UNIVERSITÀ DEGLI STUDI DELLA TUSCIA

DIPARTIMENTO PER LA INNOVAZIONE NEI SISTEMI BIOLOGICI,
AGROALIMENTARI E FORESTALI (DIBAF)

Dottorato di Ricerca in Scienze, Tecnologie e Biotecnologie per la Sostenibilità - XXX ciclo

Modelling plant-animal interactions and the role of megafauna in tropical forests

s.s.d BIO/07 ECOLOGIA

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Anno academico 2017/18

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Short abstract

Tropical forests play an important ecological role in terrestrial ecosystems and influence local and global climate. The correct functioning of tropical forests allows the provision of ecosystem services and products useful for humans, animals, and the forests themselves. Megafauna (terrestrial vertebrates with body mass >10kg) through seed dispersal, nutrient cycling, herbivory, and structural modification can have a disproportionate effect on the functioning of these ecosystems and their services. Plant-megafauna interactions might have both negative and positive effects on plant fitness as one animal can facilitate some plant species while harming others. Regardless of the outcome of each interaction, the quick disappearance of megafauna might permanently change tropical forest plant composition, structure, and ultimately their function. However, not much is known regarding the ecological role and the ecosystem effects of megafauna in tropical forests. Most field-studies have investigated the short-term (3-5 years) consequences of changes in seed dispersal mediated by medium-large animals (vertebrates with body mass 1-2>kg), including some megafauna species. However, there is a limited knowledge of all the other processes through which megafauna can influence tropical ecosystems. Because megafauna can have a disproportionate effect on ecosystems (ecosystem structure, carbon cycling, biodiversity), it is important to understand the implications of their rapid decline. The wide-reaching ecological role of megafauna is relevant not only for conservation but also for management and climate policy.

To advance the knowledge of the ecology of megafauna and overcome some of the limitations of plant-animal interaction research I propose the use of vegetation models. Mechanistic vegetation models can incorporate knowledge from observational and experimental studies to simulate plant-animal interactions at diverse spatio-temporal scales and in diverse environmental conditions. Yet, the role of animals is rarely considered in these models. Given the increasing evidence suggesting the importance of megafauna in terrestrial ecosystems, these models might be missing a key ecosystem component by not considering the influence of megafauna, and animals in general. Thus, I devoted the first part of my thesis to a literature review of megafauna-plant interactions in tropical ecosystems and highlighted the most pressing research gaps. I then developed a series of examples, with algorithms and data useful for parametrization, on how to implement the most studied animal processes in different types of vegetation models.

In the second part of the thesis, I studied the effects of disturbance by the forest elephant (*Loxodonta cyclotis* Matschie, 1900) in the Congo Basin, a poorly studied processes by one of the last and threatened megafauna species in a region of high ecological and political importance. I evaluated how different densities of forest elephants and intensity of disturbance can change forest dynamics and function in terms of forest composition, forest structure, productivity, and carbon stocks. I tested the hypothesis that by clearing the understory and influencing forest regeneration patterns, forest elephants can change forest dynamics and structure, possibly increasing carbon stocks. My methodology included the analysis of forest inventory data and results from long-term simulations of the mechanistic vegetation model Ecosystem Demography 2 (ED2). I first compared forest inventory plots from sites with different intensities of elephant disturbance (absent, low, high). I then implemented a disturbance by forest elephants in ED2 based on existing literature. I simulated scenarios with different disturbance intensities along a gradient of elephant density within a closed-canopy lowland forest in the Congo Basin. The analysis of the forest inventory data showed that at the local level elephant disturbance can have significant effects on basal area and stem density. The simulation results highlight that, in closed-canopy forests, elephant disturbance promotes a forest dominated by very large slow-growing and shade-tolerant trees, and as a result a forest with higher carbon content. The density of elephants and the intensity of their disturbance determine magnitude, rate, and direction of their effect at the landscape level. The results show that forest elephants might be one of the factors that have shaped Central African tropical forests typical structure and higher carbon content compared to other tropical forests. These results are important for the conservation of forest elephants and for forest management, suggesting that forest elephants do not undermine the carbon sequestration potential of tropical forests but could reduce plant functional diversity over the long-term if present at very high densities within the same area.

Overall, the results of my thesis suggest that megafauna can have a transforming role in tropical forests and their loss could lead to different magnitudes and direction of changes in species composition, forest structure, and carbon stocks. Additionally, I have shown the importance of including animal processes in vegetation models and that these models can be an important tool to study plant-animal interactions. Implementing animal-plant interactions in vegetation models can be achieved with minor modifications regardless of the ecosystem or the model type. Finally, given the role of megafauna in the tropics and in other ecosystems, and that their

loss is a driver of global change, models could benefit from including the effects of megafauna to improve their accuracy and forecasting potential.

Keywords: animal-plant interactions, carbon stocks, forest modeling, defaunation, megafauna

Extended abstract

Megafauna (terrestrial vertebrates with body mass > 10 kg) can have a disproportionate effect on the functioning of tropical forests and their ecosystem services. Megafauna interact with plants and the ecosystem in a variety of ways (herbivory, seed dispersal, trampling, nutrient cycling, etc.). Field-studies in tropical forests have focused mostly on seed dispersal and how changes in megafauna populations can influence short-term tropical forest dynamics and regeneration. However, field studies usually investigate only the immediate effects of loss of megafauna over small areas. In addition, all other megafauna-plant interactions have been poorly studied. To overcome some of the limitations of field studies, I have developed a series of examples on how to incorporate animal processes in mechanistic vegetation models to study plant-animal interactions. In addition, I investigated the role of disturbance by megafauna on forest dynamics and structure through a case study of the forest elephant (*Loxodonta cyclotis* Matschie, 1900) in Congo Basin closed-canopy forests.

La megafauna (vertebrati terrestri di taglia > 10 kg) può avere un effetto sproporzionato sul funzionamento delle foreste tropicali e dei loro servizi ecosistemici. La megafauna interagisce con le piante e l'ecosistema in molteplici forme (erbivoria, disseminazione e predazione di semi, calpestio, riciclo di nutrienti, etc). Gli studi in situ in foreste tropicali si sono focalizzati principalmente sulla disseminazione e su come cambiamenti nelle popolazioni di megafauna possano influire sulle dinamiche a breve termine delle foreste tropicali e sui processi rigenerativi. Tuttavia gli studi in situ sono di breve durata e coprono delle aree limitate, inoltre tutte le altre interazioni megafauna-piante sono state poco studiate. Per ovviare ad alcune delle limitazioni degli studi in situ, ho sviluppato una serie di esempi per dimostrare come incorporare i processi animali in modelli di vegetazione per studiare le interazioni animali-piante. Inoltre, ho valutato gli effetti del disturbo da megafauna sulla struttura e le dinamiche forestali prendendo come caso di studio l'elefante delle foreste (*Loxodonta cyclotis* Matschie, 1900) *nelle foreste del Bacino del Congo.*

Key words: megafauna, vegetation modelling, ecosystem functioning, forest dynamics, plant-animal interactions

Introduction

Tropical forests play an important ecological role in terrestrial ecosystems and influence local and global climate. The correct functioning of tropical forests allows the provision of ecosystem services and products useful for humans, animals, and the forests themselves. However, the loss of medium and large mammals (body mass >1-2 kg) due to illegal hunting could result in changes in plant biodiversity and species composition, forest functioning, and genetic biodiversity with unpredictable consequences for forest ecosystems. These changes have been tied directly and indirectly to the loss of different functions performed by animals and changes in plant-animal interactions. Among tropical forest vertebrates, megafauna species (body mass >10 kg) are of particular interest because they can have a disproportionate effect on ecosystem structure and function by consuming high quantities of biomass, distributing nutrients, and reducing tree establishment. The role of megafauna has been studied mainly in relation to their role as seed dispersers while other processes such as disturbance and nutrient cycling are mostly unknown. The consequences of defaunation are still highly debated because results from field studies are often site-specific and of short duration with unknown long-term consequences for tropical ecosystems. To overcome some of the limitations of field studies I have developed methodologies to implement in vegetation models the effects of animals which are often not considered. These models can simulate long-term dynamics and would allow investigating changes in forest ecosystems linked to changes in plant-animal interactions. I then used one of the methodologies I have developed to study the effect of megafauna disturbance on African tropical forests dynamics. African tropical forests are of particular interest because they are one of the largest terrestrial carbon sinks and hold the highest diversity of extant megafauna species. In particular, the forest elephant (*Loxodonta cyclotis* Matschie, 1900) is the largest animal by far in tropical forests but its role as an agent of disturbance has been studied only sporadically over short periods. I investigated the effects of disturbance by forest elephants in the Congo Basin through a combination of analysis of forest inventory data and simulations with the vegetation model Ecosystem Demography 2 (ED2). I tested the hypothesis that elephants clear the understory and increase the mortality of small plants, thus reducing the competition for resources among plants and changing recruitment rates. Forests with and without elephants might differ in trees size class distribution, plant productivity, and possibly carbon stocks.

