task was to quantify total AGB losses and to reconstruct a hypothetical pre-disturbance AGB level. The methodology-dependent trade-off inherent in DBH reconstruction and height correction of the first task (see above) happened to be the closest we could get to an estimate of pre-disturbance AGB of trees' living stems. We could hence confidently assume to have reconstructed the pre-disturbance AGB of these living stems already, before subsequently deducting the apparent tree canopy losses during damage assessment. By reversely assessing the AGB lost from shrubs and subadults, we determined a comparable value for shrub-like growth. Adding canopy losses from shrubs and trees to

living, AGB yielded the pre-disturbance AGB. In a final step we made use of the procedures tested and employed on living stems to also included AGB of dead stems attached to gullivers (Fig. 7D). In doing so we were able to reconstruct pre-disturbance AGB where severe disturbances had caused total topkill of trees, in some cases leaving behind only small shrub-like gulliver regrowth. Our method quantifies a minimum amount of AGB lost to disturbance during the lifetime of living trees and shrubs. Even without comparing our disturbed sites to undisturbed reference sites which are often hard to find (McNellie et al., 2020), we were able to estimate an approximate pre-disturbance AGB level, and to document the substantial biomass losses especially in savanna sites, where nearly half of living woody individuals' biomass had been lost. These rates are in the same range as have been found in some studies for disturbance impacts like elephants (Ben-Shahar, 1993; O'Connor and Page, 2014) but exceed those found elsewhere (Tripathi et al., 2019).

The growth classes required to design separate workflows for AGB and AGB loss estimation have proven useful, especially with regard to seemingly young gullivers that instead are a result of previous topkill events and were found to be resprouts from large remaining root stocks. Differentiating them from other shrubs of similar aboveground dimensions will be needed to better estimate belowground biomass, demographic processes, and regrowth potential under future disturbance regime shifts (Chidumayo, 2014; Lévesque et al., 2011; Morrison et al., 2016).

AGB loss estimations uncovered both differences and similarities between the two vegetation types. Although savanna and woodland sites were spatially close and both sites had similar disturbance regimes and soil conditions (Sandhage-Hofmann et al., 2021) woodland carried much higher stand-level AGB than savanna vegetation. On the other hand, we found that mean losses per damage type were surprisingly similar across vegetation types, with AGB lost from tree canopies being most important. This highlights the necessity to take at least this damage type into account. With the proposed procedures of DBH reconstruction, height correction, and damage assessment also solely stem-based approaches could be streamlined for dryland ecosystems and other disturbance-prone ecosystems (Anderegg et al., 2020). Where disturbance levels are less severe, the damage assessment may be used as an independent module, but in our case, damages were so massive that damage quantification was dependent on height correction and DBH reconstruction procedures to first reconstruct a pre-disturbance AGB. With our workflows, species-wise assessments of disturbance losses are also possible, which is essential to understand community-level effects, and to predict future disturbance shifts as well as their consequences for ecosystem functioning and services (Burton et al., 2020). Previously, studies often quantified AGB losses for few species (Chabi et al., 2016; Moncrieff et al., 2011) or in a single species only (Bennett et al., 2014; Neke et al., 2006; Werner and Peacock, 2019). Moreover, the damages recorded in woody growth could themselves be used as indicators for a site's disturbance history and disturbance regime by harnessing the historical archive contained in trees (Moncrieff et al., 2011).

Although our method provided new insights into the complex disturbance regime of drylands and its impact on woody biomass, it has several limitations. First, our method does not deliver total AGB losses, and where it estimates former AGB of dead stems it only regards living individuals. Also, topkill events and other damages that date back a long time at some point might have become partly or fully compensated by regrowth. Secondly, severe recent damages can potentially mask older damages. However, unless long-term disturbance exclusion experiments or repeated monitoring of individually marked trees are undertaken, these uncertainties are unavoidable (Morrison et al., 2016; Werner and Peacock, 2019; Werner and Prior, 2013). While long-term studies would obviously yield more accurate estimates on AGB loss dynamics, they might be impractical or even impossible due to time constraints or a lack of undisturbed control sites (McNellie et al., 2020). Yet many of the disturbance regime shifts drylands will be facing in the future cannot be studied via historical risk data or historical reference state comparisons

as unprecedented global change is underway already and its future impacts can not necessarily be extrapolated from historical baselines (Anderegg et al., 2020). Either way, our proposed methodology could be the next best option.

5. Conclusions

We have proposed a novel methodology for the estimation of woody aboveground biomass in disturbance-prone ecosystems such as drylands. This includes a stratified sampling design along growth classes, an integration of all woody growth forms, and a damage assessment on an individual level, harnessing the disturbance archive of woody plants. Our method encompasses small, disturbed, and irregular woody growth forms, while keeping sampling effort within reasonable limits. It can easily be attuned to other ecosystem types or research questions. Extensive supporting material will facilitate the application and adaptation of our methodology.

Our study highlights the importance of a suitable methodology when assessing woody biomass in disturbance-prone ecosystems, thus avoiding substantial errors in biomass estimation. Considering intensifying disturbance regimes in ecosystems worldwide, the adoption of our methodology becomes even more pressing. Global environmental change and disturbance regime shifts demand for novel tools to estimate AGB and AGB losses, which may operate with one-time inventories, instead of relying on long-term observations. While our method requires more calculation and data processing steps, the greater detail and deeper insight into woody biomass and disturbance effects on it are worth the effort.

Declaration of Competing Interest

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

Contributions

AL and LK conceived the ideas and designed the methodology. LK, DN, MD and AL collected the field data. Calculations and statistical analyses were performed by LK, DN and MD. LK, DN and AL designed conceptual figures. LK wrote the manuscript. All authors contributed

13

critically to the drafts and gave final approval for publication. The authors declare to have no conflicts of interest.

Preprint

A preprint version of this manuscript was made available through the data repository of the Future Rural Africa project (Kindermann et al., 2020) and can be accessed via https://www.trr228db.uni-koeln. de/DOI/doi.php?doiID=5.

Availability of Data

The data used in this article is published via co-submission with a Data in Brief article (Kindermann et al., in review) and made available via Mendeley repository under DOI: 10.17632/3cs85wd3gb.1. Eventually, this and further datasets will be also made available through the data repository of the Future Rural Africa project (https://www. trr228db.uni-koeln.de/site/index.php).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.ecolind.2021.108466.

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14

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15

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Supplementary Material

Practical Guidelines for Data Acquisition and Biomass Estimation

Sampling Strategy

The stratified sampling along growth classes demands tactical consideration on how to place the cut-offs for each class along the plot. Usually, a representative number of saplings was reached after 500-750m² in our study system, and beyond this range only adult-sized trees were recorded. If necessary, a further cut-off can be made between adult-sized gullivers (AG) and less damaged adults (AA). For dense vegetation, the overall plot size might have to be chosen to be smaller than the standard size. Even agricultural fields can be assessed with our method; in this case plot areas ought to be measured with a GPS device and should be identical with the field itself, as they usually only contain very few trees and where they do trees might be lined up along the edges. Trees which are growing near the edges of a plot may receive a note on how much of their biomass falls inside the plot margins as to correct for that when aggregating AGB on a unit per area basis. As a general rule, individuals might be omitted if > 50 % of their biomass volume or the stem itself are outside the plot margins.

Allometric Measures

As many trees in highly disturbed ecosystems have irregular growth forms, measuring circumference at breast height is not always possible, but circumferences can be taken at various other heights in order to infer DBH by own local calibrations (Molto et al., 2013). In cases where stems were branching below 130 cm, the circumference was taken below the branching and the height of this alternative measure was noted as well and later used to calculate our own local regressions between basal diameter, DBH, and measurement height (see Data in Brief, Eq. 5). For some heavily damaged trees a second circumference measure cannot be derived, hence a surrogate DBH (DBH_{est}) will later be estimated from their basal circumferences (see Supplementary Figures 2 & 3)). Also, if the bases of stems are partially missing, an educated guess has to be made of the basal circumference before severe damage occurred (usually, this is not too complicated to achieve if the general curvature of the stem is visible and a missing section can be guessed). Note: When adopting our methodology, the allometric measurement procedure can be further streamlined according to the targeted allometric models. Therefore, some of the measurements taken here might not be mandatory for other applications and allometric models, although taking full sets of measures for all individuals will render later application of future allometric models possible. It also allowed for us to have our own locally calibrated models of DBH – height relationships, which is favourable (Molto et al., 2013; Sullivan et al., 2018).

We measured specific wood density (SWD) following the 'wood specific gravity' protocol in (Pérez-Harguindeguy et al., 2013). We sampled the stem wood of 2-20 individuals per species, using a 2-threaded increment borer (Haglöf Sweden®, inner diameter 5.15 mm). If this was not possible (e.g. in shrubs), we collected stem pieces with a saw. In total, we took 412 samples from 65 species according to the species' abundance. Bark was removed and

each sample was measured in length, and five separate diameter readings were taken with callipers to determine wood fresh volume. Wood samples were stored in paper envelopes and later oven-dried (105 °C) until no further weight reduction could be detected. Their weight was determined using standard laboratory fine scales (with a division of 0.001g). Dry weight and fresh green volume were used to calculate SWD, and measurements were averaged per species. Where own measurements of SWD are impractical, we advise researchers to derive SWD values from global trait databases such as TRY or the Global Wood Density Database (Chave et al., 2009). Alternatively, another allometric model may be applied, which does not rely on SWD as a proxy.

Own Model Calibrations and Validation

To extend applicability of the chosen stem-based allometric model by Chave et al. (2014, Model 4) we employed trees with reliable measures from our dataset to develop two models for estimating missing or misleading allometric proxies in damaged trees (Eq. 3 & Eq. 4 in main text). When exploring relation between basal stem circumference (or basal diameter (BD), respectively) and stem diameter at breast height (DBH) in n = 375 stems which had both measures taken in the field, we found a convincingly linear relationship (see Supplementary Figure 2A). The trees used for this linear model covered a size range from 3.5 to 97.4 cm in DBH and 16 to 351 cm in basal circumference, respectively. The derived linear model (Eq. 4 in main text, R^2 = 0.9639) was used to estimate a surrogate DBH (DBH_{est}) value for another n = 1,378 stems in which DBH measurement had not been possible in the field, either through low branching of the stems or as a result of stem damages complicating or preventing reliable measurements.

We discovered, that many gulliver trees exhibited a disturbed allometric relation between stem circumference and measured height (see Figure 3 in main text): for a given stem size (which can be considered to be an age proxy) they had a much lower height than non-gulliver trees. Considering the fact, that generic allometric stem-based models such as Chave et al. (2014) are established in and for considerably less damaged trees we found it questionable to feed such disturbed allometries into the model formula. For that reason, we developed another auxiliary model that for a given stem circumference (and hence age) estimates the height that was to be expected for a stem of that age and size. For this procedure we only used the least damaged tree growth class (AA, see Figure 1 and Table 1 in main text) for which height measurements are most reliable as damages are low or absent. We also included individuals for which we had to estimate a missing DBH value, and from each individual only regarded the biggest stem (because this is most representative for the maximum height measured in the field). Following the procedure suggested by Mensah et al. (2016) and Mensah et al. (2018) the so formed subset of n = 781 tree individuals was then randomly split into a calibration data set (80 %, n = 625 trees) for model calibration while the remaining n = 156 trees (20 %) formed an independent validation dataset. The calibration dataset covered a DBH range from 3.5 to 84.7 cm and a range of field height measurements from 100 to 2,100 cm. The validation dataset covered a DBH range from 3.8 to 90.7 cm and a range of field height measurements from 130 to 1,850 cm. The calibration dataset was

2

further used to calibrate i) a linear model, ii) a power law model, and iii) an exponential model (see Supplementary Table 1) and models' fit metrics were compared, where the power law model showed highest R^2 (0.7504).

Supplementary Table 1. Three alternative models for predicting former height from stem diameter at breast height (DBH) as developed from calibration dataset of n = 625 trees.

Model	Type	Formula	Multiple R^2
i)	Linear Model	Height = 258.75 + 22.09 * DBH	0.6739
ii)	Power Law Model	LN(Height) = 4.72595 + 0.63385 * LN(DBH)	0.7504
iii)	Exponential Model	LN(Height) = 5.70 + 0.035 * DBH	0.5986

Following workflow by Mensah et al. (2016) and Mensah et al. (2018) model fits were then explored visually by using the validation dataset. In the validation dataset all three models were employed to predict height values from given stem circumferences. For the power law model an additional correction factor (Correction Factor (CF) = exp(RSE^2/2)) was computed to correct for the systematic error of back-transforming log values to real values (Mensah et al., 2018; Mensah et al., 2016). Then linear models between observed and predicted values in the validation dataset were used to visually compare models' fit (see Supplementary Figure 1, exponential model not shown because of bad fit).
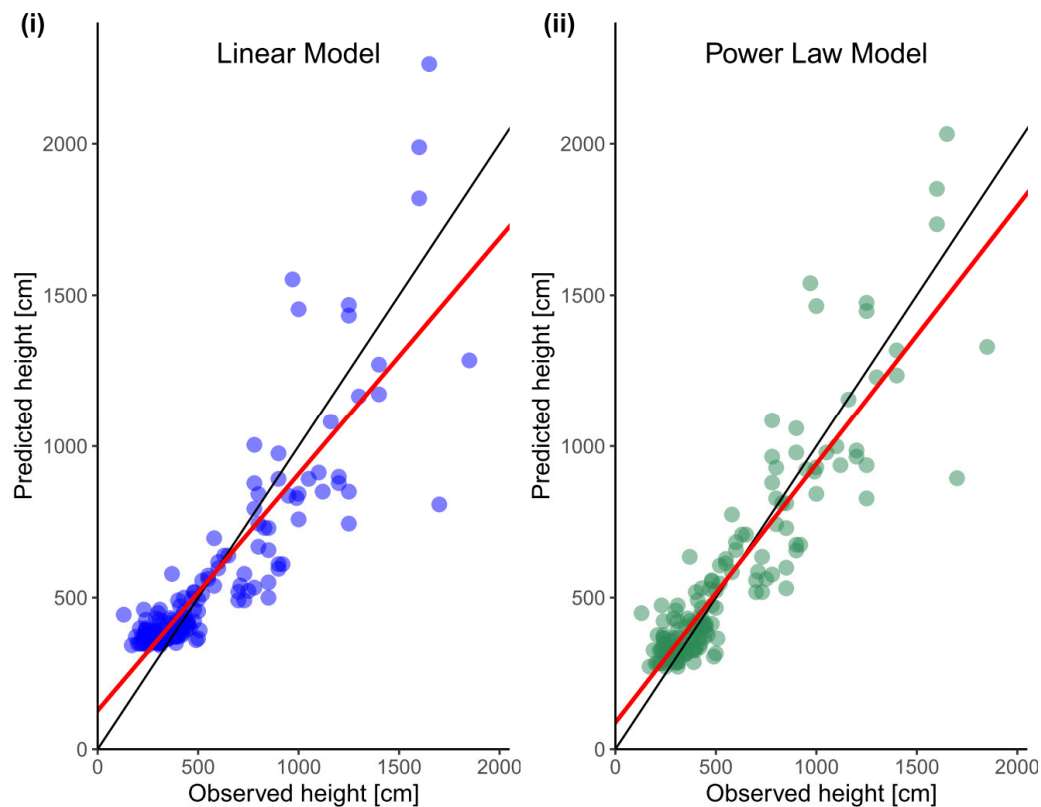
Supplementary Figure 1: Visual model comparison between i) Linear Model, and ii) Power law model by plotting observed vs predicted heights from the validation dataset (n = 156 trees) and linear

3

models between observed and predicted values. Model fit of power law model (ii) is better than linear prediction model (i), as indicated by closer match between linear regression of observed and predicted values (red lines) with the 1:1 equity line (black line).

As power law model (ii) exhibited a better fit than linear and exponential model, it was chosen to estimate corrected heights in severely damaged gulliver trees of the main dataset (Supplementary Figure 2B).
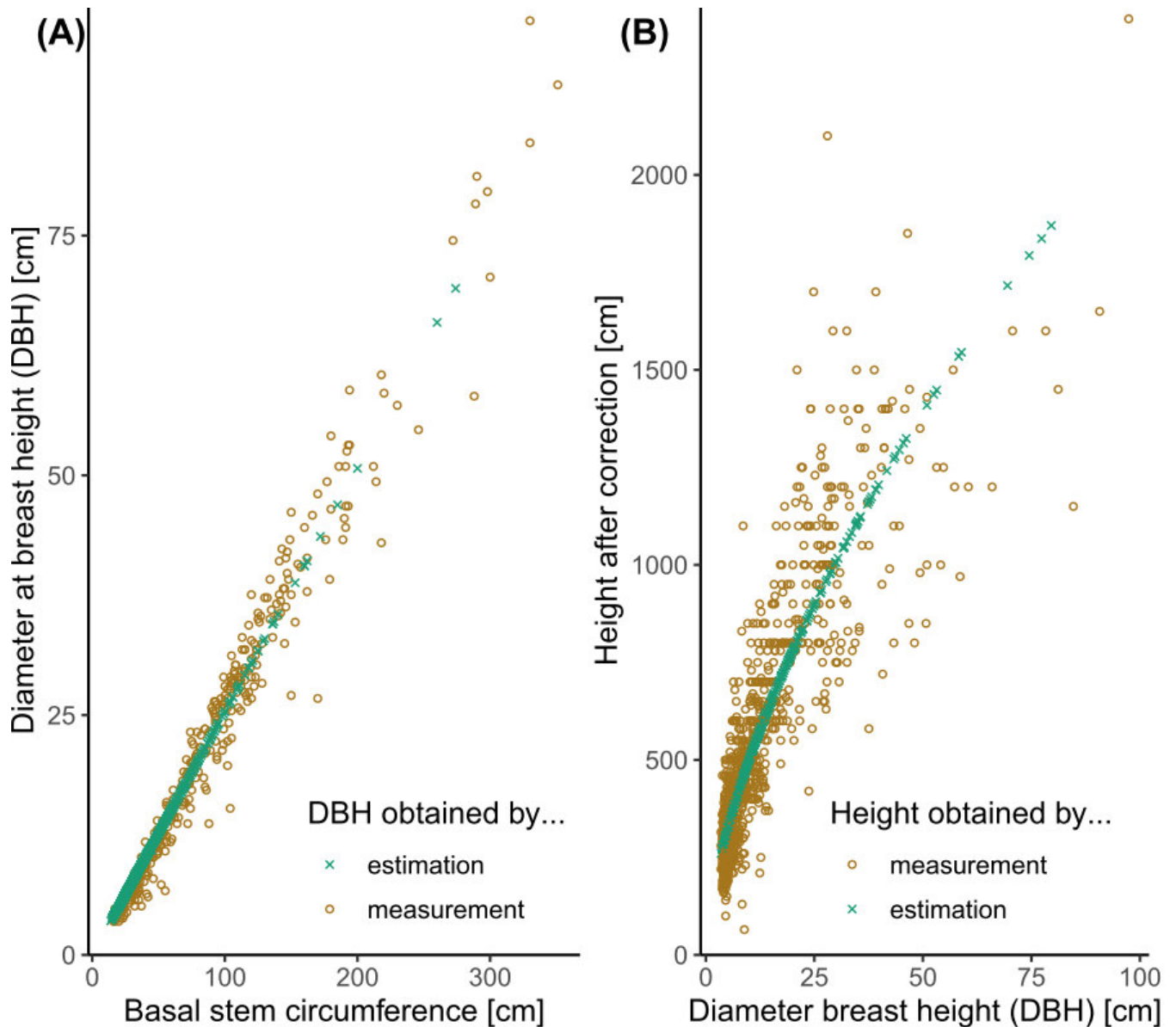
Supplementary Figure 2: *Measured and reconstructed size proxies. A) Linear relation between basal stem circumference and diameter at breast height (DBH) as found in measurements of undamaged stems (golden circle symbols, n = 375) allowed for reconstruction of unmeasurable DBH in gulliver trees through estimation (DBHest, green cross symbols, n = 1,378) via Eq. 4 (R^2 = 0.9639), see main text. B) Power law relationship between height and DBH found in calibration dataset of n = 625 undamaged and marginally damaged trees (golden circle symbols) allowed for reconstruction of pre-disturbance height in gulliver trees (hest, green cross symbols) via Eq. 3, see main text.*

4

1) derive formula:
h = exp(4.72595 + 0.63385 * LN(DBH))
$(R^2 = 0.75)$

4) use formula 1) to estimate former height:
h_{est} = exp(4.72595 + 0.63385 * LN(DBH))

2) derive formula:
DBH = 0.7968*circ at base /π
$(R^2 = 0.9639)$

5) combine formulas 3) & 4)
h_{est} = exp(4.72595 + 0.63385 * LN(DBH_{est}))

3) use formula 2) to estimate missing DBH measurement:
DBH_{est} = 0.7968*circ at base /π

height **h** (if biomass losses <30%)

height **h_{est}** (because biomass losses ≥30%)

height **h_{est}** (because biomass losses ≥30%)

Supplementary Figure 3: Measuring and inferring size parameters in adult trees of different damage conditions. While undamaged and slightly damaged Adults (AA) are measured with their real height and DBH, adult-sized Gullivers (AG) require workarounds, depending on how severely the damages altered their crown and stem properties: From AAs in the dataset 1) a DBH-height relationship, and 2) a relation between basal stem circumference and DBH were inferred. These formulas were used to calculate missing height and stem dimensions: For AGs which had been damaged so severely that a major stem was lost, 3) a former DBH could be estimated (DBH_{est}) from the basal circumference of the stump; 4) original pre-disturbance height of AGs can be estimated from actually measured, but also inferred, DBH values. Through this procedure, misleading height measurements (grey broken arrows) could be discarded and instead lost biomass was calculated by making use of the former height information contained in gulliver trees' basal circumferences. Broken lines and arrows symbolize field measurements; solid lines and arrows symbolize values used for AGB estimations;
AGB = aboveground biomass, DBH = stem diameter at breast height; est = estimated, h = height; AGB in [kg], DBH and h in [cm].

5

Damage Assessment

For each woody individual in the tree inventory, a detailed damage assessment was conducted. The main damaging agents should all be listed independently, as was the case for the following possible disturbances in our study: fire, elephant, other browsers, woodcutting, abiotic stress. Other disturbance agents, e.g. insects or storm, were subsumed under "other", but notes were taken to further identify the disturbance. When comparing healthy to damaged trees a general idea can be derived on how much of the biomass has been lost in the latter. It is helpful to visualize what a healthy tree individual would look like (i.e. straight stem with a regular, well-proportioned crown) and then pay attention to scars of lost branches or firemarks on the bark, which are indicators for the causes that led to irregular growth forms of damaged trees. With a little bit of practice observers will get a general good feeling for how different species exhibit past disturbances.

If a dead adult-sized stem is present, it is measured with basal circumference and a note is taken to mark it as dead and identify the presumed topkill agent. Its biomass will be calculated independently and is not included into the percentages of lost biomass as recorded on live stems and in crowns. This also helps to stratify the disturbance losses on small living regrowth, which all in all would only make up for < 1 % if the dead adult-sized stem was to be counted in; by calculating lost biomass for the dead stem independently, the total of 100 % of living regrowth biomass can be split up to several disturbance agents. Note that indicated biomass losses summed up over all disturbance agents cannot exceed 99 %, but as estimating unproportionally big losses from dead adult-sized stems is done, overall biomass losses will be represented, even if the living individual is small now.

Methodological obstacles and biomass partitions

In part, our methodology follows the rather straightforward sequence of measuring few dendrometric proxies of a tree, estimating its AGB from an allometric model, and then deducting a percentage of AGB lost to a recorded disturbance. For all but the slightly damaged trees though there are methodological obstacles:

Problem 1: A damaged tree's dendrometric measures do not fit the usual allometric relationships between height and stem diameter (Moncrieff et al., 2011). Solution 1: The stem diameter still informs us about the tree's original height; therefore, the latter can be estimated from the former.

Problem 2: DBH measurement is impossible due to damages on the stem. Solution 2: Whenever possible we took both measures, basal circumference and DBH. From a rather undamaged subset of trees in our dataset we derived a regression between basal circumference and circumference at breast height (Eq. 4) and used this formula to estimate missing DBH values.

6

Problem 3: A damaged tree is likely to adopt an atypical growth form. Solution 3: Two different allometric models are deployed for shrub-like and tree-like growth forms, but across all species. For one growth class, these two models even have to be combined within one and the same individual if dead stems and regrowth are of different growth forms (AG3).

Problem 4: Substantial damages in dead stems may exceed the retained living AGB by orders of magnitude. Solution 4: Those damages must be quantified separately through circumference measures of dead stems, DBH reconstruction from basal circumference, height reconstruction from DBH and subsequent feeding of those values into allometric stem model.

Reflecting the problems and solutions outlined above, it becomes clear, that calculation of standing AGB and estimation of AGB losses to disturbances are two distinct procedures, which cannot be decoupled as the unit of observation still is the woody individual. This potentially complicates the methodological demands, but as we will demonstrate a woody individual can be broken down to certain biomass partitions, which can be calculated separately.

7

Supplementary Table 2. *Biomass partitions which were independently calculated and then combined according to growth class specifications to reflect biomass stocks and losses. AGB = aboveground biomass, act = actually alive, calc = calculated by stem measures, reclost = recorded losses from damage assessment, dead = dead adult-size stems, ex = extrapolated from alternative allometric measures.*

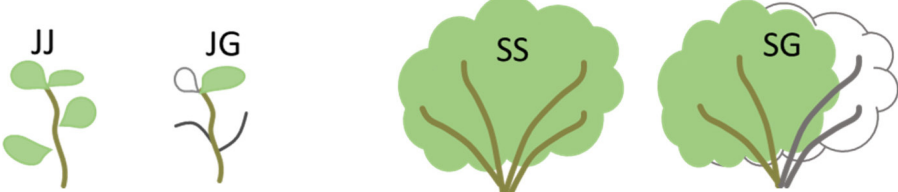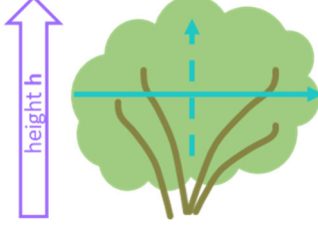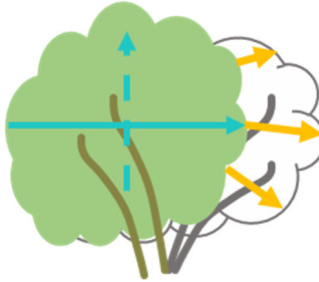| Acronym	Biomass Partition	Description
AGB_{act}	Actual AGB	Trees: What remains of AGB_{calc} after crown damages are deducted
		Shrubs and shrub-like gulliver regrowth: biomass as represented by their (damaged) canopy measurements; directly estimated with formula by (Conti et al., 2019)
$AGB_{reclost}$	AGB losses recorded during damage assessment	Trees: Estimated biomass losses (crown, branches) in relation to AGB_{calc}; deducted % damages from AGB_{calc} (as AGB_{calc} was calculated from undamaged stem measures and (corrected) height)
		Shrubs: Estimated biomass losses (branches) in relation AGB_{act}; is added to AGB_{act} to obtain pre-disturbance AGB (AGB_{ex}) as AGB_{act} was calculated from damaged crown dimensions
AGB_{dead}	AGB of dead stems (on a living individual)	Dead stems attached to a living gulliver; this biomass is calculated independently from AGB_{calc} by dead stems' own stem measures
AGB_{calc}	AGB as calculated from allometric measures by Chave et al. (2014) formula	Adult-sized trees only; biomass as represented by their (undamaged) allometric measures (height in AGs was corrected to h_{est}); not incorporating the visible losses in e.g. crown biomass; → close to what usual studies would have done, but more accurate than that, as we also included damaged stems which had no proper DBH (by estimating DBH_{est} from their basal circumference, see Supplementary Figure 3)
AGB_{ex}	Extrapolated pre-disturbance AGB	Hypothetical AGB of for an individual if it were undamaged: - for undamaged and slightly damaged adults (AA): $AGB_{ex} = AGB_{calc}$ - damaged adults with a dead and a living stem (AG2a and AG2b): $AGB_{ex} = AGB_{calc} + AGB_{dead}$ - for sub-adult classes (JJ, JG, SS, SG): $AGB_{ex} = AGB_{act} + AGB_{reclost}$ - for shrub-like gullivers with a dead stem (AG3): $AGB_{ex} = AGB_{act} + AGB_{reclost} + AGB_{dead}$

8

Calculation Procedure per Growth Class

The calculation procedure is slightly different in each of the growth classes. For a better understanding of the procedure and a complete formulary and detailed workflows for each growth class are presented here.

Supplementary Table 3. Formulas and biomass partitions combined to calculate each growth class' AGB and AGB losses; auxiliary colour coding according to Supplementary Figure 3 and Supplementary Figure 4 below; AGB = aboveground biomass, act = actually alive, calc = calculated by stem measures, CD = mean canopy diameter, dead = dead adult-size stems, DBH = diameter at breast height, est = estimated from alternative allometric measures, h = height, reclost = recorded losses from damage assessment.

Growth class	AGB_{calc}	AGB_{dead}	$AGB_{reclost}$	AGB_{act}
JJ, SS, JG, SG	----	----	AGB_{act} * biomass loss %	Conti et al. (2019) eq. based on CD and h
AA	Chave eq. based on DBH, h & SWD	----	AGB_{calc} * biomass loss %	AGB_{calc} - $AGB_{reclost}$
AG1	Chave eq. based on DBH, h_{est} & SWD	----	AGB_{calc} * biomass loss %	AGB_{calc} - $AGB_{reclost}$
AG2a	Chave eq. based on DBH, h & SWD	Chave (2014) eq.; based on DBH_{est}, h_{est} and SWD	AGB_{calc} * biomass loss % + AGB_{dead}	AGB_{calc} – (AGB_{calc} * biomass loss %)
AG2b	Chave eq. based on DBH, h_{est} & SWD	Chave (2014) eq.; based on DBH_{est}, h_{est} and SWD	AGB_{calc} * biomass loss % + AGB_{dead}	AGB_{calc} – (AGB_{calc} * biomass loss %)
AG3	----	Chave (2014) eq.; based on DBH_{est}, h_{est} and SWD	AGB_{act} * biomass loss % + AGB_{dead}	Conti et al. (2019) eq. based on CD and h

See detailed workflows per growth class in Supplementary Figure 4 where also AGB partitions are visualized in colour code from Supplementary Table 3.

9
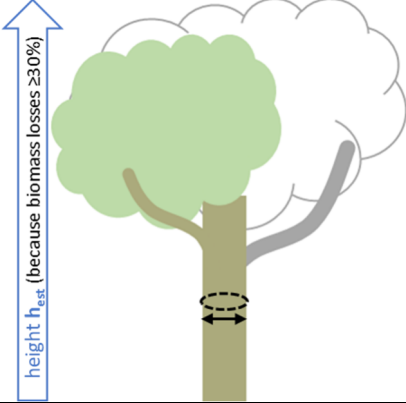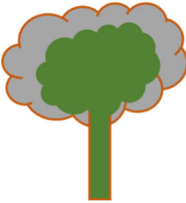
Supplementary Figure 4: *Detailed visual workflow of AGB and AGB loss estimation per growth class. Growth classes are abbreviated as: AA = undamaged and slightly damaged adult trees, AG = adult-sized gulliver trees, JJ = undamaged and slightly damaged juveniles; JG = juvenile-sized gullivers, SS = undamaged and slightely damaged saplings and shrubs, SG = sapling and shrub gullivers; AGB = aboveground biomass, act = actually alive, calc = calculated by stem measures, CD = mean canopy diameter, dead = dead adult-size stems, DBH = diameter at breast height, est = estimated from alternative allometric measures, h = height, reclost = recorded losses from damage assessment.*
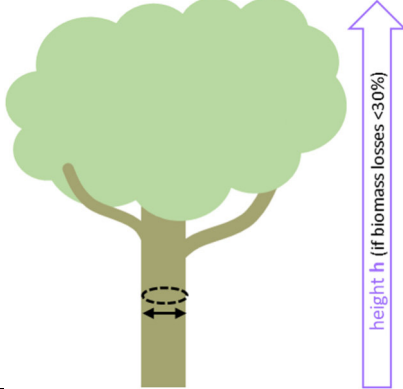
JJ, JG, SS, SG	
Icons	
Size parameters	Mean Canopy Diameter (CD) and height (h)
Biomass partitions	$AGB_{reclost} = AGB_{act} *$ **recorded losses (%)**
	$AGB_{act} = \exp(-0.370 + 1.903 \, \mathrm{Ln}(CD) + 0.652 \, \mathrm{Ln}(h)) * 1.403$

10
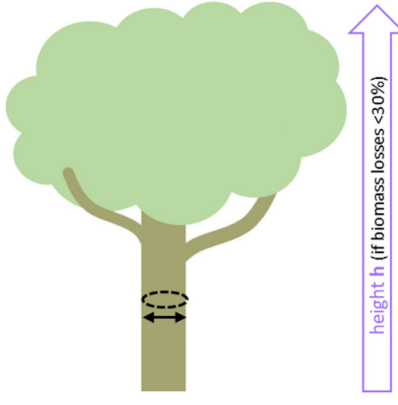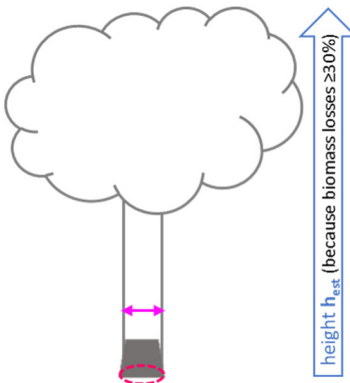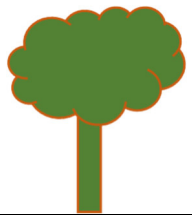
Supplementary Figure 4 continued.

AA	undamaged	slightly damaged
Icon	AA without damages	AA with damages <30%
Size parameters	Height (h) and DBH as measured in the field	
Biomass partitions	Estimating AGB as represented by stem properties and height: $$AGB_{calc} = 0.0673 * (SWD * DBH^2 * h)^{0.976}$$ (formula by Chave et al. (2014))	
		Calculating AGB lost to damages according to damage assessment: $AGB_{reclost} = AGB_{calc} * \text{recorded losses (\%)}$
	Actually living biomass for undamaged individuals: $AGB_{act} = AGB_{calc}$	Actually living biomass for slightly damaged individuals: $AGB_{act} = AGB_{calc} - AGB_{reclost}$

11
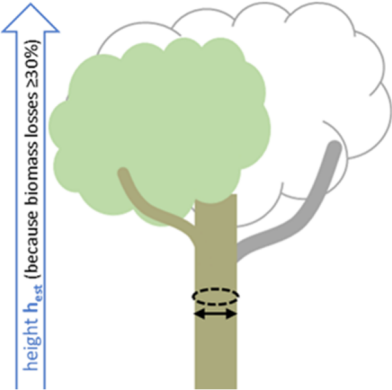
Supplementary Figure 4 continued.

AG1	Heavily damaged, but in crown only
Icon	
Size parameters	DBH as measured in the field; former height (h_{est}) estimated from DBH
Biomass partitions	Estimating AGB as represented by stem properties and corrected height: AGB_{calc} **= 0.0673 * (SWD * DBH^2 * h_{est})$^{0.976}$** (formula adopted from Chave et al. (2014))
	Calculating AGB lost to damages according to damage assessment: $AGB_{reclost}$ = AGB_{calc} * **recorded losses (%)**
	Actually living biomass retained after damages: AGB_{act} = AGB_{calc} - $AGB_{reclost}$
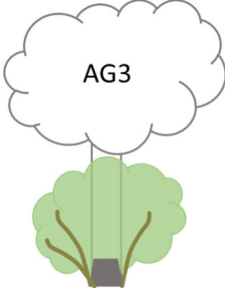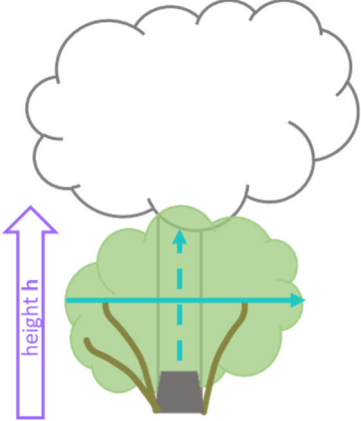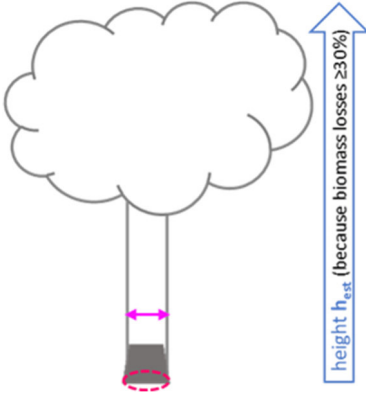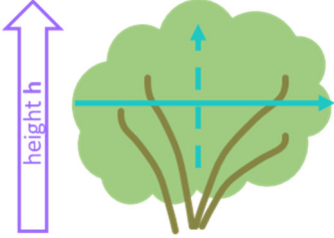
Supplementary Figure 4 continued.

AG2a	Heavily damaged, but all damage in form of a dead stem	
Icon		
Size parameters	Height (**h**) and DBH as measured in the field for the living stem	Former DBH (**DBH_{est}**) as estimated from dead stem's basal circumference; former height (**h_{est}**) estimated from **DBH_{est}**
Biomass partitions	Estimating AGB of the living stem as in AAs: **AGB_{calc} =** **$0.0673 * (SWD * DBH^2 * h)^{0.976}$** (formula adopted from Chave et al. (2014)	Estimating AGB lost within the dead stem from estimated dendrometrics: **AGB_{dead} =** **$0.0673 * (SWD * DBH_{est}^2 * h_{est})^{0.976}$** (formula adopted from Chave et al. (2014)
	Calculating damages on the living stem: **$AGB_{reclost}$ = AGB_{calc} * recorded losses (%) + AGB_{dead}**	
	Without damges on the live stem: **AGB_{act} = AGB_{calc}**	With minor damages on the live stem: **AGB_{act} = AGB_{calc} - $AGB_{reclost}$**

13

Supplementary Figure 4 continued.

AG2b		
Icon		
Size parameters	DBH as measured in the field; former height (h_{est}) estimated from DBH for the living stem. 	Former DBH (DBH_{est}) as estimated from dead stem's basal circumference; former height (h_{est}) estimated from DBH_{est}.
Biomass partitions	$AGB_{calc} =$ $0.0673 * (SWD * DBH^2 * h_{est})^{0.976}$	$AGB_{dead} =$ $0.0673 * (SWD * DBH_{est}^2 * h_{est})^{0.976}$
	$AGB_{reclost} = AGB_{calc} * \text{recorded losses (\%)} + AGB_{dead}$	
	$AGB_{act} = AGB_{calc} - AGB_{reclost}$	

Supplementary Figure 4 continued.

