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- 1 *Prediction of Forest Parameters and Carbon Accounting under different Fire Regimes in*
- 2 *Miombo Woodlands, Niassa Special Reserve, Northern Mozambique*
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5 ***Highlights***

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- 7 • FORMIND accurately predicts miombo carbon dynamics in Niassa Special Reserve.
- 8 • Shift from annual to 3 years fire intervals reduces C emissions in 4tC/ha/year.
- 9 • C fire projects have potential to generate revenue for improved reserve management.
- 10 • Further research is needed fire management vs changes in different carbon pools.
- 11 • Awareness raising is key to reduce fire policy and implementation barriers.
- 12

ABSTRACT

Miombo woodlands are the most extensive dry forest type in southern Africa, covering ca. 1.9 million km² across seven countries. Fire is a key ecosystem process that has structured miombo for the last 200,000 years. However, how fires affect the ecosystem's functioning is not well understood. In this study, we used the individual-based forest model called FORMIND to analyze the carbon balance in the miombo woodlands of Niassa Special Reserve (NSR), northern Mozambique. The 42,000 km² NSR represents the most important conservation area in Mozambique (~31% of the total conservation area in the country) and of miombo woodlands worldwide. Long-term inventory data from 2004 to 2019 for NSR were used to calibrate FORMIND. The primary ecosystem processes of this model are tree growth, mortality, regeneration, and competition. Fire is set as one of the main factors that affect these processes, after the woodland reaches an equilibrium at 200 years of age. We also calculated the Net Present Value (NPV) of carbon credits resulting from altering the fire regime (e.g., reducing or eliminating fires). The FORMIND model successfully reproduced important characteristics of the woodlands (aboveground biomass, stem size distribution and basal area). NPV estimates of above-ground woody biomass carbon stocks were highly dependent on the woodland age. The maximum NPV estimates were generated for a 30-year project starting with 200-year old woodlands (the current forest age) at 192-1,339 USD based on a realistic range of carbon values (i.e., 3-20 USD MgCO₂e⁻¹). While fire plays an important role in miombo woodlands by reducing stock and changing species composition, its effects on the capacity of the woodland to mitigate the effects of climate change varies depending on the age of stands. Our results show that FORMIND model reliably reproduce the field inventory data, thus can be used to improve carbon accounting standards. We recommend the development of a fire management system to sustain the miombo woodlands of NSR for multiple reasons. NSR is a globally significant protected area, but perhaps more importantly it could become a regional example for how to improve miombo woodland management. Given that miombo woodlands provide a myriad of ecosystem services to rural Africans, investing in improving fire management could increase the benefits to local communities. Altering fire regimes could improve habitat quality and promote greater resilience to climate change while sequestering carbon. In addition, local employment opportunities in fire management could be created via carbon financing from a carbon project. However, much more outreach and education will be needed to local and national stakeholders for fire management to be perceived more positively and realize the potential to generate multiple benefits for nature and people.

Key words: FORMIND gap model, Ecosystem dynamics, carbon accounting, fire management, fire policy

50

51 **1. Introduction**

52 Tropical forests, storing over half of terrestrial carbon in less than 10% of the global land area
53 (Pan et al., 2011), may become a carbon source in the near future with the current rate of rapid
54 deforestation and degradation (Mitchard, 2018). Although the rate of deforestation has slowed in
55 many parts of the tropics recently, the trend of rapid net forest loss has continued in Africa every
56 decade since 1990 (FAO, 2020). United Nation's declaration of the Decade of Ecological
57 Restoration (2021-2030) is calling for a global restoration movement for protecting and reviving
58 ecosystems around the world for people and nature (UN, 2019). However, it would cost more
59 than USD 318 billion per year to achieve the goals globally (FAO and Global Mechanism of the
60 UNCCD, 2015). Even with proportionally high government spending on protected area
61 management and supports from international donors, the current level of funding was estimated
62 to be less than one third of what is needed to reverse the trend of forest loss and declining
63 wildlife population in Africa (Lindsey et al., 2018). In countries with weak forest governance,
64 market-based mechanism can complement other policy instruments and to fill the wide funding
65 gap (Lambin et al., 2014; Global Mechanism of the UNCCD and CBD, 2019).

66

67 Developing international carbon trading mechanisms, e.g., Reducing Emissions from
68 Deforestation and Forest Degradation (REDD+), has been hailed as a way to bring new sources
69 of funding to conservation while mitigating climate change (e.g. REDD+ and the Paris
70 Agreement in 2015, UN-REDD Programme, 2016; UNFCCC, 2015). However, Africa and its
71 dry tropical forests and woodlands remain one of the least studied forested ecosystems in the
72 world, despite their global importance as carbon sink and habitats for critically endangered
73 species, as well as sources for food, energy and livelihoods of the world's poorest (Schröder et
74 al., 2021; Sunderland et al., 2015; Dewees et al., 2010). Filling the funding gaps with carbon
75 financing would require clear understanding of dominant ecosystem processes, such as fires, and
76 their impacts on emission. This study presents a way of incorporate uncertainties related to fire
77 ecology and its influence on the ecosystem's structure and function into carbon accounting
78 standards.

79 How to account for cyclical human-induced fires in carbon accounting is an important
80 consideration for calculating a reference emission level and setting realistic carbon emission
81 reduction targets, as well as reducing uncertainty and risks associated with carbon projects. We
82 assumed no other risk factors for ensuring permanence of emission reduction during the project
83 period, other than fire. Some of the carbon accounting systems, such as Verified Carbon
84 Standards, developed methodologies to incorporate fire management in the baseline calculations
85 using process-based models (e.g., VM0026 and VM0029, VCS 2014; 2015). However, the
86 methodologies mostly focus on fire-caused tree mortality and do not account for other
87 ecosystem-wide changes due to frequent fires. An empirical study from Australian savanna
88 demonstrated that active fire management during the early dry season (EDS) can significantly
89 reduce the overall emission from fires by reducing fire occurrence, intensity, and extent, which
90 present global opportunities for emission reduction throughout dry tropics (Lipsett-Moore et al.,
91 2018). Based on this study, Tear et al. (in review) estimated that EDS fire management in Africa
92 could generate USD \$1.5–\$44.4 M per protected area at USD \$5 ~\$13 MgCO₂e⁻¹ reflecting the
93 current price at voluntary carbon markets. Hofstad and Araya (2015) argued that carbon
94 sequestration payment had to be at least USD \$15 MgCO₂e⁻¹ to avoid degradation of dry tropics

of Africa after accounting for 1.85% biomass reduction after fire and opportunity cost of lost revenue (based on the charcoal trade around miombo woodlands of Tanzania). Globally, carbon prices in the range of US\$50–100/tCO₂ by 2030 may be required to cost-effectively reduce emissions to achieve the temperature goals of the Paris Agreement (World Bank, 2020). Attracting more buyers to terrestrial carbon projects is one way to promote higher carbon prices, which would require increasing investors' confidence in carbon accounting while reducing risks associated with carbon projects. However, existing carbon accounting methods and policies have been largely ambiguous about the impacts of fire management, such as prescribed burning (Ning and Sun, 2017). Ground-truthing accuracy of process-based models and examining long-term effects of recurring disturbances, as well as the impacts of active fire management, are imperative for improving carbon accounting standards and developing other outcome-based conservation objectives. Investments for carbon sequestration can be combined with biodiversity offsets and other funding to conserve megafauna species with efforts for eco-tourism and community development, which would amplify subsequent social and economic benefits, especially in rural areas (Mwakalobo et al., 2016). Integrated fire management programs for prevention, firefighting, and prescribed burning, such as Working on Fire in South Africa, have shown to create opportunities for job training and development that generate rural income flows, which in turn address underlying drivers of human-caused fire ignitions, such as rural poverty (Giordano et al., 2012).

Miombo woodlands cover a vast swath of southern Africa – spanning approximately 1.9 million km² across seven countries including: Angola, Democratic Republic of Congo, Malawi, Mozambique, Tanzania, Zambia and Zimbabwe (Dziba et al., 2020; previously reported to be 2.7 million km² by White, 1983). They host ca. 8,500 plant species, of which 54% are endemic (White, 1983) and support livelihoods of over 100 million people (Deweese et al., 2010). Miombo is also recognized for its diversity of landscape habitats that support a large variety of wildlife species, including the last remaining megafaunal assemblages of the world (Mittermeier et al., 2003). Miombo vegetation ecology is largely driven by its woody component, which represents 95% of the ecosystem's biomass (Frost, 1996; Chidumayo, 1997; Ribeiro, 2013; Ribeiro et al., 2020). Extraction of wood fuel, (illegal) harvesting of wood as well as land use conversion to agriculture and settlements have been noted as key drivers of deforestation in the miombo region (~1% per year) (Campbell et al., 2007; Bond et al., 2010; Allan et al., 2017). With improved forest governance through community-based management in several miombo countries (Deweese et al., 2010) and established protected areas to set a baseline (Ribeiro et al., 2013), developing carbon projects in the miombo region can reduce deforestation and degradation while improving livelihoods (Bond et al., 2010). However, lack of information on carbon cycles, especially the role of frequent disturbances such as fires, is a major constraint to developing management strategies and payments for ecosystem services (Williams et al., 2008).

Fires and humans have coexisted in the miombo woodlands for more than 200,000 years (Morris, 1970) and play an important role in maintaining the ecosystem's structure and function. Human-caused fires interacting with other factors have been widely studied in the broader miombo region. However, the complexity of natural and anthropogenic fires and their interactions with other processes, including climate change, energy extraction, forest demographics and grass layer, are not well-understood primarily due to a lack of comprehensive studies. Analyzing the heterogeneous structure and dynamics of miombo woodlands on a local

scale poses a challenge due to limited accessibility to some areas and lack of updated data. Process-based Forest models offer away to understand complex interactions of ecosystem processes and disturbances such as climate, fire, herbivory, land use/land cover changes, and their impacts on the structure and function of miombo woodlands. They simulate forest processes such as tree growth, mortality, and regeneration, which in turn helps understanding how processes such as fire determine the existence of savannas and woodlands in the global context (e.g., Bond et al., 2005).