Methods

Forest inventory data

I obtained forest inventory data from the Ndoki Forest (1.5-3° N, 16–17° E) near the Nouabalé-Ndoki National Park (NNNP), Republic of the Congo (DRC) and from LuiKotale research site (2°47'S, 20°21'E) at the southwestern edge of the Salonga National Park, Democratic Republic of the Congo (DRC). Both sites are located in primary forests with very low human disturbance. In LuiKotale elephants have been absent for nearly 30 years and in Ndoki the population density is 0.56 individuals/km^2. The forest inventory was carried in both sites in lowland closed-canopy forest. Both data sets include all trees with DBH ≥ 10 cm measured in an area of 15 ha in LuiKotale and 4.6 ha in Ndoki. Because LuiKotale data are more extensive, I have used them for validating the model. The Ndoki plots were half positioned on elephant trails and half off trail, I classified them as high disturbance intensity and low disturbance plots respectively. The forest data was analyzed by calculating above ground biomass, basal area, and the distribution of tree sizes fitted with a Weibull distribution.

Choice and description the Ecosystem Demography 2 vegetation model

As disturbance is a process that influences plants according to specific patterns, I have chosen the mechanistic vegetation model ED2 because it has a well-developed implementation of disturbance. ED2 simulates the competition for resources (light, water, and nutrients) among plants and uses environmental data (climate and soil) to simulate plant responses to the environment such as photosynthesis, respiration, and resource allocation. In addition, ED2 reproduces the forest vertical and horizontal structure through diameter at breast height (DBH), height and a crown size. Microenvironment and light conditions at different heights are simulated according to biophysical functions that account for the penetration of radiation through the canopy and microclimate conditions considering also plant-environment feedbacks. ED2 simulates trees as cohorts in a non-spatially explicit fashion, and uses three plant functional types (early, mid, and late successional) to represent functional diversity in tropical forests. Cohorts in ED2 are grouped in patches, which are a collection of cohorts with a similar disturbance history and vertical structure. ED2 can represent the heterogeneity of forest structure with a series of gaps of different ages without representing individual trees. Thus, ED2 structure is suited to study disturbance by elephants which is mostly dependent on plant height and size.

Elephant disturbance in ED2

I implemented a new disturbance type (by elephant) in ED2 that triggers a size-dependent mortality. This disturbance event is described by the disturbance rate, which depends on the density of elephants per km^2, and by the plant mortality rate which is size dependent and varies according on the intensity of the disturbance. I determined the value for these parameters based on two studies of forest elephants in Kibale National Park. In the model, elephant disturbance mortality is, depending on the intensity of disturbance, between 1.4% and 4.2% per year for trees of size <10 cm DBH, and 1.4% for trees >10 and <30 cm DBH. Following the literature, I estimated that at a density of 0.74 individuals/km^2 the area disturbed yearly by elephants is 14% of the total area available to them. This estimate was used to calculate the disturbance rate and to simulate a range of elephant density scenarios. During a first phase, I simulated a lowland closed-canopy forest at a site in the Democratic Republic of Congo (latitude -2.7, longitude 20.4) from bare ground for 500 years. Then, I validated this initial simulation with forest inventory from the same location and compared above ground biomass, basal area, and class size distribution. In a second phase, starting from the forest state achieved in phase one, I ran eight simulations with different elephant densities for another 1000 years, in addition to one without elephant disturbance (control forest). I also evaluated three scenarios of increase disturbance intensity (mortality) to produce a sensitivity analysis. I then compared all the scenarios with the control forest and analyzed changes in forest properties (mean tree size, size class distribution, functional composition, Net primary productivity (NPP), and above ground biomass (AGB)). To corroborate the results from the simulation, I analyzed forest inventories data from sites with different degrees of elephant disturbance (high, low, no elephants).

Results

Analysis of forest inventory data

The analysis of the forest inventory data from LuiKotale and Ndoki Forest shows a clear difference in the density distribution of class sizes (Weibull distribution) between the plots under high elephant disturbance intensity and the low and no disturbance plots (figure 1). The Weibull distribution shape and scale parameters indicate that in plots where disturbance intensity is high there is a lower frequency of small trees compared to large trees and the median DBH is higher. The difference is more subtle between the plots with no and low disturbance.

As the disturbance increases so does the frequency of trees larger than 40 cm. A similar pattern is observed in the number of stems >10 cm and basal area (table 1).

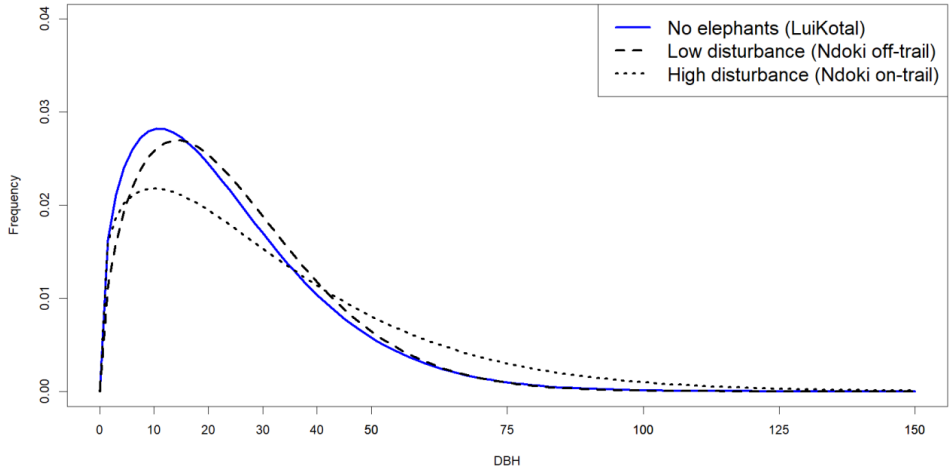

Figure 1. Weibull distribution of forests under different elephant disturbance intensities. Note that the function is fitted with data starting from 10cm DBH.

Data source	Stems/ha	Mean tree size (m^2)	Basal area (m^2/ha)	AGB (Mg/ha)	Shape	Scale
Model	411 (11)	0.088	36 (0.5)	380 (87)	1.71 (0.02)	31.46 (0.59)
No elephants (LuiKotale)	438 (52)	0.075	33 (7)	432 (122)	1.41 (0.01)	26.09 (0.24)
Low disturbance (Ndoki off-trail)	335	0.075	25	370*	1.54 (0.03)	27.85 (0.69)
High disturbance (Ndoki on-trail)	399	0.148	59	1015*	1.26 (0.02)	33.87 (0.93)
Central Africa (Lewis et. al 2013)	425	0.074	31.5	429		

Table 1. Stems per hectare, mean tree size, basal area, AGB, Weibull shape and scale. Standard deviation across years or plots is indicated within parentheses. Model results are from the average of the last 50 years of the spin up simulation. LuiKotale average is calculated across 15 one-ha plots. Ndoki plots, 200 m^2 each, have been aggregated and standard deviation could not be calculated. *Calculated considering a mean density of 0.65 provided by Lewis et. al 2013 and height allometry for Central Africa by (Feldpausch et al. 2011).

Model results from the elephant density scenarios

Medium-term effects after elephant introduction (0-250 years)

Two separate trends can be observed in terms of AGB (figure 2). At densities 0.25-2 a small initial decline is followed by an increase (~1 Mg/ha/year) leading to a rather stable state with AGB higher than control. AGB gains are between 10%-38% (39-146 Mg/ha) with the highest gains at intermediate densities 0.5-1. At densities 3-5 a sharp decline (~2.5 Mg/ha/year) is followed by a highly variable state where AGB is between -3% and -29% (13-113 Mg/ha) lower than control. BA declines initially at all densities, but while at densities 0.25-1 it returns to levels pre-disturbance, at high densities 2-5 BA is reduced up to ~40% (20 m^2/ha) compared to the control (36 m^2/ha). In terms of functional composition, the disturbance causes a heavy loss of early successional PFT and an increase in late and mid successionals (figure 3). At very high densities 4&5 mid successionals start to decline but only after 150-200 years.

Long-term effects after elephant introduction (250-1000 years)

At all elephant densities, aside from 5 and 0.75, this type of continuous disturbance leads to an equilibrium forest with higher AGB compared to control. The higher the elephant density the shorter time it takes to reach equilibrium but the trajectory can be oscillatory (densities 0.25-0.75) or more direct (1-5) (figure 3). At lower densities 0.5-0.75 there is still not a clear equilibrium, but the trajectories of BA functional composition show a trend towards a forest dominated by late successional, like most of the other simulations. Thus, functional diversity is lost only after 500 years at high elephant densities (3-5), while at the other densities mid and late successional PFTs, and in some cases early successionals, persist even after 1000 years. The oscillations between high and low AGB states are due to competition between mid and late successionals and AGB always increases faster (~1 Mg/ha) than it declines (~0.4 Mg/ha). Only at the highest density the equilibrium AGB is lower than control, although only by 1-2%.