AG3		
Icon	AG3	
Size parameters	Mean Canopy Diameter (CD) and height (h) for the living shrub-like part of the gulliver tree.	Former DBH (DBH_{est}) as estimated from dead stem's basal circumference; former height (h_{est}) estimated from DBH_{est} for calculating dead stem's biomass.
Biomass partitions	AGB_{act} = exp(−0.370 + 1.903 Ln(CD) + 0.652 Ln(h))*1.403	AGB_{dead} = 0.0673 * (SWD * DBH_{est}^2 * h_{est})$^{0.976}$
	$AGB_{reclost}$ = AGB_{act}* recorded losses (%) + AGB_{dead}	

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Chapter 3

Dataset on woody aboveground biomass, disturbance losses, and wood density from an African savanna ecosystem

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Adjoining dataset published with Mendeley data repository
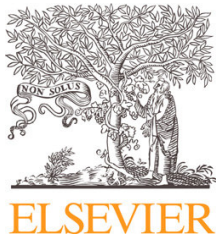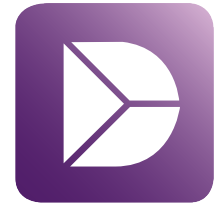
Data Article

Dataset on woody aboveground biomass, disturbance losses, and wood density from an African savanna ecosystem

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ARTICLE INFO

ABSTRACT

This dataset comprises tree inventories and damage assessments performed in Namibia's semi-arid Zambezi Region. Data were sampled in savannas and savanna woodlands along steep gradients of elephant population densities to capture the effects of those (and other) disturbances on individual-level and stand-level aboveground woody biomass (AGB). The dataset contains raw data on dendrometric measures and processed data on specific wood density (SWD), woody aboveground biomass, and biomass losses through disturbance impacts. Allometric proxies (height, canopy diameters, and in adult trees also stem circumferences) were recorded for $n = 6,179$ tree and shrub individuals. Wood samples were taken for each encountered species to measure specific wood density.

These measurements have been used to estimate woody aboveground biomass via established allometric models, advanced through our improved methodologies and workflows that accounted for tree and shrub architecture shaped by disturbance impacts. To this end, we performed a detailed damage assessment on each woody individual in the field. In addition to estimations of standing biomass, our new method also delivered data on biomass losses to different disturbance agents (elephants, fire, and others) on the level of plant individuals and stands.

The data presented here have been used within a study published with Ecological Indicators (Kindermann et al., 2022) to evaluate the benefits of our improved methodology in comparison to a standard reference method of aboveground biomass estimations. Additionally, it has been employed in a study on carbon storage and sequestration in vegetation and soils (Sandhage-Hofmann et al., 2021).

The raw data of dendrometric measurements can be subjected to other available allometric models for biomass estimation. The processed data can be used to analyze disturbance impacts on woody aboveground biomass, or for regional carbon storage estimates. The data on species-specific wood density can be used for application to other dendrometric datasets to (re-) estimate biomass through allometric models requiring wood density. It can further be used for plant functional trait analyses.

Specifications Table

Subject	Biology; Plant Science: General
Specific subject area	Savanna ecology; disturbance ecology; global change ecology; disturbances impacting woody aboveground biomass
Type of data	Table Image Graph Figure
How the data were acquired	We stratified our sampling into two vegetation types (savanna and savanna woodland) and three levels of elephant population densities (high, medium and low); for details see [2]. Each stratification level was sampled with ten replicate plots per site ($n = 60$). A systematic but flexibly attunable plot design was employed; for details see [1]. Basic tree size proxies (height, stem circumferences, canopy diameters) were taken in the field with the aid of meter sticks and measuring tapes. For very large trees, a clinometer PM-5 by Suunto was used for height determination. A two-threaded increment borer by Haglöf Sweden (inner diameter 5.15 mm) was used for extraction of wood cores from tree stems while in shrub species, a saw was used to cut stem pieces [3]. Fresh wood samples were measured in length by using a meter stick and a total of five diameter readings on each wood sample were taken with calipers. Wood samples were first air-dried and later dried in standard laboratory drying ovens at 105°C until no further weight reduction was detected [3]. Their weight was determined using standard laboratory fine scales (with a division of 0.001g).

	Field measurements were digitalized in MS Excel, and data preparation including all estimation procedures for aboveground biomass were conducted in a spreadsheet. Data analysis was conducted with opensource software R [4] and RStudio [5], using packages dplyr [6], rstatix [7], and reshape2 [8]. Data exploration was performed visually using R packages ggplot2 [9], and scales [10].
Data format	Raw
	Analyzed
	Processed
Parameters for data collection	Data collection considered all woody tree and shrub species and individuals of all sizes, age classes, and damage levels were recorded with dendrometric proxies (height and canopy diameter). For adult-sized stems (> 15 cm basal circumference), additional stem circumference readings were taken, see [1] for details. Specific wood density was measured in 2-10 healthy, mature individuals per species, depending on species' abundance.
Description of data collection	On all plots, woody individuals of all species, sizes, and damage levels were measured non-destructively. For each sampled individual, we recorded (i) species identity, (ii) height, and (iii) canopy diameters. On living stems > 15 cm circumference at the base we recorded (a) basal circumference, (b) circumference at 130 cm aboveground, and where (a) or (b) was impossible (c) a stem circumference at an alternative section of the stem and its corresponding height. Dead stems were measured at the base if living regrowth was present. A representative number of individuals in each species was sampled for wood density measurements.
Data source location	Institution: University of Potsdam – Institute of Biochemistry and Biology, Faculty of Science, University of Potsdam, Germany; Collaborative Research Center TRR228 'Future Rural Africa', project A01 ('Future Carbon Storage')
	Region: Zambezi Region; National Parks Mudumu and Bwabwata as well as Communal Conservancies Wuparo and Mashi
	Country: Namibia
	Latitude and Longitude: 18°04.000′S; 23°25.000′E (see detailed coordinates for each plot in data file)
Data accessibility	Repository name: Mendeley Data
	Data identification number: DOI: 10.17632/3cs85wd3gb.5 [11]
	Direct URL to data: http://dx.doi.org/10.17632/3cs85wd3gb.5
Related research article	L. Kindermann, M. Dobler, D. Niedeggen, A. Linstädter, A new protocol for estimation of woody aboveground biomass in disturbance-prone ecosystems. Ecol. Indic. 135 (2022) 108466. https://doi.org/10.1016/j.ecolind.2021.108466

Value of the Data

- The data provide dendrometric measurements and estimates of woody aboveground biomass (AGB) as well as AGB losses from savanna and savanna woodland sites in north-eastern Namibia that differ in elephant population densities, and also in the level of damages by other disturbance agents including fire. The data are important to assess tree and shrub biomass in disturbance-prone ecosystems and disturbance impacts on woody vegetation.
- Data are useful for dryland ecologists, global change ecologists, or conservation biologists interested in the effects of elephant and fire disturbances on woody vegetation. They can also be of interest for carbon storage assessments.
- Data can be exploited to analyze structural and compositional characteristics of the study area, providing e.g., information for national or regional conservation policies.
- Data can also provide useful information to compare the pros and cons of the adoption of a new method [1] to record AGB of highly disturbed woody plants in disturbance-prone ecosystems.
- Data on tree species' 'specific wood density' (SWD) may be used to (re-) analyze existing dendrometric datasets from the region with new allometric equations requiring this proxy e.g. [12].

1. Data Description

Data Table: The dataset presents the results of tree inventories conducted along steep gradients of elephant disturbances in African savannas and woodlands located in Namibia's semi-arid Zambezi Region (18°04.000'S; 23°25.000'E). Data were collected in 60 plots (25 × 40 m). The data table contains six spreadsheets: a basic information spreadsheet, a detailed legend, and four data spreadsheets. The first data spreadsheet (data prop) contains aboveground biomass data as derived with our proposed method for n = 6,179 trees and shrubs on 60 plots, distributed over four sites, two vegetation types, and three levels of elephant density. Several aboveground biomass (AGB) partitions are given for each woody individual: the individually estimated AGB, the individual's AGB scaled to a unit per area basis [kg ha^{-1}], and AGB losses to various recorded disturbance agents (elephants, fire, woodcutting, browsers other than elephant, abiotic stress). The second data spreadsheet contains mean specific wood density (SWD; also known as 'wood specific gravity' [3]) values per species as derived from our measurements. The third data spreadsheet contains the raw data of dendrometric proxies taken in n = 6,179 trees from which AGB values in 'data prop' have been calculated, see [1] for details. The last spreadsheet contains geographical coordinates for each of the *n* = 60 plots.

Fig. 1: In Fig. 1 we describe and illustrate the six growth classes with sub-types and list the metric criteria they are defined by.

Fig. 2: In Fig. 2 we present photographic examples for the growth class of adult-sized gullivers trees and its sub-types (see details on growth classes below).

Fig. 3: In Fig. 3 we present a rough visualization of mean aboveground biomass (AGB) and AGB losses to main disturbance agents per vegetation type and elephant density level.

Supporting Material: This file contains supporting material illustrating the biomass estimation method with which the data in spreadsheet 'data prop' has been generated. All formulas are presented and detailed workflows of AGB estimation are illustrated for each growth class. A detailed illustration of workarounds for extrapolation of missing dendrometric proxies from measurable proxies is given as well.

2. Experimental Design, Materials and Methods

2.1. Study design

The data presented here is an exemplary dataset that relates to a research article [1], which presents a novel approach to estimate individual- and stand-level woody aboveground biomass (AGB) in disturbance-prone ecosystems such as drylands. The methodology consists of field sampling routines and workflows for a non-destructive estimation of AGB and AGB losses in woody vegetation, harnessing the archival function of trees for disturbances. The method was tested with the aid of large tree inventories collected along steep gradients of elephant disturbances in semi-arid savanna ecosystems located in Namibia's Zambezi Region. The dataset consists of the raw data on dendrometric proxies taken in the field, individual-level AGB estimates and AGB loss estimates generated with the proposed method, and species-wise mean values on specific woody density (SWD).

Our data were collected in savannas located in Namibia's Zambezi Region; for more information on the study area, see [1]. Sampling was stratified into two vegetation types (savanna and woodland) and three disturbance classes with low, medium, and high elephant densities; see Sandhage-Hofmann et al. (2021) [2] for details on this study design. Sites with 'medium' and 'high' elephant densities were located in the national parks Mudumu and Bwabwata, and least-disturbed sites with 'low' elephant densities were located in the respective adjacent communal conservancies Wuparo and Mashi. While the Mudumu-Wuparo set represented open, savanna-like vegetation ('savanna'), the Bwabwata-Mashi set represented a more closed savanna woodland ('woodland'), yielding a total of 6 sites (2 vegetation types x 3 elephant density levels each).

Growth Class	Abbr.	Size criteria	Explanation	Icon
Non-Gullivers (Damage criterion: biomass loss < 30 %)				
Juvenile	JJ	- Height < 50 cm - Basal stem diameter < 5 cm	Very young woody plants	
Sapling	SS	- Height ≥ 50 cm - Basal stem diameter < 5 cm	Young trees, but also most shrubs fall into this category	
Adult	AA	- Basal stem diameter ≥ 5 cm	Trees with a rather undisturbed life history, which managed to grow to adult stage; can also include individuals which have outgrown a severe damage event from the distant past and compensated major AGB losses since	
Gullivers (Damage criterion: biomass loss ≥ 30 %)				
Juvenile-sized Gulliver	JG	- Height < 50 cm - Basal stem diameter < 5 cm	Very small woody plants with a considerable loss of AGB	
Sapling-sized Gulliver	SG	- Height ≥ 50 cm - Basal stem diameter < 5 cm	Small trees and shrubs with a considerable loss of AGB	
Adult-sized Gulliver	AG	- Basal stem diameter ≥ 5 cm	Adult trees with a high loss of AGB, where AGB losses alternatively manifest ...	
	AG1		... entirely in crown and branches	
	AG2a		... mainly from an adult-sized dead stem; additional losses in crown of living adult-sized stem < 30 %	
	AG2b		... as a dead adult-sized stem and additional losses in crown of living adult-sized stem ≥ 30 %	
	AG3		... as a dead adult-sized stem, with no living adult-sized stems retained	

Fig. 1. The six growth classes with sub-types and the metric criteria they are defined by.
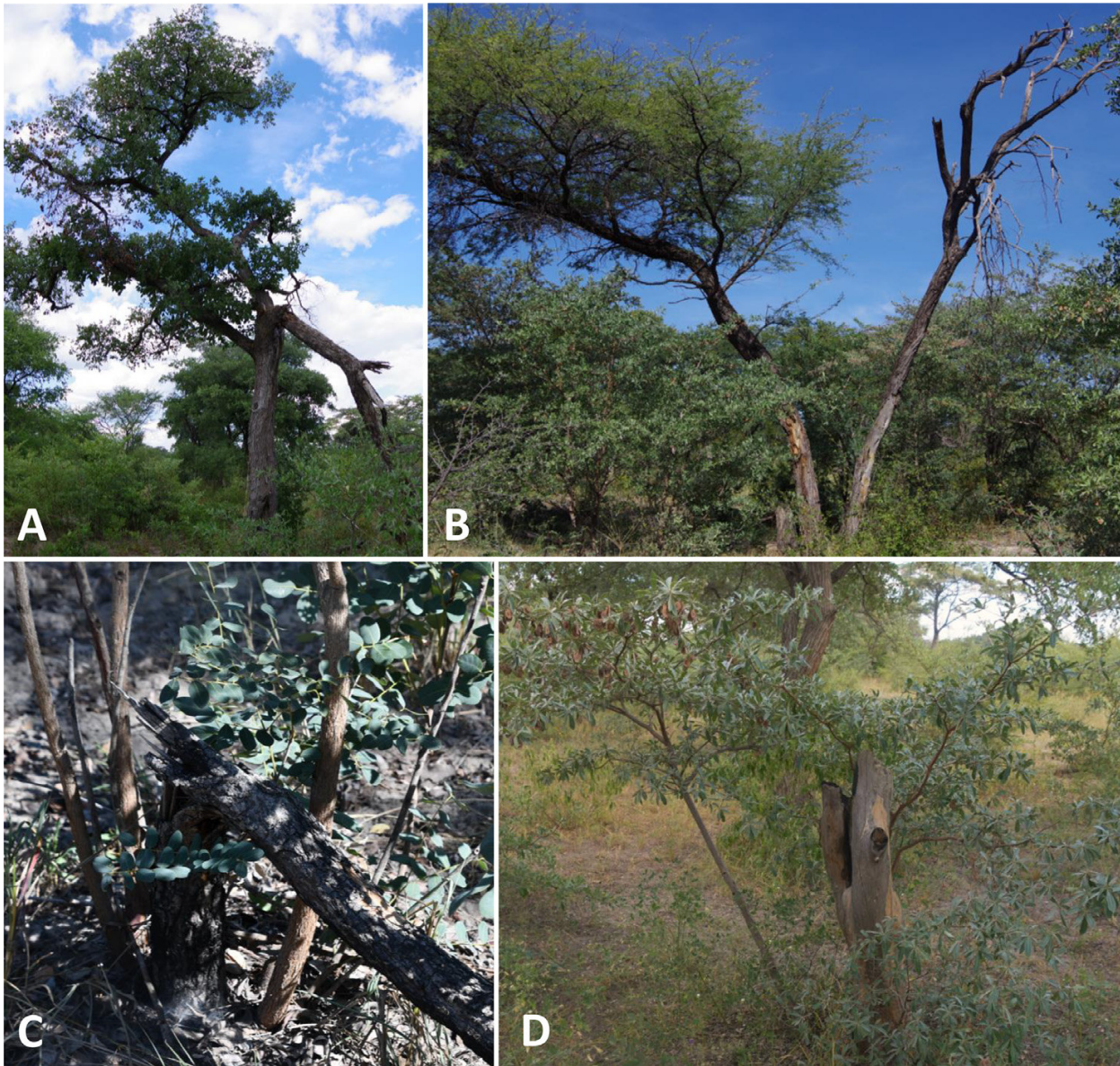
Fig. 2. Photographic examples for the main growth class of adult-sized gulliver trees (AG). A) Adult-sized gulliver type 1 (AG1) with extensive losses in crown biomass; note that a conventional stem-based allometric model would have missed the extensive canopy losses, while a purely canopy-based or remote sensing approach would underestimate the extensive stem's biomass; B) Adult-sized gulliver type 2 (AG2) which lost one out of its two big stems to disturbance topkill while the other stem remained rather undamaged and lives on; note that a remote sensing approach would probably not have linked the dead stem and its losses to the living stem; C) Adult-sized gulliver type 3 (AG3) which has lost its single main stem to topkill through elephant browsing and is now resprouting as a multi-stemmed shrub from the live root remains; only an individual-based method can explain the atypical shrub-like growth form in this tree species (*Burkea africana*); D) AG3 which has lost its main stem to topkill through fire and is now resprouting as a multi-stemmed shrub; only with an individual-based damage assessment can this very old gulliver individual be told apart from a younger sapling of similar canopy dimension and only then can biomass losses and regrowth potential be assessed reliably.

In both national parks, areas of high elephant density were retrievable in close proximity (usually ≤ 1 km) to permanent water sources, while medium-density levels were found in greater distance [13,14]. Ten independent observation plots with a minimum distance of 80 m to each other and a size of 1000 m² (25 × 40 m) were sampled per site (6 sites x 10 plots = 60 in total). Sampling took place from September to November 2018, and from April to June 2019.
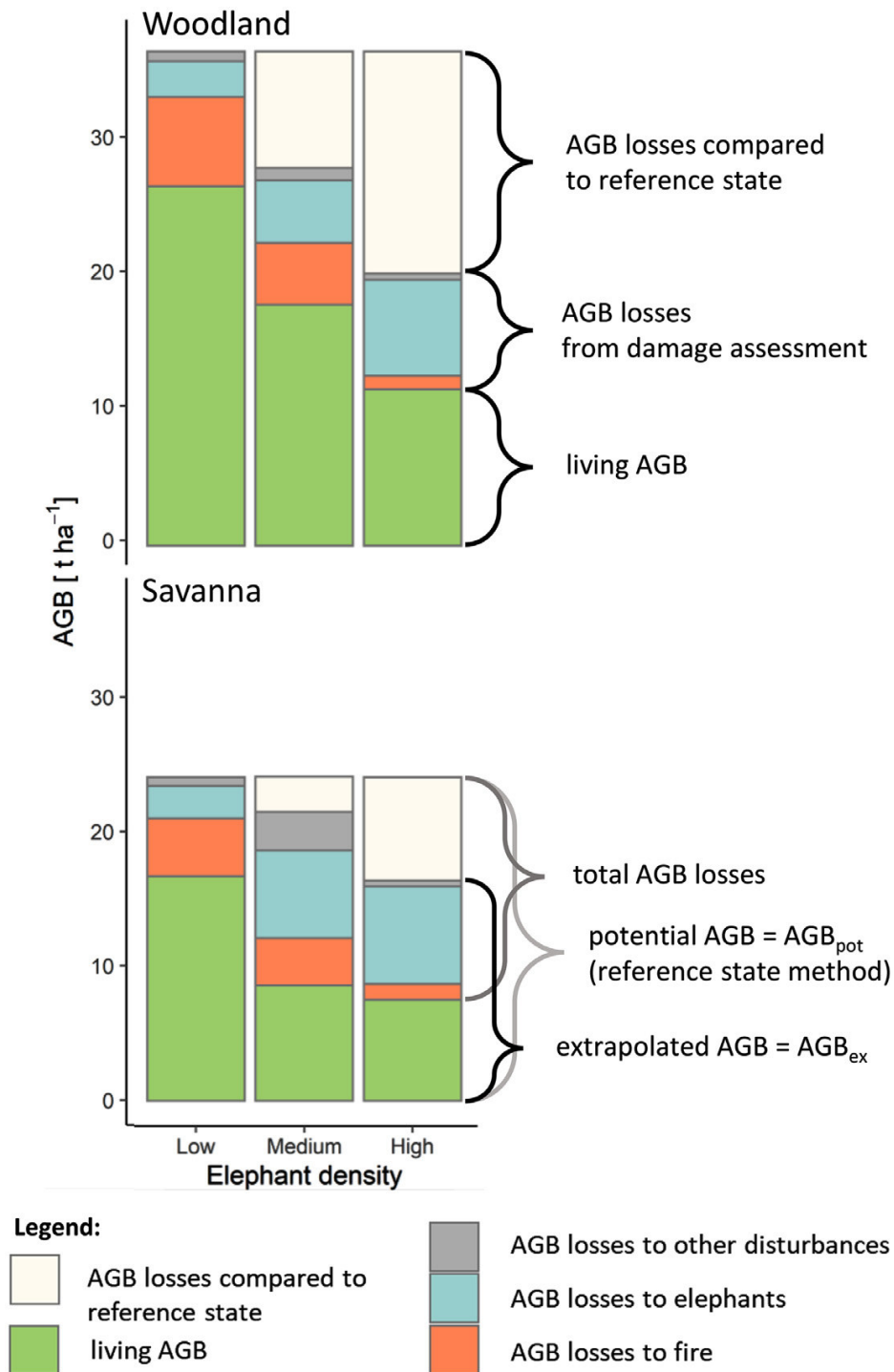
Fig. 3. Mean aboveground biomass (AGB) and AGB losses to main disturbance agents per vegetation type and elephant density level. AGB$_{ex}$ = assumed pre-disturbance AGB level as extrapolated from damage assessment, AGB$_{pot}$ = maximum potential AGB level per vegetation type as derived from AGB$_{ex}$ at the reference state of low elephant disturbance. 'Other' disturbances comprise woodcutting, storm, insect pests, and unidentifiable disturbance agents. Outlier plots were excluded here.

2.2. Data acquisition

2.2.1. Sampling approach

The original study [1] presents and tests a sampling protocol for an assessment of woody individuals within a stand, including small and highly damaged ones. To this end, six growth classes were defined as the basis for class-specific measurement protocols i.e., three comparatively undamaged classes, and three heavily damaged 'gulliver' growth classes (see Fig. 1 for details and class definitions). While the original definition of a gulliver only refers to heavily

damaged individuals which are seemingly juvenile and not reproductive [15,16], we extended this definition to encompass all heavily damaged individuals, irrespective of their true age or reproductive status. According to our definition, gullivers are heavily damaged woody individuals for which their height does neither reliably predict their age nor AGB (see Fig. 2 for examples).

As suggested by Kershaw et al. [17], a flexible sampling strategy with a nested plot design was used for inventories. Each of the 60 plots had a standard size of 1000m² on which all adult-sized, healthy trees were recorded. Nested within this plot (i.e. on a smaller subplot area, usually with a size of 750–1000 m²), all adult-sized gulliver trees were recorded. Again, nested within this first subplot, on a second subplot with an even smaller sampling area (usually within the range of 250-750 m²), all saplings were recorded in addition to the adult trees. Nested within that second subplot was the third, smallest subplot with fixed size of 100 m², on which we usually recorded every woody individual, including those belonging to juvenile growth classes.

The practical sampling procedure was as follows: After laying out the borders of the entire 1000 m² plot and of the smallest, fixed-sized subplot of 100 m², data recording started on this subplot. Here, all woody individuals were identified to species level, recorded with allometric measures, and subjected to a damage assessment. Only in cases where the abundance of juveniles was very high (> 100) the recording of juveniles was stopped after 40-60 m². On the remaining plot area, only saplings and adults were then recorded on the progressively larger subplots until a representative number (usually 15-20 individuals for all species) was reached. We recorded the respective subplot area for each growth class to allow subsequent upscaling from individual AGB values to a unit per area basis (Eq. (6)). This sampling design has been honed for dryland vegetation in particular because sparse woody vegetation with singular large trees requires large plot sizes [18] while very high numbers of small and juvenile individuals would make it extremely time-consuming to record all individuals on the full plot area [17]. Using a minimum height threshold for woody individuals to be recorded, as is often done in other ecosystems [12,19], was found to be impossible in our study, as with gullivers the height alone is an insufficient proxy for an individual's age due to severe and chronic disturbances in the ecosystem [14]. Using a minimum stem circumference for woody individuals to be recorded, as is often done in other ecosystems [19,20], was not possible in our study region as that would have excluded the extensive contribution of shrubs to overall AGB [1,21].

Combining the growth class system with a nested plot design where the sampling area was flexibly decided for most growth classes allowed for an adjustment of the sampling effort according to plots' population densities and species richness. The stratified sampling along growth classes required practical consideration on how large the sampling area for each class needs to be in each plot. Where species richness was low, and most trees and shrubs were damaged by the same disturbance agent in a similar manner smaller sampling areas were sufficient to represent the vegetation and the disturbance impacts therein. On the other hand, where species richness was high and woody growth had been affected by multiple disturbance agents larger sampling areas were required to record adequate data. For instance, plots with few species, an even distribution of individuals across growth classes, and a high number of juveniles was sufficiently represented by recording juveniles on a reduced sampling area of 50 m², further saplings and shrubs on 300 m², and highly damaged ('gulliver') adult trees on 500 m². In contrast, a plot with many species, a heterogenous growth class distribution, and a clumped and/or sparse vegetation was better represented by recording juveniles on a larger area (100–150 m²), saplings/shrubs on 500–750 m², and all adult trees – including highly damaged ones – on the full 1000 m² plot area. The guidelines of what was considered a 'representative number of individuals' [17] in each plot, has been determined along the following guiding questions:

- Is the part of the plot covered so far representative for the whole plot in regard to number and species composition of the growth class in question?
- Do we need to sample a bigger area to also reliably capture the damage levels and their heterogeneity for this growth class?

- How well does the sampled plot area represent its surrounding? Does it need to be enlarged to counterbalance patchy or clumped vegetation patterns or to cover a sufficient number of individuals?

When tree biomass estimations on an individual level are accumulated for a stand level, they are usually expressed on a unit per area basis e.g., as kg biomass ha^{-1} or t biomass ha^{-1} [19,22]. To upscale our individual-level biomass data, we needed to note the realized sampling area per growth class. For each growth class per plot, a factor for upscaling was then calculated by dividing 1 ha by the realized sampling area for each growth class and then multiplying individual biomass estimates by the respective upscaling factor; this yields values on a unit per area basis which were summed up per plot to express total AGB in the unit kg ha^{-1} or t ha^{-1}.

Beyond the dataset presented here, our approach of a stratified sampling also allowed us to capture irregular sampling units like agricultural fields by measuring an entire field's area with a GPS device, recording all adult trees within the field and along the field margins, and combining that with suitable rectangular subplots for the sampling of juveniles and saplings.

2.2.2. Allometric measurements

As the trees on our plots often had irregular growth forms which is typical for highly disturbed ecosystems [23], measuring circumference at breast height was not always possible. In these cases, we measured stem circumferences at various other heights to infer diameter at breast height (DBH) by own local calibrations [24]. In cases where stems were branching lower than 130 cm above ground level, the circumference was taken below the branching and the height at this alternative measure was recorded as well to calculate regressions between basal diameter, DBH, and height. For some heavily damaged trees, a second circumference measure was not derivable, hence a surrogate DBH (DBH_{est}) was later estimated from their basal circumferences (see Supplementary Fig. 1). Also, if stem bases were partially missing, an educated guess had to be made of the basal circumference that was present before the severe damage occurred. In most cases, this was easy to achieve as the general curvature of the stem was still visible and a missing section was extrapolated.

Please note that, when adopting our methodology, the allometric measurement procedure could be further streamlined according to the targeted allometric models. Therefore, some of the measurements taken here might not be mandatory for other applications and allometric models, although taking full sets of measures for all individuals will render later application of future allometric models possible. It also allowed for us to have our own locally calibrated models of DBH – height relationships, which is favorable [24].

We recorded separate sets of dendrometric proxies for the six growth classes, see Fig. 1 and Kindermann et al. [1]. For subadults, we recorded (i) height and (ii) the widest canopy diameter of living tissue and a second measure orthogonal to the first. For adults, we recorded (i) height of highest living tissue, and (ii) stem circumferences for all adult-sized stems at the base and at breast height (130 cm), if possible. These separate procedures for tree-like adults and shrub-like subadult individuals were necessary to enable the subsequent use of two allometric models. This was required because tree-like individuals (or part of individuals) are better captured by stem proxies while shrub-like individuals (or parts of individuals) are better captured by canopy dimension proxies [21].

For adult-sized gullivers, we also recorded the basal circumference of adult-sized dead stems (if any were present) and noted those stems as "dead". Recording big dead stems may seem laborious but from our experience only required little extra effort while this information later became highly valuable to quantify lost biomass fractions (see below). For the special case that the living woody individual attached to such a dead stem contained no living adult-sized stems (growth class AG3; see Fig. 1 and Supplementary Fig. 2), we recorded canopy diameters instead, as was done in subadults. The reason is that the living biomass of the shrub-like parts of the individuals later needed to be estimated from the canopy dimensions, while the extensive biomass loss through topkill of the former tree-like growth could only be estimated from the dead stem's

proxy measurements. This specialized estimation procedure was justified by the fact that a very high number of individuals belonged to this growth class [1].

2.2.3. Damage assessment

For each woody individual in the tree inventory, a detailed damage assessment was conducted. The main disturbance agents in our study were recorded independently. These were fire damage, elephant browsing, browsing by other herbivores, woodcutting, and dieback due to abiotic stress. Other disturbance agents e.g., insect herbivory or storm damage, were subsumed under "other", but if possible identified by a comment. Distinguishing the main disturbance agents was possible through their specific damage patterns. We used healthy trees and shrubs in comparison to damaged ones to estimate how much of the biomass had been lost in the latter. It was helpful to visualize what healthy individuals of the same species looked like (e.g., straight stem with a regular, well-proportioned crown) and then pay attention to the deviations. Scars of lost branches or firemarks on the bark were used as indicators for the causes that led to irregular growth forms of damaged trees. The damage assessment was performed by visually estimating the percentage of AGB lost to different disturbance agents [following 25]. A score of 0% damage was assigned to completely intact woody individuals without any apparent lost branches or scars. A damage estimate of 99% damage was assigned to individuals after total topkill. From our experience, the best way to ensure consistency in assessment was for the entire team to conduct joint assessments at the beginning of a field session, as practiced for other observer-dependent field records such as visual cover estimations [26]. We jointly estimated the percentage of biomass lost and calibrated our individual estimations against each other. Estimates from different researchers had only negligible variance after a short time of joint calibration.

Please note that adult-sized dead stems (> 15 cm basal circumference) attached to a living gulliver were not included into this estimation of percentage biomass lost. Instead, they were recorded independently, as their former biomass often exceeded the retained living biomass by orders of magnitude (see e.g. Fig. 2D). Dead adult-sized stems were measured with basal stem circumference and annotated as 'dead'. The presumed topkill agent was identified, if necessary two joint topkill agents were listed. This procedure helped to stratify the disturbance losses on small living regrowth, which would only make up for < 1% if the dead adult-sized stem was to be counted in; by calculating lost biomass for the dead stem independently, it was possible to split up the total of 100% of living regrowth biomass to several disturbance agents. Please note that indicated biomass losses summed up over all disturbance agents cannot exceed 99%.

2.2.4. Specific wood density

For AGB estimation with the allometric model of Chave et al. [12] we measured species' specific wood density (SWD) following the 'wood specific gravity' protocol in Pérez-Harguindeguy et al. [3]. We sampled the stem wood of 2-20 individuals per species, using a 2-threaded increment borer (Haglöf Sweden®, inner diameter 5.15 mm). For sampling of wood cores, we selected healthy and rather straight stems, as otherwise the corer often became stuck. We aimed to sample both sapwood and core wood as they can have different specific weights in many tree species. Where drilling was not possible (i.e. in shrubs), we collected cylindrical stem sections instead, preferably a straight piece without any branching. In total, we took 412 samples from 65 species according to the species' abundances. Bark was removed from the end of the core or peeled off the stem pieces, respectively. Each sample was measured in length, and five separate diameter readings along the sample were taken with calipers to determine wood fresh volume. Wood samples were stored in paper envelopes and later oven-dried (105 °C) until the weight was constant. Dry weight and fresh green volume were used to calculate SWD (dry weight per fresh volume), and measurements were averaged per species.

2.3. Estimation of aboveground biomass (AGB)

2.3.1. Stocks vs losses

Unlike other studies on carbon storage, we not only aimed to quantify actual standing biomass stocks and carbon stored therein, but also took an interest in carbon losses to better understand joint processes of carbon storage and loss in a disturbed ecosystem. When adapting existing methods from standard protocols and creating our own workflows we realized, that quantifying stocks and estimating losses could not be covered by the same procedure, although these traits are interdependent. Part of our methodology therefore follows the rather straightforward sequence of measuring a living tree, estimating its biomass from an allometric model, and then deducting an estimated percentage of biomass lost to a recorded disturbance. For slightly damaged trees ($<$ 30% biomass loss), this was the best procedure, but several problems arose when we applied the procedure to heavily damaged individuals, which we briefly report here with the respective methodological solutions.

Problem 1. A damaged tree's allometric measures did not fit the usual allometric relationships between height and stem measures [23]. For example, if severe elephant damages reduced a tree to half of its original height, its new height was relatively shorter compared to its stem diameter. As a solution, the stem diameter was used to inform us about the tree's original height, and the height of the standing stem allowed for an estimation of biomass loss.

Problem 2. While DBH is a widely used metric in forestry, carbon studies, and allometric models, it can be fraught with problems in disturbed ecosystems: stems were branching lower than the height of 130 cm or a stem was simply broken off, torn, or burnt below or at that height. Our solution here was to use basal stem circumference as the measurement threshold for the definition of adult trees. Moreover, whenever possible, we measured both the basal circumference and DBH for each stem with $>$ 15 cm basal circumference. Additionally, from a healthy subset of trees in our dataset we derived a regression equation between basal circumference and DBH (Eq. (4)) and used this equation to determine DBH values (DBH$_{est}$) for heavily damaged trees which were lacking a measurable DBH.

Problem 3. Damaged trees often displayed an atypical growth form when regrowing, and many species in our study region were observed to be growing in tree-like as well as shrub-like architectures [27]. Hence, an a-priori separation between shrub and tree species for an adoption of species-wise allometries was not possible. To address this problem, two different allometric models were applied across all species, with one for shrub-like individuals or plant parts, and another for tree-like individuals, respectively (see below). Hence, in some cases, the two models had to be combined to estimate an individual's biomass.

Problem 4. While small damages were deducted from the calculated biomass, huge damages were impossible to express in relation to living biomass, as they often exceeded the living biomass by orders of magnitude. As a solution, those damages were quantified separately, through circumference measures of dead stems which were fed into the allometric stem-model.

These problems and solutions illustrate that the calculation of standing biomass and the estimation of biomass losses to disturbances were two distinct procedures, yet not to be decoupled as the unit of observation still was a woody individual.

2.3.2. Estimation procedure of AGB and AGB losses

An estimation procedure for AGB and AGB losses was designed for each of the six growth classes; see Supporting Material (Supplementary Table 2 and Supplementary Fig. 2) for further details. For the comparatively undamaged non-gulliver growth classes, AGB estimation was done with the aid of a stem-based model for adults, and with a canopy-based model for subadults. Please note that the two specific models used here may be replaced by whatever local stem- and canopy-based models you prefer or will be available in the future. Separate estimation workflows were performed for four subtypes of adult-sized gullivers (AG) to account for their distinct, irregular growth forms shaped by severe disturbances (see Fig. 2 and Supplementary Fig. 2). The first type (AG1) had more substantial biomass losses than non-gulliver adults ($\geq$ 30%), but still a regular growth. Here we only added a height correction to the standard method of AGB calcu-

lation to reflect pre-disturbance height. The second type (AG2a) had both dead and living stems. As living stems bore comparatively undamaged crowns, a height correction was not necessary for them. Here, biomass losses in the form of dead stems were estimated based on their basal stem diameter. From a dead stem we were able to measure at least one proxy (basal circumference) which still held information about the tree's pre-damage dimensions. Adult-sized gullivers of type AG2b showed a combination of damages seen in the former two subtypes i.e., they displayed both severe damages in living stems' canopy and had dead stems. We thus performed a height correction for living canopies (as done for AG1) and then estimated dead stems' biomass (as done for AG2a). Finally, AG3 gullivers had a shrub-like appearance after having experienced topkill of their former main stem and had at least one major dead stem. The living biomass was thus a regrowth from the root system. In this case, AGB losses were estimated as for dead stems in types AG2a and AG2b, while living AGB of the shrub-like part was estimated via the canopy-based allometric model also used for AGB estimation in subadults. For the specific formulas applied in the procedure see the next section. A detailed visual workflow of AGB and AGB loss estimation for each growth class is provided in the Supporting Material.

2.3.3. Formulas

For AGB estimation of shrubs and subadult growth classes, we used the generic, canopy-based model developed by Conti et al. (2019) [21] (Eq. (1)). It estimates aboveground biomass (AGB, in [kg]) from mean crown diameter (CD, in [m]) and height (h, in [cm]). The canopy-based model was also used to estimate living AGB fractions of adult-sized gullivers, where these fractions met the size criteria of subadults (AG3).

$$AGB = \exp\left(-0.370 + 1.903\,Ln(CD) + 0.652\,Ln(h)\right) * 1.403 \tag{1}$$

For adult trees, we used the generic, stem-based model by Chave et al. (2014) [12]. It estimates aboveground biomass (AGB, in [kg]) from specific wood density (SWD, in [g cm^{-3}]), stem diameter at breast height (DBH, in [cm] at 1.3 m above ground level) and the tree height (h, in [m]), see (Eq. (2), [12]).

$$AGB = 0.0673 * \left(SWD * DBH^2 * h\right)^{0.976} \tag{2}$$

For adult-sized gulliver trees (AG) we first reconstructed their pre-disturbance height (h_{est}, in [cm]) from their DBH by using a regression developed from adult non-gulliver trees (AA) in our dataset (Eq. (3), see [1]), before feeding these values into the stem-based model. In cases where $h_{est} < h$, we kept the initial height reading h.

$$h_{est} = \exp\left(4.72595 + 0.63385 * LN(DBH)\right) \qquad \left(R^2 = 0.75\right) \tag{3}$$

For damaged and dead stems where a DBH reading was not possible, we took a basal circumference (in [cm]) and estimated a pre-disturbance DBH (DBH_{est}, in [cm]) by a regression, again built from adult non-gulliver trees (AA) in our own dataset (Eq. (4), see [1]):

$$DBH_{est} = 0.7968 * \frac{\text{basal circumference}}{\pi} \qquad \left(R^2 = 0.9639\right) \tag{4}$$

For the few cases of stems in which neither DBH nor basal circumference were applicable (e.g. a tree that was branching below or directly at 130 cm and also had been damaged heavily from fire at the base), we took a circumference reading at an alternative height (circ(hx), in [cm]) along the stem, and the height where this reading was taken (hx, in [cm]). From these measurements we first extrapolated a basal circumference (see Eq. (5), which was derived from our own data):

$$\text{basal circumference} = \frac{130 * circ(hx)}{130 - 0.2032 * hx} \tag{5}$$

From this reconstructed basal circumference, DBH_{est} was again estimated through Eq. (4). This DBH_{est} was also used to extrapolate a former height h_{est} (using Eq. (3)) where necessary (i.e. for living stems in AG1 and AG2b, or dead stems), and both proxies were used to calculate

AGB according to Eq. (2). We advise to newly establish the latter three formulas (Eqs. (3)–(5)) whenever our estimation procedure is adapted to other regions and species communities. They can easily be generated from existing measurements in rather undisturbed trees of the same data collection. Please note, that in our example Eq. (3) is a power law function and Eq. (4) is a linear regression and their fit was quite convincing (see [1] and Supplementary Fig. 2 therein), but depending on species composition other regression types might deliver a better fit.