Utilizing long-term field data from permanent plots in a protected area in Mozambique as a case study, we evaluated the accuracy of a process-based forest gap model (FORMIND; Fischer et al., 2015) that tracks individual trees throughout their lifecycle for understanding the ecosystem processes and the feasibility of utilizing the model to improve carbon accounting standards. Given the limitations associated with the vast expanse that miombo woodlands cover, as well as the complexity of factors involved in fire ecology, it is crucial to develop ways to better incorporate local and regional scale disturbances such as fires into carbon accounting. By doing so, the revenue generated from carbon projects could be fed back into support regional fire management programs through controlled burnings. However, prescribed burning is illegal in many dry tropical countries, such as Mozambique. Modeling of specific impacts of fire management can help redefine inconsistent and often counter-productive fire-related policies in the region. Specific research objectives of this study are: 1) to evaluate accuracy of an individual modeling approach (FORMIND) in simulating the ecosystem structure and dynamics of miombo woodlands; 2) to estimate the effects of changing fire frequency on ecosystem structure and its capacity to sequester carbon; and 3) to estimate economic values of sequestered carbon from reducing fires and 4) suggest ways to improve carbon accounting standards and related policies.

2. Methods

2.1 Study site description

The Niassa Special Reserve (NSR) is a key protected area in southern Africa, representing about 31% of the total protected area in Mozambique and one of the last remnants of miombo woodlands in southern Africa. NSR is located in northernmost Mozambique with the northern end of the park bordered by the Rovuma River that marks the Tanzanian border (Figure 1). NSR covers 42,300 km² in two provinces: Cabo Delgado and Niassa, and eight administrative districts (SGDRN 2007; Ribeiro et al. 2008; Ribeiro et al. 2013) (Figure 1). The reserve was officially proclaimed in 1954 as a Game Reserve but then abandoned between 1975 and 1992 during Mozambique's Civil War. From 1997 to 2012, the reserve was managed through a public-private partnership between the Mozambican government and the previous management authority called *Sociedade para o Desenvolvimento e Gestao da Reserva do Niassa* (SDGRN, 2007). Since October 2012, the Wildlife Conservation Society (WCS) has been co-managing NSR together with the National Administration for Conservation Areas in Mozambique (ANAC) to secure the long-term future of NSR. Fire management is one of the several challenges for managing this geographically and socio-economically sensitive area.

LOCATION OF NIASSA SPECIAL RESERVE

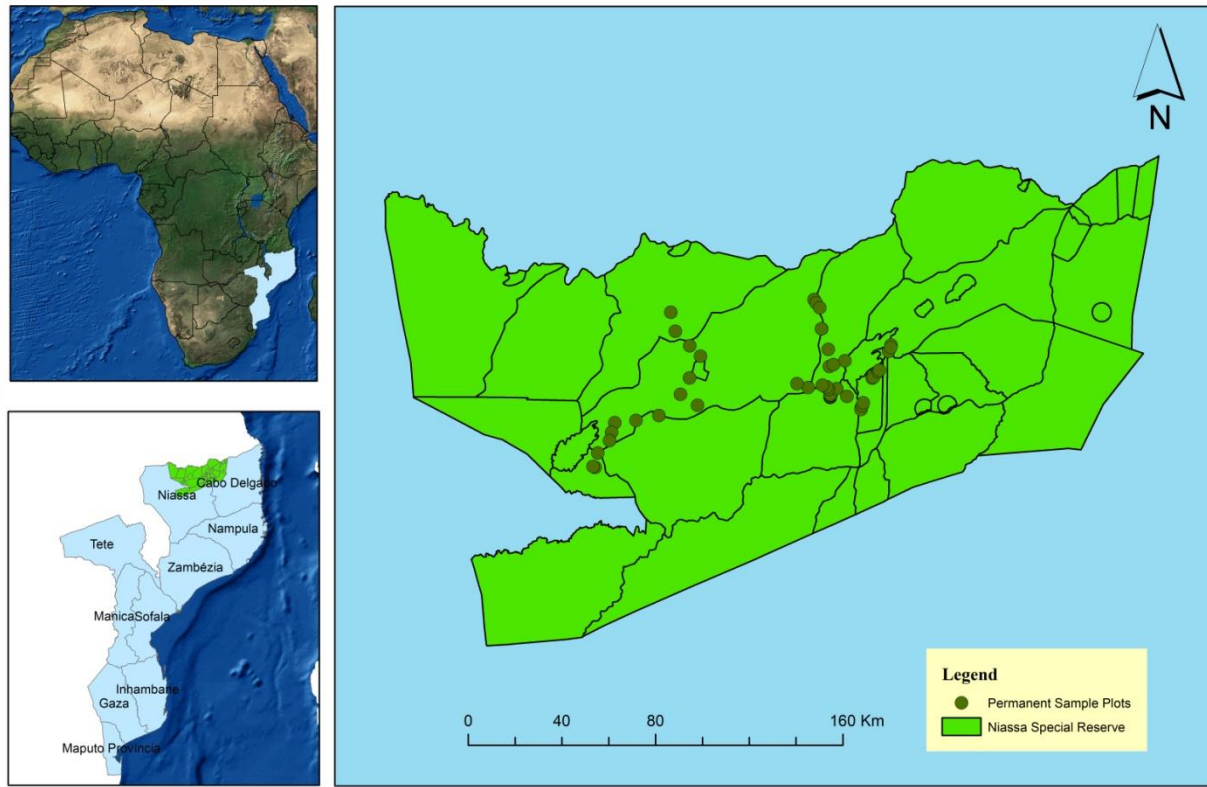


Figure 1: Geographic location of Niassa Special Reserve (NER) in northern Mozambique.

The climate of northern Mozambique is tropical dry, with a mean annual precipitation of 900 mm increasing from the east (800mm) to the west (1,200 mm) and a mean annual temperature of 25°C that ranges between 20 and 26°C during the dry season (May to October) (SGDRN, 2007; Allan et al., 2017). NSR has a gently undulating landscape on a plateau with elevations ranging between 300 and 600 m above-sea-level (Ribeiro et al., 2013). There are two major peaks in the Reserve, Mount Jao in the West (at 1,200 masl) and Mount Mecula in the East (at 2,000 masl), which are centers of biodiversity (Timberlake et al., 2004). Drainage is dominated by the Rovuma and Lugenda Rivers, which are large, free-flowing sand rivers with strong perennial flows (Booth and Dunham, 2016).

Human population inside the reserve is estimated to have increased from ~45,000 inhabitants in 2009 (SGDRN, 2010) to 60,000 in 2017 (INE, 2018). One of the main challenges for managing NSR is a growing resident population who live within ~40 scattered villages. Some people living in the major towns of Mecula and Mavago highly depend on NSR's natural resources to sustain their livelihoods (MITADER, 2015; Allan et al., 2017). Lack of alternative livelihood strategies creates conditions for unsustainable use of ecosystems, including extensive use of fire as a vegetation management tool. Ribeiro (2007) and Ribeiro et al. (2017) found that

95% of historical fires in NSR were human-caused. Fire has been an inexpensive and readily accessible tool for most human activities including: subsistence hunting, pedestrian trade involving travel to and from Tanzania, honey collection and swidden agriculture (Tilley and Abacar, unpublished data; Chande, pers. com.; Allan et al., 2017). Between 2000 and 2012, the fire frequency was estimated as once every 3.29 years on average for the whole NSR but annual burning took place in 45% of NSR and other areas burning less frequently (Ribeiro et al., 2017).

Deciduous miombo woodlands cover more than 70% of the total area of NSR (Marzoli, 2007) and are dominated by a few tree species: *Julbernardia globiflora* (Benth.) Troupin, *Brachystegia* spp., *Diplorynchus condilocarpon* (Müll. Arg.) Pichon and *Pseudolachnostylis maprouneifolia* Pax and a dense grass layer (Ribeiro et al., 2008; Ribeiro et al., 2013). Despite having lost 0.9% of its woodland cover between 2001-2014 (Allan et al., 2017), NSR's diverse ecosystems are still intact and have potential to sustain key wildlife population, including: the largest populations of elephants (~3,000-4,000) and lions (1,000-1,200) in the country, leopards, wild dogs (400-450), sable, kudu, wildebeest, buffalo, zebra and more than 400 bird species (Craig, 2009; SGDRN, 2010; <https://mozambique.wcs.org>). The woodland's ecology is largely driven by the rainfall gradient across NSR and a complex interaction between anthropogenic fires and herbivory by elephants (SGDRN, 2007; Ribeiro et al., 2008; Ribeiro et al., 2013; Ribeiro et al., 2017).

2.2. Overview of the FORMIND forest model

In general, gap models track each individual tree in a plot throughout its life history, including seedling establishment, competition for light and resources, regeneration and mortality. Considering a forest gap caused by a falling tree, for instance, the opened canopy results in increased light availability and hence the growth of sub-canopy trees and recruits (Shugart, 1984; Martinez-Ramos et al., 1989; Fischer et al., 2016). In this study, we used the FORMIND forest gap model described by Fischer et al. (2015) and Fischer et al. (2016). The FORMIND forest gap model (Köhler and Huth, 2004) is an individual- and process-based simulation model designed specifically for tropical forests and considers the complex age structure of the tree community. As with the classic individual-based gap models, seeding, mortality and tree fall are stochastic processes that through time lead to a mixed age, mixed species forest in a stable equilibrium (Armstrong et al., 2020). The simulated forest area is divided into patches according to the typical size of tree fall gaps (20 m x 20 m). The vertical leaf distribution and light availability are calculated for each patch. The biomass growth of each tree is determined based on a carbon balance including photosynthesis, respiration, biomass allocation and litter fall. Photosynthetic production in the canopy depends on local light availability. Forests of up to 1,000 hectares can be simulated over a period of several centuries. FORMIND has been extensively tested and applied to tropical forests in Panama, Malaysia, French Guyana, Venezuela, Mexico, Brazil, Madagascar, Tanzania, Costa Rica and Paraguay (Huth and Ditzer, 2000; Kammesheidt et al., 2001; Köhler et al., 2003; Köhler and Huth, 2004; 2007; Rüger et al., 2007, 2008; Gutiérrez and Huth, 2012; Fischer et al., 2014; Fischer et al., 2015; Armstrong et al., 2018; Armstrong et al., 2020). This is the first time, to our knowledge, that FORMIND has been applied to miombo woodlands in Southern Africa, and only the second time in Africa.

In this study the FORMIND model was used to investigate tree biomass (t/ha), density (trees/ha) and basal area (m²/ha) of the miombo woodland ecosystem in NSR. In addition, above- and belowground carbon stocks and the resulting Net Ecosystem Exchange (NEE in tC/ha/year) was calculated as the balance of carbon sequestration and carbon emissions in the ecosystem. The woodland ecosystem is considered to be a carbon sink if it absorbs more carbon than it releases (NEE is positive). If, on the other hand, the heterotrophic respiration is greater than the net primary production, the forest is a carbon source (NEE is negative). A detailed description of the FORMIND model can be found at www.formind.org and Fischer et al. (2016). In our study, the fire module of FORMIND was used to simulate the long-term impacts of fires on forest dynamics (Fischer, 2021).