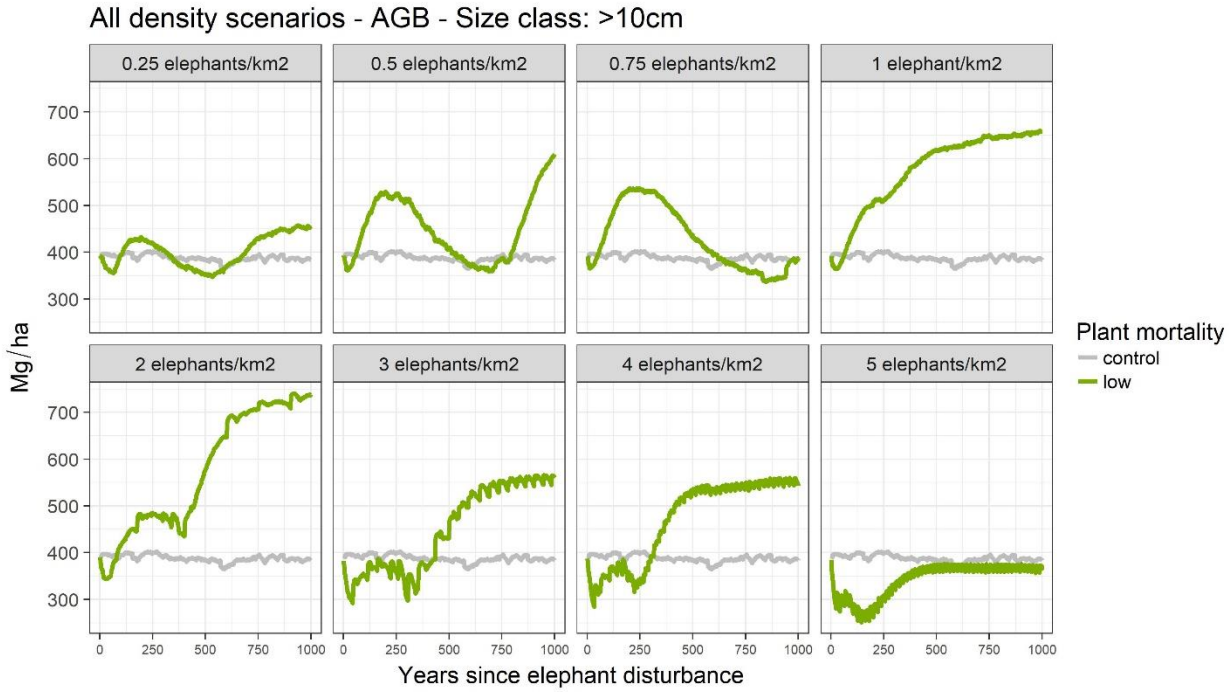

Figure 2. Aboveground biomass of trees >10 cm DBH in all elephant density scenarios.

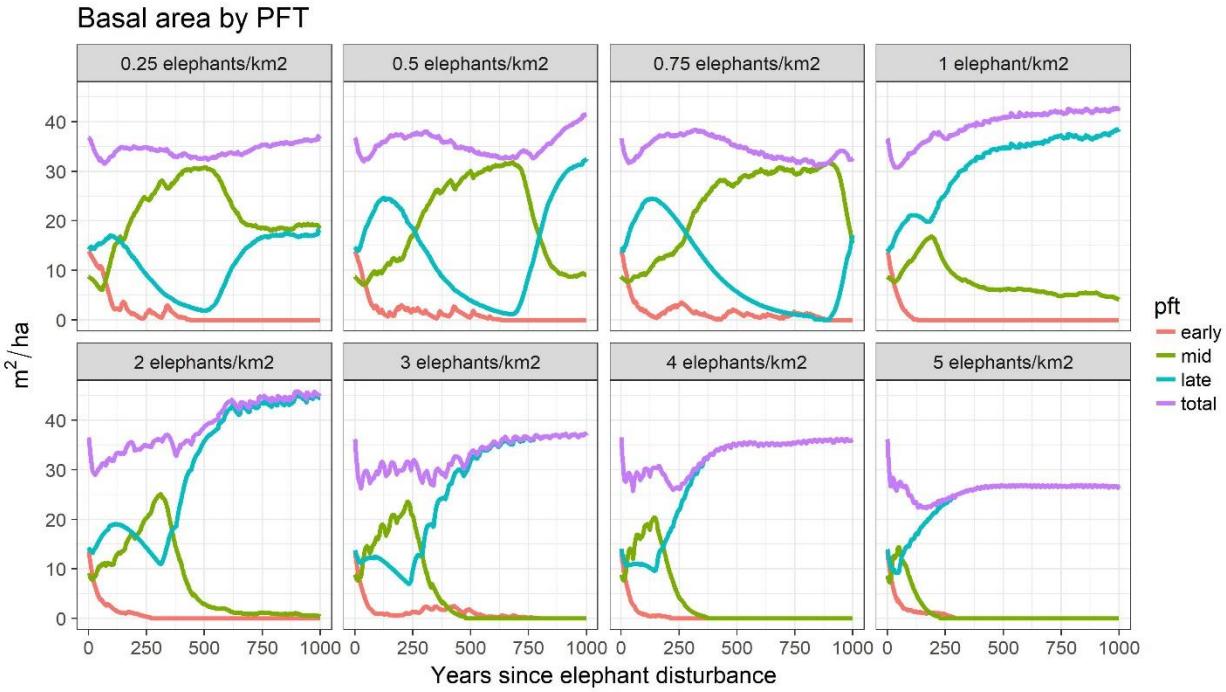

Figure 3. Basal area by PFT and total for trees >10 cm DBH in all elephant density scenarios.

Global effect on Central African forests

The presence of forest elephants across their potential range has large impacts on Central Africa carbon stocks (figure 4). Elephant range reduction leads to heavy carbon losses, ranging from 0.91 Pg of C (s.d. 0.11) up to 1.98 Pg (+/- 0.24). The current losses are also high 1.89 Pg of C (+/- 0.24) because both range (24%) and density (0.25/km^2) have decreased. Elephant introduction would have the opposite effect. The rate of change depends on different factors: the forest state, tree mortality, elephant density at introduction/extinction, and range.

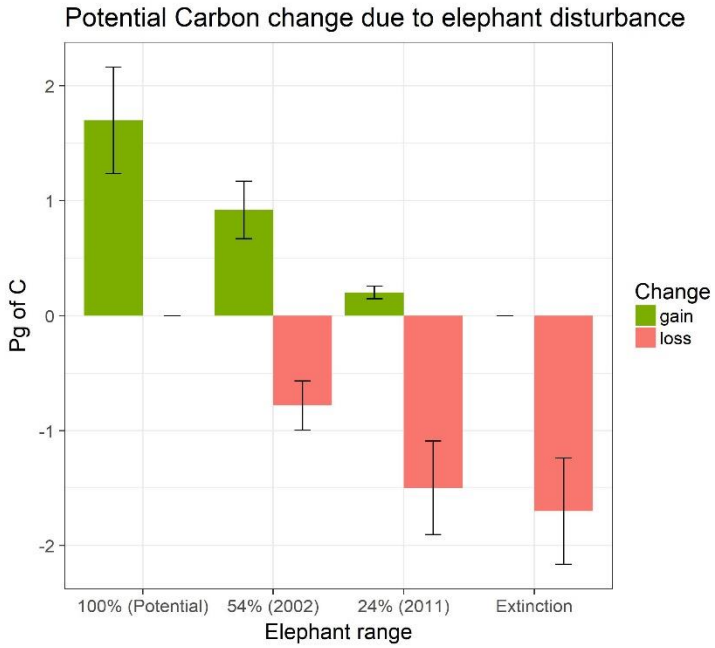

Figure 4. Changes in above ground carbon stocks due to elephant presence (gain) or absence (loss). Ranges 100% and 54% are calculated with a density of 0.5, 24% is calculated with a density of 0.25 (Maisels et al., 2013).

Plant productivity, macro and micro processes driven by elephant disturbance

NPP is lower in elephant disturbed forests and is negatively correlated with AGB. Much of this is related to the functional composition of disturbed forests which have a higher abundance of late successional cohorts which are less productive than early and mid successional. However, late successional have higher wood density and lower mortality and even though their annual NPP is lower, over time the standing biomass of disturbed forests increases and in certain cases remains higher than the control. Competition for light and water is also modified as the mortality in the lower class sizes (1-30cm) changes plant density and the microenvironment. The higher leaf area index (LAI) in the 50+ size class reduces the light reaching the lower size

classes. Also, water stress of trees >10 cm is lower (2-4%) due to having less cohorts. Similar effects are observed across all densities scenarios.