For trees with multiple adult-sized stems, we calculated individual stems' AGB with the same height, but with their respective measured or estimated DBH. Multiple stems' AGB was then summed up per individual. As we had used different sampling areas per growth class, we used an upscaling factor (Eq. (6)) to express individual AGB on a per unit area basis (in kg ha^{-1}); see Kershaw et al. [17] and more detailed explanations above in section 'Sampling approach'. The plot-wise sum of these individually upscaled values then reflects stand-level AGB on a unit per area basis.

$$\text{upscaling factor} = \frac{1\ \text{ha}}{\text{area covered for respective growth class}} \tag{6}$$

To calculate AGB losses for living stems and in crowns, we multiplied AGB with the estimated proportion of biomass lost due to different disturbance agents. As canopy-based models and stem-based models differ with respect to the way how they incorporate AGB losses (see [1]), AGB estimated from the canopy-based model already reflects the actual damaged state, whereas with stem-based models crown AGB losses have to be subtracted first to obtain actual standing AGB.

In dead stems, former AGB was quantified via the generic model by Chave et al. [12] with the workaround of first estimating an unmeasurable DBH from basal circumference (see Eq. (4)). A dead stem's former AGB was then added to the AGB losses that were visually estimated for the respective disturbance that had also caused the topkill. Details on calculation procedures are presented in the Supporting Material. Where AGB losses are displayed on a unit per area basis they have been multiplied by the upscaling factor, as was done for AGB.

2.3.4. Task-wise overview of our methodology

To summarize the detailed information on methods and procedures above, this is a list of the nine tasks that were performed to generate the dataset presented in this paper. Tasks 1-3 are fieldwork tasks, while the remaining six tasks are lab and office tasks.

Task 1 – determine the appropriate size of subplots (nested within 1000 m² plots) for the sampling of growth classes:
  - As a default, consider a sampling area of 100 m² for the sampling of juveniles (corresponding to the fixed-size subplot), while saplings and damaged adults are recorded on larger subplots that represent a known fraction of the plot, and non-gulliver adults are by default recorded on the whole 1000 m² plot
  - If woody individuals are very abundant, but uniformly disturbed, reduce the sizes of nested subplots for the respective growth classes
  - Where individuals are sparse and/or disturbance patterns are unevenly distributed, increase the size of the respective subplot until recorded woody individuals reflect disturbance patterns and demography of the surrounding landscape
  - Make sure to sample a sufficient number of individuals per species; we suggest choosing sampling areas so that a minimum 15-20 individuals are sampled per species, unless species are rare, and individuals are solitary

Task 2 – record woody individuals of different growth classes on progressively larger subplots:
  - Start with the 100 m² subplot (see above) where usually all individuals of all sizes and age classes are recorded: record their species name, growth class and dendrometric proxies, and estimate the percentage of biomass lost to each disturbance agent

- Progress with inventories and damage assessments to the next larger subplot (with its size flexibly decided), where you stop to record juvenile individuals but continue to record all other growth classes
- In case you chose different sampling areas for sapling and adult growth classes, create another cut-off and only record adult growth on the extended area; note final sampling areas which were realized within each plot for each growth class

Task 3 – take wood samples for woody species on the plot to estimate specific wood density (SWD):

- Check for all woody species that are present on the plot if wood samples were already taken for ten individuals; if yes, wood sampling can be skipped for this species
- For species sampled with < 10 individuals in total, select a healthy individual, and extract two wood cores from the stem(s) or cut 2–3 stem pieces

Task 4 – process wood samples to estimate SWD:

- Oven-dry wood samples and take their dry weight to determine SWD following Pérez-Harguindeguy et al. (2013) [3]
- Fill data gaps with SWD values from existing databases

Task 5 – digitize data into spreadsheets and analyze a subset of healthy individuals:

- Create a subset of all non-gulliver adult trees in your total dataset
- Perform data exploration techniques following Zuur et al. [28]
- Use this subset to parameterize Eqs. (3)–(5) for your dataset

Task 6 – fill in missing allometric size proxies:

- For badly damaged stems, a missing DBH value needs to be deduced from actually measured basal stem circumference via Eq. (4)
- The same procedure needs to be performed for dead stems, which were only measured at the base
- For adult gullivers, a pre-disturbance height needs to be estimated from the stem proxies via Eq. (3)

Task 7 – estimate AGB fractions according to the workflow designed for its respective growth class (see Supporting Material, Supplementary Fig. 2, and Supplementary Table 2):

- For tree-like individuals, estimate pre-disturbance AGB first and then deduct recorded AGB losses to gain post-disturbance AGB (i.e., actually standing, live AGB)
- For shrub-like individuals, the initial AGB estimation yields the post-disturbance value from which a pre-disturbance value can be estimated through reverse damage assessment (see Supporting Material, Supplementary Fig. 2)
- Estimate pre-topkill AGB of recorded dead stems

Task 8 – calculate AGB losses per disturbance agent:

- Fractionate estimated AGB loss from canopies according to percentage losses recorded visually in the field: multiply estimated pre-disturbance AGB by percentage loss recorded for that disturbance agent to gain AGB lost to that disturbance agent specifically
- Use the disturbance agent responsible for topkill in dead stems to allocate this additional AGB loss to a disturbance agent
- Aggregate AGB losses created by different disturbance agents into 'total AGB losses'

Task 9 – upscale individual values to unit per area:

- Multiply each individual's living AGB by the upscaling factor (Eq. (6)) needed for the respective plot and growth class
- Also use scale-up factors on all other AGB partitions e.g., AGB losses and AGB of dead stems
- Sum up these values per plot to gain overall AGB and AGB losses per plot on a unit per area basis
- For individuals growing on the plot edge, correct for the tree's or shrub's fraction falling inside the plot

Following the procedures listed above we were able to quantify woody AGB in a naturally disturbed ecosystem and also attribute fractions of AGB lost to specific disturbance agents like

elephant browsing or wildfire (see Fig. 3). Results indicate that AGB losses to wildfire are decreasing with increasing elephant densities (Fig. 3). This trend was observed for both savanna and woodland vegetation, although baseline woody AGB levels of both vegetation types were found to be markedly different (Fig. 3). We hope to have demonstrate the added value of integrating the two procedures of biomass quantification and disturbance-specific biomass loss estimation for woody biomass in savanna and dryland ecosystems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships which have or could be perceived to have influenced the work reported in this article.

Data Availability

Dataset on Woody Aboveground Biomass, Disturbance Losses, and Wood Density from an African Savanna Ecosystem (Original data) (Mendeley Data).

CRediT Author Statement

Liana Kindermann: Conceptualization, Visualization, Methodology, Data curation, Software, Formal analysis, Writing – original draft, Writing – review & editing; **Magnus Dobler:** Data curation, Software, Formal analysis, Writing – original draft, Writing – review & editing; **Daniela Niedeggen:** Data curation, Software, Formal analysis, Writing – original draft, Writing – review & editing; **Ezequiel Chimbioputo Fabiano:** Visualization, Resources, Writing – original draft, Writing – review & editing; **Anja Linstädter:** Conceptualization, Visualization, Methodology, Data curation, Writing – original draft, Writing – review & editing.

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Supplementary Materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.dib.2022.108155.

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Dataset on Woody Aboveground Biomass, Disturbance Losses, and Wood Density from an African Savanna Ecosystem

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Anja Linstädter

Description

This dataset comprises raw and processed data from two tree inventories in savanna and savanna woodland vegetation along elephant disturbance gradients in Zambezi Region, Namibia. The recorded individuals represent all age classes and damage levels (including gullivers) and were classified accordingly into six

Dataset metrics

Usage

Views: 607
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Version 4	17 January 2022
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87

Chapter 3

growth classes. The raw data contains allometric/dendrometric proxies (height, canopy diameters, and (where applicable) stem circumferences for stems >15cm at the base) which were recorded for n = 6,179 woody individuals in 60 plots (each 0.1 ha). Wood samples were taken to measure specific wood density (SWD) for each recorded species.

SWD measurements and raw data have been used to estimate aboveground biomass (AGB) per individual via allometric models. Existing methodologies and workflows had to be improved to account for damages and diverse vegetation structure as shaped by disturbance impacts. In addition to standing biomass, our proposed method also delivered data on biomass losses to respective disturbance agents (elephants, fire, and others) for each individual.

The processed data comprises estimates of living AGB on individual and unit per area basis as determined with our proposed methodology, see:
Kindermann L, Dobler M, Niedeggen D, Linstädter A (2022). A new protocol for estimation of woody aboveground biomass in disturbance-prone ecosystems. Ecol. Indic. 135, 108466, https://doi.org/10.1016/j.ecolind.2021.108466.
Our proposed approach further delivered data on pre-disturbance AGB and AGB losses to major disturbance agents. For a description of biomass partitions also see detailed legend within the

88

Data file.

Our research hypothesis was that increasing elephant densities decrease woody aboveground biomass (AGB) and increase elephant-mediated AGB losses along the disturbance gradient. Findings from the data presented here support this hypothesis. Furthermore, increasing elephant densities seem to decrease fire disturbance impacts along the same gradient. These trends can be demonstrated for two different vegetation types (savanna & savanna woodland). A comparison between the conventional standard method and our improved proposed methodology highlights the importance of suitable sampling strategies and protocols for determining biomass and carbon storage in highly disturbed dryland ecosystems. The conventional method over-estimated biomass in large but disturbed trees, while simultaneously under-estimating total biomass on a unit per area basis through omission of all smaller trees, shrubs, and highly damaged woody individuals (gullivers); see Kindermann L, Dobler M, Niedeggen D, Linstädter A (2022). A new protocol for estimation of woody aboveground biomass in disturbance-prone ecosystems. Ecol. Indic. 135, 108466, https://doi.org/10.1016/j.ecolind.2021.108466.

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Chapter 4

Conservation with elevated elephant densities sequesters carbon in soils despite losses of woody biomass

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Conservation with elevated elephant densities sequesters carbon in soils despite losses of woody biomass

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Abstract

Nature conservation and restoration in terrestrial ecosystems is often focused on increasing the numbers of megafauna, expecting them to have positive impacts on ecological self-regulation processes and biodiversity. In sub-Saharan Africa, conservation efforts also aspire to protect and enhance biodiversity with particular focus on elephants. However, elephant browsing carries the risk of woody biomass losses. In this context, little is known about how increasing elephant numbers affects carbon stocks in soils, including the subsoils. We hypothesized that (1) increasing numbers of elephants reduce tree biomass, and thus the amount of C stored therein, resulting (2) in a loss of soil organic carbon (SOC). If true, a negative carbon footprint could limit the sustainability of elephant conservation from a global carbon perspective. To test these hypotheses, we selected plots of low, medium, and high elephant densities in two national parks and adjacent conservancies in the Namibian component of the Kavango Zambezi Transfrontier Area (KAZA), and quantified carbon storage in both woody vegetation and soils (1 m). Analyses were supplemented by the assessment of soil carbon isotopic composition. We found that increasing elephant densities resulted in a loss of tree carbon storage by 6.4 t ha^{-1}. However, and in contrast to our second hypothesis, SOC stocks increased by 4.7 t ha^{-1} with increasing elephant densities. These higher SOC stocks were mainly found in the topsoil (0–30 cm) and were largely due to the formation of SOC from woody biomass. A second carbon input source into the soils was megaherbivore dung, which contributed with 0.02–0.323 t C ha^{-1} year^{-1} to ecosystem carbon storage in the low and high elephant density plots, respectively. Consequently, increasing elephant density does not necessarily lead to a negative C footprint, as soil carbon sequestration and transient C storage in dung almost compensate for losses in tree biomass.

KEYWORDS
carbon sequestration, conservation, elephants, soil organic carbon, woody biomass

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1 | INTRODUCTION

Nature conservation is one of the dominant land uses currently shaping Africa's ecosystems. Southern Africa in particular contributes to international conservation targets (Naidoo et al., 2018; Ramutsindela, 2007): the protected area almost doubled within the period from 1970 to the 2000s (Newmark, 2008), covering nowadays 22% of the total land surface in sub-Saharan Africa (WDPA, 2021). An important aspect of conservation efforts in southern Africa is to increase wildlife numbers, especially those of megaherbivores like elephants, giraffes, or rhinoceros (i.e., animals exceeding 1000 kg body weight; Owen-Smith, 2013). This effort is envisioned to compensate for the dramatic decrease of megaherbivore numbers during the past 100 years (Bocherens, 2018; wwf.org, 2018), and because megaherbivores fulfill multiple ecological functions, which cannot be replaced by smaller herbivores (Owen-Smith, 2013). These functions include cascading positive effects on biodiversity due to opening of the vegetation (Asner et al., 2016), followed by changes in fire patterns, seed spreading (Bunney et al., 2017), redistribution of nutrients (Wolf et al., 2013), and accompanied increases in other herbivore species (de Boer et al., 2015).

Increasing numbers of megaherbivores impact ecosystem functioning at different spatial and temporal scales (Dirzo et al., 2014; Fullman & Bunting, 2014; Hempson et al., 2017). Previous studies have often outlined effects on vegetation characteristics such as on aboveground biomass (Guldemond et al., 2017) including vegetation structure and composition (Cromsigt et al., 2018; O'Connor & Page, 2013; Teren et al., 2018). Those studies found that browsing megaherbivores typically exerts strong negative effects on woody aboveground biomass, for example, by increasing the mortality rates within tree and shrub populations, thus also reducing the amount of carbon stored in aboveground biomass (Smit & Putman, 2011). A particular damage can occur from elephants (*Loxodonta africana*). Due to their large size, treefall considerably increases with increasing elephant densities, thus raising public concern about potentially detrimental impacts on woody biomass in protected areas where elephant populations are increasing rapidly (Asner et al., 2016). Nevertheless, elephants are keystone species in savanna ecosystems (du Toit et al., 2014; Owen-Smith, 1988), and as such a priority for conservation measures in Sub-Saharan Africa. As elephants prefer nutrient-rich trees over nutrient-poor ones (Skarpe et al., 2014), they modulate both biodiversity and spatial structure of savanna ecosystems (Teren et al., 2018; Thornley et al., 2020) toward tree species with higher disturbance tolerance and resprouting ability (Neke et al., 2006; Ouédraogo et al., 2015). Related changes in fire frequency (Pellegrini et al., 2017), droughts, and other herbivore populations accompany this process (Zyambo, 2016).

As trees usually store more than 90% of the carbon in savanna ecosystems (Pellegrini et al., 2014), changes in tree density affect the atmospheric CO_2 balance. However, large amounts of carbon are also stored in soils (Lal, 2016). For Australian savannas, it is even estimated that 84% of the total carbon is stored in the soil (Chen et al., 2003). This soil C pool ranges from less than 25 t C ha^{-1} in

the soil's top 30 cm in dry savannas (Alam et al., 2013) to more than 80 t C ha^{-1} in the tropical savanna forests of Brazil (Leite et al., 2014). Yet, we are still lacking a mechanistic understanding of the degree to which increasing densities of megaherbivores change the soil system from a carbon sink to a source or vice versa (Andriuzzi & Wall, 2018), and how this affects the carbon storage in the entire ecosystem (Hempson et al., 2017). In general, it is assumed that shifts in the woody biomass in savannas over time shift the carbon stored in the soils in the same direction (Pellegrini et al., 2014), that is, a reduction of woody biomass should finally result in lower soil C stocks. Nevertheless, a recently published study showed opposite effects in Kenya: Megaherbivores reduced adult tree densities, but increased the size of the soil carbon pool (Sitters et al., 2020).

Surprisingly, little is known on how elephants affect soil properties (Andriuzzi & Wall, 2018; Cromsigt et al., 2018; Sitters et al., 2020). Similar to other mammal herbivores such as cattle (Munjonji et al., 2020), elephants likely exert direct and indirect effects on soils and related carbon stocks and nutrient balances. Direct effects result from trampling, which could lead to soil compaction, for example by changing soil aggregate structure (Kotzé et al., 2013; Lobe et al., 2011), and consequently infiltration capacity. Trampling also destroys aggregates, rendering the carbon stored therein vulnerable to degradation. In addition, the megaherbivores may directly affect soil C by depositing dung and urine. In this way, megaherbivores also redistribute carbon and nutrients from one place to another (Wolf et al., 2013). The passage time in an elephant's gut is usually one or two days (Beirne et al., 2019); hence, dung deposition usually occurs at places different from where the tree was originally browsed. This process increases spatial soil heterogeneity and plant nutrient availability, as also known for grazers (Veldhuis et al., 2018), but likely with different degree of material redistribution.

Indirect effects of megaherbivores on soils can include changes in vegetation composition toward a greater dominance of grasses, which finally affects soil organic matter (SOM) content, and its composition (Cromsigt et al., 2018). Stable ^{13}C isotopic tracing in soils may help to unravel this imprint. As grasses and woody plants in tropical savannas have different photosynthetic pathways, the δ^{13}C values of C_4 grasses are higher ($\sim -13‰$) than those of C_3 trees ($\sim -26‰$), which is mirrored in the soils; Liao et al., 2006; Sandhage-Hofmann et al., 2020). Thus, tracking the δ^{13}C isotope composition of SOM may help to reconstruct changes in the relative abundances of trees and grasses (Bai et al., 2013; Boutton et al., 1999). Extending these analyses to δ^{15}N stable isotope composition may provide additional indications on the overall ecosystem N use efficiency (Bai et al., 2013; Peri et al., 2012).

The Zambezi Region in north-eastern Namibia lies in an area where land conservation has increased with aspirations for higher wildlife numbers and related socio-economic development (Kalvelage et al., 2020). The region includes several national parks and community-based natural resource management (CBNRM) schemes in close vicinity. Its savanna ecosystems are representative for many other protected areas, where increasing numbers of

wildlife are a prominent goal (Asner et al., 2016). Conservation is particularly promoted within the Kavango Zambezi Transfrontier Conservation Area (KAZA TFCA), which was established in 2011. With a size of 520,000 km^2, it is the largest terrestrial transboundary conservation zone in the world. Elephant numbers rose from around 5000 in 1995 to more than 19,500 in 2018 (Stoldt et al., 2020). The effects of these rising numbers on the carbon stocks in soils are not known, particularly not for the subsoil, which may comprise more than half of ecosystem carbon storage (Batjes, 1996; Duarte-Guardia et al., 2018). Nature-based solutions are increasingly considered as important add-ons to climate change mitigation (Amundson & Biardeau, 2018), for example, via afforestation in respective climate-mitigation-related monitoring programs such as REDD+ (Quijas et al., 2018), by increasing C input into agricultural soil (Amelung et al., 2020; Smith et al., 2020; Sykes et al., 2020), or by protecting carbon in sensitive ecosystems (Goldstein et al., 2020). To our knowledge, there is no study that has investigated carbon stocks down to 1 m soil depth in relation to increasing elephant numbers outside experimental setups.

The main aim of the present study was to quantify the effects of increased elephant numbers on savanna soil characteristics, particularly on soil carbon stocks, and to assess how observable changes in the soil are related to changes in the carbon storage of woody vegetation. We test the hypotheses that higher elephant numbers (1) reduce tree cover, biomass, and the C stored therein, which (2), in turn, may reduce soil carbon stocks. This is highly relevant, as carbon removal by wild herbivores would present a trade-off between climate mitigation through increased carbon storage, and addressing the biodiversity crisis through rewilding, including the reintroduction of large herbivores to help restore self-regulating ecosystems. A rejection of this hypothesis would strengthen ideas of synergies from rising biodiversity with increased C storage (Flores-Rios et al., 2020). Hence, we sampled sites with low, medium, and high elephant density in two national parks and conservation zones of two communal conservancies. The study included the analysis of C and N storage in soils down to 1 m soil depth, together with studies on the tree layer and the C stored therein, and an assessment of the C pools in elephant dung. To unravel changes in past vegetation composition and N cycling, we also recorded soil δ^{13}C and δ^{15}N isotopes.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in Namibia's Zambezi Region (Figure 1), a central part of the KAZA TFCA (Stoldt et al., 2020). Climate is moist semiarid, with temperatures ranging from a maximum average of 10℃ or over in winter, and 36℃ or above in summer. Mean annual rainfall ranges between 550 and 600 mm (Mendelsohn, 2007) and falls highly variable during summer, between October and March. The study region is relatively flat, with an average elevation of about 940 m a.s.l.

The Zambezi Region is part of the Kalahari Basin and covered by thick deposits of Kalahari sand, on which sandy, infertile soils have developed. They are shaped by perennial rivers that formed more fertile soil along the river channels. Approximately half of the Zambezi region is dominated by soils with sand contents of more than 90%, another >10% has sand contents between >70% and 90%. On these deep, nutrient-poor Kalahari sands, Arenosols developed (FAO, 2015). The present study focused on these Arenosols in the western area of the region (Figure 1). The Zambezi Region falls in the Miombo ecoregion, an area of savanna woodlands and dry open forests in south-central Africa (Frost, 1999). Our study area is classified as 'Kalahari woodland' (Mendelsohn, 2007), where the tree layer is dominated by species such as *Terminalia sericea*, *Pterocarpus angolensis*, and *Baikiaea plurijuga*.

Approximately 21% of the Zambezi Region is covered by three national parks: Bwabwata (3.137 km^2), Mudumu (737 km^2), and Nkasa Rupara (337 km^2). As in all parts of KAZA TCFA, the main aim of these national parks is to increase biodiversity and wildlife numbers with free migration between countries (Stoldt et al., 2020). In Namibia, this is combined with models for socio-economic development of communities, which aim to involve local people in the management of natural resources and benefit by generating income for them, for example through tourism. Communal conservancies have designated conservation zones (core areas), which are intended for wildlife only. Ranging and settlements are not allowed, but in reality, activities such as grazing by livestock could occur. Population densities of elephant and other mammal herbivore species such as giraffe, buffalo, hippo, impala, wildebeest, zebra, and springbok have increased considerably in the Namibian part of KAZA since the 1960s (Stoldt et al., 2020), with elephant numbers being close to 20,000 animals now. Further increases are envisioned for the future. In the core areas of the conservancies, wildlife numbers are highly variable, but still low (Mashi-Report, 2019; Wuparo-Report, 2018).

2.2 | Study design

To assess the impact of increasing numbers of elephants on the two ecosystem compartments "soil" and "woody vegetation", the sampling was stratified into three elephant density classes: low, medium, and high population densities. Sites with medium and high elephant densities were located in the national parks Mudumu and Bwabwata, while sites with low densities were placed in the core areas of the conservancies Mashi and Wuparo (Figure 1), adjacent to the national parks. Sampling took place in September/October 2018 and in April to June 2019. In all, 10 independent observation plots (25 × 40 m) were selected per site (60 in total). Plots had a minimum distance of 200 m. All sites had a similar (flat) topography, and were located on Arenosols. They also showed no visible signs of recent fires, and displayed a comparatively homogeneous vegetation structure and composition. As elephant densities are a function of distance to water, plots with higher elephant densities were located in closer

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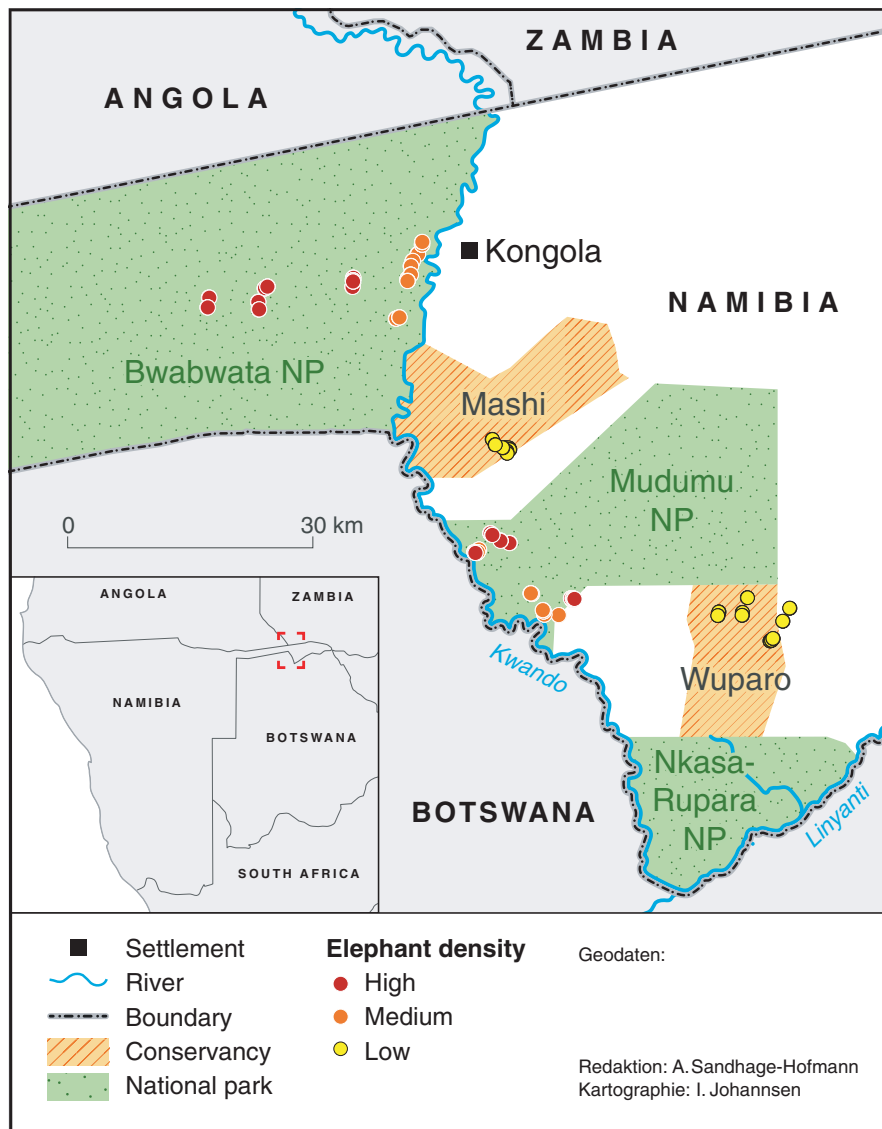
FIGURE 1 Map of the study sites. Circles for plots with low (orange), triangles for plots with medium (lightgreen) and squares (darkgreen) for plots with high elephant densities

distance to the river than those with medium densities. Minimum distance to water was 1.5 km to minimize inundation effects.

2.3 | Estimation of herbivore densities and elephant dung

For an expert assessment of recent elephant abundances on our plots, three physical indicators for elephant activities (trampling, dung deposition, and fresh damages of woody plant individuals) were combined (Linstädter et al., 2014). Elephant spoors (tracks and dung deposits) were recorded together with recent signs of elephant browsing activity (freshly broken branches, peeled barks, and torn off leaves). These three proxies were combined into an indicator for recent elephant abundance in and around the plot. Values ranged from zero (no elephants) to five (very high elephant abundances). The occurrences of other mammal herbivores (grazers, mixed feeders, and browser) were recorded by combining spoors with signs of grazing or browsing with support of local

rangers (Table S1). We also conducted severity assessments of woody biomass losses, with values ranging from zero (no losses) to five (>80% of biomass lost due to elephant browsing). Separate assessments were performed for trees and shrubs, and for old losses (>2 years) and recent losses (≤2 years), following O'Connor and Page (2013). The four values were then summed, resulting in values on an ordinal scale of 0–20. We treated ordinal data as quasi-numerical in further analyses.

Our overall approach allowed us to reach indirect conclusions about elephant densities on the plot level. In the nearby Chobe National Park (<100 km distance), it was found that, in the dry season, 4–7.7 elephants km^{-2} occurred directly at the riparian riverfront, whereas only 0.9–1.1 elephants km^{-2} occurred in the Kalahari woodlands far away from the river (Chase, 2013; du Toit et al., 2014). These values, together with our indirect density assessments, indicate for the plots under study that the average elephant densities on the investigated areas are also in this order of magnitude; that is, between <1 elephant km^{-2} in the low-density plots to >4 elephants km^{-2} in the high-density plots.

To estimate transient C pools in elephant dung, we performed visual estimations of herbivore dung cover on our plots (dung area m^{-2}) and estimated the relative contribution of elephant dung to total dung cover at each plot. We focused on elephant dung because contribution in area and size was highest. Additionally, dung of other herbivores varies widely in size and C content (Sitters et al., 2014), rendering these materials less reliable for estimating transient C pools.

$$\text{Dung} \left(C \, kg \, ha^{-1} \right) = \text{Dung cover} \left(m^2 \, ha^{-1} \right) * \text{height of bolus (dm)} * \text{density of bolus} \left(kg \, dm^{-3} \right)$$
$$* \text{dry weight} (\%) * C \text{ content} (\%) * corr, \tag{1a}$$

with bolus height set at 1.4 dm, bolus density set at 0.5 kg dm^3 (Morrison et al., 2005), dry bolus dry weight at 20% (Anderson & Coe, 1974)*C content of dry weight set at 39% (Stanbrook, 2018) and a volume correction factor corr (1/6π, to correct for the cubic shape of a bolus). To check the plausibility of our calculations, we used an alternative method to estimate average dung C pools for the sites situated in the two national parks Bwabwata and Mudumu, based on elephant densities in the two parks, and defecation rates (Equation 1b)

$$\text{Dung} \left(C \, kg \, ha^{-1} \right) = \text{Park size (ha)} * \text{elephant numbers} * \text{fresh dung per elephant} \left(kg \, day^{-1} \right)$$
$$* \text{bolus dry weight} (\%) * C \text{ - content} (\%) * 365 \, days. \tag{1b}$$

Data for the national parks were obtained from (landscapes namibia.org), fresh dung deposition set at 150 kg day^{-1} (Haynes, 2012), bolus dry weight set at 20% (Anderson & Coe, 1974), and C content of dry weight set at 39% (Stanbrook, 2018).

2.4 | Assessment of carbon stocks in woody vegetation

To accurately estimate carbon stocks in woody vegetation for our disturbance-prone study ecosystems, we developed a novel methodology to estimate biomass of heavily damaged woody individuals and stands; see Kindermann et al. (2020). We recorded tree and shrub individuals growing on the plots with their species identity and with a suite of dendrometric parameters. To keep sampling efforts in reasonable limits, we used a flexible sampling strategy with a nested plot design; for methodological details, see Kindermann et al. (2020). In brief, we stratified our sampling effort according to tree size. Small, sub-adult individuals with a height <50 cm and a basal stem diameter <5 cm were only sampled on 100 m^2 subplots, while adult individuals (height ≥50 cm, basal stem diameter ≥5 cm) were recorded on the whole plot area of 1000 m^2. For intermediate growth classes (including individuals heavily damaged by elephant browsing), intermediate plot sizes were sampled (see Kindermann et al., 2020). Canopy dimensions were recorded for sub-adult individuals while stem circumferences were additionally recorded for adult individuals. For estimating aboveground biomass (AGB) from these dendrometric proxies, we chose two different allometric models. For adult, comparatively undamaged trees, we used the updated, stem-based model by Chave et al. (2014), which is based on an exceptionally large dataset across all types of tropical forests, including African dry forests. As shrubs and shrub-like growth forms could not be covered with the stem-based model by Chave et al. (2014), we instead deployed a canopy-based shrub model calibrated in close vicinity to our study region, which shared dominant species with our dataset (Meyer et al., 2013). We estimated individuals' belowground biomass (BGB) using a root-to-shoot ratio (RS ratio). As the RS ratio decreases nonlinearly with tree size (Mugasha et al., 2013), we used an equation developed by Kachamba et al. (2016) for Miombo woodlands to determine individual RS ratios and estimate individual BGB. The AGB and BGB values were then upscaled and expressed as stand-level total woody biomass (BM$_{tot}$). Carbon stocks in woody vegetation (t ha^{-1}) were subsequently calculated as 47% of BM$_{tot}$. (Brown, 1997; Ryan et al., 2011).

2.5 | Soil sampling and analyses**

To capture differences in soil carbon stocks across different microsites that are typical for dryland ecosystems (Ochoa-Hueso et al., 2018), we distinguished between three habitat types (following Gaitán et al., 2019), and sampled under trees (subcanopy), between trees (intercanopy, mostly grass), and in bare soil without any visible vegetation cover. For each habitat type, we visually estimated their ground cover on the 1000 m^2 plots, with the three estimations summing up to 100%. We took one soil core in each of the three habitat types per plot (three cores per plot), with sampling concentrated on the 100 m^2 subplots. To analyze the effects of habitat characteristics on soil organic carbon, soil samples were treated separately; for site-level estimates, soil data obtained in the three habitat types were scaled up according to the percentages of the habitat cover. For the majority of habitat patches (153 out of 180), sampling was done to 100 cm depth, using an electrical soil auger of 6 cm in diameter. A smaller part of the plots was sampled with a hand auger up to a soil depth of 50 cm. The auger cores were divided into six depth classes (0–10, 10–20, 20–30, 30–50, 50–70, and 70–100 cm).

Each soil sample was weighted for fresh and dry weight. Dry bulk density was determined by weighing the air-dried subsamples and dividing the weight by the respective soil volume in the auger (Walter et al., 2016). Particle-size analyses were performed using the sieve-pipette method (The Non-Affiliated Soil Analysis Work Committee, 1990) according to (FAO, 2015). The concentrations of total C and N were determined by dry combustion using a CHNS analyzer (Elementar-Analysensysteme GmbH). There was no detectable inorganic C, which meant that total C was equal to organic C, hereafter SOC. The δ^{13}C and δ^5N values were analyzed using an isotope ratio mass spectrometer (Delta V Advantage IRMS, Thermo Electron Corporation) according to Equation (2)

$$\delta = \frac{R \, (\text{sample}) - R \, (\text{standard})}{R \, (\text{standard})} * 100, \tag{2}$$

where R(sample) is the ^{13}C/^{12}C and ^{15}N/^{14}N isotope ratio of the sample and R(standard) is the ^{13}C/^{12}C and ^{15}N/^{14}N isotope ratio of the standard with respect to the V-PDB standard for carbon isotopes and the atmospheric dinitrogen standard for nitrogen isotopes (Coplen et al., 2006).

We used the $\delta^{13}C$ values of soils and plant material (woody and grass biomass, from leaves of trees and tufts of grass) to estimate the relative proportion of SOC derived from C_3 photosynthetic pathways using the following equation (Boutton et al., 1998).

$$FC3 = \frac{\delta^{13}C_{soil} - \delta^{13}C_4}{\delta^{13}C_3 - \delta^{13}C_4}, \quad (3)$$

with $\delta^{13}C_{soil}$ being the measured $\delta^{13}C$ value of the soil sample, $\delta^{13}C_4$ the average $\delta^{13}C$ value of mixture of grass species (–14.3‰,), and $\delta^{13}C_3$ the average $\delta^{13}C$ value of woody plant material from *Terminalia sericea* vegetation (–27.1‰).

Carbon stocks were calculated according to Equation (3)

$$C_{stock} = SOC * BD * D/10, \quad (4)$$

where C_{stock} is soil organic carbon stocks (t ha^{-1}); SOC is soil organic carbon concentration (g kg^{-1}); BD is soil bulk density (g cm^3); and D is soil depth (cm) (Deng et al., 2016).

2.6 | Statistical analyses

The statistical analyses were performed using the R statistic package (Version 3.6.3.; lme package). All data had to be transformed with Tukey's Ladder of powers on a vector of values to achieve normality according to the Shapiro–Wilks test. To analyze the impact of different elephant densities on carbon storage in tree biomass, soil C, and N stocks, FC3, and dung, we used linear mixed models with the three elephant densities as fixed factors and site as the random effect. Tukey post-hoc tests were performed for multiple comparisons.

3 | RESULTS

3.1 | Biomass and carbon stocks in woody vegetation and dung

As expected, woody biomass losses increased significantly in the order of low < medium < high elephant density (Table 1). These changes coincided with a decline in woody tree cover in the same

direction, with the differences between sites with low and high elephant densities being significant ($p = 0.045$; Table 1). Herbaceous cover was significantly elevated at medium-density plots ($p = 0.016$), while bare ground seemed to be elevated at high animal densities, but these differences were not significant (Table 1).

According to our hypothesis, total woody biomass (AGB plus BGB) decreased with increasing elephant density (Table S2). Accordingly, the C stored in woody biomass decreased in the same direction, and plots with high elephant density contained approximately 20 t ha^{-1} less woody biomass than plots with low elephant density (Figure 2). Differences between low and high elephant density plots were significant ($p = 0.021$), despite high variability.

Elephant dung contributed to at least 70%–75% to total dung cover on all plots (individual data not shown). The quantity of carbon stored in elephant dung (calculated with Equation 1a) ranged between 24 and 328 kg C ha^{-1} (Table 2a; Figure 4) with no significant differences between plots of different elephant densities. Calculations with elephant densities per park and dung deposition (Equation 1b) resulted in comparable values of 224 kg ha^{-1} year^{-1} in Bwabwata, and 266 kg in Mudumu National Park (Table 2b).

3.2 | Carbon storage in soils

The Arenosols showed the typical predominance of sand (95.4% ± 2.6) and low contents of silt (2.5% ± 2.1) and clay (1.7% ± 1.1; $F = 6.5$, Table S3). Texture composition did not change among sites and, thus, also not with variations in elephant densities. Soil texture also hardly changed with soil depth (data not shown). The bulk density of all plots averaged 1.48 g cm^{-3} in the topsoil (0–10 cm) and increased to 1.7 g cm^{-3} in 70–100 cm soil depth. There was no significant compaction in the surface soil due to animal trampling. Overall, different densities of elephants had only small effects on bulk densities in this sandy environment (Table S4).