2.3. Model parameterization and plant species grouping

In this study, we used the dataset collected between 2005 and 2015 in 25 undisturbed permanent sample circular plots (30-m in diameter) distributed across the NSR. It is important to highlight that this is a unique dataset due to its longevity and robustness of the data collected. The dataset includes species identification, diameter at breast height (dbh-cm), height (m), basal area (m²/ha), biomass (t/ha), mortality (% of total tree number) and growth (cm/year). Some parameter values such as wood density (Zanne et al., 2009) and crown-dbh relationship (Burrows and Strang, 1964; Isango, 2007) were taken from the literature and global databases. The average Mean Fire Return Interval (MFRI) for NSR of 3.29 years was obtained from Ribeiro et al. (2017).

Plant functional types (PFTs) are non-phylogenetic groupings of species that show close similarities in their resource use and response to environmental and biotic controls (Smith and Shugart, 1997; Köhler et al., 2000). For the purpose of this study, local tree species with similar trait expressions were assigned to one of seven groups according to their maximum height and light requirements (Table 1; see Appendix A for the full species list and their traits). We used four height classes (<10m, 10-<15m, 15-<20m, 20-<30m) and three classes of shade tolerance (shade-tolerant—climax species, shade-intolerant—pioneer species, and intermediate shade-tolerant species). The grouping of tree species into shade tolerance classes was based on literature review and expert knowledge. For each of the seven PFTs, we then calculated the following variables: stem counts, aboveground biomass, average basal area, average diameter growth increment and mortality.

Table 1. Species grouping into seven plant functional types (PFT) for miombo woodlands in Niassa Special Reserve

Plant Functional Type (PFT)	Light class	Maximum Height (m)	Biomass (t/ha)	Exemplary trees
1	Shade tolerant	<10	0.023	<i>Vangueria</i> sp.
2	Intermediate shade tolerant	10-<15m	0.214	<i>Crossopteryx febrifuga</i> (Afzel. Ex G. Don) Benth.
3	Shade-intolerant	10-<15m	1.306	<i>Combretum collinum</i> Fresen.

4	Shade tolerant	10-<15m	3.012	<i>Uapaca kirkiana</i> Müll. Arg.
5	Intermediate shade tolerant	15-<20	24.990	<i>Julbernardia globiflora</i>
6	Shade tolerant	20-<30	8.137	<i>Pterocarpus angolensis</i> DC.
7	Shade tolerant	20-<30	14.876	<i>Brachystegia boehmii</i> Taub.

2.4. Model calibration simulation experiments

When the model parameters were calculated and entered into the FORMIND parameter file, simulations were run to calibrate some unknown parameter values. We performed a manual calibration to optimize a subsequent auto-calibration. The manual calibration was accomplished by running the model one hundred times, systematically changing a few unknown parameters in small increments to achieve the best simulation of the study site forest (Lehmann and Huth, 2015). Seed production and establishment of seedlings were high priority calibration variables, as there was little information in the literature and we relied on general values for the sub-tropics. In addition, mortality and light response curves were also optimized.

When the manual calibration for each of these variables determined ideal ranges for each PFT, the remaining unknown parameters were numerically calibrated (e.g., global number of seeds) by comparing the aboveground biomass, species composition, and tree density of a simulated mature forest with field data from the study region following Lehmann and Huth (2015). The parameterization was then verified by comparison of stem numbers per diameter size classes, aboveground biomass, basal area and other structural variables obtained in the model and with the field data.

We analyzed forest succession on nine hectares over 600 years, starting with bare ground conditions and without fire limitations. To assess the variability in the forest model we had 10 repeated simulation runs. Two types of analysis were conducted. First, for a comparison of the model output with field data, we calculated the mean of simulated woodland attributes over the last 600 years, based on the assumption that the woodland was in the equilibrium state for the entire period. In particular, we analyzed aboveground biomass, basal area and stem numbers (dbh>10 cm). Second, we analyzed NEE per hectare.

2.5. Model validation and scenario analysis

Most of the FORMIND model parameter values were determined from the local woodland measurements (biomass, height, basal area, dbh, mortality and growth), taken for 10 years (2005-2015) in 25 undisturbed permanent sample circular plots (30-m in diameter) distributed across the NSR. Some parameter values (e.g., wood density; crown-dbh relationship) were taken from the literature (see Appendix B). We ran the simulations for a 600-year period with three scenarios: (i) no fire; (ii) mean fire return interval (MFRI) of 3.29 years (average for the area; Ribeiro et al., 2017); and (iii) annual burnings (45% of the NSR burns annually; Ribeiro et al., 2017). Fire simulations started after 200years of simulation to allow the forest to reach the current state of NSR miombo woodlands. To validate the model, we compared the simulated

biomass, basal area and stem density with the corresponding observations from the research test sites in NSR.

2.6. Economic value of carbon projects

Based on the NEE calculations from FORMIND model, we calculated the Net Present Values (NPV) of potential carbon projects starting in different stand ages. It is important to note that the average stand age of NSR is currently about 200 years old, although the model simulates ecological changes over 600-year period (modeling starting with bare ground). We do not have site-specific data to calculate management and opportunity costs of carbon projects in NSR. Previous estimates show average costs of terrestrial protected area management and mean agricultural value (opportunity cost) in Mozambique to be USD 0.44/ha and 0.498/ha respectively (Tear et al., 2014). Mozambique is among the most underfunded countries in Africa for protected area management and additional funding to effectively manage them was estimated to be USD \$11.36 /ha/yr (median funding deficit calculated by various methods ranging from USD \$8.43/ha/yr to \$18.95 /ha/yr according to Lindsey et al., 2018). For simplicity, we used this additional funding need as the cost of a carbon project in NSR. We based this decision on the assumption that additional funding would be needed to launch and sustain a carbon project. However, we are aware this is likely an overestimate of cost, as it was intended to represent all management costs of protected areas, not just those needed for fire management and associated monitoring of a carbon project. We did not include opportunity costs of alternative land uses for two reasons: 1) NSR is a protected area with no legal alternative land use; 2) most of the human-caused fires are close linked to rural poverty and lack of economic opportunities, which can be addressed by integrated fire management. We assume carbon credits would result from changing above and below ground carbon from fire management, estimated based on changes in NEE at a single period, t ($\Delta NEE_t = NEE_t$ under Business-As-Usual – NEE_t under fire management). Net cash inflow-outflows at t (NR_t) is the difference between total revenue from carbon credits (reduced emission multiplied by carbon price, P_c) and additional management costs (MC_t): $NR_t = \Delta NEE_t \times P_c - MC_t$. NPV is a sum of discounted NR over project period ($\sum_t NR_t \times (1+r)^{-t}$). Discount rate (i) was set at 10% per year as 10~12% rates are usually employed by leading development banks when evaluating projects in developing countries (Harrison, 2010). The number of time periods (t) was set at 30 years.

Under the three fire scenarios, we projected potential economic values of sequestered carbon, and compared NPVs of 30-year carbon projects per hectare starting at different age of stands. We assumed the interventions would focus on those areas with annual burning and set NEE from annual burning as the Business-As-Usual (BAU) scenario to establish the reference emission level. We calculated the changes in NEE when fire interval is increased to the average of NSR (fire interval from 1 to 3.29) and when fires are eliminated from miombo woodlands (which is valuable for comparison but impractical and highly unlikely to happen even with fire management).

3. Results

3.1. Model testing

To test the parameterization for the miombo woodlands in the NSR, we compared the simulated biomass, basal area and tree density with field data collected in 25 undisturbed permanent sample plots, scaled to one hectare. The comparison was made for each Plant Functional Type (PFT), considering that they have the same light requirements. Our results revealed that there was an initial (first 50 years) large increase of biomass and basal area with the colonization by pioneer shade intolerant trees (PFT3 dominated by *Combretum collinum*; Figure 2). After this initial period, intermediate shade tolerant (PFT5 dominated by *Julbernardia globiflora*) and shade tolerant (PFT6, dominated by *Pterocarpus angolensis*) quickly compete with shade intolerant trees and dominate the area for the next 100 years. After ca. 200 years, when the woodlands reach an equilibrium, intermediate shade-tolerant trees (PFT5) dominate the area followed by shade-tolerant trees (PFT7 dominated by *Brachystegia boehmii*). Shade tolerant PFT6 and PFT4 follow next, while shade intolerant trees (PFT3) reach maturity at ca. 50 years and quickly decline in basal area and biomass.

When the woodlands reach an equilibrium state, at about 200 years the two dominant PFTs, i.e., the miombo characteristic species (*J. globiflora* and *B. boehmii*) make up the dominant proportion of aboveground biomass (AGB; ca. 75.5% of total biomass) and basal area (about 71% of the total basal area). They are followed by shade tolerant PFT6 dominated by *P. angolensis* with ca. 10% of total AGB and 12.7% of basal area and shade tolerant PFT4 (dominated by *Uapaca kirkiana*) representing only 5% of the total AGB and 10.2% of basal area. The remaining PFTs (1, 2 and 3) altogether are responsible for only a small percentage of the total AGB (<5%) and basal area (<4%).

The 1:1 comparison between field data calculations and simulation values for late successional phases of the simulated woodlands for AGB and basal area are presented in Figure 3 (lower and upper right graphs, respectively). It shows that the simulated AGB was ca. 54t/ha which is 1% higher than the field calculations of 53t/ha. This means the model slightly overestimated the total AGB. The same is valid for PFT5 (<1%). For the other PFTs the model was truly accurate in estimating the AGB. The total basal area was slightly underestimated by FORMIND, with values of 12 m²/ha compared to 13.5 m²/ha observed in the field, i.e., 1.1% (Figure 3). For all PFTs the model performed well in estimating the respective basal areas. A detailed evaluation of stem number distributions can be found in Appendix C.