Discussion and conclusion

The simulation results show that elephant disturbance, even at the lowest density, has a significant influence on forest structure and function. Elephant disturbance promotes a forest dominated by a higher number of large trees and less smaller trees. In most scenarios, this effect leads to a forest with a higher AGB while in others AGB decreases because elephant kill smaller trees. Clearing the understory filters the number of plants reaching size classes above 30cm and it allows trees >50 cm to become more dominant. These very large trees reduce the light environment for the lower size classes, and increase water stress of seedlings. These conditions are triggered and maintained by the disturbance of elephants which promote shade-tolerant, slow growing species. The analysis of the forest inventory data, even though limited to a small area, seem to suggest a similar conclusion. The results of the thinning performed by elephants are similar to the ones employed in tropical forest plantations which can lead to very high annual AGB accumulation rates (6-15 Mg/ha, (Lugo et al. 1988)), although in my simulations this rate is much lower (~1 Mg/ha). While treefall creates forest gaps that promote light-demanding species with low wood density the effect of elephant disturbance is the opposite. In conclusion, megafauna disturbance might cause an increase in carbon stocks through changes in plant density and forest functional composition. This process might partly contribute to the reported differences between African tropical forests and other tropical forests, in particular Amazonian ones where megafauna density is low. The time scale associated to these changes can be in the order of a few hundred years. Short-term (10-30) and year-to-year variations are small and difficult to detect at the landscape level because initially only small trees are affected. In the medium-term (50-250) the effects become evident, however there are also transitions between high and low AGB states depending on the extent and intensity of the disturbance. The long-term trends (250+) are more difficult to evaluate because there is an increased uncertainty with long-term projections and other factors influencing the magnitude and direction of change (elephant population dynamics, human disturbance, environmental conditions). Further, the modeling approach has its limitations because I had to make some assumptions and simplifications, particularly in regards to the spatial movements of elephants and the mortality rate of small trees. Data to parametrize elephant disturbance are very scarce and limit our ability to better characterize this process in a model. These results

might be useful as a guide for future data collection in the field that could help define elephant processes more accurately. Additionally, my study only addresses the effect of elephants in closed canopy forests. Future work should consider other important aspects of the ecosystem engineering of megafauna, including forest elephants: seed dispersal, nutrient distribution, and herbivory. It should also consider two-way interactions between megafauna and plants by including an ecophysiological model for megafauna populations that accounts for birth/mortality, growth, and consumption.

In conclusion, the results of my thesis suggest that megafauna can have a transforming role in tropical forests and their loss could lead to different magnitudes and direction of changes in species composition, forest structure, and carbon stocks. This has implications for conservation, forest management, and carbon stock policy. Additionally, I have shown the importance of including animal processes in vegetation models and that these models can be an important tool to study plant-animal interactions. Finally, given the role of megafauna in tropical and other ecosystems, and that their loss is a driver of global change, models could benefit from including the effects of megafauna to improve their accuracy and forecasting potential.

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1 Introduction

1.1 The multifaceted importance of tropical forests

Tropical forests play an important role for human beings, in atmosphere-biosphere interactions, and in maintaining species diversity (Gibson et al., 2011). At the local level, tropical forest ecosystem services provide forest products used for consumption (meat, medicinal plants, fruits, and seeds) and manufacturing (timber and rubber) (Lawrence et al., 2005; Stepp et al., 2002). Ecosystem services include the control of water cycle and the maintenance of a local humid climate (Boyce et al., 2010). At the global scale, tropical forests provide highly valuable natural resources that are traded, legally and illegally, on global markets. Some of these resources include animal products and live animals that are harvested for different purposes: pet trade, traditional medicine, and product manufacturing (Nellemann et al., 2014). Another global ecosystem service provided by tropical forests is carbon sequestration. In spite of occupying only 7% of terrestrial land, tropical forests play a disproportionate role in carbon cycling as they store about 25% of terrestrial carbon (Bonan, 2008). Given their importance in the global carbon cycle, tropical forests have been at the center stage in the efforts to reduce atmospheric carbon dioxide (CO2) (Maniatis et al., 2013). This ecosystem service however seems to be linked to another, the maintenance of biodiversity. Tropical forests are one of the major biodiversity hotspots (Myers et al., 2000) and hold half of world animal and plant species. Particularly, plant biodiversity might be related to a higher potential of sequestering carbon, however this is still under debate (Balvanera et al., 2014; Finegan et al., 2015; Sullivan et al., 2017).

1.2 The unknown consequences of defaunation in tropical forests

The ecosystem services provided by tropical forests depend on it ecological equilibrium, which is shifting as a consequence of environmental changes and human pressure. On one hand, climatic changes driven by anthropogenic Greenhouse Gases (GHG) emissions, are causing an increase in average temperatures, changes in rainfall patterns and possibly more intense drought events with consequences for the carbon cycle (Powell et al., 2013) and plant biodiversity (Corlett and Westcott, 2013). On the other hand, human pressure has been an ongoing threat for many decades which causes habitat loss and degradation (Achard et al., 2002) and rapid declines and extinctions in animal populations (Bradshaw et al., 2009). After

habitat loss, hunting and poaching are the biggest threats to animal populations in all tropical regions (Ripple et al., 2016). In some cases where forests are protected only from deforestation, hunting and poaching are the main drivers of animal local extinctions, which can result in a phenomenon called "empty forest" (Redford, 1992; Stokstad, 2014). Empty forests have an intact forest cover because they are usually managed or protected for timber production or carbon stocks trading schemes (i.e. United Nations, Reducing Emissions from Deforestation and forest the Degradation, REDD) but they have a low diversity and abundance of animals. Regardless of forest status, hunting for local bushmeat markets and for animal products (skins, organs, ivory) is pervasive in all tropical regions (Corlett, 2007; Wright, 2003; Ziegler, 2016). The loss of animal populations is referred to as defaunation. Animal populations of medium to large vertebrates (mammals and birds with body mass greater than 1-2 kg) are the first to disappear (Corlett, 2007; Ripple et al., 2015, 2016). These animals have co-evolved with plants for thousands of years and their disappearance from tropical ecosystems might perturb the system or shift it to a new equilibrium state. Animals interact in complex ways with plants and the environment by consuming biomass (leaves, bark, seeds, and fruits), dispersing seeds, redistributing nutrients, and altering the physical structure of the ecosystem (trampling small plants, debarking, compacting soil). These interactions can influence many plant processes: growth, recruitment, competition, mortality, and dispersal. Thus, profound changes in trophic interactions caused by animal over-exploitation may even surpass the impact of climate change on forest structure and function (Estes et al., 2011), and could furthermore amplify the predicted effects of climate change (Abernethy et al., 2013). Combined with climate change, defaunation may reduce the resilience of tropical forests and push these complex ecosystems towards a tipping point. The loss of species-specific co-dependencies (Laurance et al., 2006; Peres and Roosmalen, 2002) and biogeochemical processes (i.e.; nutrient cycling, Ripple et al., 2015; Wolf et al., 2013) connected to animals may have many cascading effects for the entire ecosystem. These effects have been examined intensively within the last decade by defaunation ecology studies with the goal of evaluating the consequences of defaunation on tropical forest ecosystems (Stoner et al., 2007; Wright, 2003).

1.3 So much for seed dispersal so much less for other processes

The vast majority of these studies were conducted in the field by examining how changes in seed dispersal affect plant recruitment and establishment at the seedling stage. The focus on seed dispersal is due to historical and ecological reasons. Historical because two seminal papers

published by Daniel H. Janzen have opened research questions regarding the role of large animals (body mass larger than 45 kg) in seed dispersal (Janzen and Martin, 1982), and dispersal as a mechanism to maintain the high plant diversity of tropical forests (Janzen, 1970) . The first question investigates the consequences of the disappearance of large animals for tree species that produce large seeds that can be dispersed by endozoochory only by large animals. The second question, also known as the Janzen-Connell hypothesis, is also related to dispersal as a process to avoid specialist enemies (herbivores and pathogens) that reduce survival of seeds and seedlings near conspecific adults (Connell, 1971; Janzen, 1970). In addition to these two long-standing hypotheses, the ecological importance to study dispersal in tropical forests lies in the high number of tree species (80% to 90%) that are dispersed by animals. Larger animals play an important role in maintaining plant diversity, not only because they disperse large seeds but also because they disperse seeds of many species by endozoochory. In fact, most defaunation studies report that the disappearance of medium-large vertebrates might lead to a shift in plant species composition towards forests with lower plant diversity and more abundant in plant dispersed abiotically (mainly wind) or by small animals (birds, bats, rodents) (Effiom et al., 2013; Rosin and Poulsen, 2016; Vanthomme et al., 2010; Wright et al., 2007). This shift happens because seeds in tropical forests have a higher chance of germinating and establishing when they are de-pulped and dispersed away from the mother tree (Janzen-Connell effect). However, other studies have shown that not always defaunation leads to changes in plant composition and that even large seeds can be dispersed effectively by smaller animals such as rodents, birds, and bats (Forget and Milleron, 1991; Jansen et al., 2012; Nyiramana et al., 2011). More evidence is emerging that the complexity of the tropical food web and redundancy in seed dispersal agents leads to site and time dependent outcomes for plant communities after changes in animal communities (Chapman et al., 2012; Howe, 2016). For example, defaunation not only affects seed dispersers but also seed predators, thus in certain cases defaunation can promote plant recruitment because it releases seeds from predation while in other cases seed predators contribute directly to increasing plant biodiversity (Paine and Beck, 2007; Wright et al., 2000). The hypothesis that the loss of medium-large animals only penalizes large-seeded trees needs further refinement, because large animals, such as primates and ungulates, disperse as many small seeds as they disperse large seeds (Chen and Moles, 2015). Seed dispersal effectiveness, defined as the "number of new adults produced by the dispersal activities of a disperser" (Schupp et al., 2010), can change in space and time according to resource availability, time of fruiting, and faunal assemblage (Howe, 2016). Hence, the same dispersal syndrome (also known as the main dispersal method/agent), even when assigned

based on observations, might not apply to all sites and at all times. For example, the primary disperser of a species might be a bird in one location and a primate in another and the two can have different seed dispersal effectiveness based on the location. Furthermore, as most studies are of short duration (2-3 years), there is limited knowledge on the long-term consequences of defaunation, an issue I discuss in more detail in section 3.1.