As is also typical for Arenosols, all sites showed low concentrations of SOC, which decreased steeply with increasing soil depth from an average of 4.6 g kg^{-1} C in 0–10 cm to 1.2 g kg^{-1} C in 70–100 cm (Table S4). Higher wildlife densities resulted in higher carbon concentrations within the top 50 cm of soil. This effect was significant for the first 30 cm of soil ($p = 0.011$) except for 0–10 cm but still visible in the subsoil. Overall, carbon concentrations in the

TABLE 1 Evidence for the presence and impact of elephants at the plot level (0.1 ha) in the three elephant density classes

Elephant density class	Woody biomass losses	Recent elephant abundances	Subcanopy (%)	Intercanopy (%)	Bare soil (%)
Low	4 ± 1.2 a	1.4 ± 0.7 a	46.6 ± 18.8 a	12.7 ± 15.1 a	40.7 ± 18.4 a
Medium	7 ± 3.3 b	2.2 ± 0.6 ab	36.2 ± 19.1 ab	23.9 ± 17.3 b	39.9 ± 19.6 a
High	11 ± 2.4 c	4.1 ± 0.6 b	32.6 ± 15.3 b	13.4 ± 20.9 a	54.0 ± 19.4 a

Note: Given are woody biomass losses due to elephant browsing (scale 0–20, where 0 is no loss and 20 is severe losses); recent elephant abundances according to physical signs of elephant presence on the plots (trampling, dung deposition, and visible damages of woody vegetation due to browsing; scale 0–5, where 0 is no animals, and 5 is very high animal abundances); and percent cover of habitat types on plots (subcanopy, intercanopy, and bare soil patches). Shown are mean values ± standard deviations. Different letters show significant differences ($p < 0.05$) for comparisons between elephant density classes.

low-density plots were up to 21% and 18% lower than in high- and medium-density plots, respectively.

Total nitrogen concentrations followed the patterns of SOC, but differences between sites were more pronounced (Table S4; significant for the top 20 cm). The plots with low elephant density stored only a quarter of the nitrogen than plots with high elephant density (top 20 cm). Hence, C/N ratios also showed significant differences among sites, with the highest values measured in plots with medium and low density.

The stratification of the soil sampling according to habitat types allowed us to differentiate SOC and N storage in three different types: woody vegetation patches, grass vegetation patches, and bare soil patches. The highest SOC concentration was found under subcanopy (4.9 g C kg^{-1}), followed by intercanopy (herbaceous; 4.3 g C kg^{-1}), and bare soil (4.1 g C kg^{-1}). The differences were not significant but indicate potential differences in SOC storage of up to 2 t C ha^{-1} across different patch types (Table S5).

When habitat-level soil organic carbon stocks were upscaled to the plot-level based cover on each plot (Table 1), we found that half of the SOC was stored in the top 30 cm of the soil. Intriguingly, SOC stocks were highest in the plots with high elephant density (30.8 t ha^{-1}), followed by those with medium (28.8 t ha^{-1}), and low impact of elephants on woody vegetation (26.6 t ha^{-1}). The differences in SOC storage between plots with low and high elephant densities were significant ($F = 6.5$, $p < 0.002$; Figure 3). Differences in total N storage followed the same directions as those in SOC (Figure S1), again with significant differences in element storage between sites of low and high elephant densities ($F = 5.12$, $p < 0.005$).

Overall, our results point to losses of 6.4 t C ha^{-1} in woody biomass at sites with high elephant density relative to the low-density sites with least impact of elephants. In contrast, SOC stocks increased by 4.7 t C ha^{-1} with increasing numbers of elephants. Hence, there was still an apparent loss of 1.7 t C ha^{-1} (Figure 4).

3.3 | Origin of soil organic matter

The stable carbon isotope composition (δ^{13}C) of the plant litter reflected the differences in photosynthetic pathways between the C$_4$ grasses (δ^{13}C = −14.3‰) and the C$_3$ woody vegetation component (δ^{13}C = −27.1‰ *Terminalia sericea*). All sites sampled showed a slight dominance of C input from C$_3$ plants into the soils, resulting in higher proportions of SOC (FC3) derived from woody vegetation (Table S5). Averaged values showed only small differences between the three levels of elephant density. However, differences became apparent when differentiating among the three habitat types: The portions of wood-derived carbon (FC3) in soil increased in intercanopy and bare soil when elephant density increased (Figure 5; Table S5), indicating an increased input of woody components into the soil.

The δ^{15}N isotopic composition of the topsoils (0–10 cm) showed also clear, significant differences among sites with different elephant densities: the site with the largest elephant impact revealed the highest soil δ^{15}N values (Figure S2). As elephant densities declined, also soil δ^{15}N values declined, both in the topsoil as well as in the subsoil (Figure S2).

4 | DISCUSSION

The results of our study showed that a shift from low to high elephant numbers reduced the amount of tree biomass and that of carbon stored therein by 6.4 t ha^{-1}. Contrary to our second hypothesis, though, SOC stocks increased with higher elephant densities by 4.7 t ha^{-1}. Consequently, soil carbon gains almost offsets woody carbon losses. We assume that two carbon input sources are responsible for this compensation: (i) the formation of SOC from decaying tree and shrub biomass, such as elephant toppled trees and broken branches lying on the ground, and decomposing tree roots and (ii) the deposition of dung

FIGURE 2 Carbon storage in woody vegetation (t ha^{-1}) at sites with different elephant densities. Different letters indicate significant differences ($p < 0.05$) between elephant densities

TABLE 2A Calculation of carbon deposited by elephant dung based on Equation (1a); elephant dung (m^2 ha^{-1})*height of the bolus (1.4 dm)*mean density (0.5 kg dm^{-3})*dry weight (20%)*C content of dry dung (39%) including a correction factor for the cubical shape of the bolus

Elephant density class	Total dung cover (m^2 ha^{-1})	Elephant dung cover (m^2 ha^{-1})	C stocks in elephant dung (C kg ha^{-1})
Low	1.3 ± 2.4	0.8 ± 1.4	24.2 ± 42
Medium	8.3 ± 9.2	5.9 ± 6.8	167 ± 194
High	15.0 ± 11.7	11.5 ± 9.0	328 ± 276

Note: There were no significant differences for comparisons between elephant density classes.

TABLE 2B Calculation of maximum amount of carbon deposited by elephant dung based on Equation (1b); size of national parks, total elephant numbers (mean age not known), daily fresh dung deposition of 150 kg day⁻¹ elephant⁻¹, dry weight of dung (20%), and C content of dry dung (39%)

National park	Size (ha)	Numbers of elephants[a]	Dung per elephants[b] (kg day⁻¹)	Fresh dung (kg day⁻¹ park⁻¹)	Dung dry weight[c] (kg day⁻¹ park⁻¹)	Carbon content of dung[d] (g kg⁻¹)	Total dung carbon production (kg day⁻¹ park⁻¹)	Daily carbon input (kg ha⁻¹ day⁻¹)	Yearly carbon input (kg ha⁻¹ year⁻¹)
Mudumu	73,700	4600	150	690,000	138,000	390	53,820	0.73	266.4
Bwabwata	128,000	6700	150	1005,000	201,000	390	78,390	0.612	223.4

Note: that these are maximum amounts based on adult elephant defecations; younger elephants defecate less.

Data taken from:

[a] landscapesnamibia.org, only Kwando east for Bwabwata.

[b] Haynes (2012).

[c] Anderson and Coe (1974).

[d] Stanbrook (2018).

from megaherbivores in plots with high elephant density. In the high elephant density plots, the dung-derived C amounted 328 kg C ha⁻¹. Adding this amount to the C gains in soils reduced the offset of C losses from browsed woody vegetation to ≤1.4 t C ha⁻¹ (Figure 4).

In the KAZA TCFA area, elephant numbers are a main indicator for the success of nature conservation. In this respect, conservation measures of recent decades have been successful, because elephant numbers have increased in Namibia's Zambezi Region (Stoldt et al., 2020). Megaherbivores play an important role in structuring natural ecosystems and their biodiversity (Estes et al., 2011; Ripple et al., 2014). However, also negative impacts of elephants have been reported, due to the decline of woody biomass, depending on elephant numbers, sex, rainfall, and distance to river (Davies & Asner, 2019; Pellegrini et al., 2017; Skarpe et al., 2014; Tanentzap & Coomes, 2012). Our results of 33% losses are in line with these studies, and support our first hypothesis that higher elephant densities lead to substantial loss of woody biomass and related C stocks. Apart from the direct impacts of elephants also other drivers such as fire, a selective browsing of nutrient-rich trees (Teren et al., 2018) and the potential interactions of these drivers with elephants may have contributed to the losses of aboveground woody biomass (Pellegrini et al., 2017). In this study, we cannot decipher the contribution of each individual factor, but following Davies and Asner (2019) we consider the impact of elephants to be the dominant one.

While the effects of elephants on woody biomass have been studied before, their effects on soil characteristics remained largely unknown. This study filled this gap. Bulk densities measured in our study were similar to those reported for other sandy soils in southern Africa (Hartemink & Huting, 2008), Yet, we did not find any indication that increasing numbers of elephants compacted the soils (Table S3). Such compaction has been observed, though, for other African savanna ecosystems under the impact of cattle grazing (Kotzé et al., 2013; Schrama et al., 2013), or high wildlife numbers (Holdo & Mack, 2014). The latter study found higher bulk densities in areas with herbivores (including elephants with a stocking density of 0.8–1.2 elephants km⁻²) than in exclusion areas without wildlife (sandy and loamy soil). Cumming and Cumming (2003) reported that trampling pressure was highest in elephant dominated wildlife areas compared with areas that lacked elephants or which were used for livestock grazing only (stocking density of elephants 1.2–3 km⁻²), which is in line with the general assumption that trampling pressure rises with rising body mass (Cromsigt et al., 2018). Yet, increased mechanical pressure is frequently associated with the breakdown of aggregates (Kotzé et al., 2013; Lobe et al., 2011). The sandy Arenosols hardly contain aggregates (Sandhage-Hofmann et al., 2015). Possibly, elephant numbers in the Zambezi Region (Table 2b) are still too low to lead to a significant compaction of Arenosols.

4.1 | Soil carbon sequestration

Many studies have observed a positive correlation between the loss of aboveground biomass and the loss of soil organic carbon, both in

FIGURE 3 Soil organic carbon stocks (t ha^{-1}) in (a) 0–30 cm and (b) 0–100 cm soil depth at sites with different elephant densities. Different letters indicate significant differences ($p < 0.05$) between elephant densities
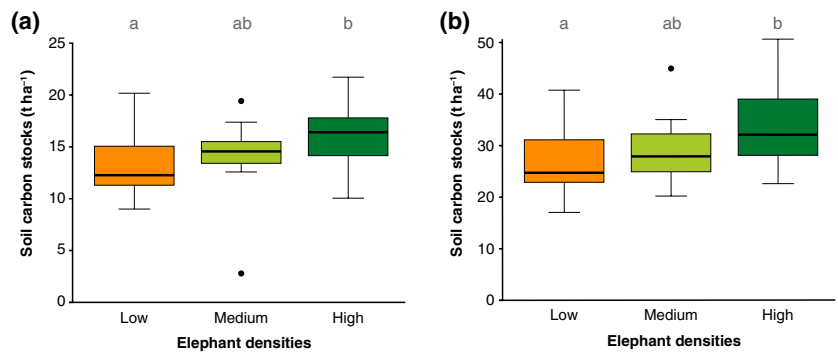
FIGURE 4 Carbon storage (t ha^{-1}) and carbon balance in woody biomass, top- and subsoils and elephant dung in plots with different elephant densities
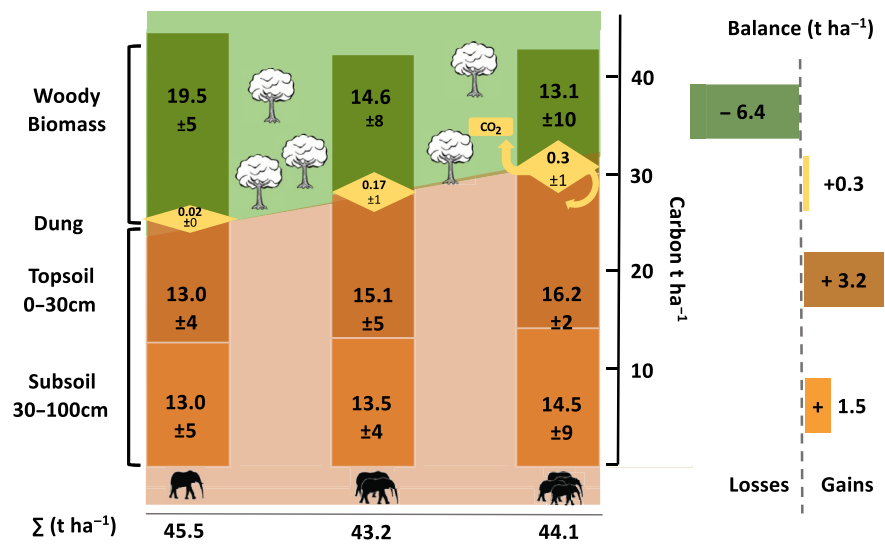
agricultural fields (Lobe et al., 2005), as well as in forests (Achat et al., 2015). Our second hypothesis was in accordance to these findings, however, our results showed the opposite. In general, soil carbon concentrations and stocks were low, reflecting the poor nutrient status of the Arenosols, but they were in line with slightly higher C stocks measured in adjacent parts of the Zambezi Region, where woodlands indicated SOC concentrations in the topsoil of 6.9 g kg^{-1} and SOC stocks for 100 cm soil depth of up to 47.9 t C ha^{-1} (de Blécourt et al., 2018). Here, we found elevated SOC stocks at sites with high and medium elephant densities (Figure 3), opposing the C storage in woody vegetation (Figure 2). Overall, in plots with higher numbers of elephants and associated megaherbivores SOC stocks increased by 4.7 t C ha^{-1}, with almost 3.2 t C ha^{-1} stored in the top 30 cm of soil (Figures 3a and 4). The remaining gain in SOC occurred in the subsoil. This finding is different from Holdo and Mack (2014), who found similar SOC concentrations in and outside a fenced area that excluded wildlife like elephants, but dissimilar bulk densities: possibly, the elevated bulk densities in wildlife-influenced areas impaired increased SOC input. However, our results are consistent with a recent experiment conducted in Kenya. Here, the composition of the animals (cattle and wildlife) was manipulated by fences. More than 20 years after the experiment started, the plots with mega- and mesoherbivores exhibited elevated SOC stocks by up to 14% (upper 15 cm) relative to plots that did not have these animals or that were grazed by cattle (Sitters et al., 2020).

Stable ^{13}C isotope tracing allows to identify the origin of the C gain. Browsing megaherbivores like elephants can change vegetation structure from a comparatively closed woodland to an open savanna (Skarpe et al., 2014). On the one hand, this can leave more space for C$_4$ grasses, forming SOC that has higher δ^{13}C values than that formed by the C$_3$ shrubs or trees (Bai et al., 2012; Boutton et al., 1998; Sandhage-Hofmann et al., 2020). On the other hand, toppling of trees by elephants, remaining browsing material, and decomposition of roots could result also in an even higher input of C$_3$-derived C into the soils. In our study, the higher elephant densities were associated with an opening of the vegetation (Table 1), but we did not detect significant changes in overall soil δ^{13}C values (−21.4‰), indicating a mixing of C$_3$- and C$_4$-derived vegetation remnants for SOC formation (Bai et al., 2012; Boutton et al., 1998; Liao et al., 2006). But we did detect changes in the origin of SOC in different habitat types: in inter-canopy and bare soil habitats portions of wood-derived C increased with rising levels of elephant densities, whereas the woody vegetation patches contained elevated portions of wood-derived C already (Figure 5; Table S5). The results are in line with those in the manipulation experiments by Sitters et al. (2020), where the authors also observed a substantial input of C$_3$-derived C into the soils induced by megaherbivores. Obviously, tree toppling and broken parts of trees do not necessarily lead to net carbon losses from the savanna ecosystem, as significant portions of this C was transferred into the soil.

100
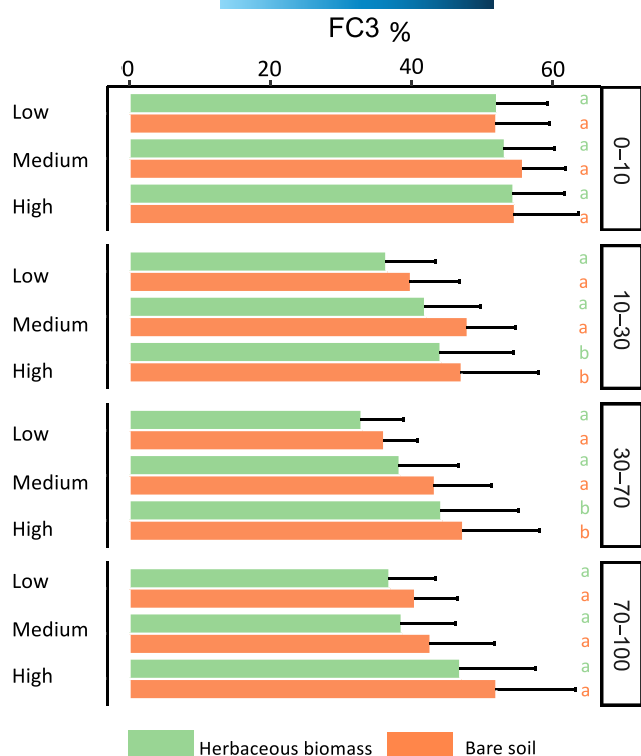
FIGURE 5 Proportion of woody biomass (FC3%) in soils under grass and bare soil patches in plots with different elephant densities and in different soil depth. Different letters indicate significant differences ($p < 0.05$) between elephant densities

In addition, there appears to be a C transfer within the ecosystem, which is directly mediated by the elephants. An adult African elephant defecates 20–30 times a day, releasing up to 100 boluses of 1–2 kg (Haynes, 2012; Stanbrook, 2018) per day, summing up to 150 kg fresh dung or 30 kg dry weight dung day^{-1}. With the given elephant numbers for the national parks (Table 2b), this makes 223–250 kg C ha^{-1} year^{-1} (Table 2b). These are maximum estimates assuming that all elephants were adults; younger elephants may defecate less than 150 kg dung day^{-1} (Coe, 1972). Hence, true total average dung deposition is likely a bit lower in the park, but will remain well in the range between our low and high elephant density plots. Our calculations based on dung cover estimates were in the same range (2a) and showed dung input values of 328 kg C ha^{-1} year^{-1} for the plots with high elephant density. Elephants accounted approximately for three quarters of the dung found on the plots. An additional input of C originates from other herbivores, where the mass of their dung typically accounts for only 2%–13% of the mass of elephant dung, and thus the carbon deposited by them (Sitters et al., 2014). This dung from other large megaherbivores, such as giraffe, zebra, and impala, megaherbivores might thus further reduce the gap between C losses and gains by another 45 kg C ha^{-1} year^{-1}.

Overall, transient storage of C in the dung of animals reduced the gap between aboveground C loss from browsing and SOC accrual to ≤1.4 t C ha^{-1} (Figure 4). The mean residence time of C storage in the dung may vary depending on habitat type, climate, nutrient stoichiometry (Sitters et al., 2014), and lignin contents (Chaudhary et al., 2020). At the dry climate of KAZA, the C loss from the dung will largely occur as CO_2, or it is taken away by small animals such as beetle and termites (Andriuzzi & Wall, 2018). Yet, there are also continued dung-C reimports, constantly replenishing the pool and compensating the losses (Zhu et al., 2020), that is, under steady-state conditions the amount of C in the dung is withdrawn from the atmosphere irrespectively of the dung turnover time. Future studies should thus include the amount of dung C into climate change mitigation calculations, because even this labile dung C may add to climate change mitigation if the decomposing dung is continuously replaced by fresh one.

Dung does not only concentrate C but also N. The N-input via dung was 0.8 kg ha^{-1} for the low, 6 kg ha^{-1} for the medium, and 11 kg ha^{-1} for the high elephant densities. Notably, both soil N and soil δ^{15}N values were thus larger at sites with higher elephant densities (Figure S2). Apparently, there was no selective browsing of N fixing trees to a degree that it would have lowered the overall soil δ^{15}N signatures. Codron et al. (2005) observed that urine and feces from browsers were generally δ^{15}N enriched compared to grazers, which is in support of our findings. The authors attributed this to more concentrated urine (and feces), and protein intake, which appears to have the primary influence on herbivore feces δ^{15}N. As N losses primarily affect lightweight N isotopes (Högberg, 1997), elevated δ^{15}N values frequently indicate lower N use efficiencies (Bai et al., 2013). Significant N losses may occur, for example, during feces formation (Masunga et al., 2006). The degree at which increasing elephant numbers also affects N_2O greenhouse gas emissions thus warrants further attention.

4.2 | Carbon storage in woody biomass, dung, and soil

Woody biomass and soils together stored 43.4–45.5 t C ha^{-1} in the savanna woodlands of the Zambezi Region. These values were in the range of savanna systems in Brazil, where between 20 and 84 t C ha^{-1} were stored in topsoils (20 cm; Abreu et al., 2017). However, the study underestimated total SOC storage across whole profile depth by up to 50% (Table S3; see Kothandaraman et al. (2020)). In general, herbaceous biomass comprises usually only between 0.5% and 10% of the carbon storage of the aboveground savanna biomass (Abreu et al., 2017; Kothandaraman et al., 2020; Pellegrini et al., 2014). The total amount depends on woody cover. Taking this low carbon storage in herbaceous vegetation into account, our estimation of aboveground and belowground carbon stored in woody vegetation captured the majority of the carbon stored in the vegetation component of the savanna ecosystem.

In our study, we found that elephants caused up to 6.4 t C ha^{-1} losses of woody biomass. However, increases in soil carbon due to rising elephant densities largely compensated for these carbon losses due to woody biomass removal (Figure 5), leaving a gap of only 1.7 t C ha^{-1} in sites with high elephant densities. Generally, SOC sequestration

is facilitated by an increase in C input (Amelung et al., 2020). Hence, the presence of animals affected the C balance of the savanna system much less than hypothesized. Even in the subsoil, a substantial part of carbon was sequestered. Obviously, the loss of woody biomass does not necessarily entail losses of SOC, and the general observation that shifts in savanna woody biomass alter carbon stocks in the same directions (Pellegrini et al., 2017) have to be reconsidered if megaherbivores are involved.

Our results should be of major interest for future biodiversity conservation measures including (trophic) rewilding. This increasingly popular approach aims to restore ecosystems through top-down interactions by repopulating them with mega-herbivore species; increasing biodiversity and combating the extinction crisis (Bakker & Svenning, 2018). Aboveground carbon removal by wild herbivores presents a trade-off between climate mitigation through increased carbon storage and addressing the biodiversity crisis through rewilding. But, as current data show, restoring elephant densities does not necessarily lead to a pronounced negative carbon footprint. A major fraction of woody biomass C is merely redistributed into soil during decomposition. Including soil into ecosystem assessment could therefore help to better align climate mitigation measures with those of biodiversity conservation, thereby linking two large scientific directions with the aim of potentially reducing joint coordination efforts for reaching the sustainable development goals. Future studies might also be needed to test these findings for soils other than the dominating Arenosols, such as well-structured soils with potential risk of aggregate disintegration. Besides, there is a research need to clarify to what extent increasing numbers of megaherbivores can be coupled to the restoration of other ecosystem services (Bakker & Svenning, 2018; Flores-Rios et al., 2020).

5 | CONCLUSION

Our study for the first time provides data of carbon stocks for the most important ecosystem compartments in relation to different elephant densities in Sub-Saharan conservation areas. Our assessments included not only C pools in woody vegetation but also in soil down to a depth of 1m and elephant dung. Conservation in Sub Saharan Africa is inextricably linked to wildlife numbers and as such, it is also one of the major aspirations of the KAZA. Since 2011, wildlife numbers have increased steadily, with largely unknown impacts on specific ecosystem compartments such as soils. The effects of elephants on vegetation structure have often been seen as initiating a decline in carbon storage of woody vegetation (Davies & Asner, 2019). Our study confirms a loss of carbon stored in woody biomass but reports an unexpected gain of carbon stored in soils. To date, the role of soils for carbon storage has been neglected in the vivid debate on ecological effects of conservation and the rising numbers of wildlife, which is surprising given that soils are a much larger terrestrial carbon reservoir than vegetation. The present study showed that increases in SOC from decaying woody material and dung inputs largely offset C losses in woody biomass.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Supplementary material for

Conservation with elevated elephant densities sequesters carbon in soils despite losses of

woody biomass

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Table S1: Evidence for the presence of recent intermediates (giraffes, impalas) and grazer (13 wild – zebras, steinbok, kudu, buffalo, hippo, buffalo, roan, sable, wildebeest, eland, tsessebe, druiker, warthog) and 3 domestic species (cattle, donkey, smallstock) abundances according to physical signs of herbivore presence on the plots (trampling, dung deposition, and visible damages of woody vegetation due to browsing; scale 0-5, where zero = no animals, and 5 = very high animal abundances).

Elephant density class	Recent Elephant abundances	Recent intermediate abundances	Recent wild grazer abundances	Recent domestic grazer abundances
Low	1.4±0.7 a	0.2±0.3 a	0.2±0.08 a	0.15±0.2
Medium	2.2±0.6 ab	0.35±0.4 a	0.4±0.2 b	-
High	4.1±0.6 b	1.35±1.1 b	0.4±0.1 b	-

Table S2: Aboveground tree biomass (ABG) and total tree biomass (BMT) including belowground root biomass. Different letters show significant differences for comparisons between elephant density classes.

Elephant density	ABG t ha^{-1}	BMT t ha^{-1}
Low	21.7 ± 7.2 a	41.6 ± 11.6 a
Medium	17.6 ±13.2 ab	31.1 ±18.5 ab
High	16.5 ±18.0 b	28.5 ± 24.0 b

Table S3: Soil texture (%) and standard deviation of sites with different elephant densities in the Zambezi region (mean over all depths). Different letters show significant differences for comparisons between elephant density classes.

Elephant density	Sand (0.05-2mm)	Silt (0.002-0.05 mm)	Clay (<0.002 mm)
Low	96.7 ±1.7 a	1.7 ±1.2 a	1.2 ±0.7 a
Medium	94.8 ±3.3 a	3.0 ±3.1 a	1.9 ±1.7 a
High	94.6 ±2.7 a	2.8 ±2.1 a	1.9 ±0.9 a

Table S4: Average bulk density, carbon and nitrogen concentrations including standard deviation for low, medium and high elephant density plots. Different letters show significant differences for comparisons between elephant density classes.

Elephant density		Bulk density g cm⁻³	Carbon concentrations g kg⁻¹	Nitrogen concentrations g kg⁻¹
Low	00-10 cm	1.49 ±0.1 a	4.3 ±1.7 a	0.27±0.1 a
	10-20 cm	1.52 ±0.1 a	2.7 ±0.9 a	0.19 ±0.1a
	20-30 cm	1.62 ±0.1 a	1.9 ±0.7 a	0.15 ±0.0 a
	30-50 cm	1.69 ±0.1 a	1.4 ±0.3 a	0.13 ±0.0 a
	50-70 cm	1.75 ±0.1 a	1.1 ±0.3 a	0.12 ±0.0 a
	70-100 cm	1.71 ±0.2 a	0.9 ±0.4 a	0.11 ±0.0 a
Medium	00-10 cm	1.44 ±0.1 a	4.4 ±1.4 a	0.27 ±0.1 a
	10-20 cm	1.55 ±0.1 a	3.3 ±0.9 b	0.22 ±0.1 b
	20-30 cm	1.63 ±0.1 a	2.4 ±0.5 b	0.18 ±0.1 a
	30-50 cm	1.70 ±0.1 a	1.6 ±0.5 a	0.13 ±0.0 a
	50-70 cm	1.73 ±0.1 a	1.1 ±0.3 a	0.11 ±0.0 a
	70-100 cm	1.65 ±0.2 a	0.9 ±0.4 a	0.10 ±0.0 a
High	00-10 cm	1.49 ±0.1 a	4.7 ±1.5 a	0.35 ±0.1 b
	10-20 cm	1.58 ±0.1 a	3.4 ±1.2 c	0.25 ±0.1 c
	20-30 cm	1.65 ±0.1 a	2.3 ±0.7 c	0.17 ±0.1 a
	30-50 cm	1.69 ±0.1 a	1.6 ±0.5 a	0.14 ±0.0 a
	50-70 cm	1.73 ±0.1 a	1.2 ±0.5 a	0.11 ±0.0 a
	70-100 cm	1.72 ±0.1 a	1.0 ±0.4 a	0.11 ±0.0 a

Table S5: Soil organic carbon stocks (t C ha^{-1}) of different soil cover types, means of all plots (no significant differences)

	Woody cover	Grass cover	Bare ground
0-10 cm	7.2 ±2.3	6.1 ±1.6	6.1 ±2.6
10-20 cm	5.1 ±1.4	4.8 ±1.9	4.7 ±2.2
20-30cm	3.7 ±1.1	3.6 ±1.1	3.5 ±1.1
30-50 cm	5.4 ±1.1	5.6 ±1.5	5.4 ±1.3
50-70 cm	4.2 ±1.7	4.2 ±1.2	3.9 ±0.7
70-100 cm	4.8 ±2.0	5.3 ±2.4	5.0 ±1.7
sum	30.4	29.6	28.6

Table S6: Percentage of soil organic carbon derived from C_3 plants (FC_3) and $\delta\ ^{13}C$ (‰) values in plots with different elephant density including standard deviation. Separate FC_3 values are given for three habitat types on plots with different soil cover, i.e. beneath woody vegetation (subcanopy), beneath herbaceous vegetation (grass), and beneath bare soil (bare). Different letters show significant differences for comparisons between density classes.

Elephant density	Soil depth (cm)	$\delta\ ^{13}C$ (‰)	FC_3 Subcanopy	FC_3 Grass	FC_3 Bare soil
Low	00-10	-21.4 ±2.0 a	63.0±16 a	52.1±14 a	52.0±15 a
	10-20	-19.9 ±1.9 a	49.4±15 a	38.7±14 a	42.3±14 a
	20-30	-19.2 ±1.7 a	42.4±13 a	34.2±13 a	37.5±13 a
	30-50	-18.7 ±1.4 a	37.4±10 a	30.5±12 a	35.3±10 a
	50-70	-19.1 ±1.9 a	41.2±9 a	35.5±11 a	36.9±8 a
	70-100	-20.4 ±1.4 a	38.5±6 a	36.9±13 a	40.5±12 a
Medium	00-10	-21.4 ±1.6 a	58.9±12 a	53.2±14 a	55.8±12 a
	10-20	-20.3 ±1.7 a	49.6±14 a	44.0±14 a	46.7±13 a
	20-30	-20.0 ±1.8 a	46.0±15 a	39.9±16 a	49.2±13 b
	30-50	-19.9 ±1.9 b	44.4±16 a	40.8±16 a	46.2±16 b
	50-70	-19.2 ±2.0 a	39.4±17 a	35.7±16 a	40.5±16 a
	70-100	-19.5 ±2.1 a	40.2±16 a	38.6±15 a	42.7±18 a
High	00-10	-21.4 ±2.1 a	56.7±19 a	54.4±14 a	54.6±18 a
	10-20	-20.2 ±2.6 a	47.6±21 a	44.8±19 a	46.8±21 a
	20-30	-20.1 ±2.7 a	43.4±23 a	43.3±21 b	47.5±21 b
	30-50	-20.2 ±2.6 c	45.5±21 a	47.7±20 b	46.4±20 b
	50-70	-19.8 ±2.8 a	41.1±24 a	40.6±23 a	48.3±22 a
	70-100	-20.6 ±2.8 a	44.4±24 a	46.9±21 a	52.0±22 a
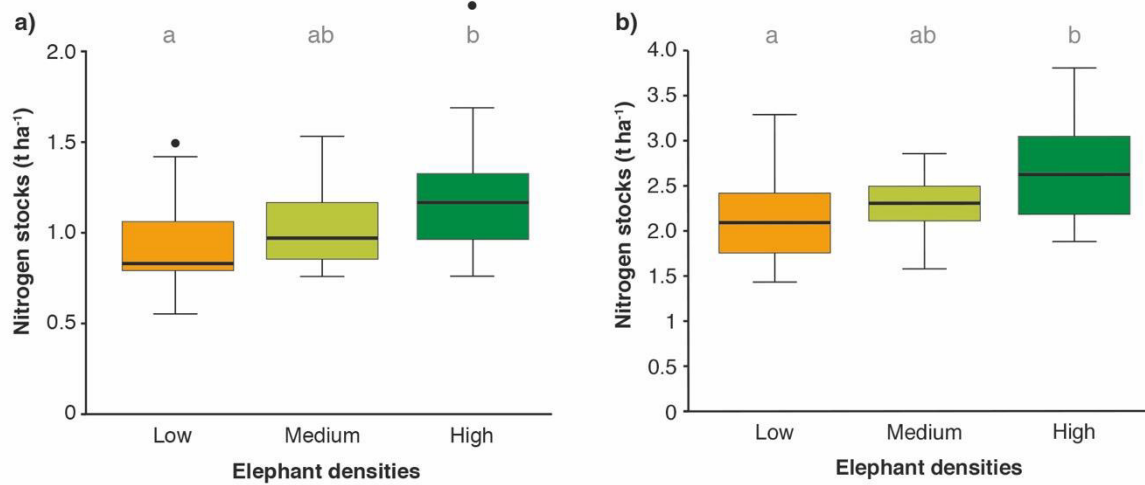
Figure S1: Total nitrogen stocks (t ha^{-1}) in a) 0- 30 cm and b) 0-100 cm soil depth at sites with different elephant densities. Different letters show significant differences (p<0.05) for comparisons between elephant density classes.
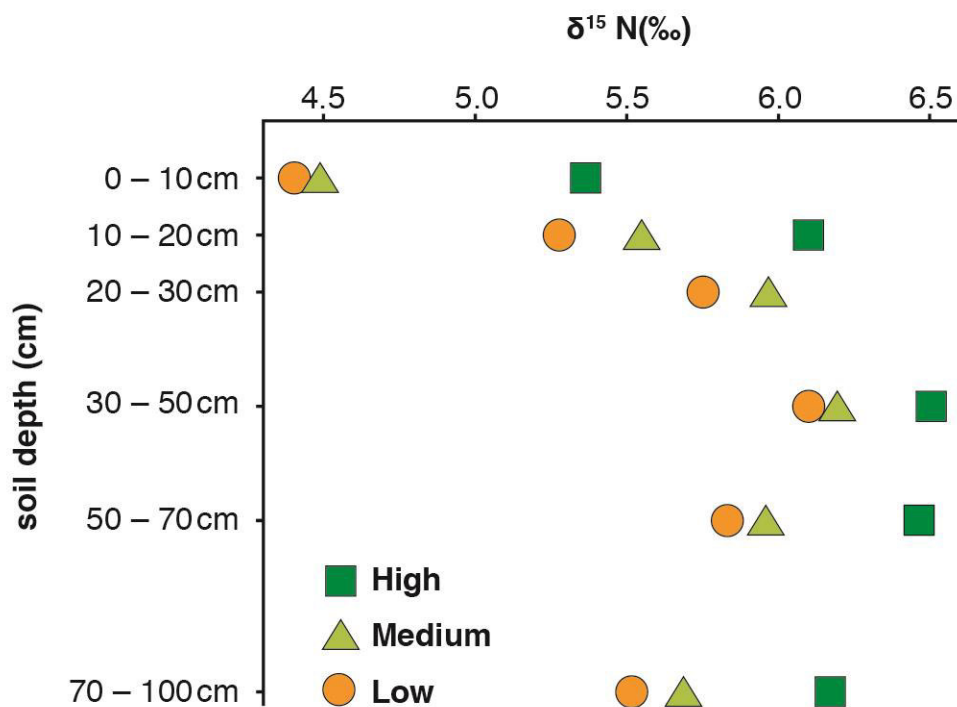
Figure S2: δ^{15}N values in six soil depth classes at sites with different elephant densities (high, medium, and low).

Chapter 5

Natural and human disturbances have non-linear effects on whole-ecosystem carbon persistence in an African savanna

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Final draft included here, all co-authors gave consent for submission in current form.

1 **Natural and human disturbances have non-linear effects on**

2 **whole-ecosystem carbon persistence in an African savanna**

3 **Running title:** Whole-ecosystem carbon persistence

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28 **Word count: 7,982 words**

29 **Abstract**

30 Disturbance-mediated shifts in carbon persistence – the inverse likelihood of experiencing

31 severe losses due to disturbances – within terrestrial ecosystems remain poorly understood

32 despite their critical role in global carbon dynamics. Moreover, huge uncertainties in

33 estimating carbon storage in disturbance-prone dryland ecosystems renders the

34 assessment of their contribution to the global carbon budget difficult. This study

35 investigated the effects of land-use change on carbon storage in an African savanna

36 landscape, focusing on agricultural intensification and wildlife conservation as major land-

37 use change pathways that alter disturbance regimes. We adapted conventional tree

38 inventory and soil sampling methods to suit dryland ecosystems, enabling robust

39 quantification of carbon storage for aboveground and belowground carbon in woody

40 vegetation (AGC and BGC, respectively), and soil organic carbon (SOC) across land-use

41 pathways and two vegetation types (savannas and woodlands). For assessing the effects of

42 environmental drivers on AGC, and whole-ecosystem carbon (C_{total}), Generalized Additive

43 Mixed Models were used. Results indicate different carbon persistence across carbon

44 reservoirs, vegetation types and along land-use change pathways. Shrub AGC always was

45 the least persistent carbon reservoir in savannas. Compared to shrub AGC in low-

46 disturbance sites, it decreased on average by 56% along the conservation pathway and by

47 90% along the intensification pathway. Tree AGC was the least persistent reservoir along

48 the intensification pathway in woodlands, with decreases of 95%. Elevated SOC stocks,

49 particularly along the intensification pathway, suggest preferential use of naturally carbon-

50 richer soils for agriculture. Strong unimodal impacts of disturbance agents, notably large

51 herbivores and woodcutting, on AGC and C_{total} indicate that intermediate disturbance levels

52 benefit carbon storage. Our findings suggest complex, interactive effects of natural and

53 human disturbances on the carbon persistence of ecosystem compartments and whole-

54 ecosystem carbon, and highlight the substantial role of locally adapted disturbance regimes

55 for carbon sequestration, offering insights crucial for carbon certification programmes in

56 drylands.