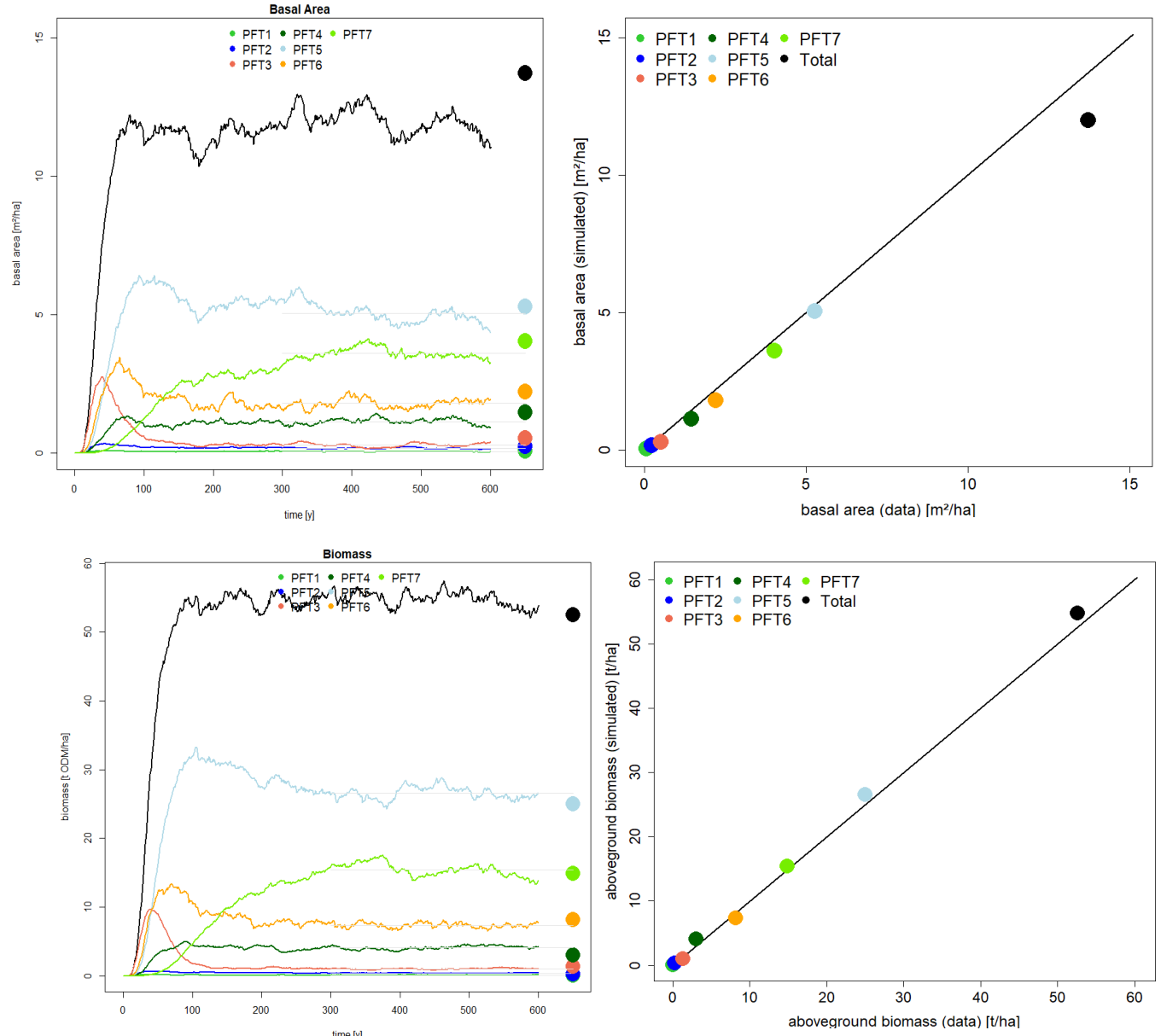


Figure 2: Simulation vs. Measurements. Comparisons between simulated variables and measurements from the miombo woodlands inventory in Niassa Special Reserve: Simulated basal area (top left), aboveground biomass (bottom left), and over time for each PFT. Right column from top to bottom: 1:1 comparison between field data calculations (x-axis) and simulation values for late-successional phase of the simulated forest for basal area in m²/ha (top right) and aboveground biomass in t/ha (bottom right).

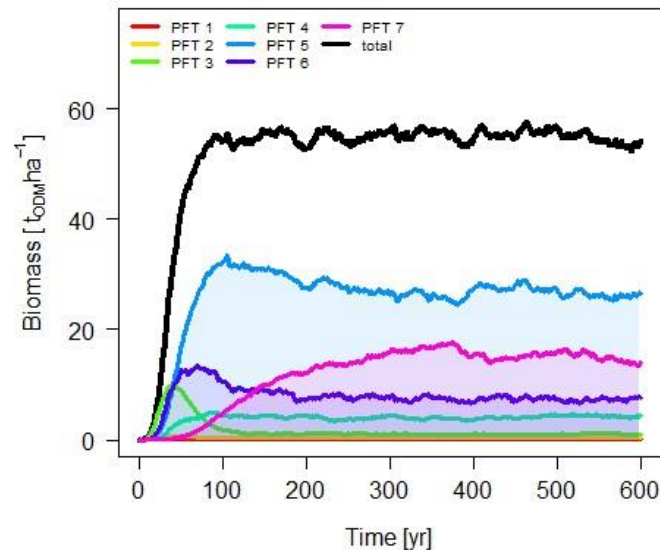
3.2. Effects of fire on woodland parameters

In the second part of the study, we evaluated the effects of fires by simulating three fire scenarios: (i) no Fire; (ii) mean fire return interval (MFRI) of 3.29 years; and (iii) annual

burnings, on ecosystem structure, composition and carbon dynamics given by the Net Ecosystem Exchange – NEE (Figures 3-6).

In terms of aboveground biomass (AGB; Fig. 3a) and basal area (Fig. 4a) our results revealed that in the *no fire* scenario (our baseline model condition), before the woodland stabilized at around 100 years, there was a short period (around 20 years) in which the shade-intolerant PFT3 (*C. collinum*) dominated the area. However, intermediate shade-tolerant PFT5 (*J. globiflora*) and shade tolerant PFT6 (*P. angolensis*) were predicted to quickly replace the shade-intolerant species at around 50 years (Figure 3a and figure 4a). After 100 years of woodlands dynamic simulation, the shade-tolerant PFT7 (*B. boehmii*) was predicted to replace the PFT6 and together with PFT5 dominate the area for the rest of the simulation period.

The second and third scenarios - MFRI of 3.29 years and annual MFRI (Figures 3b-c and 4b-c), respectively predicted the same trend of fire imposing multiple modifications to the woodland dynamics after 200 years (the assumed current forest age in this study). The first observation is that the woodland equilibrium state for AGB and basal area would be achieved at about 50 years, but would last only 150 years after which both structural parameters decline by ca. 80% for scenario 2 and by 85% in scenario 3 due to fire occurrence. After 200 years, the ecosystem was predicted to display several peaks and valleys for both AGB and basal area. During the first stabilization phase, PFT5 (*J. globiflora*), followed by PF6 (*P. angolensis*) and PFT7 (*B. boehmii*) dominated the woodlands, but they all significantly decreased in both AGB and basal area. After 200 years of simulation the shade-intolerant PFT3 (*C. collinum*) dominated the ecosystem, followed by the shade-tolerant PFT4 (*U. kirkiana*) while characteristic miombo species decreased further.



(a)

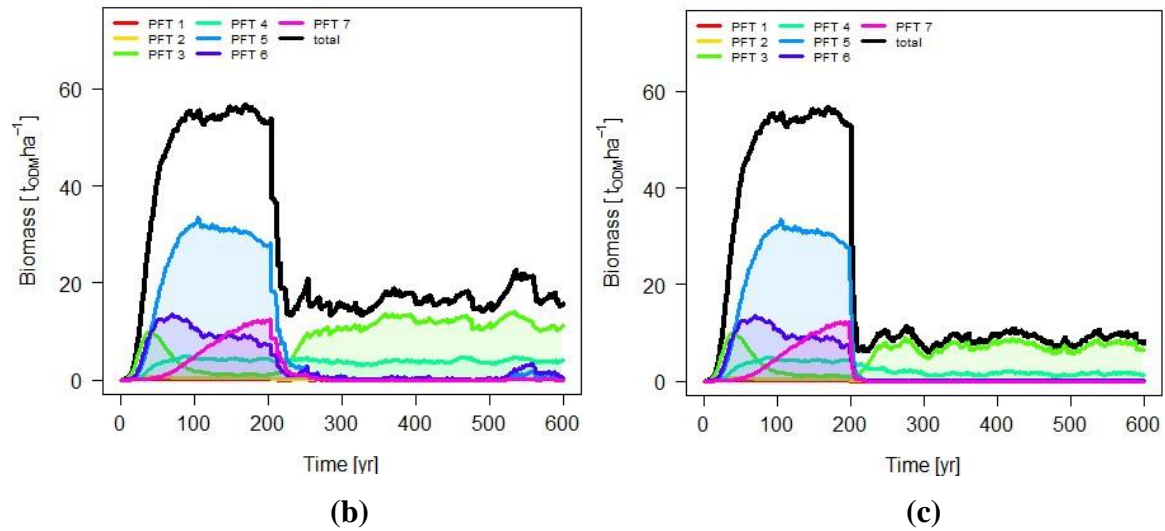
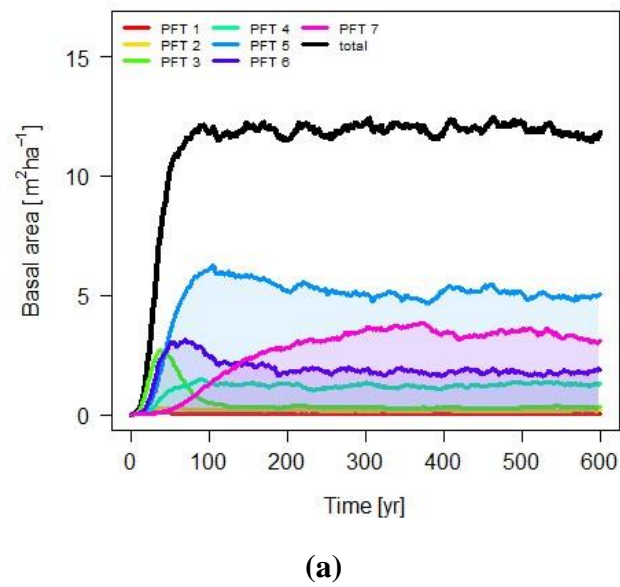


Figure 3: Simulated biomass (t/ha) of miombo woodlands in Niassa Special Reserve under three fire scenarios: (a) *no fire* scenario; (b) *3.29-year MFRI* scenario; (c) *1-year MFRI* scenario.