While there are many studies on the role of animals as seed dispersers, a large knowledge gap is constituted by the effects of large animals regarding all the other ecosystem-engineering processes through which they can influence vegetation dynamics: herbivory, nutrient distribution, trampling, uprooting, etc. Some of these processes have received little attention because they are difficult to study quantitatively in tropical forests. Also, until recently animals were considered a passive player in tropical vegetation dynamics, which were thought to be driven predominantly by climatic conditions and competition among plants. Instead, a more complex framework has been emerging in which animals are not only capable of influencing vegetation dynamics but also vegetation-atmosphere interactions.

1.4 The transforming role of megafauna

Ecosystem engineers are animal species that can have a disproportionate effect on ecosystems, not only by modifying the ecosystem physical structure but also by influencing other species across trophic levels (Jones et al., 1994). This definition is not without controversy (Wright and Jones, 2006); however, the core idea is the disproportionate influence of one species over multiple others (Chapman et al., 2012). Classical examples of ecosystem engineers are beavers (*Castor canadensis*), savanna elephants (*Loxodonta africana*), and more recently wolves (*Canis lupus*). Latest researcher has shown that also large herbivores can have transforming effects on ecosystems with effects that could be as far-reaching as influencing climate. The definition of large herbivores, which are also referred to as megafauna, can vary according to different authors and research areas, often this coincides with mammals with body mass larger than 10kg, but exceptions exist (see the definition box in section 3.1). Typically, megafauna are vertebrate mammalian herbivores, and sometimes carnivores, than can have a disproportionate effect on ecosystem function and structure when present at high or natural densities (Bakker et al., 2015; Malhi et al., 2016). There is not always a clear correlation between megafauna densities and the magnitude of their effect on ecosystems, and possibly climate. Regardless of definition, megafauna have been shown to influence a wide range of

processes: nutrient cycling and plant Net Primary Productivity (Doughty et al., 2015a; Wolf et al., 2013), ecosystem structure (Bakker et al., 2015), fire regimes (Pachzelt et al., 2015), carbon storage (Bello et al., 2015; Doughty et al., 2015b; Osuri et al., 2016; Peres et al., 2016), and GHG emissions (Smith et al., 2016; Wolf et al., 2010). There is however very limited knowledge on the ecosystem engineering role of megafauna in tropical forests and the long-term effects of their current decline on forest structure, function, and carbon cycle. In section 3.1 I present an overview of what is currently known regarding the ecosystem engineering effect of megafauna in tropical forests.

1.5 Vegetation models to study the effects of megafauna

The influence of megafauna on vegetation is becoming more evident with implications also for vegetation-atmosphere feedbacks. This fuels an increasing necessity to develop integrative methodologies that can be used to study the megafauna-vegetation-atmosphere system. These methodologies should allow not only to study the local effect of megafauna but also be scalable in time and space and allow the integration with atmospheric models, much like the coupled land-climate models. While field studies provide fine scale data, they are usually spatially and temporally limited and rarely provide any insights on the broader impacts of megafauna. A yet underdeveloped tool offering scalability and integration potential are vegetation models (VMs). VMs are process-based models that mechanistically reproduce vegetation dynamics by simulating plants lifecycle and competition for resources by using climatic and soil data to reproduce biogeochemical processes (photosynthesis, nutrient cycling, energy budgets, etc.). I provide an overview of VMs and their processes in chapter 2. VMs offer a scalable methodology that can complement field studies and incorporate observational and experimental data to simulate mechanistically plant-animal interactions. VMs can overcome some of the limitations of field studies by offering a simulated environment under controlled conditions. This would help disentangling some of the complexity of tropical ecosystems and evaluate the long-term effects of changes in animal populations. In addition, VMs may also pinpoint processes that require further examination in observational and experimental studies (Medlyn et al., 2016). Despite the advantages of VMs, there is a large methodological gap in their application to simulate plant-animal interactions, with only a handful of studies, and none of them in tropical forests. Thus, before we are able to study the effects of animals on vegetation, we need to develop methodologies to describe animal processes in VMs. In section 3.1, I present examples illustrating how to implement animal processes in VMs. I include

algorithms and examples of data that could be used to implement and parameterize the effect of animals. My examples refer to tropical forests and megafauna but the methodology is applicable to a wide range of models, ecosystems, and animals, from insects to mammals.

1.6 African tropical forests and forest elephants

In the context of the rapid loss of megafauna and their ecology, the Congo basin is an important region for several reasons. Central African tropical forests are the last ecosystem, along with the African savanna, to host a remnant of what once was a very high diversity of megafauna. While in all continents most megafauna species went extinct during the late Quaternary Megafauna Extinction (~11k years before present, Martin, 1984), in African tropical forests a high number of megafauna species still persists (e.g., forest elephants (*Loxodonta cyclotis*) , hippopotamus (*Hippopotamus amphibius*), gorillas (*Gorilla spp*) , forest hogs (*Hylochoerus meinertzhageni*)). Yet, many of these species are in the International Union for the Conservation of Nature threatened species list (Ripple et al., 2015). Thus, the Congo Basin is a priority conservation site, one of the last ecosystems where megafauna persist, and the only tropical region where it is still possible to study the ecosystem-engineering role of megafauna. To a minor extent also South-East Asia offers similar conditions, but with a lower density and diversity of megafauna.

African tropical forests, the second largest after the Amazon, play also an important part in the carbon cycle as an active carbon sink and with an average above ground biomass which is higher than other tropical forests (Fisher et al., 2013; Lewis et al., 2009). Recent research has highlighted that megafauna, and in particular forest elephants, might contribute to the difference in structure and diversity between African and Amazonian tropical forests (Terborgh et al., 2016a). African forests have lower stem densities but larger trees and higher above ground biomass than Amazonian forests and forest elephants might be one of the factors contributing to some of these differences. In fact, in Amazonian forests the largest herbivore is the tapir (*Tapirus spp*) and megafauna of comparable size to elephants have been absent for more than 10k years. Forest elephants can influence the vegetation dynamics through different processes: prevent tree establishment, clear the understory, and increase small tree mortality (Omeja et al., 2014; Terborgh et al., 2016b). Forest elephants are also important as seed dispersers as they can increase seed germination rates (Blake et al., 2009) but their effect on forest regeneration might be site dependent (Hawthorne and Parren, 2000). However, the effect of forest elephants on carbon cycling and forest regeneration is still unclear. Forest elephants

have been heavily poached for ivory and their populations rapidly declining with the loss of 60% of individuals over a period of less than 10 years (Maisels et al., 2013). The range of forest elephants is now less than 25% of its potential with a population of less than 10% of its carrying capacity. As the largest species by far in the Congo Basin, the reduction of the elephant range and population size must have important ecological consequences for African forest ecosystems. Hence, understanding the ecological role of one of the last megafauna species is paramount for both conservation and natural resource management. Furthermore, the influence of elephants on the carbon cycle of African tropical forests might have implications for climate and its policies (carbon stocks).

1.7 Objectives and scientific questions

The overarching objectives of this thesis are to shed light on the role of megafauna in tropical ecosystems and to advance the methodology to implement animal processes in VMs. My first goal is to identify the most pressing research gaps in tropical megafauna ecology and the most understudied megafauna-vegetation interactions. My second goal is to develop general approaches to implement animal processes in different types of VMs. These approaches target the necessity to overcome current limitations of field studies and the lack of modeling methodologies used to assess the influence of megafauna on vegetation dynamics and vegetation-atmosphere interactions. My final goal is to employ one of the methodologies I have developed to show the potential of VMs to tackle complex ecological questions regarding plant-animal interactions. To do so, I study the ecosystem-engineering role of forest elephants, a problematic process to assess in field studies, to identify their effect on vegetation dynamics and carbon cycling in the Congo Basin.

This thesis pursues the following research questions:

Questions regarding methodology, ecological theory, and research gaps:

- What are the main research gaps in tropical megafauna and defaunation ecology? What are the shortcomings that do not allow a better understanding of the ecological processes influenced by megafauna?

- Which modeling methodologies could be used to overcome the current research gaps and how existing vegetation models can be improved to include animal processes?

- What type of data can be used to formalize, parametrize, and calibrate animal processes in vegetation models? Can these processes be generalized with algorithms applicable to different model types?

Questions regarding megafauna ecology:

- What data is available to parameterize the disturbance effect of forest elephants in a vegetation model?