57 **Keywords**

58 African savannas, carbon pools, carbon persistence, disturbance agents, dryland

59 ecosystems, elephants, land-use change, soil organic carbon, transfrontier conservation

60 areas, woody vegetation

INTRODUCTION

Continued greenhouse gas emissions increase CO_2 concentration in earth's atmosphere and drive ongoing climate change, posing a threat to ecosystems and livelihoods worldwide (IPCC 2018). While land-use change is among the biggest threats to terrestrial carbon storage (Erb et al. 2018, IPCC 2022), retaining or increasing persistent carbon pools in terrestrial ecosystems is among the most promising means to mitigate anthropogenic climate change (Trumper et al. 2008, Saatchi et al. 2011, Cook-Patton et al. 2020).

Drylands, which cover >40% of Earth's terrestrial surface and host two billion people (FAO 2019, IPCC 2022), represent the largest, most sensitive and fastest-changing component of the global terrestrial carbon sink (Stringer et al. 2012, Godlee et al. 2021). However, their carbon storage potential is understudied (Rozendaal et al. 2022), thus undervalued (Kouamé et al. 2022), and their carbon dynamics remain insufficiently understood (Erb et al. 2018, Godlee et al. 2021). Accordingly, the contribution of drylands to global carbon stocks is often ignored in global carbon assessments (Erb et al. 2018).

In rural Africa, about 60% of carbon is stored in drylands, mostly woodlands and savannas (Trumper et al. 2008). Here, the two commonly anticipated pathways of land-use change are agricultural intensification and extended nature conservation schemes (Dittmann and Müller-Mahn 2023). These conflicting visions for the future of rural Africa, which are often found in close vicinity to each other in so-called coexistence landscapes (Fiasco and Massarella 2022, Bollig et al. 2024), also affect carbon storage differently. While land clearing in the course of agricultural intensification is frequently addressed as a main culprit for carbon losses (Balima et al. 2020, Nath et al. 2022), recent studies have shown that conservation schemes may also have detrimental effects on carbon pools. In particular, increasing populations of large herbivores reduce tree biomass (Bollig et al. 2024) and hence aboveground carbon (AGC) storage (Malhi et al. 2022). In coexistence landscapes, the joint and potentially interacting effects of different disturbance agents such as elephant browsing, woodcutting, and livestock herding are still poorly understood (Venter et al. 2018, Dittmann and Müller-Mahn 2023). Achieving such an understanding profits from modelling techniques that can flexibly account for potentially non-linear effects of drivers, which are typical for complex social-ecological systems (Messier et al. 2016, Peters et al. 2019).

91   In this context, we still lack accurate assessments of land-use change effects on carbon

92   stocks in different ecosystem compartments, as well as on whole-ecosystem carbon storage

93   (C_{total}) in dryland ecosystems. These ecosystems are typically patchy and disturbance-prone;

94   both characteristics pose specific methodological challenges for a robust estimation of

95   carbon stocks in vegetation and soil. The accurate estimation of AGC in woody vegetation

96   is methodologically challenging due to the irregular growth forms of damaged individuals

97   and because most individuals are too small for typical recording thresholds (Kindermann et

98   al. 2022b). Dryland ecosystems such as savannas and dry woodlands are typically shaped

99   by multiple disturbances such as wildfire, browsing herbivores and direct anthropogenic

100   impacts like woodcutting (Newman 2019, Owen-Smith et al. 2020, Archer et al. 2021,

101   Buisson et al. 2021), which all destroy vegetation and release carbon stored therein

102   (Osborne et al. 2018). Although disturbances have negative consequences for carbon

103   storage, they are beneficial for the biodiversity and stability of savanna ecosystems (Eriksen

104   and Watson 2009, Newman 2019). However, most protocols for carbon accounting have

105   not been designed for disturbance-prone ecosystems such as savannas, leading to flawed

106   estimates (Anderegg et al. 2020, Kindermann et al. 2022b). Frequent disturbances also

107   increase the contribution of shrub-like growth forms to woody biomass (Hempson et al.

108   2020), which need to be accounted for to not underestimate carbon stocks (Kindermann et

109   al. 2022b, Kouamé et al. 2022).

110   Disturbances (Bond and Midgley 2001) and arid climate (Ledo et al. 2018) cause woody

111   plants in savannas to have comparatively large root systems which requires consideration

112   in estimations of belowground vegetation carbon (BGC) (Mokany et al. 2006, Kouamé et al.

113   2022). However, this is hampered by the fact that root biomass in savanna ecosystems is

114   not increasing in a fixed proportion to aboveground biomass (Mokany et al. 2006, Swemmer

115   and Ward 2020). Instead, shrub-like growth forms have higher root-to-shoot (RS) ratios than

116   trees, even if they belong to the same species (Kouamé et al. 2022). Moreover, RS ratios

117   decrease considerably with tree size (Kouamé et al. 2022). It is thus surprising that in the

118   few studies assessing BGC in savannas, usually constant RS ratios are applied (see Zhou et

119   al. 2022b).

120   Soil organic carbon (SOC) stocks in topsoils of savanna ecosystems are well-known to be

121   strongly affected by natural and human disturbances such as fire (Pellegrini et al. 2020),

122   browsing herbivores (Sandhage-Hofmann et al. 2021) and deforestation (Mertz et al. 2021).

123   Frequently, carbon stocks in the subsoil (>30 cm) are influenced by land-use effects in the

124   same direction as in the topsoil (Poeplau and Don 2013, Hicks Pries et al. 2023), but subsoils

125   are rarely measured explicitly (Mertz et al. 2021, Zhou et al. 2022b). Carbon analyses are

126   usually limited to the topsoil, with the preferred sampling depth being only the top 24 cm

127   (Yost and Hartemink 2020). Only recently, subsoils gained growing interest as a carbon

128   reservoir that is also influenced by land-use change (Quartucci et al. 2023, Skadell et al.

129   2023). However, there is still a knowledge gap on SOC turnover in subsoils. This is

130   particularly unfortunate, as more than 50% of global SOC is stored in subsoils, where it is

131   less rapidly decomposed than in topsoils (Button et al. 2022). Understanding carbon

132   dynamics in subsoils is thus essential to predict the vulnerability of SOC to land-use or

133   climate change, and to assess the carbon sequestration potential of soils.

134   In savanna ecosystems with their patchy character, open areas can be distinguished from

135   vegetation patches dominated by tuft grasses, shrubs or trees (Ochoa-Hueso et al. 2018).

136   SOC stocks can vary dramatically between these habitat types (Gaitán et al. 2019,

137   Sandhage-Hofmann et al. 2022, Zimmer et al. 2024). However, previous studies exploring

138   the effects of land-use change on SOC in savannas often applied a random sampling

139   strategy, irrespective of habitat patches (Dearing et al. 2014, Zhou et al. 2022a). Upscaling

140   such averaged carbon stocks to a landscape level can lead to incorrect results. Instead, a

141   stratified sampling approach across habitats should provide more accurate SOC

142   estimations.

143   Besides posing specific challenges for quantification, carbon stored in different ecosystem

144   compartments do differ in carbon persistence, that is in the "inverse likelihood to suffer

145   severe losses to disturbances" (Kristensen et al. 2022). Previously, the concept of carbon

146   persistence was restricted to SOC, where persistence is measured as a turnover or mean

147   residence time of soil organic matter (Sierra et al. 2018). For assessing the effects of large

148   herbivores on carbon stocks, Kristensen et al. (2022) recently suggested to extend the

149   concept of carbon persistence to vegetation. Their idea is to shift away from a focus on

150   building immediate carbon stocks to a focus on whole-ecosystem carbon persistence.

151   Accordingly, persistence is assumed to increase from woody AGC over woody BGC to topsoil

152   and finally subsoil carbon stocks (Kristensen et al. 2022). As the original definition of carbon

153   persistence is not applicable to carbon storage in woody vegetation, though, an alternative

154   operationalization is required.

155   Here, we present the results of an interdisciplinary study in a Namibian coexistence
156   landscape that aims at understanding the effects of two pathways of land-use change
157   (conservation and agricultural intensification) on carbon pools in ecosystem compartments
158   that are assumed to differ in their carbon persistence. Pathways' impacts are assessed by
159   means of space-for-time substitutions, and carbon persistence is operationalized as the
160   relative change in carbon stocks between the reference state of low-disturbance sites and
161   the respective endpoints of the two pathways. AGC is quantified with the aid of a novel
162   methodology tailored to disturbance-prone ecosystems (Kindermann et al. 2022a,
163   Kindermann et al. 2022b). For BGC estimation, growth-form-specific and size-dependent RS
164   ratios are used (Kouamé et al. 2022) and damages to AGC are taken into account. SOC is
165   assessed in topsoils (0-30 cm) and subsoils (30-100 cm), stratified along habitat types.

166   We specifically ask: (1) What are the effects of the two pathways of land-use change
167   (conservation and agricultural intensification) on carbon stocks in different ecosystem
168   compartments and in the whole ecosystem? We hypothesize that carbon storage is
169   decreased along both pathways, with more persistent ecosystem compartments
170   experiencing less severe losses. (2) What is the relative importance of land-use change
171   drivers on AGC and whole-ecosystem carbon storage? We hypothesize that drivers often
172   act additively, non-linearly and interact with each other.

METHODS

1. Study area

175   Our study was conducted in Namibia's portion of the Kavango Zambezi Transfrontier
176   Conservation Area (KAZA-TFCA), which represents the collaborative effort among multiple
177   countries in southern Africa to conserve biodiversity and promote sustainable development
178   across borders (Naidoo et al. 2022). Climate is semi-arid (Prăvălie 2016); mean
179   temperatures are 36°C in summer and 10°C in winter; rainfalls occur seasonally, with a
180   mean annual precipitation of 550-600 mm (Mendelsohn et al. 2003). The dominating soils
181   are Arenosols with sandy texture and poor soil fertility (Mendelsohn et al. 1997) on which
182   two main vegetation types occur that differ in species composition and vegetation
183   structure. In open vegetation with continuous grass layer (hereafter 'savanna', (Ratnam et
184   al. 2011, Torello-Raventos et al. 2013)) the tree layer is dominated by mid-sized trees
185   (4-6 m) such as *Terminalia sericea, Vachellia erioloba* or *Colophospermum mopane*

186   intermixed with shorter species (3-4 m) such as *Combretum* spp or *Philenoptera* spp. In

187   contrast, tall-growing species (>7 m) like *Baikiaea plurijuga* and *Burkea africana* form the

188   overstorey of the more closed savanna woodlands with potential canopy cover >40%

189   (hereafter 'woodland' (Torello-Raventos et al. 2013, Skarpe et al. 2014)). Here, the lower

190   stratum (typically 1.5-4 m) is composed of *Baphia massaiensis* or smaller *Vachellia erioloba*

191   and *Terminalia sericea*.

192   Major wildlife migratory corridors intersect national borders between the five member

193   countries of KAZA-TFCA (Dittmann and Müller-Mahn 2023). Here, elephants migrate

194   between their dry-season and wet-season habitats (Brennan et al. 2020, Benitez et al.

195   2022). Between 12,000-20,000 elephants reside here in one of the country's more densely

196   populated regions, and their numbers substantially increased since the 1960s (Stoldt et al.

197   2020, Benitez et al. 2022). KAZA offers a large spectrum of land-use types including strictly

198   protected national parks, safari tourism areas and communal conservancies. In the latter,

199   local communities are allowed to manage and benefit from wildlife and protected natural

200   resources (Fabricius et al. 2013). Designated zones can be used for other land-use types,

201   like rangelands, or agriculture.

202   **2. Study design**

203   To analyse the consequences of land-use change on carbon storage within a coexistence

204   landscape, we used space-for-time substitutions (Pickett 1989) along two pathways of land-

205   use change, namely wildlife conservation and agricultural intensification (Figure 1a).

206   Conservation measures increase wildlife populations (Meyer et al. 2021), while agricultural

207   intensification converts near-natural vegetation to rangelands or agricultural fields

208   (Sandhage-Hofmann et al. 2022). These two pathways form a composite gradient from

209   conservation efforts to agricultural intensification along which the disturbance regime

210   (sensu Burton et al. 2020) changes from a dominance of wildlife impacts to a dominance of

211   anthropogenic impacts e.g. woodcutting.

212   We sampled five land-use types along the composite gradient (Figure 1a, e-g). Sites with

213   low levels of anthropogenic use and low levels of wildlife disturbance (L) served as a

214   common point of reference. These were situated in communal conservancies, distant from

215   villages (Woodward et al. 2021). For the conservation pathway, we added two elephant

216   density classes, i.e. medium (M) and high (H) densities, located in the national parks at
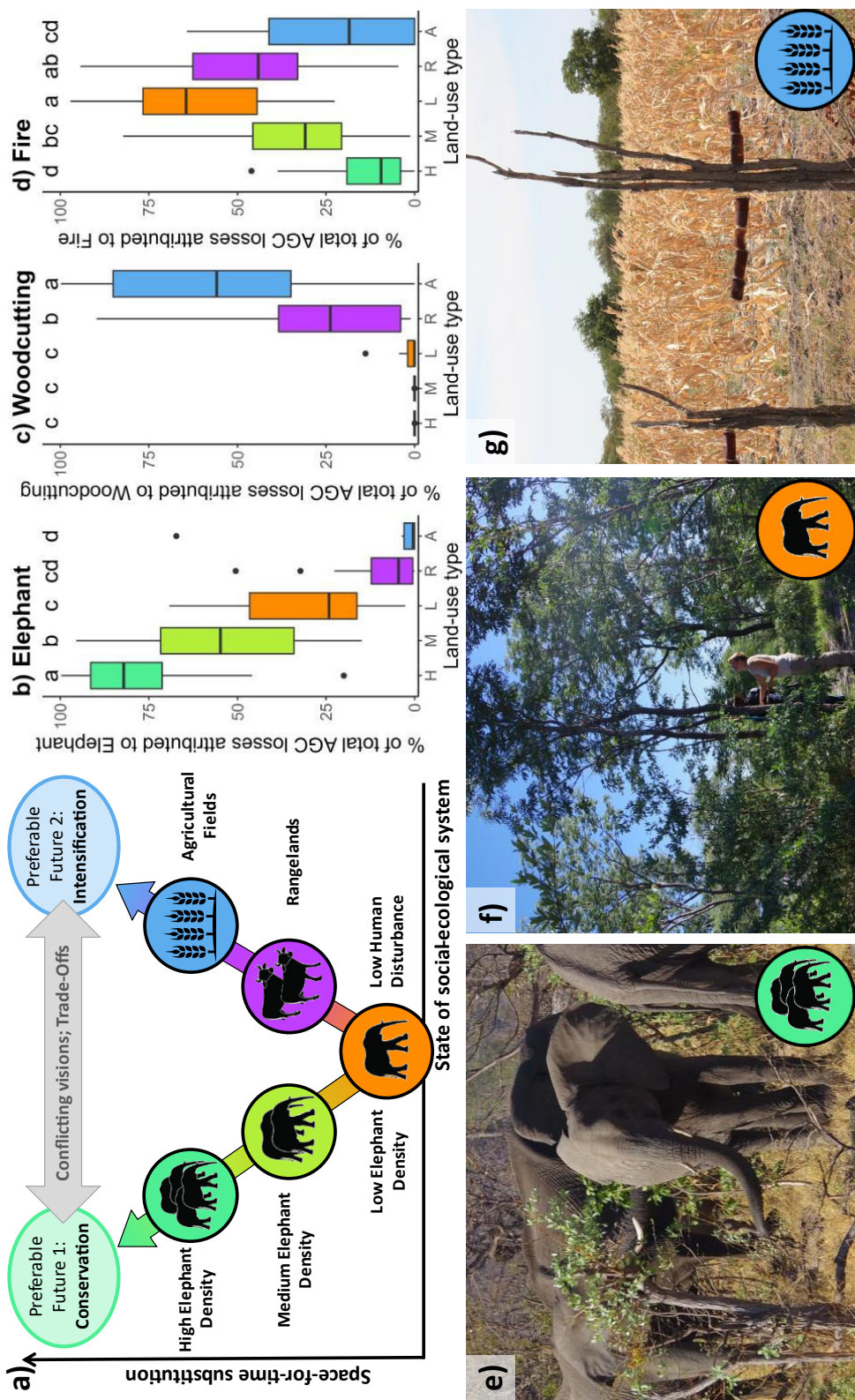
Figure 1: Study design and land-use types (High elephant density (H), Medium elephant density (M), Low elephant density and low human disturbance (L), Rangeland (R), Agricultural fields (A)); **a)** Five sampled land-use types representatively capturing two pathways of future land-use change in a space-for-time substitution; **b-d)** Relative share of three main disturbance agents on total aboveground carbon (AGC) losses recorded in living trees; super-script letters indicate significant differences in one-way ANOVA and Tukey post-hoc test; **e-g)** typical vegetation at low disturbance levels and the two respective endpoints of each pathway (icons identical to **a)**).

217   different distances to the riverfront (Figure S1)(Ben-Shahar 1993, Owen-Smith et al. 2020,

218   Wilson et al. 2021). From elephant counts conducted nearby (Chase 2013), we estimate

219   elephant density of <1 elephant km^{-2} in L sites and >4 elephants km^{-2} in H sites. For the

220   intensification pathway, we added extensively-used rangelands (R) and agricultural fields

221   (A) in communal conservancies.

222   We stratified our sampling in two vegetation types, i.e. denser woodland and more open

223   savanna vegetation and – to focus on land-use effects – aimed to minimize variation in other

224   environmental factors like soil type. To this end, we selected non-flooded Arenosol-areas

225   with high soil sand contents (>93% ±4; Sandhage-Hofmann et al. 2022) and within those

226   randomly established independent observation plots (minimum distance 80 m). This

227   resulted in five sites per vegetation type (with ten plots for L, M, and H sites, and six plots

228   for R and A sites; 84 plots in total). Plots had a size of 1,000 m² except for agricultural fields

229   where plot size corresponded to field size, accounting for lower tree densities. Sampling

230   took place in Sept-Nov 2018 and Apr-Jun 2019.

231   **3. Carbon storage assessment**

232   **Estimation of aboveground carbon storage**

233   To accurately estimate AGC, we applied a novel methodology designed for disturbance-

234   prone dryland ecosystems (Kindermann et al. 2022a, Kindermann et al. 2022b). In brief, we

235   stratified our sampling effort according to growth forms, which allowed us to sample the

236   entire size and age range of woody vegetation, including adult trees, subadult individuals,

237   heavily damaged individuals – so-called gullivers (Higgins et al. 2007) – and shrub species.

238   Small individuals (height <50 cm, basal stem diameter <5 cm) were sampled on 100 m²

239   subplots, while adult individuals (height ≥50 cm, basal stem diameter ≥5 cm) were recorded

240   on the whole plot. For other growth forms, flexible, intermediate plot sizes were applied.

241   We measured allometric size parameters, i.e. height, canopy diameters, and (for adult

242   individuals) stem circumference at base and breast height (1.3 m; converted to diameter at

243   breast height, DBH). From these measures, we estimated individuals' aboveground biomass

244   (AGB) with the aid of two allometric models for tree- and shrub-like growth forms,

245   respectively (Chave et al. 2014, Conti et al. 2019). We also subjected all recorded plants to

246   a biomass loss assessment, harnessing their archival function for past disturbances

247   (Archibald and Bond 2003, Levick et al. 2015). Specifically, we visually estimated AGB losses

248   separately for five disturbance types, i.e., elephant browsing, browsing by other herbivores,

249   woodcutting, wildfire, and other disturbances such as drought damage. These disturbance

250   agents were identified from the particular signs they caused. While elephant browsing left

251   e.g. torn branches in tree canopies, woodcutting tools left sharp wounds on stems, and

252   wildfire caused charred stems with resulting dieback in the crown. Individual AGB was then

253   corrected by recorded losses to reflect actual AGB (see Kindermann et al. 2022a,

254   Kindermann et al. 2022b).

255   For estimating adult trees' AGB with a pantropical allometric model (Chave et al. 2014), we

256   measured specific wood density (SWD, see 'wood specific gravity' in Pérez-Harguindeguy et

257   al. 2013). We sampled wood of 2-20 individuals per species (412 samples in total), using

258   two-threaded increment borers (HaglöfSweden) or stem pieces, to measure fresh volume

259   and dry weight (oven-drying at 105°C until constant weight). Species' SWD is the ratio of

260   dry weight per fresh volume. We analysed wood carbon content (CNS analyser ANCA-SL-

261   2020, PDZ-EuropaLtd) and used species-wise averages for converting AGB to AGC.

262   **Estimation of belowground carbon storage**

263   To accurately estimate BGC from AGC data, we applied size-dependent RS ratios for adult

264   trees. Based on the DBH of trees' biggest stem, we derived the RS ratio following Kachamba

265   et al. (2016), where RS ratio decreases with stem size:

266 $$RS\ ratio = \ 1.89208 \times DBH^{-0.43491}$$

267   Shrubs tend to have larger, constant RS ratios (Kouamé et al. 2022); hence, we applied the

268   fixed RS ratio of 2.16 found in a Southern African savanna (Ryan et al. 2011). We extended

269   the previously established protocol for AGC estimation (Kindermann et al. 2022a,

270   Kindermann et al. 2022b) to here also account for disturbance impacts on BGC because

271   severe aboveground damages cause BGC losses through root dieback (Zhou et al. 2022a).

272   To account for this, we developed the following procedure: From recorded biomass losses,

273   we first extrapolated individuals' pre-disturbance AGC (see details in Kindermann et al.

274   2022a, Kindermann et al. 2022b). For undamaged and slightly-damaged individuals (AGC

275   losses ≤30%), a BGC proportional to pre-disturbance AGC was calculated, as slight

276   disturbances do typically not reduce root biomass (Zhou et al. 2022b). For heavily disturbed

277   gulliver individuals (AGC losses >30%), a maximum BGC was calculated in proportion to pre-

278   disturbance AGC, as well as a minimum (post-disturbance) BGC based on actual AGC. We

279 then averaged individuals' maximum and minimum BGC as an approximation of actual BGC.

280 Individual AGC and BGC were scaled to a unit per area basis, and separately added up for

281 four carbon compartments (tree AGC, tree BGC, shrub AGC and shrub BGC), together

282 representing stand-level vegetation carbon storage (Kershaw et al. 2016).

283 **Estimation of soil organic carbon**

284 To capture SOC stocks, we distinguished three habitat types and sampled beneath trees

285 ('subcanopy'), between trees ('intercanopy'), and in 'bare soil' patches (see Sandhage-

286 Hofmann et al. 2022). We visually estimated habitat types' relative ground cover on plots

287 and took one soil core per habitat type. For most cores (180 out of 228), sampling was done

288 to 100 cm depth with an electrical auger (6 cm diameter), and for the remaining cores with

289 a hand auger (5 cm diameter) up to 50 cm depth. Cores were divided into six depth classes

290 (0-10 cm, 10-20 cm, 20-30 cm, 30-50 cm, 50-70 cm, and 70-100 cm). Dry bulk density was

291 determined by weighing air-dried subsamples and dividing the weight by samples' volume

292 in the auger (Walter et al. 2016).

293 Soil carbon concentrations were determined by dry combustion (CHNS analyser Elementar-

294 Analysensysteme-GmbH). No inorganic carbon was detected, i.e. total carbon was equal to

295 SOC. Carbon stocks were calculated as

296 SOC-stock $[t\,ha^{-1}]$ = soil carbon concentration$[g\,kg^{-1}]$ * bulk density$[g\,cm^3]$ * soil

297 depth$[cm]/10$ (Deng et al. 2016). Carbon stocks were then added up across depth classes

298 within two soil carbon compartments, i.e. topsoil and subsoil, according to a common depth

299 distinction (Schneider et al., 2021). Topsoil SOC stocks (0-30 cm) represent a carbon

300 compartment with a lower carbon persistence (Button et al. 2022, Kristensen et al. 2022),

301 while subsoil SOC stocks (30-100 cm) represent a compartment with higher persistence.

302 Missing depth classes in subsoil from sampling with the hand auger were filled in by mean

303 values of existing samples per vegetation type, land-use type and depth class. SOC data

304 obtained in the three habitat types per plot were weighed according to habitats' relative

305 ground cover.

306 **Estimation of carbon persistence**

307 For disturbance-prone savanna ecosystems, Kristensen et al. (2022) suggested a carbon

308 persistence continuum from AGC over BGC and particulate SOC dominating in topsoil, to

309 mineral-associated SOC dominating in subsoil. We adopted this approach, and further

310   subdivided woody carbon as trees are known to be more persistent than shrubs and

311   subadult growth forms (Zizka et al. 2014). Accordingly, we estimated stocks in six carbon

312   compartments for which we assumed increasing carbon persistence i.e. i) shrub AGC,

313   ii) tree AGC, iii) shrub BGC, iv) tree BGC, v) topsoil SOC, and finally vi) subsoil SOC. For each

314   carbon compartment we quantified its persistence as the relative change percentage in

315   carbon stocks between the reference state of low-disturbance sites (L plots) and the

316   respective endpoints of the two pathways (H and A plots).

317   **4. Measurement of environmental drivers**

318   We recorded a suite of potential environmental drivers of carbon storage on each plot. This

319   included land-use type (Figure 1a), disturbance regime descriptors, and soil characteristics.

320   For disturbance regimes, we estimated the ground cover of bare soil, living grass, moribund

321   material (indicating low disturbance intensity in the grass layer (Zimmermann et al. 2015)),

322   litter, charcoal, dead woody debris >2.5 cm (Aponte et al. 2014), and herbivore dung. We

323   also calculated proximity of each plot to the nearest river (proxy for elephant visiting

324   frequency (Owen-Smith et al. 2020, Wilson et al. 2021)) and to the nearest school (proxy

325   for distance to nearest larger settlement and therefore human impact (see Meyer et al.

326   2022)). Moreover, we assessed disturbance intensity and utilization of woody vegetation

327   (Walker 1976), distinguishing between browsing, wildfire, and woodcutting. Values ranged

328   from zero (no visible disturbance) to five (>90% of woody plants showing intense impacts

329   of disturbance agent). Unlike our estimations of individual biomass losses for living trees

330   and shrubs (see above), these assessments also considered dead individuals and their

331   remains as indicators of intense past disturbances. Disturbance intensity was assessed

332   separately for the tree layer (height >3 m) and the shrub layer (<3 m), as well as for old

333   (>2 years) and recent disturbance events (≤2 years)(following Walker 1976). The resulting

334   values per disturbance agent were added up, creating an ordinal scale of disturbance

335   intensity (range 0-20). To discriminate between the impact of mega-browsers (i.e.

336   elephants) on the tree layer, and the general impact of all browsers on the shrub layer,

337   browsing intensity values remained separate for these two layers (range 0-10).

338   We quantified the recent abundance of herbivore species on our plots through physical

339   indicators for herbivore activities, i.e. trampling and dung deposition (following Linstädter

340   et al. 2014). These assessments were conducted with the aid of local wildlife rangers. Values

341 ranged from zero (herbivore species missing) to ten (very high density) and were

342 subsequently added up to estimated population densities per herbivore guild: (i) wild

343 grazers and mixed feeders (13 species); (ii) domestic grazers and mixed feeders (three

344 species); (iii) mega-browsers (i.e. elephants); and (iv) other browsers (two

345 species)(Sankaran et al. 2013, Staver and Bond 2014, Szangolies et al. 2023). Disturbance

346 intensities and animal densities on ordinal scale were treated as quasi-numerical in

347 subsequent analyses.

348 To characterize soil conditions, we measured particle-size distributions (sand, silt and clay

349 contents), pH, cation exchange capacity (CEC), soil nitrogen concentration, and

350 macronutrient concentrations (Na, Mg, K and Ca) in 0-10 cm soil depth as a representative

351 part of the topsoil (0-30 cm). Particle-size analyses were performed using the sieve-pipette

352 method (IUSS-WRB WorkingGroup 2022). Soil pH was measured using a pH glass electrode

353 in distilled water (one part soil mixed with 2.5 parts H_2O). CEC was determined by

354 ammonium acetate extraction buffered at pH7 (Thomas 1983). Nitrogen concentrations in

355 [g/100g soil] were determined by dry combustion (CHNS analyser Elementar-

356 Analysensysteme-GmbH) and expressed as [%].

357 **5. Statistical analyses**

358 **Predictor selection**

359 Principal Component Analysis (PCA) was used to explore how potential environmental

360 drivers of carbon storage covaried with land-use change, and to select a reduced set of

361 predictors for statistical modelling (see Suppl. 1). Variables were scaled to unit variance and

362 zero-centred before conducting PCA. Predictor selection was based on requirements for

363 statistical models (Spearman's rank correlation coefficient <|0.75|), and models were

364 checked for concurvity issues. During data exploration, we detected strong outliers

365 (displayed as dots above boxplots), characterised by high values of carbon storage on plots

366 at the end of both pathways. These outliers were due to rare (n=10), but particularly large

367 and old tree individuals (Figure 3a) which apparently had outgrown the fire and browser

368 traps that characterize savanna ecosystems (Sankaran et al. 2013, Staver and Bond 2014).

369 We termed these tree individuals 'methusalems' and defined them to have a DBH >60 cm,

370 a size beyond which elephants can no longer topple or break stems (Caughley 1976,

371 Moncrieff et al. 2011, Stevens 2021). Moreover, farmers reported stems of such sizes to be

372   "too big to cut them" (own communication) hence, they have escaped the human

373   disturbance trap (Ouédraogo et al. 2015). To account for the disproportionally high

374   contribution of these old trees to plots' carbon storage, we included their AGC as an

375   additional predictor in modelling (see below and Suppl. 1).

376   Effects of conservation and intensification on carbon stocks

377   For assessing the effects of land-use change on carbon stocks within the six carbon

378   compartments of assumedly differing persistence (see above), we tested for differences

379   between land-use types within each vegetation type using Games-Howell test for

380   comparing groups with unequal sample sizes and variances (Sauder and DeMars 2019).

381   Prior, we checked data distribution visually with histograms and with Bartlett's test for

382   homogeneity of variance (Zuur et al. 2009).

383   Effect of environmental drivers on carbon stocks

384   For assessing the effects of environmental drivers on AGC –the carbon pool with the lowest

385   assumed persistence– and C_{total}, we first attempted generalized linear models. However,

386   unimodal behaviour of some drivers along our study's composite gradient, and non-linear,

387   additive relations between drivers and carbon storage led us to apply Generalized Additive

388   Mixed Models (GAMMs) instead (Zuur et al. 2009, Wood 2011). GAMMs were created with

389   PCA-derived predictors plus methusalems' AGC. Predictors were entered into models as

390   'thin plate regression spline' smoothers, containing a penalty term that balances the trade-

391   off between data fitting and smoothness (Wood 2017). This way the smoothing function

392   describes potentially non-linear relations between a predictor and the response variable

393   but does not require a-priori statements of the nature and shape of this relation (Wood

394   2017). A second penalty term allowed model-fitting to assign zero estimated degrees of

395   freedom to unimportant predictors, thereby effectively eliminating them from the model

396   (the 'double penalty approach' following Wood (2011)). As interactive effects of herbivory

397   and fire are common in savannas (Levick et al. 2015, Johnson et al. 2018), two interaction

398   terms were included in the models using a tensor product that decomposes predictors'

399   individual main effects from their joint interactive effect. Vegetation type was entered both

400   as a parametric effect and a random component, accounting for higher baseline tree

401   biomass in woodland sites (Figure S4, Table S2)(McNicol et al. 2018). Models were fitted

402   using the Gaussian distribution family with identity link and restricted maximum likelihood

403   as smoothness parameter selection method (Wood 2017).

404   All statistical analyses were performed in the open-source R software (RCoreTeam 2020)

405   with package mgcv (Wood 2017) for GAMMs. For data exploration, data wrangling and

406   significance tests, we used additional packages dplyr (Wickham et al. 2020), vegan

407   (Oksanen et al. 2019), corrplot (Wei and Simko 2017), rstatix (Kassambara 2020b) and

408   export (Wenseleers and Vanderaa 2022), while packages GGPlot2 (Wickham 2016), ggpubr

409   (Kassambara 2020a), cowplot (Wilke 2019) and gratia (Simpson and Singmann 2018) were

410   used for visualization.

RESULTS

411

1. Relative importance of disturbance agents along pathways

412

413   Our sampling design was clearly reflected in AGC losses attributable to disturbance agents.

414   As expected, losses along the conservation pathway were mainly caused by elephant

415   browsing (Figure 1b). Its relative share of AGC losses increased from 31% on L plots to 78%

416   on H plots. In contrast, elephant browsing was of minor importance along the

417   intensification pathway but still accounted for 7% of AGC losses in agricultural fields. AGC

418   losses along the intensification pathway were mostly attributable to woodcutting

419   (Figure 1c); its relative share increased from 2% on L plots over 30% on R plots to 58% on A

420   plots (Figure 1b). Wildfire disturbance was highest in the otherwise little disturbed

421   reference site with low land-use intensity (L). Its relative share of AGC losses decreased

422   along both pathways (Figure 1d), but particularly along the conservation pathway, i.e. from

423   61% on L plots to 14% on H plots. For absolute AGC losses recorded in living trees and shrubs

424   see Figure S2.

2. Selected environmental predictors

425

426   PCA results for our 27 environmental variables demonstrate that land-use changes covaried

427   mainly with disturbance factors (Figure S3). Our a-priori defined disturbance gradient was

428   the major source of variation in plots' environmental conditions (explained variance: 30%),

429   with human and wildlife disturbance factors displaying high factor loadings on PC1

430   (Table S1) and a clear arrangement of the five land-use types along this axis. Other

431   environmental conditions, in particular soil conditions, were the second-most important

432   source of variation (explained variance: 14%) with high factor loadings on PC2. However,

433   soil fertility parameters (such as CEC and N) varied not independently from land-use

434   changes. We selected eight predictors out of the full predictor set for subsequent statistical

Figure 2: Carbon storage per carbon compartment; **a)** Means of all compartments per vegetation type and land-use type; **b-g)** each compartment individually; High elephant density (H), Medium elephant density (M), Low elephant density and low human disturbance (L), Rangeland (R), Agricultural fields (A); significances tested with Games-Howell test for unequal sample sizes and variances (only significant pairwise comparisons are shown).

435   modelling of carbon stock dynamics (Figure S3). Four predictors reflected disturbance

436   intensities (browsing intensity in shrubs and trees, respectively; woodcutting intensity; fire

437   intensity), two herbivore densities (wild and domestic grazer density, respectively), and two

438   soil fertility (soil nitrogen content, total CEC). As mentioned before, we added the carbon

439   stored in old 'methusalem' trees as a ninth predictor to GAMMs.

3. Dynamics of compartments' carbon storage

441   Land-use change had significant impacts on C_{total} and on most carbon compartments along

442   both pathways (Figure 2). The two soil compartments together always constituted a larger

443   carbon pool than the four carbon compartments in woody vegetation (Figure 2a). As

444   expected, the carbon pools of AGC and BGC were largest on L plots (mean AGC: 7.1 t ha^{-1}

445   and 10.9 t ha^{-1}; mean BGC: 8.8 t ha^{-1} and 10.6 t ha^{-1} in savanna and woodland vegetation,

446   respectively), and became smaller with increasing disturbance severity (Figure 2a-e). The

447   impact of the intensification pathway on AGC was more pronounced (with a loss of mean

448   AGC between L and A plots by 85%, i.e. from 9 t ha^{-1} to 1.3 t ha^{-1}) than along the

449   conservation pathway (AGC loss between L and H plots by 30%, i.e. from 9 t ha^{-1} to

450   6.3 t ha^{-1}). Intermediate levels of wildlife and human disturbances on M and R plots,

451   respectively, fell between the low-disturbance reference state and the two pathway

452   endpoints. Losses of AGC along the intensification pathway (L vs. A plots) were significant

453   for all woody carbon compartments except for tree AGC in savannas, while the conservation

454   pathway (L vs. H plots) always reduced carbon stocks in shrubs, but not in trees.

455   Soil compartments responded largely opposite to land-use change compared to woody

456   compartments (see also Sandhage-Hofmann et al. 2022). Especially in the subsoil, SOC was

457   generally elevated under anthropogenic use compared to other land-use types

458   (Figure 2a, f, g). Accordingly, SOC stocks were lowest in low-disturbance environments (L

459   plots; with 27.7 t ha^{-1} and 25.8 t ha^{-1} in savanna and woodland, respectively) and higher

460   with both nature conservation (H plots; mean SOC of 33.7 t ha^{-1} and 27.6 t ha^{-1} in savanna

461   and woodland, respectively) and agricultural intensification (A plots; mean SOC 37.4 t ha^{-1}

462   and 41.2 t ha^{-1} in savanna and woodland, respectively). Carbon stocks along the

463   intensification pathway (L vs. A plots) were significantly larger for all soil compartments

464   except for topsoils in woodlands, while the conservation pathway (L vs. H plots) only led to

465   significantly higher carbon stocks in topsoils of savannas.