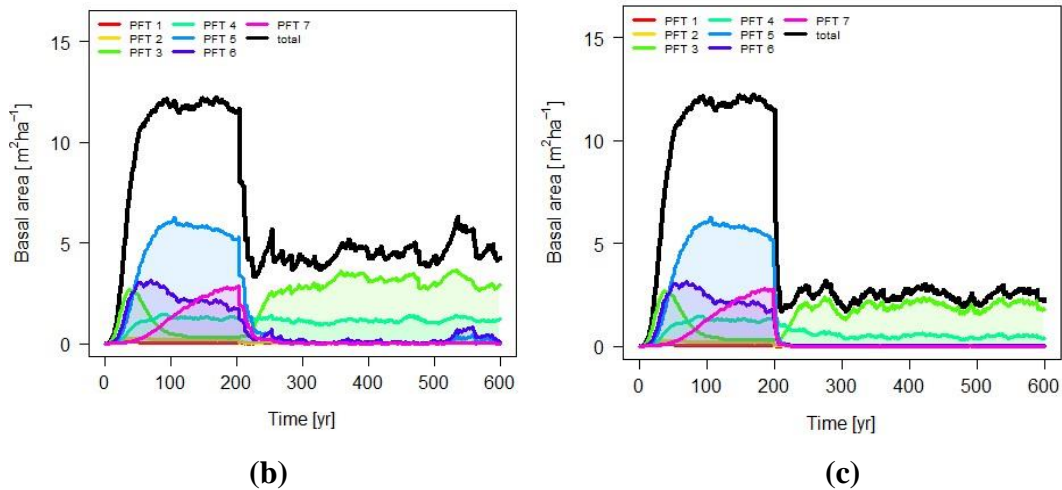
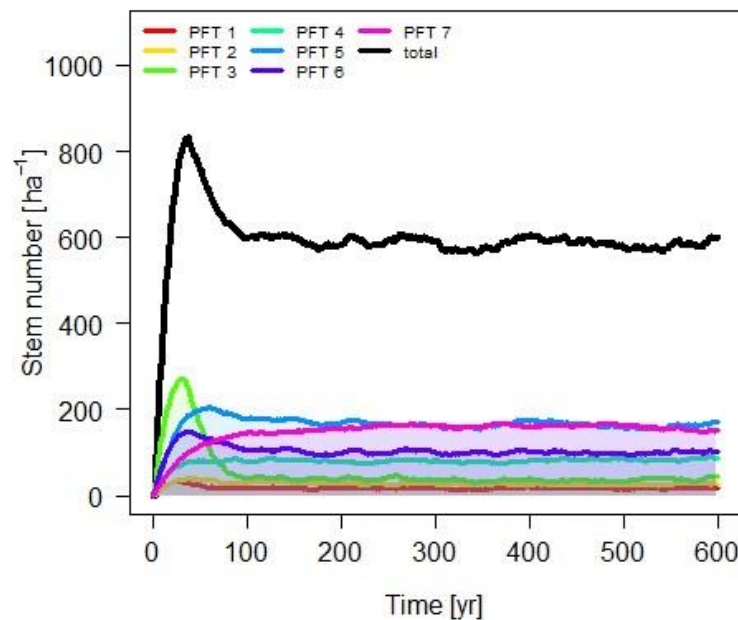


Figure. 4: Simulated basal area (m^2/ha) of miombo woodlands in Niassa Special Reserve under three fire scenarios: (a) *no fire* scenario; (b) *3.29-year MFRI* scenario; (c) *1-year MFRI* scenario.

In terms of tree density, for the *no fire* scenario (Fig. 5a) shade-intolerant PFT3 (*C. collinum*) was predicted to dominate the area for the first ca. 50 years, after which intermediate shade-tolerant (PFT5) and shade-tolerant (PFT6 and PFT 7) dominated the NSR. For the other 2 scenarios, the ecosystem predicts a short stable period of 100 years. Before this period, PFT3 (*C. collinum*) colonized the area for the first ca. 25 years, but then was replaced by characteristic miombo groups (PFT5 and PFT7). However, after 200 years of simulation (when fire started), PFT3 gain became dominant and replaced the more characteristic miombo species.



(a)

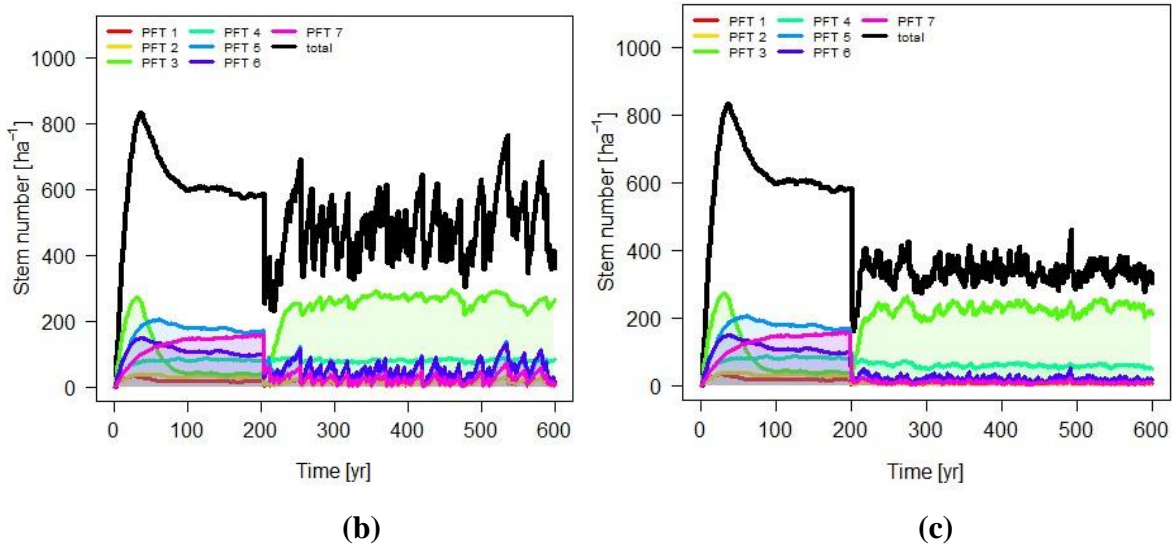
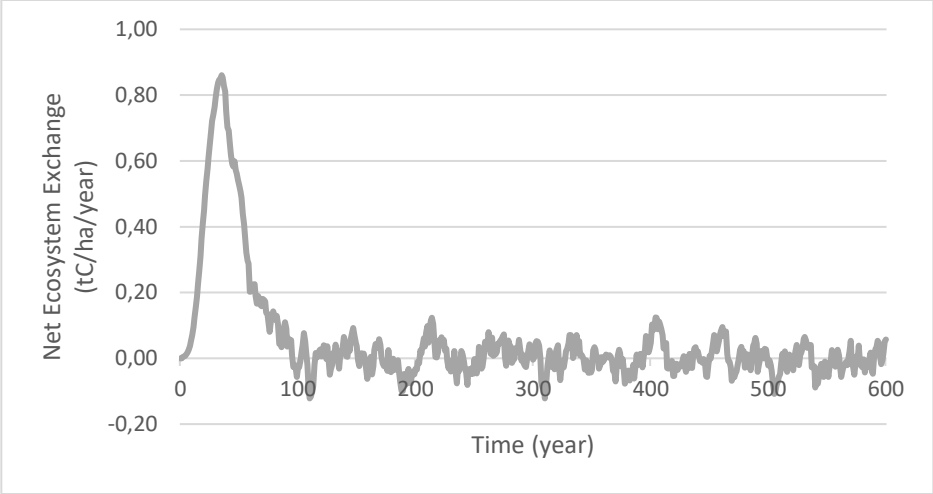


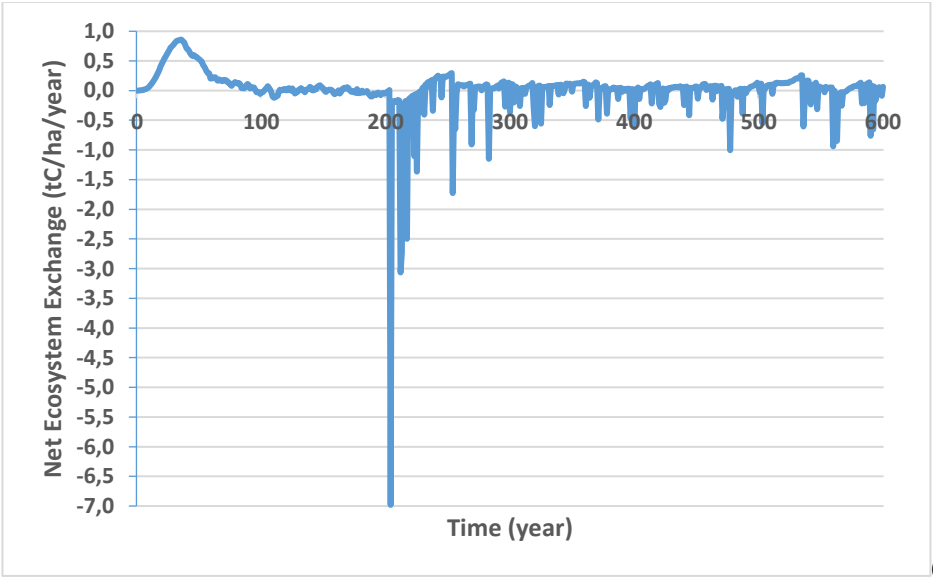
Figure. 5: Tree density (stem number /ha) of miombo woodlands in Niassa Special Reserve under three fire scenarios: (a) *no fire* scenario; (b) 3.29-year *MFRI* scenario; (c) 1-year *MFRI* scenario.

Using the simulated carbon stocks and the fluxes between these stocks, we estimated the carbon balance (Fig. 6). According to the model results, for all scenarios the woodland was a strong carbon sink during the first 50 years of simulation, due to the early growth phase in which forest grows rapidly but does not support much fire. During this phase, the woodland stored up to 0.85 tC/ha/year. For the *no fire* scenario, after about 100 years of simulation, as the forest overall growth rate slows, the NEE became more balanced, with values between ca. +0.1 and -0.1 tC/ha/yr. In the mature state, the forest was in a nearly carbon neutral state. Under the two fire scenarios (MFRI=3.29 and MFRI=1), at about 200 years of simulation when the structural parameters (biomass, basal area, and stem number) declined substantially (Fig. 3-5), the ecosystem was predicted to become a carbon source with values of -7 tC/ha/yr (MFRI is 3.29 years) and -11 tC/ha/year when the woodlands burned annually. This means an avoided loss of emissions of 4 tC/ha/year from managing fire that reduces the frequency of fire on lands that currently burn annually (i.e., approximately 45% of NSR). After the year 200 the woodland was predicted to experience intermittent C sink peaks. However, the avoidance of emissions would persist as long as the fire management program was able to prevent annual burns from occurring where they have occurred prior to the fire management program.