- What is the effect of disturbance by forest elephants on the structure and function of tropical forests in the Congo Basin?

- At which densities forest elephants have an influence on tropical forests carbon cycling and structure? What the implications for conservation and management of elephants and forests?

1.8 References

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2 Methodologies

2.1 Introduction to vegetation models

Vegetation models simulate the lifecycle of plants and the competition among them for resources. Some models go as far as including hydrology, gas fluxes, nutrient cycling, and anthropogenic and natural disturbances (e.g., fire and deforestation), and might be coupled with global climate models or earth system models to study atmosphere-biosphere interactions. These models, depending on their purpose and function, have been referred to as: dynamic global vegetation models, dynamic vegetation models, (forest) gap models, forest models, (forest) landscape models, individual-based forest models. Because there is a wide range of methodologies used to simulate plant dynamics, here I provide a general overview of the most important concepts used in these models, which I will refer to as vegetation models (VMs). In section 2.4 I will then describe more in detail the model I used in my thesis work. I chose "vegetation" instead of "forest" because some of these models also include grasses. I omitted "dynamic" and "global" because these models operate at different scales, from hectare to global, and by simulating vegetation they must be intrinsically dynamic. I will mostly refer to VMs that have been used in tropical forest studies; however, all of the models I mention are based on very similar concepts and have been used across ecosystems (boreal and temperate forests, grasslands, wetlands, etc.). Some examples are: TREEMIG in alpine ecosystems (Lischke et al. 2006), ORCHIDEE-MICT at high latitudes (Guimberteau et al. 2017), LPJ-DISP in North American forests (Snell 2014), LPJ-GUESS in boreal forests in northern Europe (Smith et al. 2008), and 3D-CMCC in southern Europe deciduous forests (Collalti et al. 2014).

2.2 General classifications of Vegetation Models

There are three broad categories of VMs as historically they were developed for different purposes. However, some of the VMs are now converging into similar products. For example, some global vegetation models are now incorporating a vertical structure to better represent light competition, and cohort-based models propose a compromise between global and individual-based models. Here I provide a general classification of VMs into three groups: Dynamic Global Vegetation Models (DGVM), cohort-based models or hybrid models (CBM), and individual-based models or gap models (IBM). I illustrate the continuum between these three groups in figure 1 with respect to geographical scale, representation of species, and

research focus. DGVMs focus on atmosphere-biosphere interactions and are part of land surface models which are coupled with Global Circulation Models in Earth System Models to simulate global climate and fluxes of energy and CO_2. CBMs run at finer spatial-scales than DGVM, still operate with PFTs but can better vegetation heterogeneity across large scales. Both CBMs and DGVMs tend to be deterministic and reproduce detailed physiological processes but to reduce computation times do not simulate single trees but rather cohorts or an average of plants in a grid cell. IBMs tend to be more focused on local processes and stand dynamics, and might have less complex energy, water, and CO_2 fluxes. For example, IBM might not account for microclimatic effects on leaf biophysical processes related to photosynthesis (evapotranspiration, canopy roughness, etc.). IBMs are used predominantly for simulations running at local scales and thus have been used with single species or a more specific set of PFTs. Instead, DGVMs have only a few PFTs to represent each biome. IBMs tend to include stochastic processes requiring several simulation to evaluate the variability of their output while DGVMs and CBMs are deterministic and given the same set of input, initial conditions, and parameters, they always produce the same output.

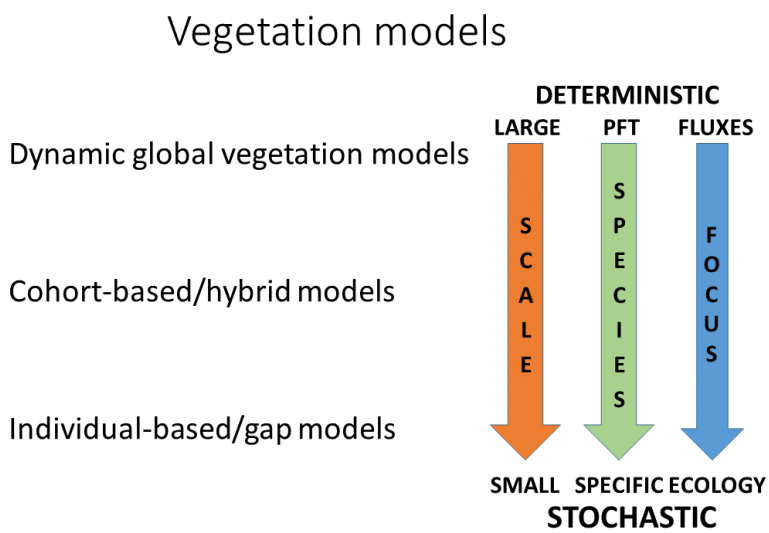

Figure 1. Characteristics of the three main groups of vegetation models according to spatial scale, representation of species diversity, and general focus. Note that the scale is fairly variable as some DGVMs are now used locally and CBM have been run on large regions.

In tropical forests, Ecosystem Demography 2 (ED2, Medvigy et al. 2009), a CBM, has three PFTs to represent tropical evergreen forests: early, mid, and late successional trees. FOREMIND (Köhler and Huth 1998), an IBM, has an even larger number of tropical PFTs and TROLL (Chave 1999), another IBM, has 163 species calibrated on French Guiana forests.

2.3 Main concepts and applications of vegetation models

VMs are deterministic and in part statistical models that simulate plant (trees and/or grasses) growth, reproduction, and death. In VMs, plants compete for resources, typically space, light, water, and nutrients. The processes most frequently simulated in VMs are establishment, photosynthesis, respiration, growth, allocation, reproduction, and mortality. These processes are simulated in lesser or greater detail based on the model's focus (Quillet et al. 2010, Snell et al. 2014). Most of these processes are simulated mechanistically through equations describing the physical and chemical relations governing each processes. For example, one seed germinates into a seedling if there is a minimum amount of light and water. However, some of these equations might also include a stochastic component. Continuing from the previous example, if many seeds are competing for resources within the same space, than a probability or random function might be used to determine which one will germinate. A similar example is mortality which can be determined by aging (a stochastic process, older plants are more likely to die) or carbon balance (a mechanistic process, plants spending too much time in negative carbon balance die). VMs are used to address a variety of research questions concerning carbon cycling, vegetation dynamics, forest response to disturbances, forest management, and atmosphere-biosphere feedbacks. The most frequently used VMs in tropical ecosystems are: DGVMs (e.g. ORCHIDEE (Krinner et al. 2005) and LPJ (Sitch et al. 2003)); (ii) CBMs (e.g. ED2, and LPJ-GUESS (Smith et al. 2001)); and IBMs (e.g. FORMIND and TROLL). As models are constantly being developed, the differences between model types are becoming more blurred, but generally, all models operate on slightly different assumptions and simulate plant processes with, respectively, increasing level of detail (Fig. 1).

Plant classification: Plant functional types, species, and traits

VMs use a simplified plant classification when simulating vegetation at large spatial scales or in ecosystems with a high number of species such as tropical forests. Plant Functional Types (PFT) are used to describe the range of plant traits found in each biome. PFTs are usually defined in models by a list of parameters that are determined by analyzing empirical data on different plant species across the area to be simulated. Plant species are aggregated into PFTs which are differentiated according to phenology, bioclimatic limits, physiognomy, and physiology. The most common PFTs reflect in some way the distribution of global biomes, as PFTs were initially conceived to be used in large scale modelling exercises. Examples of the

most common PFTs are: C3 and C4 grass, tropical broadleaf evergreen, tropical broadleaf deciduous, temperate broadleaf evergreen, temperate broadleaf deciduous, boreal needle leaf evergreen. In global models, PFTs represent the most generalizable description of plant functional diversity within a particular biome, while in more localized simulations a more precise parametrization is possible. The number of parameters that describe a PFT can range from less than 10 to almost 100. Some of the most used are: maximum height, wood density, leaf longevity, leaf turnover rate, photosynthesis related parameters, leaf/root respiration parameters, specific leaf area, leaf carbon to nitrogen ratio, dispersal distance, etc. In situations where a mono dominant forest or a forest plantation is simulated, it is possible to simply use a single species. In these cases, usually the species to be simulated is well studied and much data are available to describe its characteristics within a model. Recently, two new approaches have been proposed: trait-based modeling (Scheiter et al. 2013, Fyllas et al. 2014) and a reduction of parameters allowing a large number of species to be described (Marechaux and Chave 2017).

Trait-based models adopt a different approach than the PFT-based one by characterizing individual plants with a list of traits and the concept of species or PFT does not exist. Individuals with the set of traits most advantageous in a particular environment survive and reproduce so traits are passed on to the following generation of plants. Trait-based models in which traits are hereditary are initialized with individuals with a random set of traits, this is the case for the aDGVM model (Scheiter et al. 2013). Instead, models that only simulate one generation, or do not have inheritable traits, assign trait values based on field measurements of such traits, this is the case of the TFS model (Fyllas et al. 2014). Such measurements should be from a location with similar environmental conditions as the site being simulated. These models represent one of the latest developments and are probably the future of vegetation modeling as they overcome the limitations of PFTs which do not account for the heterogeneity of plant diversity within the same biome and for trait intraspecies variability across environmental gradients (latitudinal and elevational).