Figure 3: a) All adult trees (basal stem diameter >5 cm) recorded in this study; individuals' actual aboveground carbon (AGC, [kg]) in relation to stem diameter at breast height (DBH, [cm]) of biggest stem; for heavily damaged gulliver trees the non-measurable DBHs were reconstructed from basal stem circumference (see Kindermann et al. 2022a,b); vertical dashed line indicates threshold beyond which a tree was considered to be a methusalem (DBH>60 cm); b-c) Ratio of combined belowground carbon pools (BGC + SOC) to AGC per plot; b) as a function of tree canopy cover in plot [%]; dashed black line shows linear model across all land-use types, coloured lines show trends per land-use type; c) per land-use type; colour coding indicates land-use types: High elephant density (H), Medium elephant density (M), Low elephant density and low human disturbance (L), Rangeland (R), Agricultural fields (A); point shapes indicate vegetation type; super-script letters indicate significant differences according to one-way ANOVA and Tukey post-hoc test; all y-axes log-scaled.
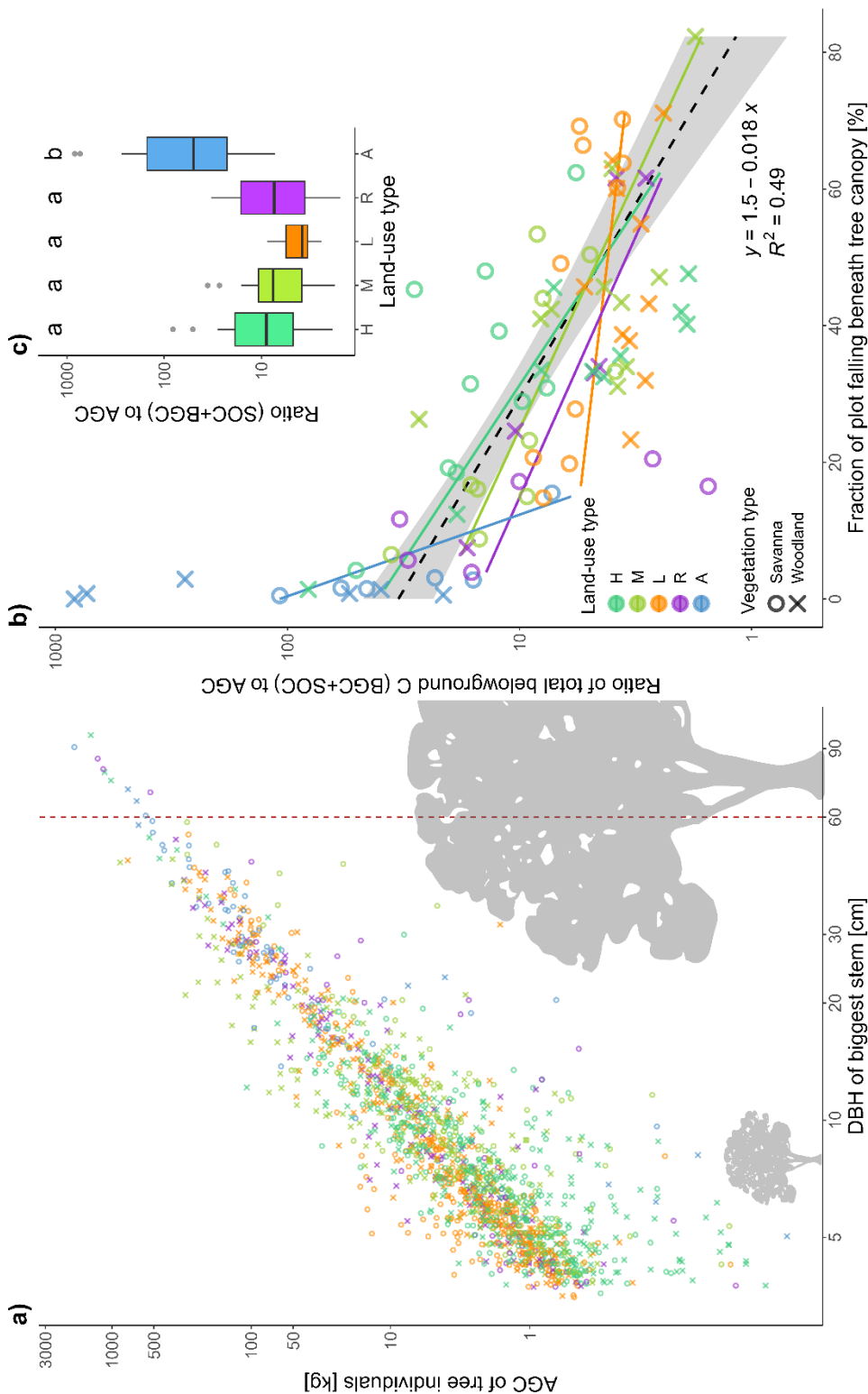
466   In woody vegetation, we found an enormous range of carbon changes (-95% to +2%, Figure

467   2b-e) across the different compartments, indicating pronounced differences in carbon

468   persistence against disturbance. The largest losses (-95%) were observable along the

469   intensification pathway for adult AGC in woodland vegetation. The second-lowest carbon

470   persistence in woodlands (i.e., second largest carbon loss) was found for shrubs, where

471   equal reductions in carbon stocks (-75% to -81%) occurred along both pathways and in all

472   compartments. In contrast, carbon losses along the conservation pathway were negligible

473   for adult AGC (-4%) and even turned to a carbon gain for adult BGC (+2%). In savannas, the

474   lowest carbon persistence was found for shrubs along the intensification pathway; here,

475   similar losses (-90% and -91% for shrub BGC and AGC, respectively) were found as for adult

476   trees in woodlands. Shrubs also constituted the least persistent carbon stocks along the

477   conservation pathway, however with less pronounced losses (-56% for both BGC and AGC).

478   Carbon losses in savannas only ranged from a maximum of -91% to a minimum of -19%.

479   Comparing carbon stocks of belowground carbon pools (BGC and SOC) to the aboveground

480   carbon pool (AGC) revealed that the ratio of belowground to aboveground carbon stocks

481   was altered by land-use change; it was significantly higher in agricultural fields than in all

482   other land-use types (Figure 3c). Along both pathways, the ratio also became increasingly

483   negatively correlated to trees' canopy area (Figure 3b, $R^2 = 0.49$). Individual RS ratios

484   differed between growth forms (Figure S5).

4. Drivers of AGC and C_{total}

486   The nine predictors of carbon storage performed well in GAMMs, especially for AGC

487   (explained deviance 84%, adjusted $R^2 = 0.801$, Table S3, Suppl. 2). Browsing intensity in

488   shrub and tree layer, density of wild grazers, and woodcutting intensity were significant

489   drivers of AGC (p <0.001). While wildfire intensity alone did not significantly alter AGC, we

490   found significant interactive effects with browsing intensity (Figure S6). AGC of the few

491   methusalem individuals (n=10) remained a highly significant term in the model selection

492   process and dropping it from model formulas caused reduced explanatory power.

493   Four of the drivers showed non-linear effects (see also Figure S7) on AGC: Browsing

494   intensity in tree layer, wild grazer density, woodcutting intensity, and the methusalems' AGC

495   (Figure 4b-d, i). For several drivers, moderate levels of disturbance first caused AGC to

496   increase before effects were tipping over into a loss of carbon under further intensifying
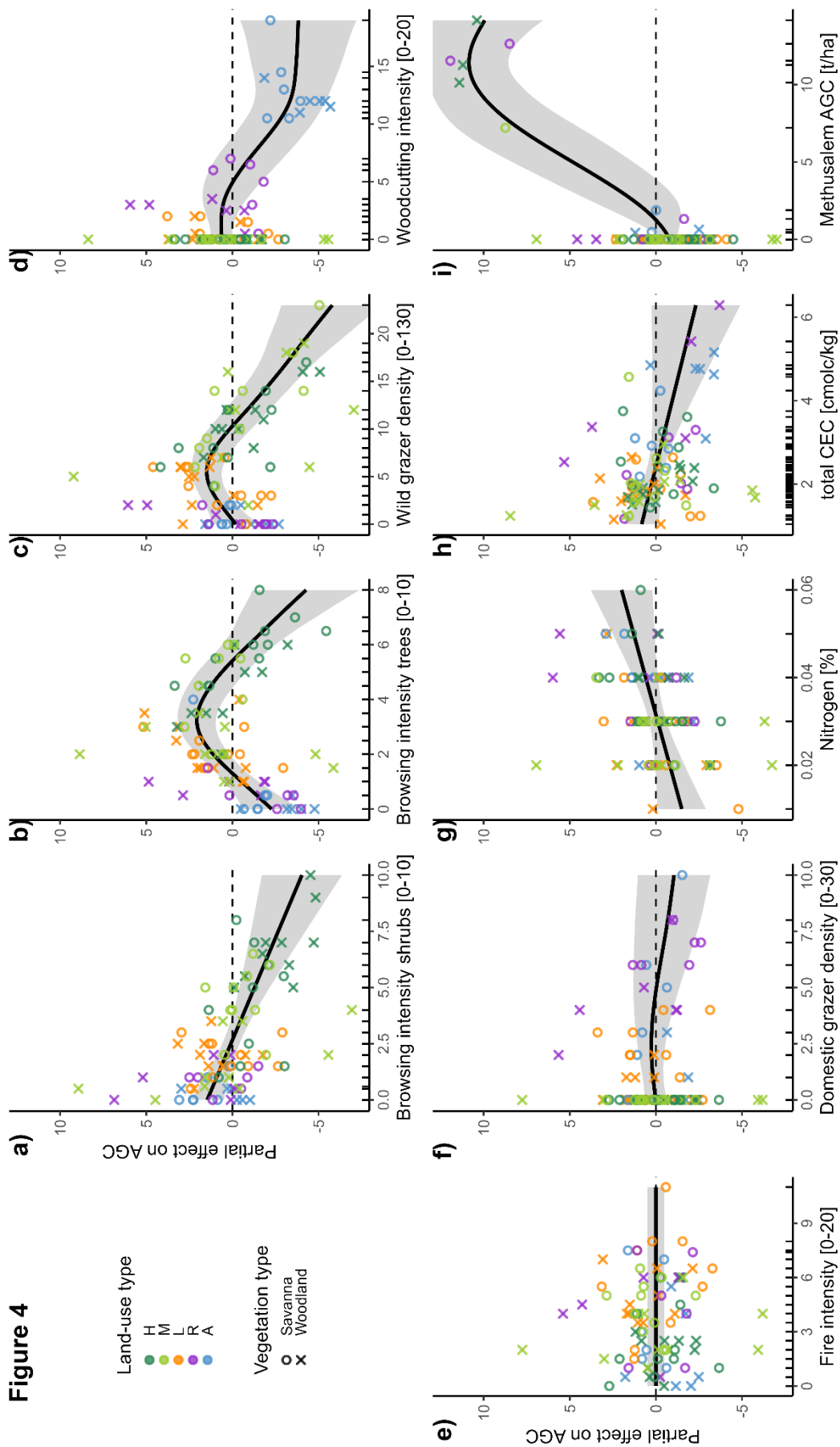
Figure 4

Figure 4: Visual representation of Generalized Additive Mixed Model (GAMM); partial effects demonstrate the impact each predictor has on aboveground woody carbon (AGC) storage in conditions where all other variables were held at fixed values; units of predictors are given on x axes; dashed horizontal lines indicate the mean around which the GAMM centres all values; colour coding follows land-use types: High elephant density (H), Medium elephant density (M), Low elephant density and low human disturbance (L), Rangeland (R), Agricultural fields (A); point shapes indicate vegetation type.
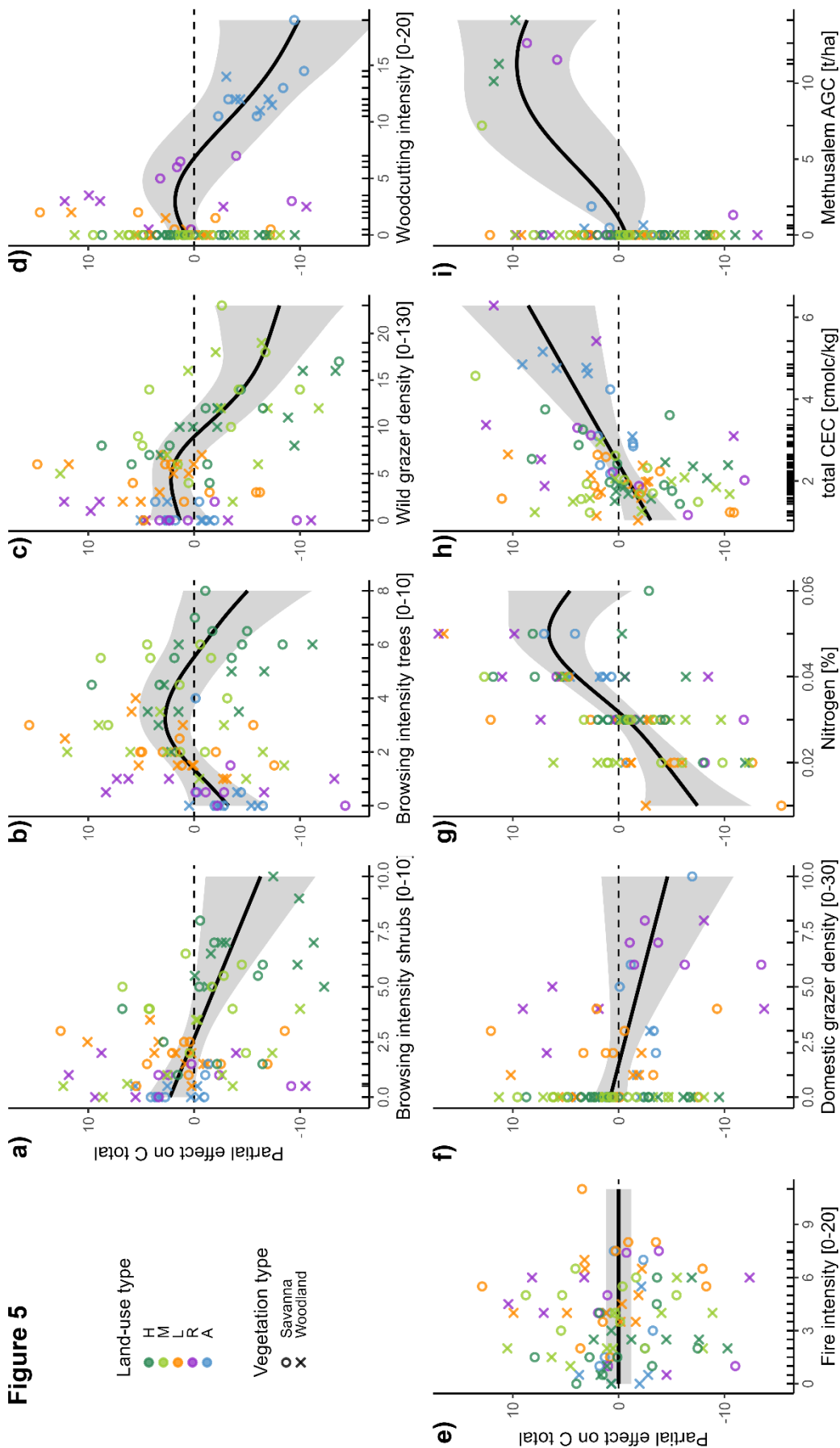
Figure 5: Visual representation of Generalized Additive Mixed Model (GAMM); partial effects demonstrate the impact each predictor has on whole-ecosystem carbon (Ctotal) storage in conditions where all other variables were held at fixed values; units of predictors are given on x axes; dashed horizontal lines indicate the mean around which the GAMM centres all values; colour coding follows land-use types: High elephant density (H), Medium elephant density (M), Low elephant density and low human disturbance (L), Rangeland (R), Agricultural fields (A); point shapes indicate vegetation type.

497   disturbance levels. Contrary to browsing intensity in the tree layer, browsing in the shrub

498   layer reduced AGC linearly (Figure 4a). Wildfire intensity was the only disturbance predictor

499   that was selected out of the model with its smoother set to a flat function with zero impact

500   on the response variable (Figure 4e, Table S3). Domestic grazer density only had

501   insignificant disturbance impact on AGC (Figure 4f); erasing it from the initial model formula

502   lowered the explanatory power of the model, though. Whereas soil nitrogen content

503   linearly increased AGC, other nutrients (total CEC) were related to a reduced AGC

504   (Figure 4g-h), with both terms being marginally significant predictors in the model.

505   The a-priory land-use types were not used in modelling because land-use differences were

506   captured through predictor variables (Figure S3) but employed in visualization to assist

507   interpretation of GAMMs. Non-surprisingly, their alignment along the disturbance gradient

508   was visible in graphs for browsing intensity, wild grazer density, woodcutting intensity and

509   domestic herbivore density. The remaining drivers showed no particular patterns with land-

510   use types. The two vegetation types in this study, namely savanna and woodland, differed

511   significantly in AGC in that woodland's AGC especially in trees was often higher than in

512   savanna vegetation under a similar disturbance regime (Figure S4). Consequently, the

513   parametric effect for vegetation type was significant, indicating that the difference in

514   baseline AGC values required different model intercepts, but aside from that vegetation

515   types were modelled jointly i.e. they formed no patterns in the GAMM outputs.

516   Applying the same model formula that worked best for AGC to C_{total} largely yielded similar

517   model outcomes (Figure 5, Table S4). This was surprising given the relatively small

518   contribution of the AGC pool to C_{total}. While explanatory power was lower (deviance

519   explained = 68%), nearly the same set of model terms that was significant in the AGC model

520   remained significant for C_{total}. The six disturbance predictors and methusalem biomass even

521   retained similar partial effect patterns (Figure 5a-f, i). Fire intensity again was only relevant

522   in interaction with browsing intensity in tree layer (Figure S6) but was otherwise selected

523   out of the model (Figure 5e). The most notable difference between the two models was the

524   more pronounced positive influence of soil fertility (soil nitrogen, CEC) on C_{total} (Figure 5g-h).

DISCUSSION

526   In the context of global environmental change, the impact of land-use on carbon storage is

527   anticipated to vary significantly, depending on the direction of land-use change, leading to

528   concomitant changes in disturbance regimes (Ramesh et al. 2019). Our space-for-time

529   substitutions confirmed that both, agricultural intensification and wildlife conservation,

530   shifted disturbance regimes (Figure 1). Non-surprisingly, the importance of the two key

531   disturbance agents (elephant browsing and woodcutting) increased in opposite directions

532   along the composite gradient from conservation efforts to agricultural intensification, and

533   both effects spanned two orders of magnitude. In sites with high elephant densities, around

534   80% of losses in woody aboveground carbon (AGC) recorded on living trees and shrubs were

535   attributable to elephant damages, with the remaining 20% mostly attributable to wildfires.

536   Our results refine earlier findings from the study area (Sandhage-Hofmann et al. 2021) by

537   considering multiple disturbance agents, and are in line with other studies discussing

538   elephant browsing as an essential driver of AGC losses in conservation areas with high

539   elephant densities (O'Connor and Page 2014, Davies and Asner 2019, Malhi et al. 2022).

540   The relative importance of wildfires stems from active fire management in the national

541   parks, where sites are burned around once every second or third year (MET 2009, Pricope

542   and Binford 2012).

543   Following Kristensen et al. (2022), we assumed that the persistence of carbon reservoirs

544   within an ecosystem would increase from AGC over BGC and topsoil SOC to subsoil SOC.

545   We further assumed that AGC of small woody plants (shrubs and subadults) would be less

546   persistent than tree AGC. However, our results highlight that the persistence of carbon

547   compartments did not always follow such a clear order (Figure 2). As expected, soil

548   compartments always displayed the highest carbon persistence, even with higher carbon

549   levels. Equally in line with our expectations, AGC constituted the least persistent carbon

550   pool. With land clearing for the establishment of agricultural fields, AGC was reduced by

551   73% in savannas and 94% in woodlands (Table S2 and Figure S4), which is in the range of

552   reductions reported previously for sub-Saharan Africa (Ouédraogo et al. 2015, Balima et al.

553   2020, Meyer et al. 2021). The range of changes in woodlands (-95% to +2%) was much

554   higher than in savannas (-91% to -19%). In line with Kristensen et al. (2022) and Zizka et al.

555   (2014) and our own hypotheses, carbon compartments in small woody plants were always

556   the least persistent in savannas. However, in woodlands, this compartment had the lowest

557   persistence only along the conservation pathway, while carbon stocks in trees were the

558   least persistent along the intensification pathway. Hence, both the direction of land-use

559   change and the vegetation type played a strong role for the persistence of tree versus shrub-

560 layer AGC. In summary, both the absolute and the relative persistence of carbon
561 compartments can vary between ecosystems.

562 Carbon stored in the shrub-layer – that includes the heavily damaged Gulliver individuals –
563 contributed considerably to whole-ecosystems carbon stocks, i.e. up to 11% to AGC and
564 even up to a third to BGC. This result is similar to recent findings from root excavations in
565 West Africa (Kouamé et al. 2022). Ignoring this ecosystem compartment as is the case in
566 previous studies (Mitchard et al. 2011, McNicol et al. 2018, Sichone et al. 2018) would thus
567 have resulted in an underestimation of whole-ecosystem carbon (C_{total}) stocks. Our results
568 highlight that the novel estimation routine for root-shoot (RS) ratios developed in this study
569 is more efficient in capturing the disproportional changes in BGC due to variations in
570 damage or size than fixed RS ratios methods. Where long-lived, immobile lifeforms like trees
571 evolved to resist, persist and resiliently survive chronic disturbances aboveground, more
572 emphasis thus needs to be directed to their belowground organs (Paul et al. 2019, Kouamé
573 et al. 2022). More generally, our findings support the need to employ suitable methods
574 when assessing carbon stocks in disturbance-prone ecosystems, in particular with respect
575 to diverse growth forms and belowground organs (Kindermann et al. 2022b, Zhou et al.
576 2022b, Ottaviani et al. 2024).

577 As anticipated, SOC stocks appeared to be more persistent to land-use change than AGC
578 and BGC, and even purportedly increased along the conservation pathway. As has been
579 found before (Sandhage-Hofmann et al. 2021), carbon removed from the AGC pool via
580 elephant browsing is not necessarily lost from whole-ecosystem carbon storage, but likely
581 redistributed through dung or topkill of trees, and sequestered again in soils (Sitters et al.
582 2020). Intriguingly, we also found elevated SOC stocks on rangelands and agricultural fields,
583 both for topsoil and subsoil SOC. As subsoil SOC has been frequently reported to be highly
584 persistent (Wallenfang et al. 2015, Shi et al. 2020), it is unlikely to respond to land-use
585 impacts in a study area where agricultural activities including ploughing only commenced
586 in the 1950s (Bollig and Vehrs 2021), and livestock-keeping only started in the early 20th
587 century (Bollig and Vehrs 2020). We therefore conclude that the elevated SOC stocks date
588 back to a positive selection bias during settlement processes (Wallenfang et al. 2015). That
589 is, present day farmers' forefathers deliberately spared the more infertile soils and
590 established their villages on more fertile land (Mertz et al. 2021). For agricultural fields, our
591 findings also reflect a site selection by farmers informed by an intricate local knowledge of

592   natural soil fertility and its indicators, such as the occurrence of certain tree species

593   (Wallenfang et al. 2015, Mertz et al. 2021). Our findings also put a common claim of local

594   farmers into perspective, i.e. that if there were no national parks, they could expand

595   agricultural activities to that land (personal communication, 2018-2022 but also see Meyer

596   and Börner (2022)).

597   Our findings for the ecosystem-level ratio of total belowground carbon (BGC plus SOC) to

598   AGC revealed how carbon pool persistence influenced potential carbon losses (Figure 3). In

599   low-disturbance environments, the ratio was stable across plots of varying canopy cover,

600   while it drastically dropped with reduced canopy cover under conditions of higher

601   disturbance. This together with the higher SOC stocks in agricultural fields significantly

602   increased the relative importance of belowground in relation to aboveground carbon pools.

603   Hence, in low-disturbance environments, a higher tree cover does not imply an altered ratio

604   between belowground and aboveground carbon stocks, corroborating earlier assumptions

605   that, in savanna ecosystems, a low woody cover does not necessarily lead to lower SOC

606   inputs (Ryan et al. 2011). Presumably, this is due to higher carbon inputs from a denser

607   grass layer (Zhou et al. 2022a), which is a limitation of our study.

608   We found a surprisingly high variability of C_{total} between plots due to the contribution of

609   few, exceptionally large methusalem trees to some plots' carbon storage (Figure 3).

610   Methusalems' advanced age as deducted from stem circumferences indicates that these

611   tree individuals have escaped common disturbance traps (Staver and Bond 2014) in times

612   when human, cattle and wildlife populations in the region had been largely diminished

613   through war, diseases and excessive trophy hunting, respectively (Skarpe et al. 2014,

614   Osborne et al. 2018, Bollig and Vehrs 2021). Methusalems' importance for AGC and C_{total}

615   became even more obvious in statistical modelling (see below).

616   Disentangling the additive effects of overlapping disturbances through GAMMs revealed

617   that many drivers of AGC and C_{total} acted non-linearly on carbon storage (Figures 4, 5). The

618   effect of woodcutting intensity was non-surprisingly shaped like a depletion curve, gradually

619   flattening in agricultural fields where most trees had been cut and therefore AGC was nearly

620   depleted. Importantly, other disturbances were found to have strong unimodal effects

621   whereby intermediate disturbance intensities were associated with the highest carbon

622   storage. Especially increasing browsing intensity in the tree layer and wild grazer density

623   initially increased AGC before reaching a threshold beyond which further disturbance

624   reduced AGC. Hence, carbon storage in disturbance-adapted savanna ecosystems seems to

625   benefit from moderate herbivore disturbances, as has been argued before (Cromsigt et al.

626   2018, Malhi et al. 2022). Interestingly, drivers of C_{total} exerted similar effects as in AGC

627   model, although explanatory power of the C_{total} model was lower pointing to increased

628   unexplained variation. Our results do not support the hypothesis by Kristensen et al. (2022)

629   that large herbivores' presence would decrease topsoil SOC while increasing subsoil SOC.

630   However, they provide evidence for a shift of carbon from labile pools in vegetation to more

631   persistent, slow-turnover SOC pools (Sandhage-Hofmann et al. 2021, Kristensen et al.

632   2022). This supports the postulation that large herbivores can aid climate change mitigation

633   through ecosystem carbon stabilization (Malhi et al. 2022). However, as our results point to

634   a non-linear effect of browsing intensity not only on AGC but also on C_{total} this mechanism

635   evidently has limitations: once AGC stocks are fully depleted, the positive effect of

636   disturbances on persistent carbon stocks may cease.

637   Finding a decreasing effect of CEC as a proxy for soil fertility on AGC seems counter-intuitive

638   yet has recently been reported from a study nearby where it was found to have an indirect

639   effect through density of larger trees (Godlee et al. 2021). In contrast, soil nitrogen content

640   increased AGC and especially C_{total} seems to be limited by soil fertility. This hinds to the

641   "hoard it or use it" conundrum (Janzen 2006) of maximizing inert, persistent carbon at the

642   expense of decomposing SOC as a means of replenishing nutrients fostering plant growth.

643   It further undermines claims of some broadly advertised afforestation projects likely

644   overstating the potential carbon gains of tree planting and disturbance suppression (Bond

645   et al. 2019, Zhou et al. 2022b). Instead, conserving near-natural disturbance regimes will be

646   vital for conservation of biodiverse, fully-functioning savannas (Skarpe et al. 2004, Newman

647   2019).

648   Although wildfire typically is a dominant disturbance factor in savannas, with pronounced

649   negative effects on carbon storage (Zhou et al. 2022b), when accounting for additive effects

650   of other disturbance agents we did not find a significant, solitary influence of fire in our

651   analysis. In contrast, we often found highest carbon stocks in sites where recorded losses

652   from fire on living trees and shrubs were relatively highest, coinciding with plots of low

653   herbivore and human disturbance which supports the notion that savanna trees are highly

654   resistant and persistent to fire (Bond and Midgley 2001, Charles-Dominique et al. 2018).

655 Furthermore, the interactive disturbance of fire and browsing had moderate but complex

656 effects on carbon storage. It should be noted that fire disturbance was not a main focus of

657 this study and thus we deliberately excluded recently burned sites in sampling. Therefore

658 the relative dominance of fire losses in living trees and shrubs on low-disturbance plots

659 might be a function of low herbivore abundance allowing the accumulation of high fuel

660 loads, leading to more fire damages due to high fire temperature (Kristensen et al. 2022,

661 Malhi et al. 2022).

662 Notably, the AGC contribution of a few exceptionally large tree individuals (methusalems,

663 Figure 3a, Figure 4, 5) was retained as an important driver of current carbon storage.

664 However, they will eventually be dying of old age, and when they do are unlikely to be

665 replaced by a new methusalem cohort under the current or presumed future disturbance

666 regimes (Skarpe et al. 2004). Albeit being massive, their large positive influence on carbon

667 storage cannot be regarded sustainable or future-proof (Stringer et al. 2012). Rather, they

668 should be viewed as 'material legacies' or 'transient artefacts' of a past ecosystem state

669 decades ago when disturbance intensities were unnaturally low (Skarpe et al. 2004,

670 Johnstone et al. 2016). This finding highlights inevitable net carbon losses in the future

671 which should be factored in for future carbon accountings.

CONCLUSION

673 Despite their critical role in global carbon dynamics, land-use mediated shifts in carbon

674 persistence within dryland ecosystems are poorly understood. Our study provides evidence

675 that carbon persistence is not a fixed attribute of carbon pools as previously assumed.

676 Within the carbon pool of lowest assumed persistence, i.e. aboveground woody carbon,

677 persistence varied between the two growth forms of shrubs and trees, but also between

678 land-use change pathways and with vegetation type. We also found strong unimodal

679 impacts of disturbance agents such as elephant browsing and woodcutting on woody

680 aboveground carbon and whole-ecosystem carbon storage, indicating that intermediate

681 disturbance levels will benefit carbon storage. However, effects of altered disturbance

682 regimes were overlain by other environmental factors such as a-priori soil conditions:

683 Farmers had deliberately chosen slightly better soils for their rangelands and agricultural

684 fields. Hence, larger carbon stocks in agricultural soils were partly attributable to a pre-

685 selection of fertile land. We therefore conclude that complex, interactive effects of

686 environmental conditions including human management interventions shape the
687 persistence of different carbon compartments in drylands, highlighting the crucial role of
688 locally adapted disturbance regimes for carbon sequestration. Moreover, understanding
689 carbon storage in drylands needs to acknowledge the high spatial variability of edaphic
690 conditions, the concomitant decisions of land-users, and the importance of ecological
691 legacy effects such as the occurrence of methusalem trees. Carbon certificate programmes
692 should incorporate our findings on the differential persistence of carbon pools in drylands.

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SUPPLEMENTARY Material

to manuscript by Kindermann et al

"Natural and human disturbances have non-linear effects on whole-ecosystem carbon persistence in an African savanna"
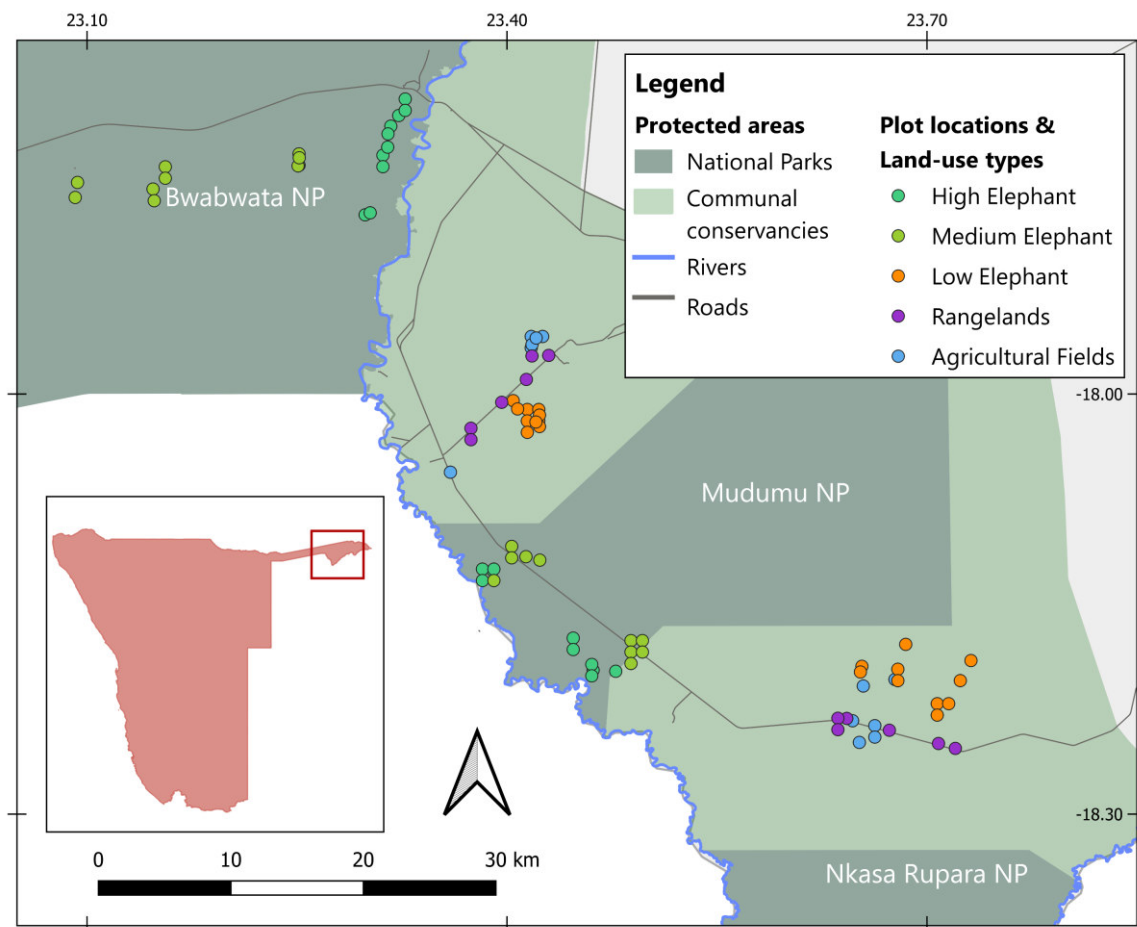

Figure S1: Study area and plot locations with land-use type classification. We stratified our sampling in two vegetation types, with the northern set representing denser savanna woodland – comprised of Mashi conservancy and Bwabwata National Park, while the southern set – with more open savanna vegetation – comprised of Wuparu conservancy and Mudumu National Park.
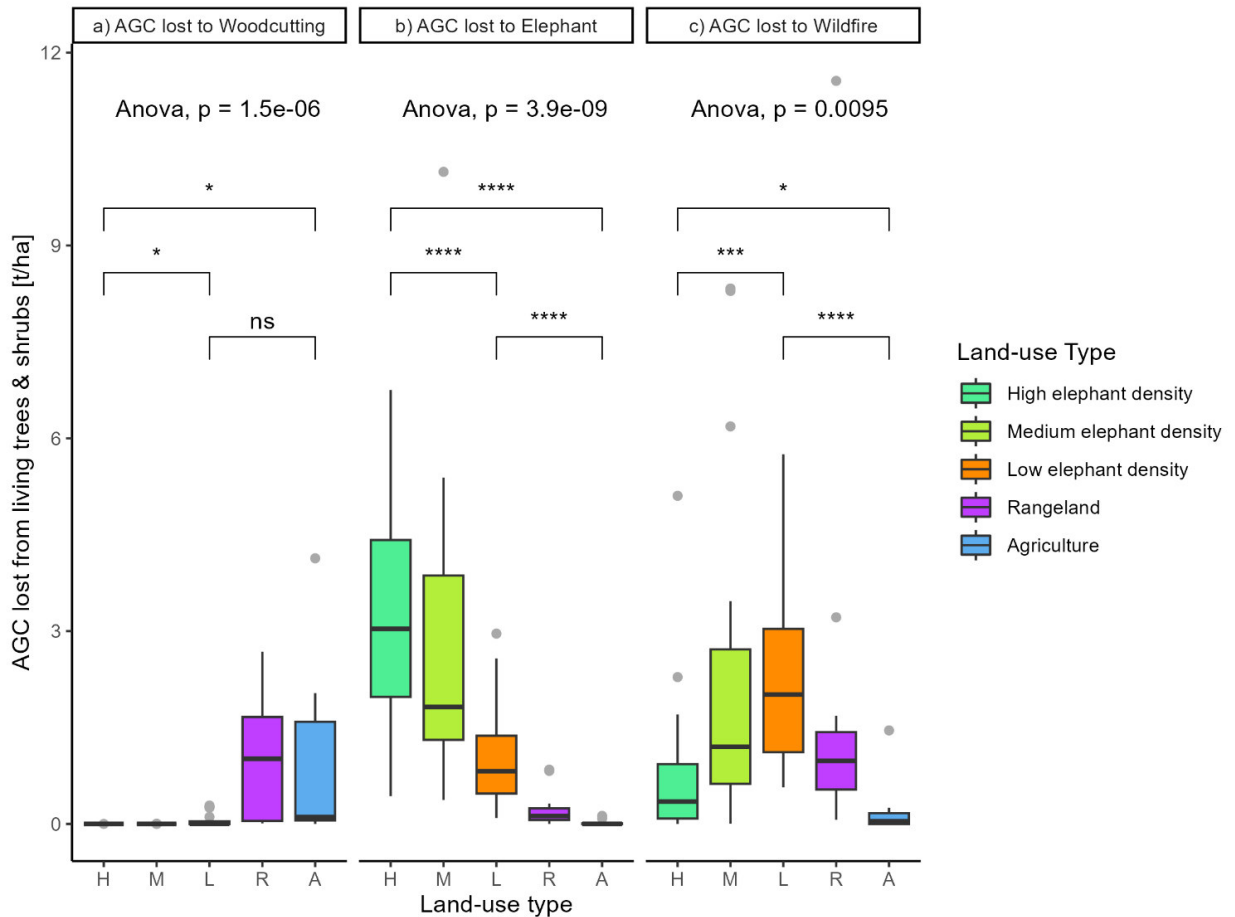
Figure S2: Absolute biomass losses to the three main disturbance agents recorded in damage assessment on living woody individuals per plot; a) Woodcutting damages, b) Elephant browsing damages, c) Wildfire damages. H = High elephant density, M = Medium elephant density, L = Low elephant density and low human disturbance, R = Rangelands, A = Agricultural fields. Overall significant differences between land-use types were tested with one-way ANOVA (see superscript p-values); asterisks denote significant differences (according to T-test) between pairwise comparisons of reference state (L) and respective endpoints of the two land-use change pathways towards agricultural intensification (A) and wildlife conservation (H).

Suppl. 1: Environmental drivers and predictor selection

The five sampled land-use types are well represented by the environmental variables and disturbance indicators employed in this study and nicely align along the two divergent pathways of anticipated future change (**Figure S3**). The first principal component axis of the PCA biplot is mainly determined by variables related to anthropogenic use such as woodcutting intensity, presence of domestic herbivores, and the distance to settlements, and accounts for 30% of the variation between plots. The second PC axis is mainly determined by browsing intensity in woody vegetation and the presence of wild herbivores contrasting to wildfire intensity, accounting for another 1 % of variation in the dataset; cumulative proportion of variance covered by the first three PC axes is 53%.