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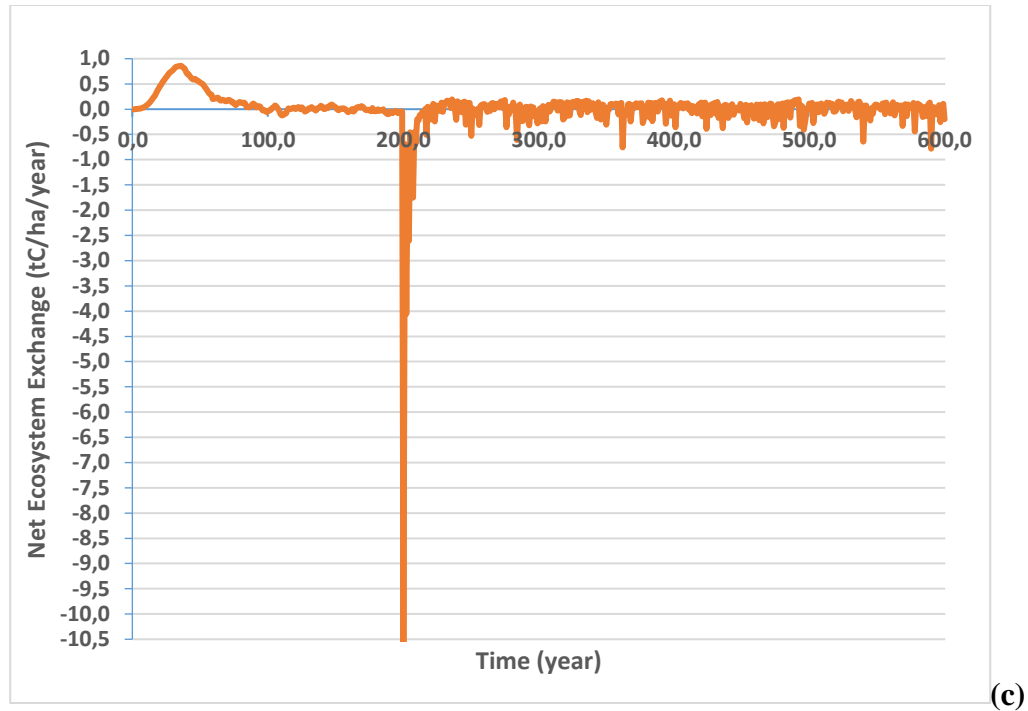
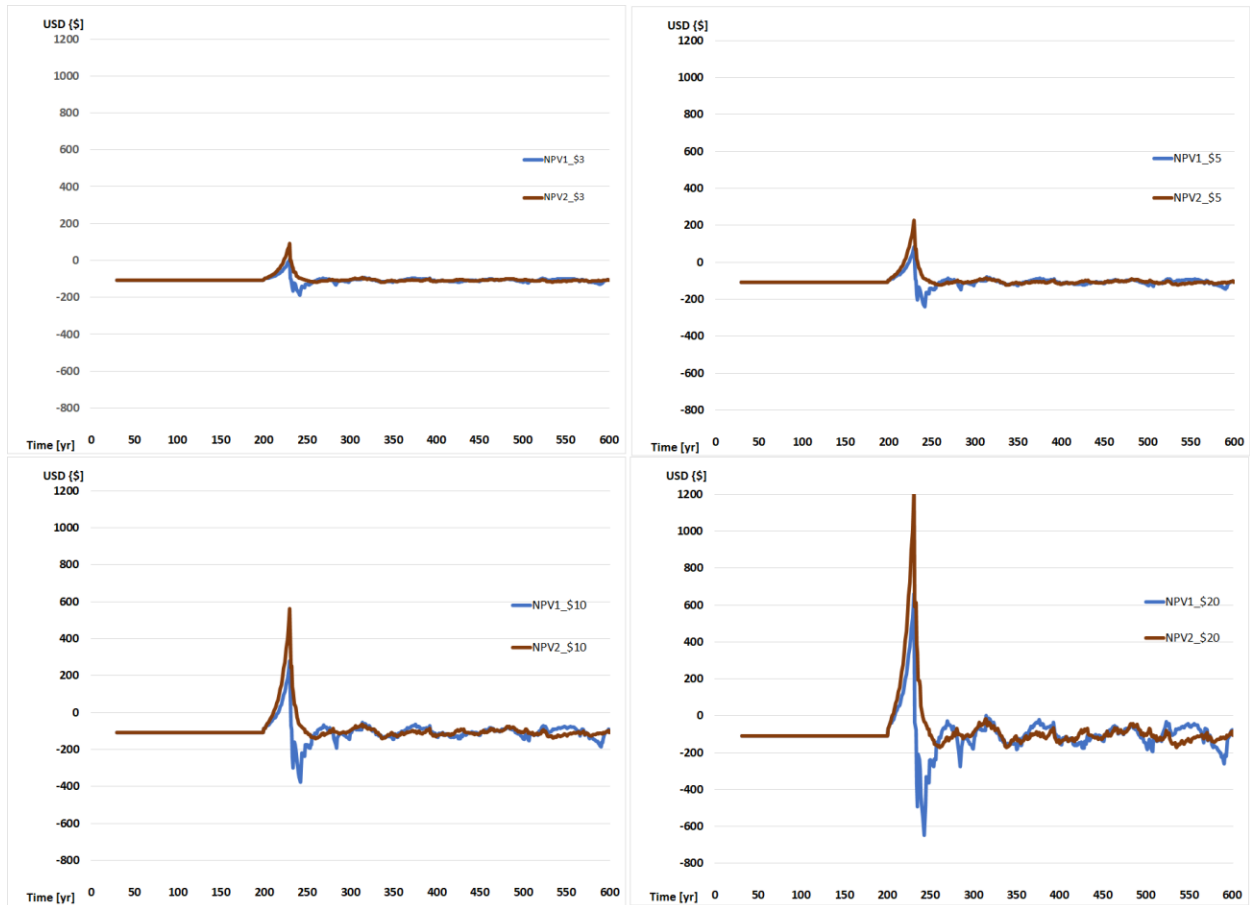


Figure. 6: Simulated Net Ecosystem Exchange (NEE; tC/ha/year) of miombo woodlands in Niassa Special Reserve under three fire scenarios: (a) *no fire* scenario; (b) *3.29-year MFRI* scenario; (c) *1-year MFRI* scenario.

3.3. Economic values of fire management

We evaluated potential carbon values from reducing or eliminating fires based on three fire scenarios and NEE calculations described above (Figure 7). According to the latest survey of voluntary carbon market, volume-weighted average forest carbon price ranges from USD\$ 2.49 to \$7.69 $\text{MgCO}_2\text{e}^{-1}$ depending on project types (Forest Trends' Ecosystem Marketplace, 2020), although USD\$10-\$20 $\text{MgCO}_2\text{e}^{-1}$ may be necessary to make a carbon project profitable in miombo woodlands (Hofstad and Araya, 2015). We performed sensitivity analyses at different carbon prices (USD\$3 ~\$20) at 10% discounting rate per ha.



517

518 **Figure. 7:** Net Present Value (NPV) of reducing annual fires per hectare: NPV 1 for increasing
 519 fire intervals from annual to 3.29 years; NPV 2 for eliminating fires. Simulations for four
 520 different price scenarios are as follows: USD \$3 MgCO₂e top left, \$5 MgCO₂e top right, \$10
 521 MgCO₂e bottom left, and \$20 per MgCO₂e, bottom right. (1 tC=3.67 Mg CO₂e with 10%
 522 discount rate for a 30-year project).

523 These predictions suggest that carbon values are only positive in woodlands around 200 years
 524 old (the present forest age). The maximum NPV can be achieved for a 30-year project starting in
 525 200year-old woodlands for increasing fire intervals (NPV1: USD \$7.8- \$662 per ha) or
 526 eliminating fires (NPV2: USD 93 -\$1,231/ha). However, the carbon values calculated here are
 527 only accounting for changes in NEE due to interventions to reduce or eliminate fires, and do not
 528 include potential values of carbon from reducing biomass removals, such tree harvesting and
 529 fuelwood collection. They also do not account for the value of the avoided emissions of
 530 4t/ha/year from decreasing the fire interval from annual burns to every 3.29 years. Applying the
 531 lowest carbon value of USD \$3 MgCO₂e would produce \$12/ha/year, which is higher than the
 532 median funding deficit of USD \$11.36 /ha/yr identified by Lindsay et al. (2018). Using current
 533 market values of \$5 MgCO₂e would produce \$20/ha/year, which is higher than the high end of
 534 the funding deficit range of \$18.95 /ha/yr (Lindsey et al., 2018), which would obviously be
 535 significantly higher should carbon market values increase (e.g., \$10-20 MgCO₂e). Furthermore,
 536 this study does not specifically address the actual emission reduction potential of fire
 537 management of shifting fires from the late to early dry season (Lipsett-Moore et al., 2018), which

could produce additional revenue. What this study does show is that the overall carbon balance of miombo woodlands as a carbon source or sink does depend on the age of the woodlands, and that mature miombo woodlands provide the highest NPV, and that younger aged stands of miombo woodlands would require longer project periods to generate positive economic returns if the majority of project area consisted of woodlands that were considerably younger than 200years-old.

4. Discussion

In this study, we parameterized the FORMIND gap model in NSR, northern Mozambique which is to our knowledge the first attempt for miombo woodlands in southern Africa (except see Bowers, 2017 for the GapFire model in Kilwa District, Tanzania). The simulation results showed that the model successfully reproduced measured basal area and aboveground biomass because observed biomass values were used to calibrate the model. The data used in this study comes from one of the few long-term (10+ years) monitoring projects for miombo woodlands of southern Africa. Thus, the results of the study can provide a justification to use the model to improve carbon accounting methodology.

Given the longevity and robustness of the field data, model uncertainties were minimized to only 1% overestimation and underestimation for basal area and biomass, respectively. It is more likely that this level of error is driven by uncertainties in grouping the NSR species into plant functional types (PFTs), and due to prominence of other growth forms (e.g., grass) that in general are not simulated by FORMIND. In this study, PFTs were defined based on light requirements (or shade tolerance) and maximum height based on Kolher et al. (2000). The idea behind this grouping was to reduce noise and redundancy in species dynamics, thus simplifying plant community descriptions (Duckworth et al., 2000). However, in the context of open miombo woodlands (which dominates our study area), tree species are exposed to nearly equal amounts of light and thus there may not be clear breaks between different PFTs and therefore the grouping can be considered subjective and arbitrary. On the other hand, it might be much more important to define PFTs according to their response to fires (e.g., bark and leaf thickness; Duckworth et al., 2000), but given the lack of data regarding the particular traits affecting plant resistance to fire, this option was not available. Kazmierczak et al. (2014) suggested that finding a suitable number of PFTs for a specific research question in a simulation study is not resolved. This study reinforced the findings of Fischer et al. (2016) that this approach allows for a realistic description of species dynamics in forests. While we acknowledge the limitations associated with species grouping, the model is robust in reproducing the main structural and compositional characteristics of the miombo woodlands in NSR, which outweighs these limitations. Further investigation on species traits and light responses are needed to improve our capacity to model this complex ecosystem.