A third approach is to parametrize single species instead of PFTs. This is usually performed in simulations where forests are composed by one or a few tree species. Many VMs used to stimulate temperate and alpine forests work at the species level. In tropical forests, the first approach to represent high species diversity in a VM was proposed by Marechaux and Chave (2017) who parametrized 163 species in the model TROLL by using 7 species-specific parameters.

Spatial and temporal resolution

Typically, VMs represent the landscape by dividing it in grid cells. The size of each cell can vary considerably from one model to another and range from one hectare to several kilometers. Inside each cell, the smallest unit is usually an average number of plants, a gap or a tree, each gap is the size of the crown of an adult tree (20m x 20m). The environmental conditions are homogeneous in each cell: temperature, precipitation, radiation, humidity, soil, etc. The temporal resolution at which processes are simulated can also differ among models. The models working at fine temporal resolutions simulate processes such as photosynthesis with a resolution of a few minutes, while other models might aggregate fine scale processes and present monthly or yearly estimates. For example, models that do not compute photosynthesis hourly will estimate monthly or yearly gross primary production. Clearly, models working at a fine temporal scale will need climate data at hourly or daily time steps. The spatial resolution of the environmental data is one of the limiting factors when representing landscape heterogeneity, as the same environmental data leads to very similar results and in some cases the same exact results in non-stochastic models.

Vegetation structure

There are two common methods to represent horizontal and vertical forest structure. The simplest is called "big leaf" and it does not represent the vertical structure of the forest but aggregates all properties of plants within a gap or cell into one individual "big leaf". The methodology is used in DGVM running over large spatial scales (continental or global) as it reduces computation time at the cost of no information on forest vertical structure and reduced capability of representing landscape heterogeneity. Although now some DGVMs are starting to include equations represent vertical structure (e.g. ORCHIDEE-CAN). Individual-based gap models instead keep track of trees vertical structure and the different light environments between the ground and the canopy, this requires more computing time and thus it limits the spatial extent at which these models can simulate. A third approach to retain vertical structure while reducing computation time was proposed by Moorcroft et. al (2001) in the Ecosystem Demography (ED) model. Instead of simulating individual plants or "big-leaf", ED uses cohorts which represent an average of plants with the same height and vertical structure. Collections of cohorts are then enough to simulate the vegetation heterogeneity without simulating single plants. I explain ED2, the successor of ED, in more detail in the section 2.4.

Soil

Soil processes in VMs are probably one of the most simplified and less developed. Most VMs have two carbon pools (fine and coarse roots) and use a fixed decomposition rate for litter which in some cases might be temperature dependent. Only some models have phosphorus and nitrogen pools. Soil processes in VMs are modelled following dedicated soil models such as CENTURY (Parton et al. 1987) from which only some processes are incorporated in VMs (Quillet et al. 2010). VMs with more complete soil processes include hydrology and percolation and multiple soil layers of different depths. A better representation of soil processes is an active area of development.

Dispersal

Dispersal is a process highly relevant to study plant-animal interactions but like soil related processes is not as well represented, particularly in DGVMs where dispersal is not considered. In individual-based models, where the geographical position of single plants is known, dispersal has been implemented but with simplified functions mostly through a generic dispersal kernel function (Snell et al. 2014). At the moment, IBMs might be the most suited option to study seed dispersal related processes; however, they have rarely been used for this purpose.

Input data and initial state

The main inputs of VMs are: meteorological forcings, soil composition, forest structure, and species/PFTs composition. Climate data is a critical input for VMs as many processes are driven by radiation, temperature, and humidity. Large-scale simulations utilize global reanalysis such as the NCEP reanalysis (Kalnay et al. 1996) or the ERA-Interim reanalysis section (Dee et al. 2011). These are climatic time series data that include air temperature, humidity, wind, solar radiation, precipitation, and pressure which are needed to drive the VMs. For more local simulations, data from local weather stations or from eddy covariance towers can be used. The disadvantage of global reanalysis is their poor precision, particularly in areas where ground data is limited. Given that the representation of soils are not detailed, soil input data includes only soil composition (percentages of sand, clay, silt) at different depths. There are global soil databases, for example the one provided by the Food and Agriculture Organization of the United Nations (Fischer et al. 2008), or for local simulations field data can

be used. Information regarding forest structure can also be used to initialize the simulation, in addition to field measurements, this data could also be derived from remote-sensing products (Smith et al. 2008). Data on vegetation structure and composition are needed unless the VM starts from bare ground. In this case, a spin up period is needed to reach an equilibrium state in the simulation when the variation of vegetation properties is minimal. Lastly, the inputs should include which PFTs or species will be part of the simulation. In case of a prescribed initial state this PFTs/species composition will be paired with the data on structure and composition collected at or near the site to be studied. Four simulations from bare ground, seeds/seedlings from all PFTs are introduced at the same time and only a subset will eventually persist according to each PFT preferred bioclimatic conditions and the result of competition.

The common advantage of most VMs is that being process-based models the underlying mathematical functions should hold under different environmental conditions. This allows the possibility of driving the models with past, present, and future environmental data to study how vegetation might respond to changes in climatic conditions, disturbance regimes, land use, and plant-animal interactions.

Output data

The output data of VMs is quite extensive in terms of quantity and variety of forest parameters and fluxes. Output variables can include plant density, net primary production, biomass (above and below ground), leaf area index, and forest composition and structure (PFT/species, age and size structure), fluxes (CO2, energy, water), mortality and growth rates. Some of the VMs that simulate leaf biophysical properties also provide outputs that include leaf transpiration, light use efficiency, and leaf vapor pressure deficit, and more.

Scopes and applications of vegetation models

VMs have been developed for a wide range of scopes and thus cover a broad spectrum of applications. DGVMs are used to represent the terrestrial biosphere component in coupled biosphere-atmosphere models to study climate. DGVMs are used in both paleoclimate and climate research to study the biogeography of biomes and the responses of vegetation to climatic changes (Friedlingstein et al. 2006, Quillet et al. 2010, Snell and Cowling 2015). As well, DGVMs have been used for other purposes, for example to study grassland management (Chang et al. 2016) or wetland dynamics (Ringeval et al. 2012). Instead, the core idea behind forest gap models is the ecological theory of forest succession which is driven by the formation of large canopy openings (gaps) (Horn 1974). These gaps create a new light environment that

allows light-demanding and fast-growing species to establish and thrive until shade tolerant and slow-growing species overtake the space. Forest gap models try to simulate this dynamic and for this reason they are focused on medium and small-scale ecological processes. This approach makes them better suited for localized forest ecology and management applications. Some examples of their application are: the effect of disturbances such as tree fall and browsing on forest regeneration (Rammig et al. 2007), the effect of selective logging on forest dynamics (Köhler and Huth 2004), the consequences of fragmentation on forest composition (Pütz et al. 2011), and evaluation of growth and yield for forest management (Glauner et al. 2003).

Vegetation models to study plant animal interactions

VMs have not been fully exploited to study plant-animal interactions in spite of the advantages that these models provide over experimental approaches. In part, the lack of animal related processes in VMs might be due to a relatively low interest of forest modeling ecology for animal processes as well as the complexity of VMs which are usually developed incrementally by adding and validating one process at a time. However, a few studies have already shown how VMs can be used to implement plant-animal interactions such as browsing, folivory, and trampling by a variety of taxa from insects to large herbivores (see table 1). I discuss the advantages of VMs to study plant-animal interactions in section 3.1. Even though section 3.1 is focused on megafauna and tropical forests, many of the examples I provide can be applied to other ecosystems and animals.