Figure S3: *Principal component analysis (PCA) of all potential drivers of carbon storage assessed for each plot (dots). Drivers highlighted i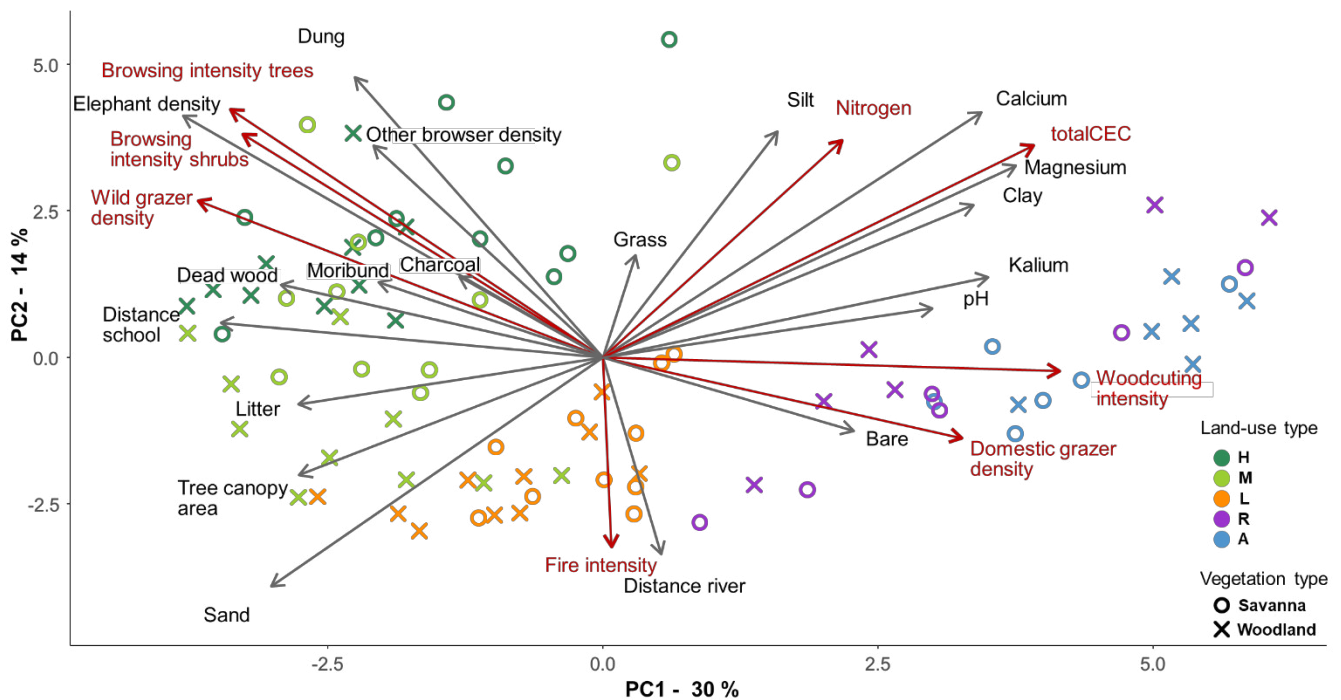n red with thick arrows were selected as predictors for further modelling. Abbreviations: totalCEC = total cation exchange capacity in soil; Nitrogen = soil nitrogen content; Groundcover estimations in subplot: Bare = fraction of bare ground; Litter = leaf litter; Grass = grass and other herbaceous vegetation cover; Moribund = moribund grass cover; Charcoal = cover of charcoal particles; Dung = dung cover; DeadWood = cover of dead woody debris > 2.5 cm; AGC of methusalem trees was not included in PCA as it only concerned very few plots and therefore had non-visible arrow in PCA biplot.*

Our central reference point for assessing land-use change impacts consists of areas that are under no specific land-use and only mildly disturbed by wildlife or humans (L). These low-disturbance areas were often found in further distance from the riverbank with soils tending to be sandy and the disturbance regime being dominated by wildfires but otherwise being mostly undisturbed. Diverting from there, plots belonging to the conservation pathway are shaped by increasing levels of herbivore densities in wild browsers as well as wild grazers and mixed-feeders (see **Figure S3**). The higher the herbivore disturbance levels, the lower the fire intensity appears to be. Conservation pathway plots were found in greater distance to schools, representing further distance from larger settlement areas. In plots belonging to the agricultural intensification pathway on the other hand increasing levels of anthropogenic disturbances were recorded such as woodcutting activities and density of domestic grazer species. Notably, the spreading of plots along the agricultural intensification pathway were driven also by soil fertility indicators that seem to be positively related to intensifying anthropogenic land-use.

Out of the eight predictors selected after PCA (see highlighted in red in **Figure S3**) six are disturbance factors, and two represent soil resources: Browsing intensity in the tree layer (>3 m) and shrub layer (<3 m) are complemented with wild grazer density as evident from tracks and dung counts to represent the disturbance of increasing levels of wild herbivores through ongoing conservation actions. Browsing intensity was highly correlated to elephant density and density of others browsers, hence these factors had to be excluded from modelling. Woodcutting intensity (including methods like ringbarking and field

clearing as typical for shifting agriculture practices) and domestic grazer density as evident from livestock dung and tracks represent the direct and indirect anthropogenic disturbances under agricultural intensification schemes. Fire intensity of wildfires was included in the models to represent fire as a typical disturbance agent of savanna ecosystems and loaded strongly on the second PC axis. Lastly, soil Nitrogen content and total Cation Exchange Capacity (CEC) were chosen as predictors of edaphic resources, thereby comprising several nutrients. Soil sand content was correlated negatively and clay content was positively correlated to nutrients and hence both were unsuitable for modelling together with nutrient contents. Groundcover variables loaded less heavy on the PC axes and were highly correlated to each other and to selected disturbance predictors. Distance to river and distance to settlement were excluded from further analysis as they directly represent the sampling approach by which we assured the coverage of steep disturbance gradients. Tree canopy area was excluded from the further analysis as it is directly related to tree biomass and hence carbon storage per plot.

Table S1: *Loadings of potential environmental predictors on first three axes of Principal Component Analysis (PCA, see **Figure S3**); highlighting follows a gradient from most negative values (red) to most positive loadings (blue); * predictors selected for modelling (in red font).*

| Potential environmental drivers of carbon storage	loading on PC1	loading on PC2	loading on PC3
Elephant density	-0.254	0.275	-0.151
Wild grazer density *	-0.245	0.178	-0.052
Distance to nearest school, i.e. to larger settlement	-0.231	0.039	0.125
Browsing intensity tree layer *	-0.226	0.282	-0.001
Browsing intensity shrub layer *	-0.218	0.253	-0.093
Sand content in soil	-0.201	-0.261	-0.228
Dead woody debris ground cover	-0.195	0.082	0.018
Litter ground cover	-0.185	-0.054	0.059
Tree canopy area	-0.184	-0.134	0.042
Dung ground cover	-0.150	0.319	-0.033
Other browser density (aside from elephant)	-0.139	0.241	-0.302
Moribund grass cover	-0.136	0.085	0.349
Charcoal particle ground cover	-0.087	0.091	0.128
Fire intensity *	0.005	-0.216	0.202
Grass ground cover	0.020	0.116	0.493
Distance to nearest river	0.035	-0.224	0.131
Silt soil content	0.106	0.257	0.282
Nitrogen concentration in soil *	0.145	0.247	-0.143
Bare ground cover	0.152	-0.084	-0.441
pH of soil	0.199	0.055	-0.086
Domestic grazer density *	0.217	-0.092	0.064
Clay soil content	0.224	0.173	0.137
Calcium concentration in soil	0.229	0.279	-0.076
Kalium concentration in soil	0.233	0.091	-0.129
Magnesium concentration in soil	0.250	0.218	0.100
total CEC (cation exchange capacity of soil) *	0.261	0.241	-0.008
Woodcutting intensity *	0.277	-0.016	-0.055
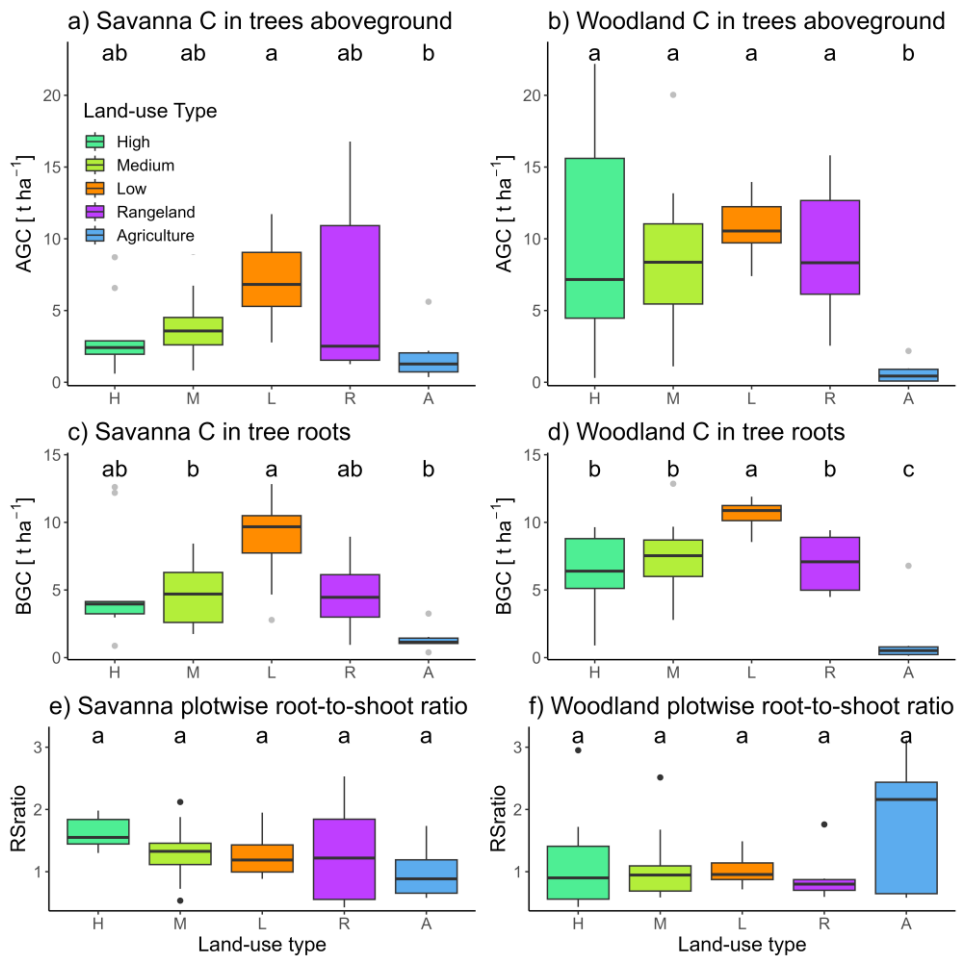
Figure S4: *Carbon storage and root-to-shoot (RS) ratios on plot-level of trees and shrubs combined, for savanna and woodland vegetation, respectively; a-b) aboveground carbon storage (AGC); c-d) belowground carbon storage (BGC) in roots; e-f) plot-level RS ratio from estimated AGC and BGC. H = High elephant density, M = Medium elephant density, L = Low elephant density and low human disturbance, R = Rangelands, A = Agricultural fields; C = carbon.*

Table S2: *Mean carbon storage per land-use type, C pool, and vegetation type; AGC = aboveground carbon stored in trees and shrubs, BGC = belowground carbon stored in trees' and shrubs' root biomass, SOC = soil organic carbon 0-100 cm soil depth.*

Vegetation type	Land-use type	mean AGC [t ha⁻¹]	AGC loss [%] to Low	mean BGC [t ha⁻¹]	mean SOC [t ha⁻¹]	C stock sum [t ha⁻¹]
Savanna	High	3.2 ± 2.5	54.9	5.1 ± 3.9	33.7 ± 5.5	42.0
	Medium	4.0 ± 2.4	43.7	4.6 ± 2.3	30.1 ± 6.9	38.7
	Low	7.1 ± 2.7	0	8.8 ± 3.1	27.7 ± 4.4	43.6
	Rangeland	6.3 ± 6.9	11.3	4.7 ± 2.9	30.3 ± 10.1	41.3
	Agriculture	1.9 ± 1.9	73.2	1.4 ± 1.0	37.4 ± 2.9	40.7
Woodland	High	9.4 ± 7.7	13.8	6.3 ± 2.9	27.6 ± 2.8	43.3
	Medium	8.8 ± 5.3	19.3	7.5 ± 2.8	26.5 ± 3.9	42.8
	Low	10.9 ± 2.0	0	10.6 ± 1.0	25.8 ± 6.1	47.3
	Rangeland	9.1 ± 5.0	16.5	7.0 ± 2.2	39.4 ± 9.5	55.5
	Agriculture	0.7 ± 0.8	93.6	1.5 ± 2.6	41.2 ± 4.2	43.4
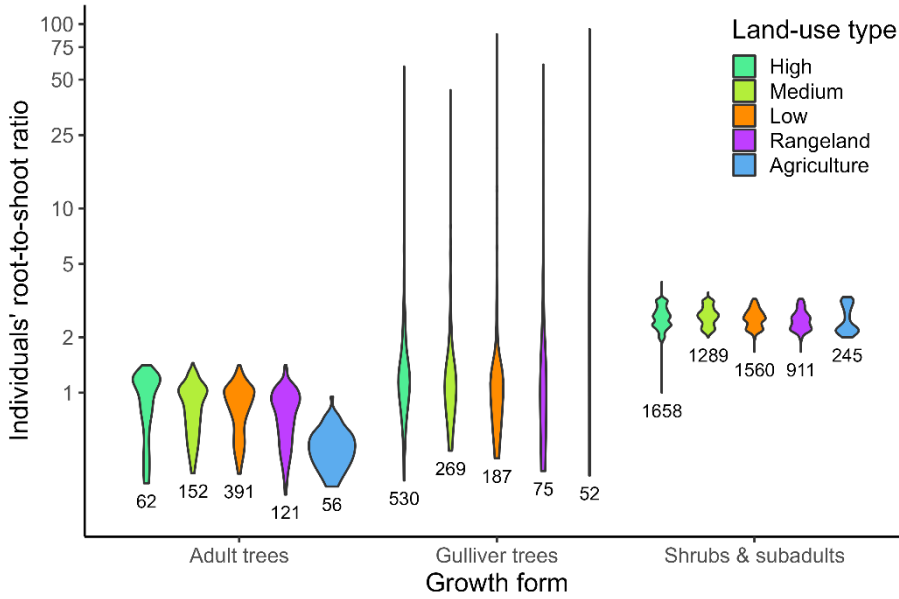
Figure S5: *Root-to-shoot ratio of all tree and shrub individuals (n=7,558) that were measured with dendrometric proxies; calculated after biomass loss assessment as BGCact/AGCact. Adult trees = basal stem diameter >5 cm & aboveground biomass losses <30%; Gulliver trees = adult trees with aboveground biomass losses >30%; Shrubs & subadults = shrub species, subadult trees (basal stem diameter <5 cm) and shrub-like gullivers; numbers below each violin plot indicate number of individuals included in each group.*
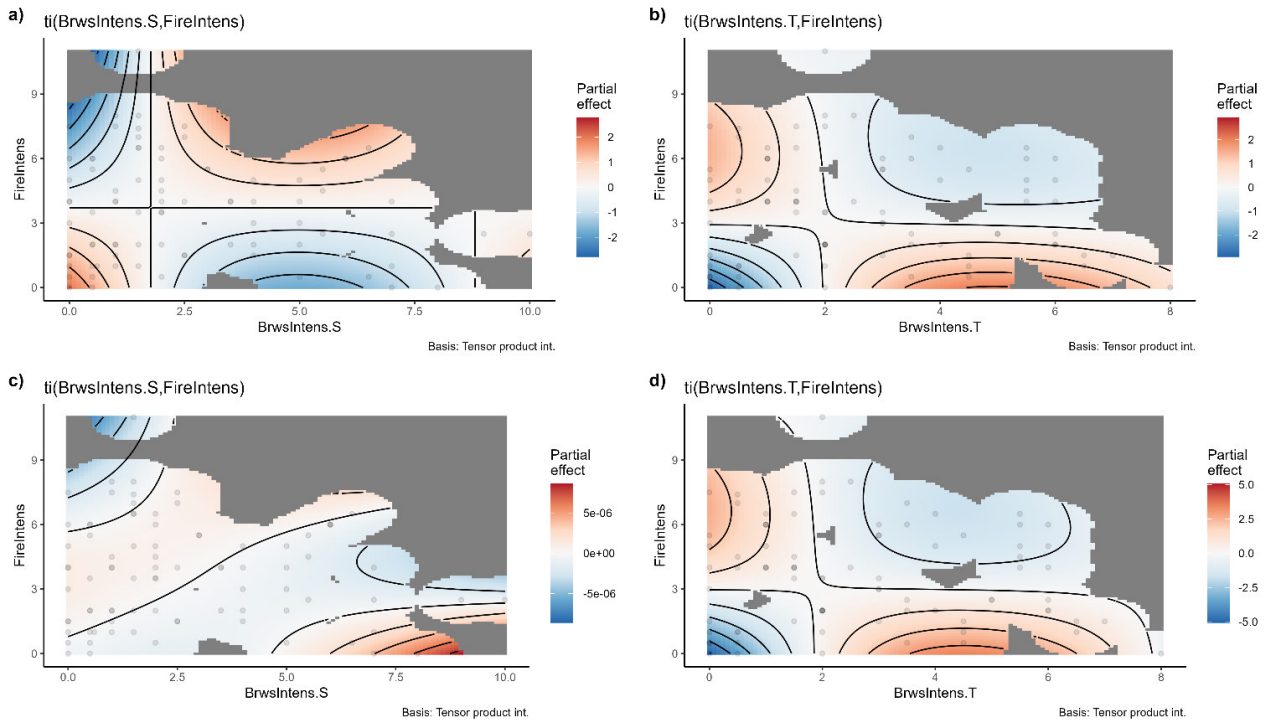
Figure S6: *Partial effect plots for interaction term smoothers displaying the joint, interactive effect of fire intensity (FireIntens) with browsing intensity (BrwsIntens) for both GAMM models; in tree layer (.T, >3 m) and shrub layer (.S, >3 m), respectively; a) & b): AGC model, c) & d) C_{total} model; red hues indicate a joint positive effect on carbon stocks while blue hues indicate a joint negative effect on carbon stocks.*

Suppl. 2: Generalized Additive Models (GAMs)
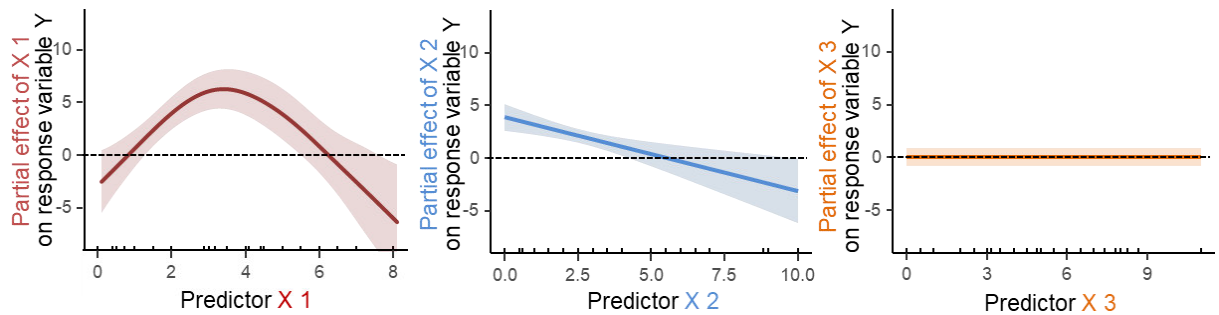
Figure S7: *Example of what a GAM output typically looks like for three hypothetical predictors (X 1 to X 3), see description below.*

In this example (Figure S7) the visual GAM outputs would be interpreted like this:

➢ If we could hypothetically hold all other predictors in the model at fixed values and only let X 1 vary, the response variable would first increase at lower levels of X 1 but eventually tip over and undergo reduction where X 1 exceeds values of ~3.5. This predictor therefore is demonstrated to have an essentially unimodal and non-linear effect on the response variable.

➢ Holding all other predictors in the model at fixed values and only allowing X 2 to vary, we would observe a negative linear effect of X 2 on the response variable; this also indicates that the GAM has detected no evidence of improved model performance by allowing X 2 to have a non-linear influence on the response variable and has therefore reduced its smoother to a linear model term.

➢ Smoother curve for predictor X 3 is identical with the horizontal mean zero line as the GAM has found this predictor to be non-significant for modelling the response variable; in such a case X 3's impact on the model is "set to zero" (i.e. the GAM assigns zero estimated degrees of freedom (edf) to X 3), meaning it is effectively selected out of the model.

Table S3: *Model summary AGC*

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	4.827	0.539	8.951	0	***
	veg_typeWoodland	3.281	0.801	4.095	0.0001	***

Component	Term	edf	Ref. df	F-value	p-value	
B. smooth terms	s(veg_type)	0	2	0	0.0019	**
	s(BrwsIntens.S)	0.924	9	1.343	0.0003	***
	s(BrwsIntens.T)	2.61	9	2.383	0	***
	s(WildGrzDens)	2.568	9	3.285	0	***
	s(WoodcutIntens)	1.91	9	1.482	0.0003	***
	s(DomGrzDens)	0.87	9	0.147	0.5877	
	s(FireIntens)	0	9	0	0.8574	
	s(Nitrogen)	0.837	4	1.284	0.011	*
	s(totalCEC)	0.765	9	0.361	0.032	*
	s(MethusalemAGC)	2.015	9	10.925	0	***
	ti(BrwsIntens.S,FireIntens)	0.814	4	1.092	0.0133	*
	ti(BrwsIntens.T,FireIntens)	1.525	4	1.719	0.0049	**

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05 < '.' < 0.1

Adjusted R²: 0.801, Deviance explained 0.839

-REML: 208.453, Scale est: 5.417, N: 84

Formula: **AGC** ~ veg_type + s(veg_type, bs='re') + s(BrwsIntens.S) + s(BrwsIntens.T) + s(WildGrzDens) + s(WoodcutIntens) + s(DomGrzDens) + s(FireIntens) + s(Nitrogen, k = 5) + s(totalCEC) + s(MethusalemAGC) + ti(BrwsIntens.S, FireIntens, k = 3) + ti(BrwsIntens.T, FireIntens, k = 3)

Table S4: *Model summary C_total*

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	42.474	1.277	33.261	0	***
	veg_typeWoodland	2.581	1.894	1.363	0.1774	

Component	Term	edf	Ref. df	F-value	p-value	
B. smooth terms	s(veg_type)	0	2	0	0	***
	s(BrwsIntens.S)	0.855	9	0.657	0.0081	**
	s(BrwsIntens.T)	2.059	9	0.866	0.0109	*
	s(WildGrzDens)	2.164	9	2.029	0.0001	***
	s(WoodcutIntens)	1.721	9	1.062	0.002	**
	s(DomGrzDens)	0.685	9	0.241	0.0521	.
	s(FireIntens)	0	9	0	0.7793	
	s(Nitrogen)	2.02	4	5.735	0	***
	s(totalCEC)	0.88	9	0.814	0.0037	**
	s(MethusalemAGC)	1.413	9	1.764	0.0001	***
	ti(BrwsIntens.S,FireIntens)	0	4	0	0.755	
	ti(BrwsIntens.T,FireIntens)	1.366	4	1.523	0.0094	**

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05 < '.' < 0.1

Adjusted R²: 0.618, Deviance explained 0.684

-REML: 275.764, Scale est: 30.304, N: 84

Formula: **C_total** ~ veg_type + s(veg_type, bs='re') + s(BrwsIntens.S) + s(BrwsIntens.T) + s(WildGrzDens) + s(WoodcutIntens) + s(DomGrzDens) + s(FireIntens) + s(Nitrogen, k = 5) + s(totalCEC) + s(MethusalemAGC) + ti(BrwsIntens.S, FireIntens, k = 3) + ti(BrwsIntens.T, FireIntens, k = 3)

Note: edf = estimated degrees of freedom, AGC = aboveground woody carbon, Brws = browsing, CEC = cation exchange capacity, C_total = whole-ecosystem carbon storage, DomGrz = domestic grazers & mixed-feeders, Intens = intensity, S = in shrub layer (<3 m), T = in tree layer (>3 m), veg_type = vegetation type, WildGrz = wild grazers & mixed-feeders.
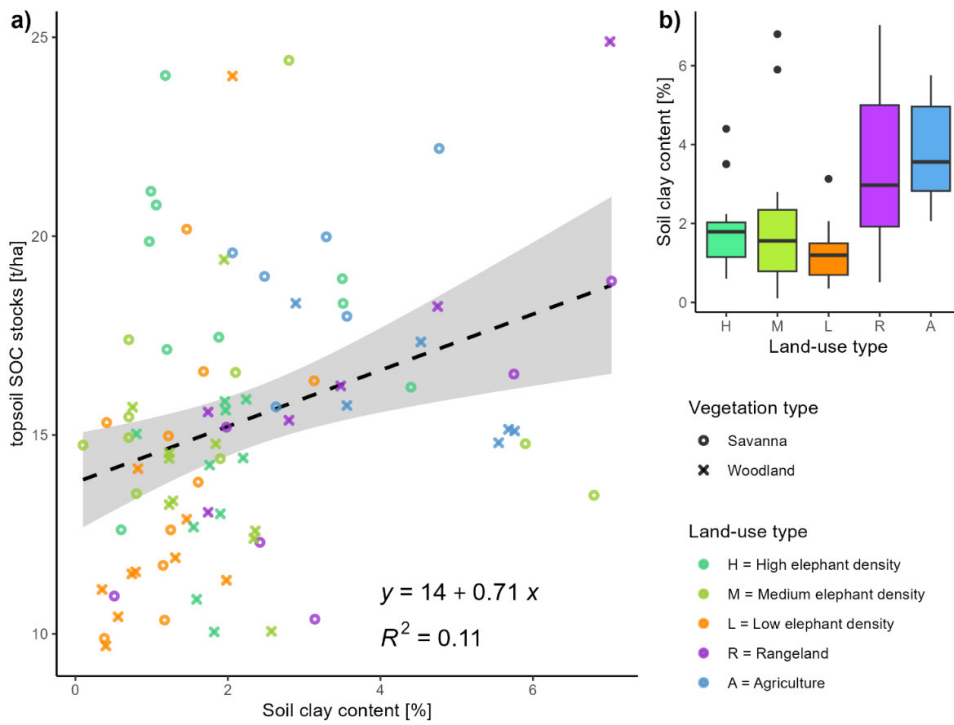
Figure S8: *Relation between soil texture and topsoil SOC. Although texture and in particular soil clay content is relevant for soil carbon storage it was not found to be a significant factor in GAMM for Ctotal. Higher clay contents in rangelands and agricultural fields hind to a selection bias through farmers.*
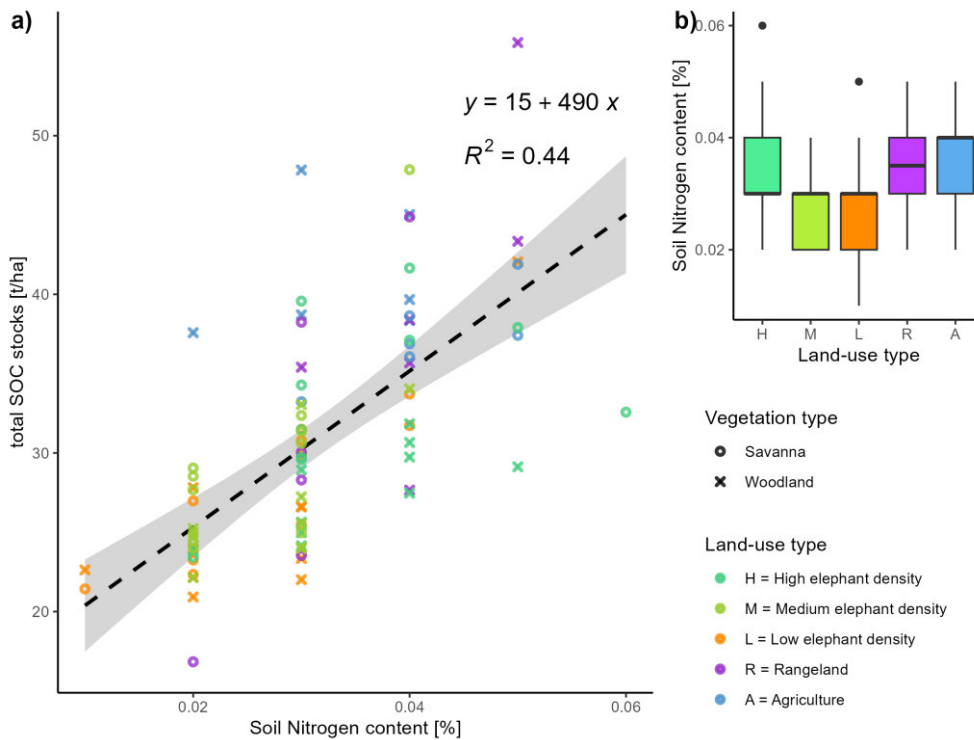
Figure S9: *Relation between soil Nitrogen content and SOC stocks.*
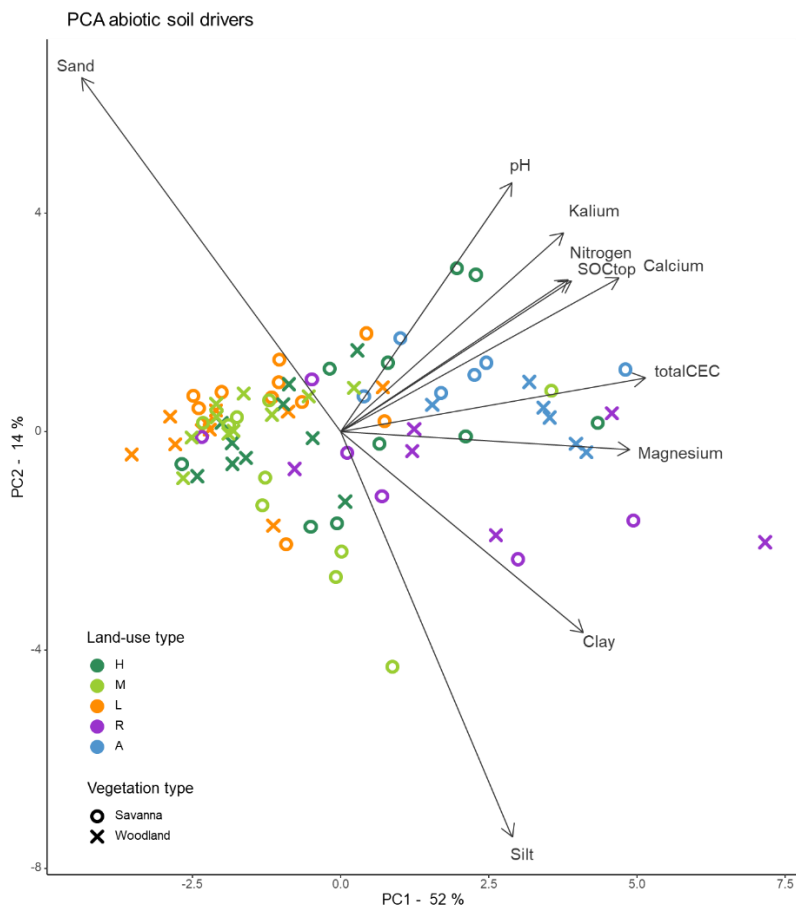
Figure S10: *Principal component analysis (PCA) on soil resources and abiotic soil variables; Woodland and Savanna vegetation types are not created by soil type differences, but rangelands and agricultural fields are characterized by more fertile soils; H=High elephant densities, M=Medium elephant densities, L=Low elephant densities and low human disturbance, R=Rangelands, A=Agricultural fields.*

Chapter 6: Synthesis & Discussion

Methodology

In my thesis and the papers included in it, I have demonstrated and analysed weaknesses of existing methodological approaches to carbon storage estimation in open and disturbance-prone ecosystems such as savannas. Furthermore, I identified sources for both potential over- and underestimations of carbon storage which have resulted from application of unspecific standard forestry protocols to a disturbance-prone ecosystem. Moreover, I have quantified the resulting uncertainties introduced by specific error sources, which is a requirement for many carbon accounting protocols (Kachamba et al. 2016). For instance, where tree inventories use minimum size thresholds commonly applied in forest inventories, only a small fraction of tree individuals are recorded in a savanna ecosystem. My case study showed that the conventional method would have recorded only 266 bigger trees while in the same subset of my thesis data my proposed method captured more than 6,100 woody individuals of varying sizes, age classes and disturbance states. As such, the conventional method would only have accounted for 4.3% of the individuals. This discrepancy would have resulted in a substantial underestimation of woody biomass on stand level (up to 90%), as demonstrated for two savanna vegetation types and three levels of increasing elephant disturbance (**Figure 10** and **Figure 11**).
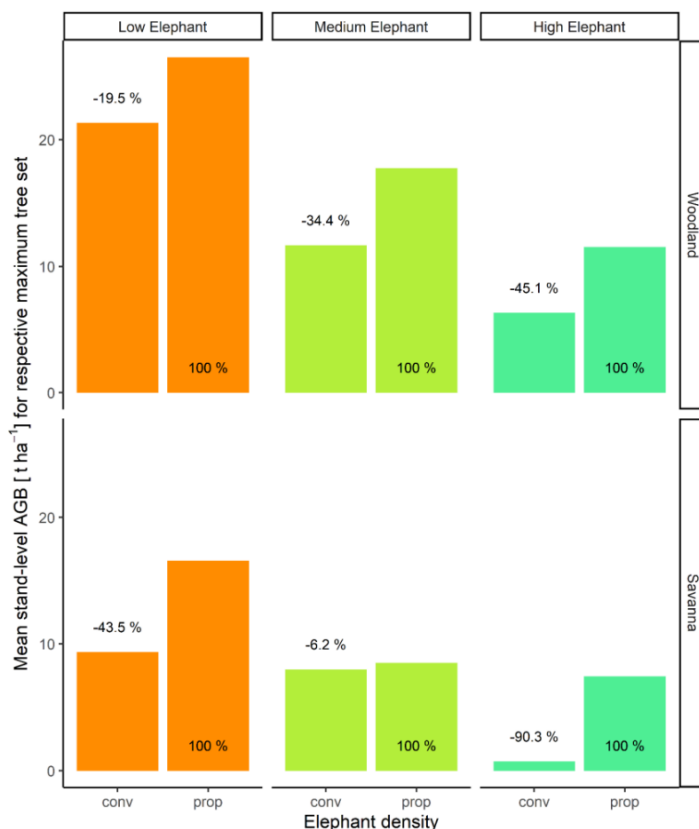
Figure 10: Mean stand-level aboveground woody biomass (AGB) estimated with my proposed method in Chapter 2 & 3 (prop) and relative underestimation thereof when applying conventional size threshold of DBH ≥ 5 cm (conv). Method comparison was tested in two vegetation types (savanna & woodland) and across three levels of increasing disturbance from low elephant densities in communal conservancies to high elephant densities at national parks' intensely frequented elephant spots. Figure taken from pre-print version of Chapter 2 (Kindermann, L., Dobler, M., Niedeggen, D., Linstädter, A., 2020. Improving estimation of woody aboveground biomass in drylands by accounting for disturbances and spatial heterogeneity. Preprint, Institute of Crop Science and Resource Conservation (INRES), Bonn, Germany. DOI: 10.5880/TRR228DB.5).
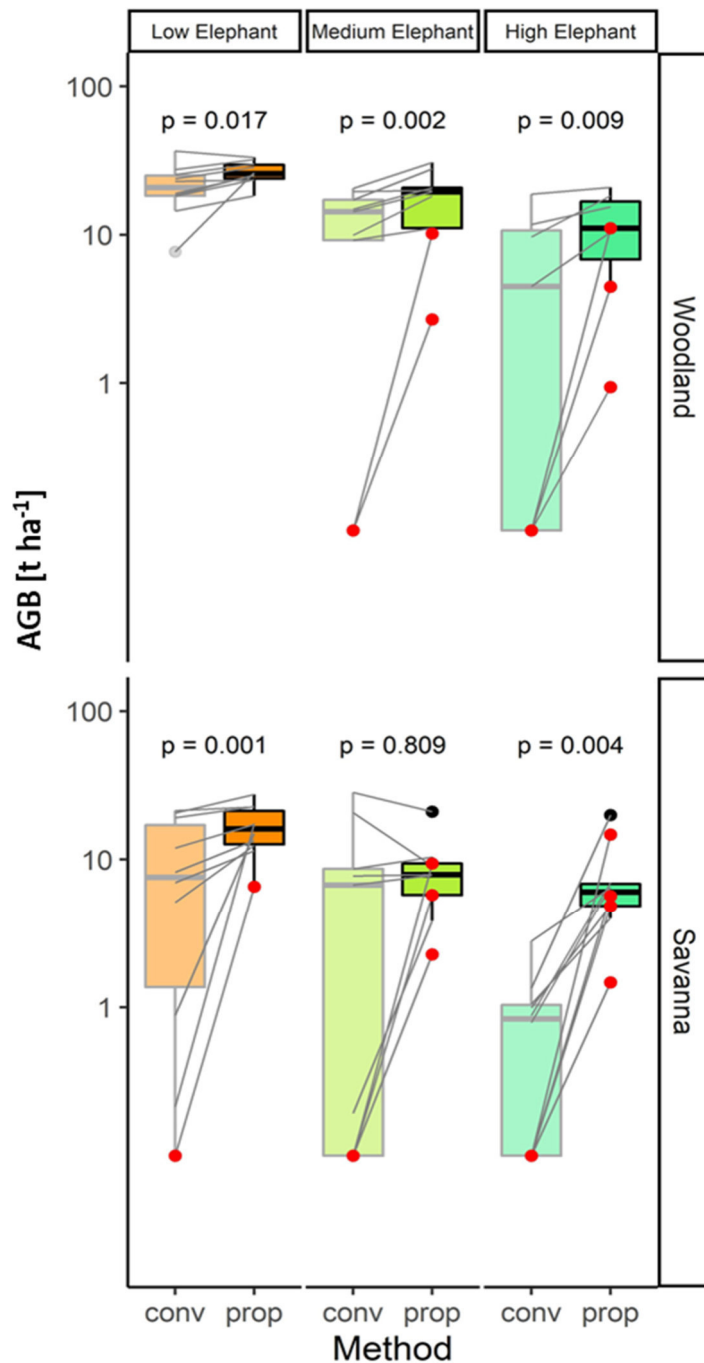
Figure 11: *Stand-level aboveground woody biomass (AGB) when employing a method with conventional forestry size threshold (conv; DBH ≥ 5 cm, n=266 trees) in comparison to method proposed in Chapter 2 (prop; n=6,179 trees, shrubs & gullivers that were subjected to damage assessment) across three levels of increasing disturbance from low elephant densities in communal conservancies to high elephant densities at national parks' intensely frequented elephant spots. Observation plots devoid of any trees above the conventional size threshold would have yielded zero AGB with conventional forestry method and are highlighted in red; significant differences between conventional and proposed method were tested with pairwise two-tailed T-tests; method comparison was reproduced across two representative vegetation types: open scrub savanna and taller, more closed savanna woodland vegetation.*

Figure taken from pre-print version of Chapter 2 (Kindermann, L., Dobler, M., Niedeggen, D., Linstädter, A., 2020. Improving estimation of woody aboveground biomass in drylands by accounting for disturbances and spatial heterogeneity. Preprint, Institute of Crop Science and Resource Conservation (INRES), Bonn, Germany. Online available at DOI: https://doi.org/10.5880/TRR228DB.5).