Our study has also demonstrated that fire plays an important role in ecosystem's carbon dynamics and structural parameters. With the *no fire* scenario, the ecosystem attained an equilibrium at around 100 years when the structural parameters (basal area, biomass and tree density) stabilized for the next 500 years. Although this is an unrealistic scenario, it is important from a comparative perspective. The miombo indicator species (PFT5, PFT6 and PFT7) became the most dominant groups, which represents well what the miombo woodlands are (Frost, 1996; Gumbo and Chidumayo, 2010; Ribeiro et al., 2008; Ribeiro et al., 2013; Goncalves et al., 2017

and many others). However, it is the occurrence of any fire regime (MFRI 3.29 years or annual burnings) that radically changes the woodland's dynamics after 200 years of age. The ecosystem reached equilibrium at 50 years of simulation and remained in this status for 150 years, after which all structural parameters (basal area, biomass, stem number) declined dramatically and established a much lower equilibrium level (compared to the no fire situation) due to the occurrence of any fire. These trends concur well with the theory that the miombo woodlands are a non-equilibrium ecosystem (Ellis, 1994), which results from a combination of rainfall patterns and fire occurrence (Frost et al., 1996).

Given the presence of fire for over 200,000 years in miombo woodlands, important and pragmatic outcomes of this study that could guide future fire management are the comparisons between the two fire regimes (annual fire vs. fire interval of 3.29 years), rather than no fire scenario. For example, there was a much higher decline in the structural parameters from annual burning than 3+ years during the second stabilization phase (after 150 years of simulation). During this period, species composition did not differ between the two fire regime scenarios and the area was dominated by PFT3 (*Combretum collinum*). However, this latter conclusion contradicts previous observations in the miombo woodlands. For instance, Ribeiro et al. (2008) indicated that under annual burnings Combretaceae species (PFT3) replace *Julbernardia* and *Brachystegia* species while a MFRI of 3-4 years allows miombo species to dominate the ecosystem. The same was observed by Trapnell (1959) in his 50-year fire experiment in Ndola, Zambia. This contradiction may be justified by the complexity of factors (including soils, precipitation and disturbances) affecting the miombo woodlands, which are not completely captured in both field studies and modeling. However, compositional results would not have a major influence on C sequestration and thus provide an important indication that altered vegetations types as a result of fire management would not substantially alter the estimated carbon budgets for a carbon project.

To our knowledge, this is the first attempt to estimate NEE in the miombo woodlands. Despite its novelty, we anticipate that the values observed in this study are accurate given the long-term observations (10+ years) and robustness of the field data. Regardless, more field work is needed, particularly to differentiate changes in fire regimes to overall fire emissions, and impacts to above and below-ground carbon stocks. It is of global significance to climate change mitigation to identify which fire regime scenarios convert miombo ecosystems from a carbon sink into a carbon source, especially when compared to the *no fire* scenario (Figure 3). While this study revealed an estimated reduction of 4 tC/ha/year when fire regimes shift from annual burns to the landscape average of 3.29-year MFRI, it does not provide results in terms of fire emissions benefits from shifting fire seasonality as opposed to fire frequency (e.g., Lipsett-Moore et al. 2018; Russel-Smith et al., 2021). As ecosystem structural changes (basal area and biomass) due to annual burnings there was an influence the woodland's capacity to sequester carbon. This would surely add to the emissions dynamics of NSR and should be included if a C project is to be designed.

On another note, recent predictions for southern Africa indicate that under the low-emission scenario RCP2.6, summer temperatures will increase by about 1.5°C above the 1951–1980 baseline until 2050, and will remain at this level until the end of the century. A dipole pattern of wetting in tropical east Africa and drying in southern Africa emerges in both seasons and in emission scenarios with both temperature increase and decreases in rainfall between 10–30 % (IPCC, 2014). These anticipated changes may increase the likelihood of fires and their impact on

the ecosystem's capacity to mitigate the effects of climate change, a key ecosystem service from miombo woodlands. Given that Africa comprises the vast majority of the global carbon emissions from burning savanna (Lipsett-Moore et al., 2018), the importance of managing fires in this ecosystem cannot be overstated. Emissions from fires can be reduced by active fire management to increase fire interval and reduce fire intensity. Several studies reveal that EDS fires are less destructive than LSD fires, which tend to be burn in higher temperature (Trapnell, 1959; Guy, 1989; Chidumayo, 1997; Archibald et al., 2013, Ribeiro et al., 2017) and have potential to reduce emissions (Bowers, 2017, Lipsett-Moore et al., 2018; Russe-Smith et al., 2021).

Our attempt to calculate C value from managing fire indicate that at maturity (around 200 years - which is likely the current state of the woodland), the NPV resulting from eliminating fire was significantly higher than that from reducing fire frequency, but this is an unrealistic management objective. It is more important to take into consideration that fires are part of the miombo ecology and that these forests generate many non-timber forest products (e.g., honey, mushrooms, other food) as well as fuelwood. We calculated the potential values of carbon due to NEE changes without accounting for opportunity costs of forgone economic activities. Given the long history of fire- human coexistence in this landscape, opportunity cost of eliminating fires would be much higher than that for reducing fire frequencies.

In addition, miombo woodland structure is only one of several carbon pools influenced by fire. Altering fire management from burning too frequently (e.g., annually) can also result in increasing the amount of carbon sequestered in the soil and in aboveground living woody biomass (as it does not burn). All of these carbon pools have existing methodologies that could collectively account for many more carbon credits within the same project area coming from the same, single management action (i.e., fire management) (Lipsett-Moore et al., 2018). Increase of soil carbon also increases nutrient cycling and water retention, which build ecosystems resilience to climate change – in particular to drought and flooding (e.g., Bossio et al., 2020). A recent global meta study of 66 economic valuation studies (559 observations) showed that the largest economic value of dryland ecosystems is from water regulation function (217.9 out of total 586 Int\$/ha/yr in 2007) (Schild et al., 2018). Thus, it is important to recognize the role of fires for maintain the overall ecosystem function. The results of this study suggest that there is ample need to better link more specific studies that document changes in miombo woodland dynamics in relation to fire management with the predictions of FORMIND and other similar models.

The results from this study reveal that a fire management plan can be developed to allow beneficial fires for people and the ecosystem considering the site conditions and age of woodlands, which can be assisted by process-based modeling, such as FORMIND. Managing fires, such as maintaining a 3-year MFRI, instead of trying to eliminate fires, can ensure co-benefits of carbon projects for improving local livelihood and biodiversity. It is important to highlight that fire frequency has high spatial variability across NSR as indicated by Ribeiro et al. (2017). According to the study, 45% of the area burns annually with clusters in the eastern and central northern portions of the reserve, while 27% of the area burns every 3-4 years especially in western NSR. Based on this spatial fire distribution and on our results, we recommend to focus fire management on the sectors where fire occurs annually by conducting EDS fires to reduce the impact of annual late dry season fires as also suggested by Russel-Smith et al. (2021).

If managed effectively, carbon projects can promote benefit-sharing, address social equity concerns, as well as improve the effectiveness of the project activities (Doerr and Santin, 2016). However, fire management is still emerging in the miombo region and very few initiatives have been implemented (the Mpingo Conservation Initiative in Tanzania is one of the fewest; Khatun et al., 2017). This maybe a result of the fact that fire is a legally prohibited activity in most of the miombo countries. On the other hand, fire management in practice is complex and requires an understanding of a complex mix of cultural, biophysical, political and economic factors. To date, there have not been enough multidisciplinary studies focused specifically on addressing this complexity, which limits our ability to design appropriate fire management activities. Revising fire policies to allow prescribed fires in EDS to reduce fuel load should be considered to produce a fire regime that reduces the occurrence, risk and extent of LDS fires (Commonwealth of Australia, 2014). As the use of fires by local people in and around NSR for agriculture occurs towards the end of the dry season, addressing local agricultural practices should be part of the fire management program in the region. It is important to stress that developing integrated fire management requires an investment in resources (human, equipment, etc.), as well as consideration of traditional fire practices to better understand the cultural aspects. Still the Western bias that frames wildfires as “a public enemy” to fight prevails in the region (Doerr and Santin, 2016). Local and regional policies must be adapted to fit this new approach to fire management, but successful fire management in the miombo region can only be achieved after considering rural people’s perceptions and practices.

5. Conclusions

The results of our study revealed that the FORMIND gap model successfully reproduced the structural parameters (biomass and basal area) of the miombo woodlands in Niassa Special Reserve (NSR). The model also predicted that fires substantially influence ecosystem’s ecological dynamics and carbon cycle in the long-run. Annual and triannual burnings substantially reduced biomass and basal area and converted the ecosystem into a carbon source, decreasing its capacity to mitigate the effects of climate change (not considering potential positive changes in other carbon pools). In addition, fire imposed changes in species composition, by which PFT3 (*Combretum collinum*) replaced the miombo typical species (*Julbernardia* and *Brachystegia*). While our model predicted that reducing fire frequency generates a lower carbon value in comparison to eliminating fire, miombo woodlands are fire-dependent ecosystems. Therefore, it is not practical to consider eliminating fire. Furthermore, the elimination of fire dramatically increases the risk of catastrophic fire that damage woodlands, wildlife, and human habitation. Therefore, our study predicted that supporting fire management plans with an objective of maintaining the 3.29-year MFRI is more beneficial to sustaining miombo woodland structure and function than annual burning, and can generate significant carbon revenues from avoided carbon emissions that could at least cover the cost of implementation, and at best generate enough revenue to fill existing funding gaps necessary to ensure effective habitat management. Finally, while the results of our study reveal that fire management is a key activity in NSR, more research is needed to improve our understanding of the complex interactions among the varied socio-economic and biophysical factors in this region. In addition, more education and awareness raising is needed with local decision makers and national policy advisers if the multiple benefits of carbon financing from fire management can be secured for the benefits of nature and people. Our results show that FORMIND model can be

used to incorporate ecosystem changes affected by fires in dry tropics. Improved carbon accounting methodology can be applied in other similar ecosystem types, but ground truthing will be necessary.

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.

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Appendix A Full species list and their traits

Species name	Tree counts	potential height	Average of growth dbh (05-09)	Average of growth dbh (09-15)	Average of growth (05-15)	Annual periodic growth	Average of API 05-15 (kg)	Wood Density (kg/m3)	Category of shade-tolerance*	PFT Grouping
<i>Boscia angolensis</i>	1	5	-0.050	-2.500	-2.550	-0.255	-0.006		ST	1
<i>Bosciasp</i>	1	5	2.200	0.100	2.300	0.230	0.005		ST	1
<i>Vangueria sp.</i>	2	7	0.150	2.550	2.700	0.270	0.142	657	ST	1
<i>Vitex sp</i>	1	8	0.000	6.700	6.700	0.670	0.288	644	ST	1
<i>Ehretiasp</i>	1	8	0.000	5.200	5.200	0.520	0.283		ST	1
<i>Hugonia angolensis</i>	1	8	0.000	5.600	5.600	0.560	0.284		ST	1
<i>Maytenus sp.</i>	2	9	0.033	4.167	4.200	0.420	0.191	713	ST	1
<i>Vangueria arandii</i>	1	9	0.000	6.300	6.300	0.630	0.286		ST	1
<i>Annona senegalensis</i>	23	11	1.011	0.161	1.172	0.117	0.071	518	IST	2
<i>Stereospermum kunthianum</i>	4	15	0.614	-7.325	-6.711	-0.671	-0.114	603	IST	2
<i>Markhamia obtusifolia</i>	10	15	0.000	5.680	5.680	0.568	0.284	622	IST	2
<i>Faurea decipiens</i>	1	10	5.100	0.700	5.800	0.580	0.285	651	IST	2
<i>Bauhinia tomentosa</i>	12	11	1.505	-0.370	1.135	0.114	0.037	670	IST	2
<i>Crossopteryx febrifuga</i>	17	11	1.521	2.227	3.747	0.375	0.052	806	IST	2
<i>Markhamia zanzibarica</i>	11	12	-0.419	1.165	0.747	0.075	0.038		IST	2
<i>Cassia abbreviata</i>	1	15	0.000	25.900	25.900	2.590	0.313	883	SI	3
<i>Ximenia caffra</i>	3	12	-1.625	2.650	1.025	0.103	0.069	463	SI	3
<i>Combretum fragrans</i>	1	10	0.000	0.000	0.000	0.000	0.000	646	SI	3
<i>Parinaricuratelifolia</i>	9	13	1.580	0.170	1.750	0.175	0.031	673	SI	3
<i>Vachellia nilotica</i>	4	10	0.877	0.557	1.433	0.143	0.048	763	SI	3
<i>Combretum elaeagnoides</i>	2	12	0.050	0.200	0.250	0.025	0.001	857	SI	3
<i>Flacourtia indica</i>	13	10	0.303	-0.522	-0.219	-0.022	-0.043	860	SI	3
<i>Ximenia americana</i>	1	10	-2.586	-4.386	-6.971	-0.697	-0.249	867	SI	3

<i>Combretum apiculatum</i>	10	13	0.115	0.276	0.391	0.039	0.001	870	SI	3
<i>Combretum collinum</i>	10	18	1.045	-2.178	-1.134	-0.113	-0.045	880	SI	3
<i>Swartziamadagascariensis</i>	18	15	1.537	2.958	4.495	0.450	0.100	950	SI	3
<i>Vachelliabreviata</i>	2	10	4.300	1.480	5.780	0.578	0.103		SI	3
<i>protea sp.</i>	1	10	0.960	1.440	2.400	0.240	0.003		SI	3
<i>Strychnos spinosa</i>	3	10	0.667	0.600	1.267	0.127	0.002		SI	3
<i>Vitex payos</i>	3	10	0.200	0.600	0.800	0.080	0.002		SI	3
<i>Combretum hereroense</i>	46	12	0.724	0.270	0.994	0.099	0.030		SI	3
<i>Combretum sp.</i>	6	12	1.169	-3.916	-2.746	-0.275	-0.103		SI	3
<i>Combretum molle</i>	3	13	0.590	-0.753	-0.163	-0.016	-0.001		SI	3
<i>Combretum paniculatum</i>	2	15	0.300	0.100	0.400	0.040	0.001		SI	3
<i>Combretum zeyheri</i>	32	15	0.046	-0.612	-0.566	-0.057	0.034		SI	3
<i>Senegaliasenegal</i>	9	15	4.492	1.417	5.908	0.591	0.193		SI	3
<i>Turraea floribunda</i>	1	15	0.000	0.000	0.000	0.000	0.000		SI	3
<i>Psychotria sp.</i>	4	10	2.850	-1.550	1.300	0.130	0.001	575	ST	4
<i>Lannea discolor</i>	7	15	1.119	-1.258	-0.139	-0.014	0.030	413	ST	4
<i>Tarennapavettoides</i>	2	12	0.550	1.000	1.550	0.155	0.002	508	ST	4
<i>Uapacakirkiana</i>	24	14	0.671	-1.237	-0.565	-0.057	0.019	556	ST	4
<i>Brideliacathartica</i>	27	12	0.989	2.204	3.193	0.319	0.120	587	ST	4
<i>Ochna schweinfurthiana</i>	1	10	0.600	0.200	0.800	0.080	0.001	620	ST	4
<i>Diospyros kirkii</i>	83	14	0.902	-0.270	0.632	0.063	0.007	636	ST	4
<i>Catunaregan spinosa</i>	41	10	0.519	-0.305	0.214	0.021	-0.009	688	ST	4
<i>Ormocarpumkirkii</i>	3	15	1.367	1.113	2.480	0.248	0.004	742	ST	4
<i>Dalbergia nitidula</i>	27	12	0.937	-0.047	0.890	0.089	0.043	821	ST	4
<i>Monotesengleri</i>	26	15	1.565	0.250	1.815	0.181	0.033	843	ST	4
<i>Zanhaafricana</i>	2	12	0.400	0.200	0.600	0.060	0.001	857	ST	4
<i>Dalbergia melanoxydon</i>	1	15	2.200	1.100	3.300	0.330	0.008	1152	ST	4
<i>Grewia monticola</i>	1	15	0.960	1.140	2.100	0.210	0.002		ST	4

<i>Hugoniaorientalis</i>	28	15	0.644	-0.538	0.107	0.011	-0.013		ST	4
<i>ozoroainsigna</i>	1	15	0.960	2.100	3.060	0.306	0.004		ST	4
<i>Vangueria tomentosa</i>	2	15	3.580	1.320	4.900	0.490	0.146		ST	4
<i>Uapaca nitida</i>	23	20	2.361	-1.080	1.280	0.128	0.047	690	IST	5
<i>Mimusopssp</i>	3	20	1.700	8.133	9.833	0.983	0.294	729	IST	5
<i>Pseudolachnostylisma prouneifolia</i>	157	20	0.853	-0.034	0.820	0.082	0.001	750	IST	5
<i>Philenopteraviolacea</i>	7	21	1.325	-2.304	-0.978	-0.098	-0.052		IST	5
<i>Julbernardiaglobiflora</i>	289	25	0.990	-1.991	-1.000	-0.100	-0.016	707	IST	5
<i>Milettia stuhlmannii</i>	20	30	3.127	-1.965	1.162	0.116	-0.039	714	IST	5
<i>Sclerocarya birrea</i>	9	20	2.660	-8.002	-5.342	-0.534	-0.028	446	SI	6
<i>Pterocarpus angolensis</i>	47	20	1.097	-2.254	-1.158	-0.116	-0.002	558	SI	6
<i>Diplorhynchus condylocarpon</i>	261	20	0.966	-0.225	0.741	0.074	0.033	586	SI	6
<i>Strychnos madagascariensis</i>	8	20	0.212	-3.223	-3.012	-0.301	-0.073	633	SI	6
<i>Burkea africana</i>	45	20	1.033	0.112	1.145	0.115	-0.004	761	SI	6
<i>Pteleopsis myrtifolia</i>	14	20	0.939	0.879	1.818	0.182	0.022	771	SI	6
<i>Berchemia discolor</i>	2	20	-0.650	-1.075	-1.725	-0.173	-0.139	895	SI	6
<i>Pericopsis angolensis</i>	23	27	1.079	0.357	1.436	0.144	0.012	850	SI	6
<i>Ochna leptoclada</i>	14	20	-0.349	-1.813	-2.161	-0.216	-0.092	545	ST	7
<i>Syzygium guineense</i>	5	20	1.000	-0.048	0.952	0.095	0.001	681	ST	7
<i>Lannea schweinfurthii</i>	3	20	0.000	6.333	6.333	0.633	0.286		ST	7
<i>Brachystegiaspiciformis</i>	34	25	0.427	-2.698	-2.271	-0.227	-0.021	588	ST	7
<i>Brachystegia allenii</i>	38	25	-0.209	-2.099	-2.307	-0.231	-0.053	646	ST	7
<i>Brachystegia manga</i>	46	25	0.996	-0.021	0.976	0.098	0.030	655	ST	7
<i>Brachystegia boehmii</i>	145	25	0.739	0.213	0.952	0.095	0.031	684	ST	7
<i>Terminalia sambesiaca</i>	77	30	1.029	-0.787	0.242	0.024	-0.010	630	ST	7
<i>Loeseneriella crenata</i>	4	30	2.336	-2.413	-0.078	-0.008	-0.061		ST	7
<i>Brachystegia microphylla</i>	2	35	0.300	0.850	1.150	0.115	0.003		ST	7

*ST – Shade-Tolerante; IST - Intermediate Shade Tolerant; SI – Shade-Intolerant

Appendix B. Wood density and crow-dbh relationships

Plant Functional Type	Mean Wood density (kg/m ³) - Zanne et al., 2009
PFT1	655.25
PFT2	622.8571429
PFT3	759.9230769
PFT4	645.8181818
PFT5	825.5714286
PFT6	693.1666667
PFT7	663.2857143

Species or woodland type	Model	Location/MAP	Source
<i>Brachystegiaspiciformis</i>	$cr = (-0.302 + 40.703 \times bd - 26.220 \times bd^2)/2$	Near Harare, Zimbabwe/ 825 mm	Burrows & Strang (1964)
<i>Julbernardiaglobiflora</i>	$cr = (-0.258 + 35.266 \times bd)/2$	Near Harare, Zimbabwe/ 825 mm	Burrows & Strang (1964)
<i>Parinaricuratellifolia</i>	$cr = (0.324 + 22.931 \times bd)/2$	Near Harare, Zimbabwe/ 825 mm	Burrows & Strang (1964)
Miombo	$Cr = 0.073 + 0.113 \times DBH + 0.136 \times ht$	Iringa district, Tanzania/ 565-900 mm	Isango (2007)

cr=predicted crown radius (m), bd=basal diameter (m), DBH=diameter at breast height (m), ht=height (m)

Appendix C. Evaluation of stem number distributions