Furthermore, my analyses also demonstrate that damage assessment of individual trees can be crucial if they have sustained multiple, chronic and occasionally severe disturbance events. In contrast, adhering to a method that solely relies on a few allometric proxies and ignores large portions of missing biomass would have resulted in mean relative biomass overestimation on individual tree level of 23% to 368% (**Figure 12**).
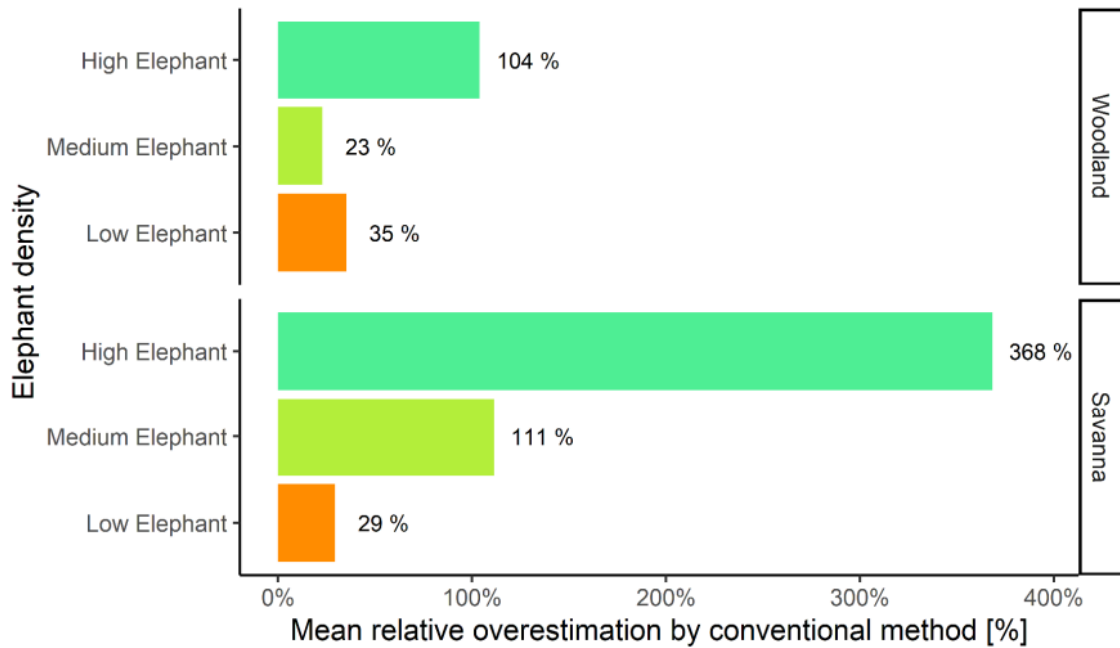
Figure 12: *Mean relative overestimation of individual trees' aboveground biomass in absence of a suitable damage assessment that in my proposed method corrects allometric estimations from size proxies according to apparent missing portions of trees' crowns and stems; see damage assessment as proposed in Chapter 2 and Chapter 3. Figure taken from pre-print version of Chapter 2 (Kindermann, L., Dobler, M., Niedeggen, D., Linstädter, A., 2020. Improving estimation of woody aboveground biomass in drylands by accounting for disturbances and spatial heterogeneity. Preprint, Institute of Crop Science and Resource Conservation (INRES), Bonn, Germany. DOI: 10.5880/TRR228DB.5).*

Importantly, my analyses demonstrate, that first of all, my proposed estimation method was more accurate in that it certainly reduced spread of data i.e. biomass estimates for plots belonging to the same land-use type showed much smaller variance than with conventional approaches (see **Figure 11**). Second of all, the potential errors introduced by application of unsuitable methods were strongly increasing with higher disturbance levels in woody vegetation, which indicates the increasing relevance of adapting methods to ecosystem-level disturbance the more disturbed the vegetation becomes (**Figures 10-12**).

I further demonstrate that improved alternative protocols and adapted methodologies can increase the accuracy of carbon storage assessments when different growth forms, their specific allometries and their often-disturbed state are properly integrated into measurement protocols and estimation procedures. This becomes apparent when analysing also belowground woody biomass due to particularly high root-to-shoot ratios that can be found in savanna ecosystems. Specifically, I can demonstrate that shrubs and subadult growth hold relatively large carbon reserves in their roots compared to adult trees (as was to be expected), but even they are often dwarfed by some severely disturbed gullivers' root-shoot-ratios at an order of magnitude (see **Figure 13**).

This improved data accuracy and reduced uncertainty is especially relevant to making better spatial predictions and inform policy and program developments in relation to 'pro-poor' carbon storage (Stringer et al. 2012).
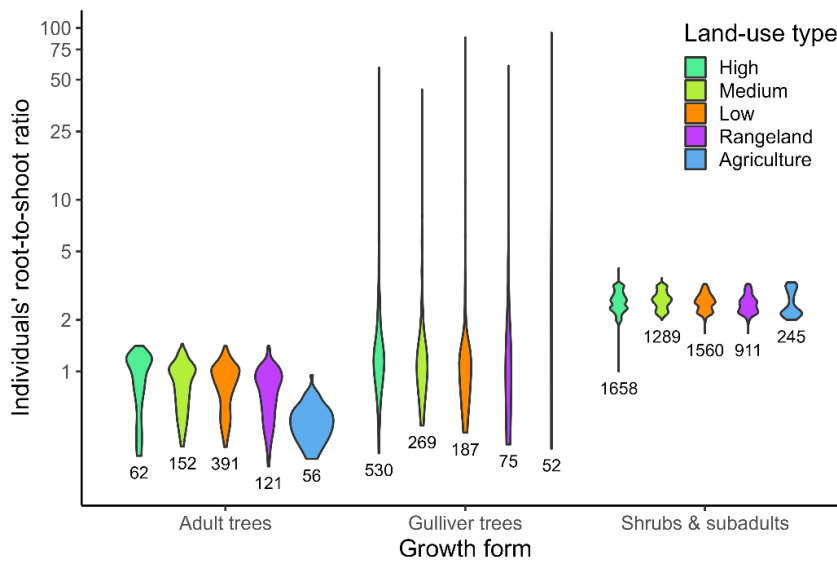

Figure 13: Individuals' root-to-shoot ratio of all recorded individuals; calculated after damages i.e. biomass loss assessment as [BGC/AGC]. Adult trees = basal stem diameter ≥5 cm & aboveground biomass losses <30%; Gulliver trees = basal stem diameter ≥5 cm & aboveground biomass losses ≥30%; Shrubs & subadults = shrub species, subadult trees (basal stem diameter <5 cm) and shrub-like gullivers. Numbers below each violin plot indicate number of individuals included in each group. Figure taken from Supplementary material of Chapter 5.

I have been able to demonstrate in Chapter 3 that the proposed methods and workflows can be implemented without unduly increasing the amount of work needed. In addition, the damage assessment does not only function to increase carbon storage estimation accuracy, but also serves another twofold purpose: it can i) quantify how much biomass is currently missing through disturbance impacts likely imposed by which disturbance agent and ii) be used for estimating pre-disturbance woody biomass levels from already disturbed vegetation (see **Figure 14**). This way, my proposed method can improve reference state comparisons also in landscapes in which currently no fully undisturbed reference state can be found. This is likely the case in many savanna ecosystems as total exclusion of disturbances in such open landscapes can only be accomplished by large-scale firebrakes, elephant-proof fencing, and with decades of experimental set-up (see for example Singh et al. 2018, Davies and Asner 2019, Coetsee et al. 2023) and therefore hinders space-for-time substitution approaches in ecology (McNellie et al. 2020). Furthermore, the method can be employed to harness the archival function of trees which in their distinctly altered growth forms, broken branches , scorch marks and cutting scars retain a record of their past disturbance experiences (Moncrieff et al. 2011, Levick et al. 2015) and can therefore be used to assess recent and past disturbance levels in a given landscape (Stringer et al. 2012, Johnstone et al. 2016, Tripathi et al. 2019, Rozendaal et al. 2022). For instance, **Figure 14** demonstrates that the low-disturbance reference sites in my space-for-time substitution are by no means un-disturbed, but trees and

shrubs growing there display high losses from wildfires and also damages attributable to elephant browsing. This demonstrates that even areas which are largely un-used are subjected to naturally strong disturbances although they are neither used for agriculture nor as a national park. Quantifying the biomass losses from this reference state and adding them to biomass currently alive and standing allows estimation of potential total biomass under disturbance-exclusion (see **Figure 14**).
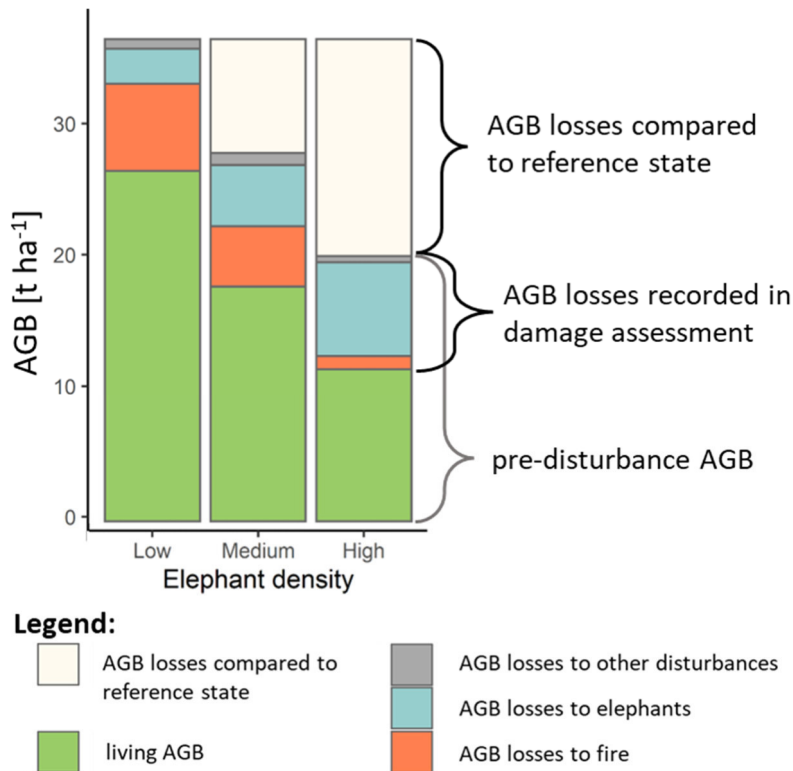
Figure 14: Mean stand-level aboveground woody biomass (AGB) of living trees, shrubs and gullivers and their recorded biomass losses per disturbance agent as evident from individual damage assessment. Across a gradient of increasing elephant density, the lowest elephant disturbance level can serve as a reference state comparison after its pre-disturbance AGB has been reconstructed from standing, living AGB plus recorded AGB losses. In relation, missing AGB at higher disturbance levels which cannot be accounted for during damage assessment on living trees is therefore considered to reflect AGB losses from tree and shrub mortality. Results shown here only represent woodland vegetation type. [Figure adapted from Chapter 3]

Materials and tools needed to apply the method were constraint to a minimum and can easily be obtained from average hardware stores or supplemented. For instance, where measuring of wood carbon content via CNS analyser is impossible, suitable values can be derived from my published data or e.g. the Global Wood Density Database (Chave et al. 2009, Zanne et al. 2009). I have designed the workflow in such a way that it can be freely adjusted to other researchers' needs, other disturbed ecosystems or research rationales, and be combined with other existing or potentially future allometric models. This method, the raw data or the results presented here will hopefully advance the general undertaking of estimating carbon storage in savannas or other disturbed ecosystems.

Interdisciplinary research and concepts

Interdisciplinary predictor sets

As argued above, the interconnections between human future-making, social concepts, economic plans and natural resources are strong and numerous in social-ecological systems. It is therefore not surprising that factors from all these sub-systems influence land-use decisions and land-use change in the study region. Through interdisciplinary work with my colleagues, I was fortunate to draw on a large set of variables during predictor selection in Chapter 5, including detailed edaphic and soil fertility indicators, distance of my observation plots to larger settlements which have been assessed in the central economic household survey of *Future Rural Africa*, and the detailed knowledge of wildlife species and wildlife ecology which my collaboration partners from University of Namibia and the national park rangers kindly shared with me. I will certainly continue to draw on these predictors and insights for future research and hope to further overcome disciplinary obstacles and barriers of scientific integration.

Drivers of carbon storage

Analyses in Chapter 4 demonstrated how closely vegetation carbon storage and soil carbon storage in conservation areas are linked. Although conservation areas with elevated elephant densities suffer a loss of woody aboveground biomass in relation to reference states with low elephant density, a larger fraction of the carbon previously contained in shrubs and trees is sequestered again in the soil organic carbon pool. In relation to Chapter 4 the analyses in Chapter 5 uncovered, that not all losses in aboveground carbon storage previously attributed to elephants are actually caused by elephants, but some also by fire. While Chapter 4 leans on the space-for-time substitution alone, the analysis of data on individual damage assessments in living trees and shrubs (Chapter 5, Figure 1b, d) demonstrates, that roughly a fifth of the biomass losses are attributable to disturbance by fire. National parks in Southern Africa are now subjected to active fire management, after decades of fire suppression in the name of nature conservation efforts had been found to have detrimental unintended consequences such as bush encroachment and rare but devastating late-dry-season fires (Davies et al. 2019, Nieman et al. 2021). However, these detailed biomass loss and disturbance impacts drawn from the archival function of trees have the disadvantage to only capture disturbance impacts on living vegetation, at least in a onetime assessment, and being oblivious to disturbance effects which are so severe that they cause not only biomass losses or topkills, but in fact cause tree mortality. Consequently, data on absolute biomass or aboveground carbon (AGC) losses from such a damage assessment can be misleading in so far that they can be high in areas of low disturbance levels, see Chapter 5, Figure S2. This demonstrates, how extensive

the sustained biomass losses in living savanna vegetation can be where species are adapted to live through them, regenerate and continue growing. To analyse in how far severe damages render tree individuals to subsequent death would therefore require a re-assessment after some years, but would help to quantify sustainable, i.e. in part survivable, disturbance intensity levels. The phenomenon outlined above led me to analyse the particular drivers of carbon storage via Generalized Additive Models (GAMs) which can help to disentangle additive effects of several predictors (see **Box 7**). However, the individual biomass losses were not used as predictors in those models for the circumstances outlined above. Instead, disturbance intensity assessments on plot level were employed here, specifically because they also regard signs of tree mortality and dead trees, see Chapter 5. The modelling of the drivers on carbon storage, including disturbance intensity from fire and browsing herbivores, then revealed, that the impact of fire disturbance alone did not result in reduced woody biomass or carbon storage. However, the models for both AGC and C_{total} contained two interaction terms for fire intensity in interaction with browsing intensity in tree and shrub layer, respectively (see Chapter 5, Figure S6, Table S3 and Table S4). The visual outputs of this interactions (here **Figure 15**, adapted from Chapter 5, Figure S6) demonstrate that the interaction between these two disturbances is complex and contrasting between tree and shrub layer.
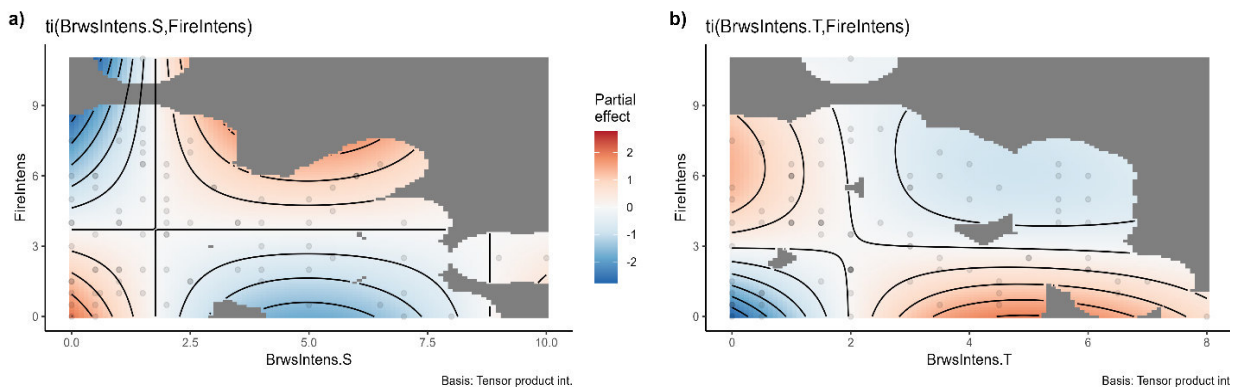
Figure 15: *Partial effect plots for interaction term smoothers displaying the joint, interactive effect of fire intensity (FireIntens) with browsing intensity (BrwsIntens) for GAM on aboveground carbon storage (AGC); in a) shrub layer (.S, >3 m) and b) tree layer (.T, >3 m), respectively; red hues indicate a joint positive effect on carbon stocks while blue hues indicate a joint negative effect on carbon stocks. [Figure taken from Chapter 5 Suppl.]*

In the shrub layer, non-surprisingly, low browsing intensity together with low fire intensity drives high AGC, but the same holds true for intermediate browsing intensity at intermediate fire intensity (red hues in **Figure 16a**); in contrast, both high fire intensity without browsing of the shrub layer and also intermediate browsing intensity at low-fire intensities were related to low levels of AGC (blue hues in **Figure 16a**). Interestingly, the pattern seems to be exactly opposite for the interactive effects of fire with browsing in the tree layer (see **Figure 16b**). In comparison to the shrub layer, higher fire intensities in interaction with browsing in the tree layer expresses less pronounced

impacts on AGC which matches the observation that woody vegetation taller than 3 m often escaped the fire trap, i.e. the height in which ground fires commonly harm or kill woody vegetation (Asner and Levick 2012, Levick et al. 2015). The analogous elephant trap, however, is higher off the ground, as elephants mainly target trees in layer of 5-9 m (Asner and Levick 2012), which implies that for a tree to reach a save height it would need to grow taller than 9 m. This height was rarely acquired by trees in the open savanna vegetation type (n=38) but reached more often in the woodland vegetation type (n=117), which partly explains why vegetation type is a significant predictor in the model. Interestingly, my analysis demonstrates, that at low fire intensities a low browsing intensity in the tree layer is related to overall lower AGC, and increasing browsing intensity in the tree layer is related to higher AGC. One possible explanation is that browsing in the tree layer opens up the canopy and therefore allows more woody vegetation in the shrub layer. The other possible explanation is that this result is an effect of few but very old and big trees ('methusalems') which have escaped both the fire and the browser trap in historical times of unnaturally low disturbance intensities in the study area (Skarpe et al. 2014, Bollig and Vehrs 2021). The high partial effect of methusalems' AGC on overall AGC is a strong indicator that this could be the case, however this theory remains to be tested in my future work. For instance, the dendrometric measurements of stem diameters in connection with a dendrochronological analysis of existing wood core samples allows growth-rate estimations and therefore an age-determination of large trees in my dataset (Coetsee et al. 2023). In connection to historical wildlife and fire data this could reveal which large trees in my dataset were already well-established and grown through fire and browser trap at the onset of elephant conservation and active fire management, respectively. In a hybrid-historical reference state comparison (McNellie et al. 2020), this would allow me to ascertain if not many more large trees from my dataset can be regarded to be methusalems. This question is relevant in so far, as we cannot expect a new cohort of methusalems to establish in this region under current and projected near-future disturbance levels and therefore would have to expect current carbon storage to decline once all methusalems die of old age; the larger the actual set of methusalems is, the stronger this phenomenon will impact future carbon storage. Also of interest is the question in how far vegetation types will still differ in their vegetation structure if no more large trees will establish, and in how far the savanna vegetation type may be better adapted to this future than the woodland vegetation type of this study area, as the former presumably contains more species that can withstand continuous, intense elephant browsing, such as *Terminalia sericea*.

Conceptual future-making framework fosters transdisciplinary integration

The overarching concept of future-making that shapes the collaborative research centre *Future Rural Africa* reinforced my research within a highly interdisciplinary context. In my research, I have

focused on practices of future-making that are expressed as land-use change. Decisions like allocating land to communal conservation efforts or alternatively to agricultural production are driven by very basic needs but follow logics of future-making in so far, that people hold ideas of the future and anticipate certain outcomes when advocating for one option or the other. Especially one inherent dichotomy that is typical for rural Africa is the decision between extension of wildlife conservation areas versus intensified agricultural production. In my research I have conceptualized this future-making in the form of two alternative land-use change pathways (agricultural intensification versus wildlife conservation) which formed the conceptual foundation for my land-use change analyses (see **Box 1**). As such, these pathways have more dimensions apart from the natural-ecological one and therefore, the integration of results across disciplines working on the same social-ecological system was essential to grasp the larger picture.

For instance, jointly selecting representative and comparable land-use types for a harmonized sampling design has already proven very useful on the level of closely related disciplines. In my case, I aimed to produce a joint dataset together with the soil sciences in which all plot observations are supported by entire data overlap. Whereas I would have likely opted for a fully randomized plot selection within each land-use type and stratified across two vegetation types, the soil scientists raised my awareness for the heterogenous soil conditions in the larger study region and opted for randomized sampling not only within land-use and vegetation types, but also within one and the same soil type (deep sandy Arenosols, in our case). By following this approach, the joint analyses in Chapter 4 and Chapter 5 became possible. This way, we discovered that much of the aboveground woody carbon destroyed and consumed by elephants was in fact not lost from the ecosystem but rather redistributed to the soil compartment. The detailed recognition of soil types even allowed us to uncover the highly interesting selection bias through farmers who, among the deep Arenosol areas in the study region, had successfully managed to identify the more fertile and carbon richer patches, which became essential for putting our results of carbon persistence into perspective.

This insight has also decisively shaped our research rationale for subsequent research in the current funding phase of *Future Rural Africa*, in which we aim to understand to what extent ecological knowledge of farmers or their wealth and education level impact their site selection when planning new fields (see e.g. additional publication No. 4: "Unravelling the relationship between rural farm household wealth, carbon storage, and natural resources in Namibia's Zambezi Region" that is currently in preparation). This research will again require joint analyses with economists in our project, but also it will link our work to historians of project *A02 Past Futures*, who aim to reconstruct historic settlement processes in the region that led to the allocation of land to different communities. Without their insights, we would never be able to rule out such cofounding factors from solely focusing on our plant-ecology and soil science results. Moreover, in ongoing research

we investigate whether farmers value trees as a natural resource base or rather an obstacle and to what extent household wealth of farmers determines whether they retain which trees in their fields. It will be of interest to investigate the farmers' ideas and motivations to make these kinds of decisions, which principally is a form of future-making. This question again connects us to anthropologists working in the region of study and I would like to collaborate with them to jointly analyse their results from qualitative interviews with quantitative interviews on local ecological tree knowledge that I have gathered.

Figure 16: *Deep sandy soils in the study region; Wuparo Conservancy, Namibia, 2018; source: own photo.*

With part of the data gathered for my thesis I am currently participating in an interdisciplinary publication between soil sciences, agricultural economics, and anthropology (project *A04 Future Conservation* of *Future Rural Africa*) in which we seek to understand how past, current and future refaunation processes with either wildlife or livestock impact the social-ecological system (Publication is currently under review with Conservation Biology, but can be accessed as a preprint: Bollig et al. 2024). While interdisciplinary data analysis, especially across distant disciplines as in the above example, have proven to be demanding and time-consuming, the joint framework of future-making as a focal point has efficiently guided our debates and our work process.

The same holds true for another interdisciplinary publication in which I am currently analysing my data on woody vegetation together with virologists from project *B02 Future Infections*, with whom

I have created a joint dataset, again through close collaboration and harmonized joint sampling design achieved through extensive planning in the past. Guided by the One Health approach, I am using my vegetation data, their data on mosquito species, and data on wildlife and domestic herbivores to calculate abundance and biodiversity at several ecosystem levels. We complement this analysis by literature-derived traits on mosquito species' known medical importance to test the hypothesis that higher diversity in one ecosystem level cascades to other trophic levels and thereby dilutes potentially threatening mosquito species in the species pool. We aim to understand if medical threats from mosquito-borne diseases can be buffered through high biodiversity, which would be directly beneficial to humans. This publication is currently under preparation but in an advanced stage (see additional publication No. 3: "Mosquito-borne disease risks in African savannas: A One-Health perspective on the role of land-use change").

Figure 17: *Elephant's footprint on the ground; researcher's foot for scale (EU size 42); Wuparo Conservancy, Namibia 2018.*

Persistence

Another example in which inter-disciplinary collaboration informed my research is the concept of persistence as applied in Chapter 5 of this thesis. The integration of data from the soil sciences into my analyses had proven essential, especially after results of Chapter 4 had indicated the strong link between soil organic carbon (SOC) stocks and woody vegetation biomass where a large fraction of the former was derived through elephant feeding on the latter. Despite this link, that in Chapter 4 also only had been analysed for the conservation pathway, SOC and aboveground woody carbon (AGC) are still inherently different compartments of the ecosystem. While vegetation often undergoes comparatively fast changes as it is directly exposed to all sorts of disturbance impacts such as woodcutting, fire or browsing by mega-herbivores, SOC stocks on the other hand are a typical slow-turnover carbon pool that often only changes on decadal time scales and can be centuries old (Shi et al. 2020, Kristensen et al. 2022, Zhou et al. 2022b). From historical reconstructions conducted by project partners (Bollig and Vehrs 2021) but also others (Skarpe et al. 2014) I knew that land-use and human population in the study region had undergone several major

fluctuations since the 19th century due to war, diseases, colonial policies and resource exploitation. I therefore had to recognize that areas now sampled as representatives of a certain land-use type (such as rangeland, cropland or national park) with a high likelihood had been un-used, under-utilized and largely devoid of farmers and animals for longer timespans in recent history (Skarpe et al. 2014, Bollig and Vehrs 2021). This could have had problematic implications within the framework of my space-for-time substitution approach (see **Box 1**) as that largely draws on the concept of holding sampling sites of one land-use type as representatives of a past state in the larger area and compare it to others as if they were fixed, distinctly different land-use categories. In light of the historic analyses, however, we had to recognize, a) that land-use change differences have happened fairly recently in relation to lifetimes of large trees and centuries-old SOC stocks, b) that also sites we use as a reference state have undergone a certain amount of change as both human and wildlife populations have been distinctly increasing all over the study area during the past decades, and c) that we have to be aware of lag-effects rooted in the period of very low human and wildlife disturbance levels.

For analysing changes of carbon stored in compartments of different reaction times across such a land-use gradient a suitable concept was needed. We found the solution in the concept of carbon persistence as recently proposed by Kristensen et al. (2022) in which persistence is the inverse likelihood of carbon stored in a certain compartment to experience losses through disturbances. In their approach, carbon stored in different ecosystem compartments is thought to fall along a general continuum from aboveground biomass as the least persistent to SOC as the most persistent carbon pool (Kristensen et al. 2022). However, my collaborating soil science partners informed me that within their discipline the term 'persistence' is rather narrowly defined and describes the stochastic process of turnover or the measurable mean residence time of soil organic matter (Sierra et al. 2018). In a collaborative effort we have succeeded to integrate these different perspectives and reconceptualize carbon persistence as the relative change in carbon storage between the low-disturbance reference state and other land-use types in the space-for-time substitution. As such, persistence is still a means to quantify changes in carbon storage, although these are not purely absolute but relative changes (in comparison to sites with similar historic background but different recent land-use change). The relative comparison hence accounts for the fact that historical lag-effects are potentially present in all land-use types. Moreover, this conceptualization of persistence allowed us to assess relative persistence of different carbon compartments in comparison to each other. We therefore were able to test to what extent the hypothesized persistence continuum proposed by Kristensen et al. (2022) actually reflected the relative changes in carbon storage observed by us, see Chapter 5 for results. In summary, we did not require detailed measurements of absolute turnover rates or residence times sensu Sierra et al. (2018) but gained valuable insights

regarding which ecosystem compartments are the fastest to participate in the carbon cycle. This proved especially important in recognizing the higher SOC stocks in rangelands and agricultural fields as not being caused by actual land management – for which the timespan of cultivation cannot have been sufficiently long enough given the historical perspective – but instead led us to attribute them to a selection effect of knowledgeable farmers who chose better soils before establishing settlements and fields (also see **Figure 18**).
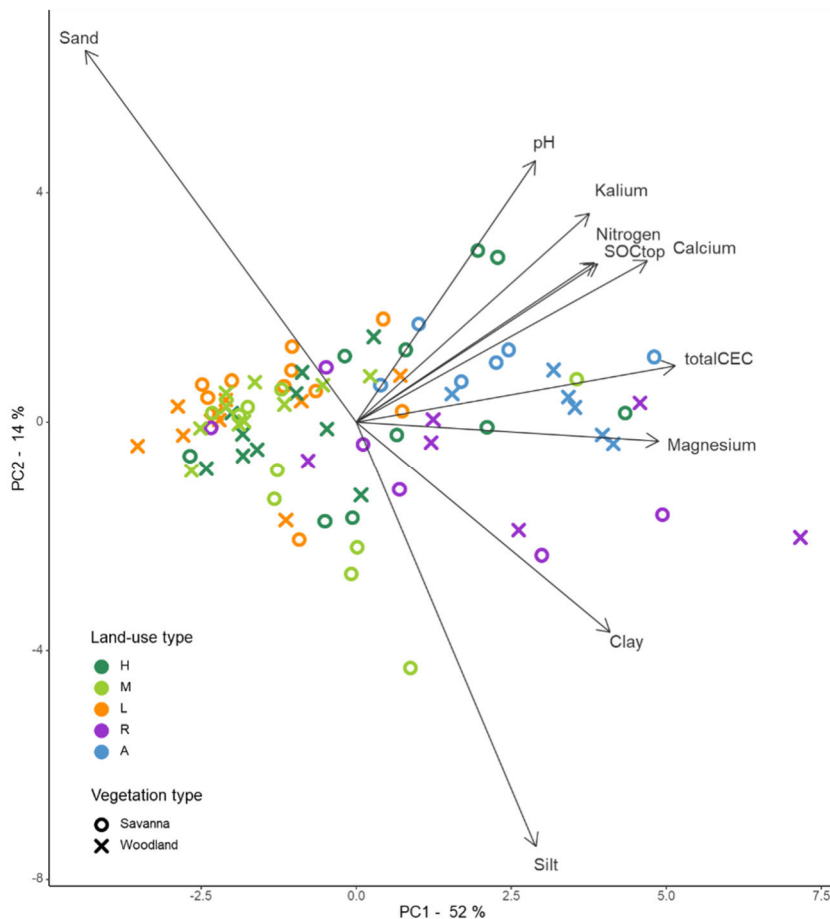
Figure 18:
Principal component analysis (PCA) on soil resources and abiotic soil variables; Woodland and Savanna vegetation types are not created by soil type differences, but rangelands and agri-cultural fields are characterized by more fertile soils.

H = High elephant densities,
M = Medium elephant densities,
L = Low elephant densities & low human disturbance,
R = Rangelands,
A = Agricultural fields.

[Figure taken from Supplementary material of Chapter 5]

Integrating the notion of the past into my analysis also helped me to understand that some of the large and old trees which massively impact woody carbon stocks today, in fact managed to establish themselves under un-naturally low disturbance levels before growing to near indestructible size. At disturbance levels present in the area today i.e. with high wildlife numbers, active fire management, and increasing human impacts these 'methusalem trees' are remnants of the past, but unlikely to be replaced by a new cohort once they eventually die of old age. These trees are therefore not representing a 'future-proof' carbon pool.

In general, the interdisciplinary work in a large-scale collaborative research centre like *Future Rural Africa* has given me the opportunity to interact, debate, discuss and work with researchers of many different disciplines and backgrounds, especially also with my African collaboration partners at

University of Namibia (UNAM) for which I am immensely grateful. I am aware that this interaction and multi-lateral learning experience has deeply impacted my research interests, opened my eyes for many new perspectives, and has sensitized me to other research backgrounds and knowledge systems. It has certainly encouraged me to attempt further interdisciplinary collaborations.

Implications for management and carbon certificates

The results presented in this thesis have several implications for carbon storage assessments, carbon accounting and management of natural resources, which I would like to present here while being well aware that the larger complex of decision-making for the future needs to integrate many further considerations outside of the scope of this thesis. My recommendations would be:

1. If carbon accounting is to be done in savanna ecosystems the protocols have to be adapted so that they actually reflect true carbon storage levels, otherwise countries with high share of dryland vegetation and savanna ecosystems, especially where large wildlife populations reside, are at a disadvantage as compared to international standards.

2. The protocols applied should be able to integrate across the mosaic landscape of different land-use types that open savanna ecosystems and especially integrated conservation landscapes always are. They should also account for elements typical to local agricultural practices and seek to understand e.g. the carbon sink potential of rotational shifting agriculture (Ziegler et al. 2012, Nath et al. 2022). In that sense, remote sensing applications have to be treated with care, as many processes of land-use change can be misidentified or are invisible from above (Tietema 1993, Stringer et al. 2012).

3. Carbon storage assessments in savannas should seek to recognize and integrate important potential carbon sinks like protected areas (Grace et al. 2006, Chidumayo et al. 2011), root biomass (Chidumayo 2014), extensive rangelands (Stringer et al. 2012), agroforestry (Garrity et al. 2010), secondary forest formations (Mertz et al. 2021) or rotational fallow systems (Ziegler et al. 2012, Nath et al. 2022).

4. Carbon certificates applicable to this study region and similar regions in rural Africa should regard that not all loss of trees or shrubs is equal to whole-ecosystem carbon loss. Where for instance wildlife browsing redistributes carbon from woody biomass to soil compartments (see Chapter 4 and Chapter 5) this carbon is not lost to the ecosystem and has not volatilized into the atmosphere. Instead, a suitable carbon certificate employed here would recognize that this carbon in fact has been sequestered into a more persistent carbon pool where it is more likely to withstand future disturbances.

5. The non-linear effects of certain disturbance drivers on not only woody carbon storage but also whole-ecosystem carbon storage (see Chapter 5) are indicators of non-linear ecological

processes, potentially leading to tipping-point behaviours which can entail degradation of the ecological system (Milkoreit et al. 2018) and therefore should be regarded with great care. Especially the effect of elephant browsing in the tree layer needs to be observed more closely. Where larger threats to functional vegetation structure, plant diversity and resource stability are identified, the control of elephant population sizes may need to be regarded, or at least a debate should take place from which state onwards future elephant populations would be 'overabundant' and problematic (Balfour et al. 2007).

6. Sources of carbon storage loss should be identified. It is necessary to acknowledge, for instance, that freely roaming elephants cause substantial carbon losses also outside national parks (see **Figure 14**). Should policies attempt to establish programs which through payments for ecosystems services aim to safeguard trees and the carbon stored therein from destruction, these policies need to define a way of not holding people responsible for the damages caused by elephants or wildfires.

7. Carbon sequestration into the soil carbon pool should be regarded as an ecosystem service which potentially brings many co-benefits such as soil fertility and increased water holding capacity (Stringer et al. 2012, IPCC 2022). Applications such as production of biochar from bush encroachment should be explored further and, after proven viable, should be fostered in agricultural management techniques and farmers should be encouraged to sustainably apply it (IPCC 2022, Angombe et al. 2023).

8. Not only conservation efforts should be shared across neighbouring countries in a framework such as KAZA, but also agricultural techniques and local knowledge that has been proven to increase yields while safeguarding tree resources should be shared, e.g. Namibian farmers in Zambezi Region could benefit from the knowledge on agroforestry approaches known more widely and for a long time to farmers in Zambia (personal communication, Zambia & Namibia 2018–2022; Garrity et al. (2010)).

9. Restoration of healthy savanna ecosystems, including native tree species and near-natural disturbance regimes (Davies et al. 2019), should be supported for their stability and the additional ecosystem services they provide (Stringer et al. 2012). In contrast, large-scale afforestation programs with planted monocultures of non-native tree species should be prohibited for they are not ecologically sustainable due to their unforeseeable impacts. For an overview of the manifold reasons to avoid afforestation of savanna drylands such as its spatial demands, its questionable effectiveness, the potentially adverse effects, and the social, economic and ecological costs see Bond et al. (2019).

Future-making perspective to carbon storage/conservation?

Having said that, I want to emphasize the point that the carbon perspective is by no means the only perspective for future savanna ecosystems. Focusing on financial incentives and monetization of ecosystems through carbon income should never obscure the essential need to restore and conserve intact ecosystems and ecosystem functions (Aguirre-Gutiérrez et al. 2023), which I hope to have made evident throughout. While carbon storage can have essential benefits in form of related ecosystem services, others are inevitably trading-off against carbon storage and therefore detailed and sound assessments prior to program planning or investments are vital (Stringer et al. 2012). The same holds true for REDD+ programs and the baseline values they use for reporting their claimed effectiveness; these baselines need to be chosen well and assessed rigorously in order to make REDD+ work effectively (West et al. 2023). Furthermore, I want to emphasize that whatever carbon projects may be planned for the future of rural Africa, investments need to be 'future-proof', i.e. resilient in the face of potential developmental challenges that lie ahead (Stringer et al. 2012). They are more likely to be sustainable if they are not only focused on carbon storage, but on multiple ecosystem services at once and oriented towards effectively reducing poverty on several levels (Stringer et al. 2012).

Drawing on the many conversations I had with colleagues, conservationists, wildlife rangers, interview partners, farmers and other inhabitants of communal conservancies directly bordering the national parks, I know that the future of integrated land-use and conservation is by far not without problems and challenges. Living with and farming next to wildlife is a difficult task, which needs to be acknowledged in decision-making (Cassidy and Salerno 2020) if in the future this conservation approach should be supported by local communities. To ensure fairness and livelihoods under such conditions requires sound governance, improved compensation payment systems to farmers, and generally conditions that give people a vision of the future that they all can aspire to. In line with Palomo et al. (2014), where true social-ecological conservation is the goal it requires participatory community-involvement and bottom-up processes of future-making to form truly cooperative multifunctional landscapes. From my experience, many people deeply care for trees, are excited to share knowledge on trees, and derive and value a multitude of benefits from trees around their villages. In my opinion, farmers are interested to learn how trees can help their agricultural practices and many of them will likely participate in tree protection, not only if there are carbon credits to sell for them. However, being able to make this decision of protecting trees can only be expected from people who have a sound basis of income and secure livelihood conditions for their families. Without those, the future of trees and shrubs will be uncertain.

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