Animals/Guild	Ecosystem	Location	Interaction	Model	Authors
Ungulates	Alpine forest	Switzerland	Browsing	Vegetation+tree model – IBM	(Rammig et al. 2007)
Deer	Temperate deciduous forest	USA	Browsing	ZELIG – IBM	(Holm et al. 2013)
Large razers	Forest and savannah	Sub-Saharan Africa	Grazing + trampling	LPJ-GUESS – CBM	(Pachzelt et al. 2015)
Insects (folivores)	Temperate mixed forest	USA	Dispersal	ED2 – CBM	(Medvigy et al. 2012)
Savanna elephant	Savanna	South Africa	Herbivory + uprooting	aDGVM - IBM	(Scheiter et. al 2012)

Table 1. Examples of studies that have implemented animal processes in a VM

2.4 Choice of vegetation model and forest inventory data

One of the main goal of my thesis was to analyze the effect of disturbance by forest elephants in closed-canopy tropical forests. To study this process two aspects of forest elephants ecology

should be considered in relation to the vegetation model of choice. The first is an explicit representation of the forest vertical and horizontal structure, in addition to trees size structure. Forest structure is a key information because elephants interact differently with plants according to the plant height and size. Also, elephants affect a range of ecological processes such as mortality, establishment, and regeneration. Hence, not all VMs might be suited to study the effect of forest elephants. Both IBMs and CBMs offer more flexibility in simulating the above mentioned ecological processes compared to DGVMs because IBM/CBM represent in detail forest vertical, horizontal, and size structure. The second aspect to be considered is the spatial scale at which forest elephants operated. Elephants have large home ranges (Schuttler et al. 2012) and at high densities they might affect forests at the landscape scale and at the same time have a strong influence at the stand level (Omeja et al. 2014). CBMs might thus be more appropriate to study the disturbance by elephants because these models are more scalable than IBMs while still simulating ecological processes with enough details. DGVMs work at a scale that is probably too coarse to capture impacts of elephants at the stand scale as their big leaf approach does not provide details on the size structure of forests. This limitation does not allow to reproduce some of the plant-animal interaction details. There are only a few models that have been used to model tropical ecosystems and that are not a DGVM type of model. Additionally, previous modeling in Africa has been performed only at the continental scale which leaves only a few choices of potentially useful VMs. Among the CBMs used in tropical forests, I have chosen the Ecosystem Demography 2 model (Moorcroft et al. 2001, Medvigy et al. 2009) witch in his initial version by Moorcroft et. al (2001) was primarily developed to study tropical forests. ED2 simulates processes such as competition for resources between cohorts, vertical and horizontal vegetation structure, and has a fine representation of the microclimate which is useful as elephant disturbance influences the understory and might change competition for water, light, and space among plants. Furthermore, the fine scale reproduction of biophysical processes down to the leaf-level offer detailed data to pinpoint the specific mechanisms that elephant disturbance might trigger and the consequences for recruitment, mortality, and growth. Another interesting feature of ED2 is the way it handles disturbance processes. ED2 allows to describe disturbance events that can trigger specific size classes of trees. ED2 can have multiple disturbances and each one can be calibrated in terms of disturbance mortality rate. Disturbance rate is defined by the fraction of the total simulated area which is disturbed within a known period of time. Mortality rate describes the fraction of plants that are killed following a disturbance event. This is particularly useful because it allows to create a disturbance that is size-dependent which is needed to simulate the differential impact

of elephants on different plant size classes. Finally, ED2 has been developed and used extensively to study Amazonian tropical forests. This provides a good starting basis and an interesting opportunity to apply and validate ED2 to African tropical forests that are rarely simulated in VMs. I provide a more detailed description of ED2 in section 3.2.

Field-data

Forest inventory data was obtained from Stephen Blake (Max Planck Institute for Ornithology) for the study site in the Nouabalé-Ndoki National Park, Republic of the Congo and from François Bretagnolle (University of Burgundy) and David Beaune for the study site in the LuiKotale research site at the southwestern edge of the Salonga National Park, Democratic Republic of the Congo. Both data sets include tree surveys in primary forests with tree species vouched against herbarium species and with the help of local botanists. The surveys included all trees with a diameter at breast height larger than 10 cm. I will discuss the details and spatial extent of the two data sets in section 3.2.

2.5 References

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3 Results and discussion

3.1 Assessing the role of megafauna in tropical forest ecosystems and biogeochemical cycles - the potential of vegetation models

(Manuscript accepted with minor revisions – Journal: Ecography)

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3.1.1 Abstract

Megafauna (terrestrial vertebrate herbivores > 5kg) can have disproportionate direct and indirect impacts on forest structure, function, and biogeochemical cycling. We reviewed the literature investigating these impacts on tropical forest dynamics and nutrient cycling as it relates to ecology, paleoecology, and vegetation modelling. We highlight the limitations of field-based studies in evaluating the long-term consequences of loss of megafauna. These limitations are due to inherent space-time restrictions of field-studies and a predominant focus on seed dispersal services provided by large animals. We further present evidence of a research gap concerning the role of megafauna in carbon cycling in tropical ecosystems. Specifically, changes in aboveground biomass might not be noticeable in short-term studies because of slow vegetation dynamics requiring decades to recover after disturbance. Nutrient cycling has received even less attention in relation to the role of large herbivores in tropical forests. We present an approach to investigate the effects of megafauna through new perspectives and with different tools (i.e., vegetation models) which enable the simulation of long-term dynamics under different environmental or megafauna extinction scenarios. Vegetation models could allow increased integration between plant-animal ecology and biogeochemistry research. Thus, we conceptualize ideas on how plant-animal interactions could be integrated into vegetation models to further our understanding of the role of large herbivores in tropical forests.

Box 1

Definition of terms

In this review paper we refer to the terms "megafauna" and "large animals" as one group and we focus on herbivores. These terms have previously been used in different contexts referring to different sub-groups of animals. For instance, the term "megafauna" has been used frequently in the paleontological literature to refer to animals larger than 45 kg (Martin, 1984).. More recent studies used different thresholds from 100 kg for megafauna and large herbivores (Gill, 2014; Ripple et al., 2015) to a differentiation between large herbivores (45-999 kg) and megaherbivores (> 1000 kg) (Malhi et al., 2016). For existing species across a broad geographic range we find that a context-based (Hansen and Galetti, 2009) and functional-based definition is more appropriate. Thus, our definition of megafauna includes the larger extant species that are also keystone species or ecosystem engineers. Hence, it includes species that substantially impact ecosystem function and/or structure. Following our definition and in line with defaunation studies, Amazonian megafauna would include spider monkey (*Ateles spp.*, 9-11kg) and woolly monkey (*Lagothrix spp.*,7-9kg) (Peres et al., 2016). In tropical Africa defaunation studies include large primates > 5 kg, duikers 6 > kg (Vanthomme et al., 2010), and red colobus (*Procolobus rufomitratus*, 5-11 kg) (Chapman et al., 2012). Similarly in southeast Asia: Bornean gibbon (*Hylobates muelleri*), Langurs (*Presbytis hosei*, 6-7 kg), and Red-giant flying-squirrel (*Petaurista petaurista*, up to 3 kg) could be considered megafauna (Harrison et al., 2013). While some of these species body mass is lower than previously used thresholds for megafauna, they might be the largest functionally extant species in a particular habitat, and thus should be considered megafauna at the current time.

3.1.2 Introduction

The largest threats to vertebrate populations are habitat loss, forest fragmentation, and unsustainable hunting for human consumption (i.e., the 'bushmeat crisis') (Chiarello, 1999; Hoffmann et al., 2010; Kinnaird et al., 2003; Michalski and Peres, 2007; Weinbaum et al., 2013). Evidence suggests that faunal population decline and species loss may lead to severe alteration of ecosystem functioning (Dirzo et al., 2014; Galetti and Dirzo, 2013). This process could be a driver, rather than a consequence, of global change with unpredictable repercussions on the long-term sustainability of ecological processes (Dirzo et al., 2014; Laurance et al., 2012; Sutherland et al., 2013). As extinction risk caused by human consumption is correlated to body size (Ripple et al., 2016), large animals (see Box 1) are declining more rapidly. Large animals fulfil many ecological niches, directly and indirectly influencing a large range of processes (see fig. 1; seed dispersal and germination, biogeochemical cycles, plant regeneration and growth, etc.) (Dirzo and Miranda, 1991; Vanthomme et al., 2010; Wright et al., 2007a). For example, empirical studies across the tropics show that defaunation and fragmentation dramatically affect the tree-seed disperser network with cascading long-term effects on forest structure and dynamics (Abernethy et al., 2013; Kurten, 2013; Laurance et al., 2006; Poulsen et al., 2013; Wright et al., 2007b). However, we still have a limited overview of all processes related to large animals removal on forest regeneration and plant species composition because these empirical studies primarily focus on the short-term consequences of changes in seed dispersal and predation. Therefore, the net effect of these changes is still unclear because of ambiguous results, lack of long-term experiments, and the largely unexplored megafauna-carbon connection. As a recent analysis also suggests, changes in vegetation dynamics due to changes in megafauna densities can be subtle and difficult to detect in the short to medium term (Harrison et al., 2013). Thus, detecting long-term changes associated with the absence of megafauna poses a difficult task as adult tropical trees are long-lived, and we currently are unable to observe their dynamics over multiple generations. Furthermore, the connections to carbon cycling have only recently been examined (Dos Santos Neves et al., 2010; Osuri et al., 2016; Peres et al., 2016). As a result, limited evidence is available to provide long-term projections concerning the linkages between megafauna, forest dynamics, and carbon cycling. Investigating vegetation-animal feedbacks is particularly relevant in tropical forests, given their ecological importance as biodiversity hotspots and economical value as carbon sinks (Lewis, 2006) in relation to the UN REDD+ initiative (Hinsley et al., 2014). Another incentive for research is the unknown ecological role of large animals in these biomes (Ripple et al., 2015; Wright et al., 2007a) and the long-term consequences of their functional extinction.

Indeed, little is currently known on how the loss of megafauna might change biodiversity, ecosystem services and functioning.

To overcome these problems, we propose an approach that relies on vegetation models (VMs) to complement current studies and integrate knowledge from different fields. VMs developed for tropical biomes (Fischer et al., 2016; Marechaux and Chave, 2017; Moorcroft et al., 2001) have been designed to simulate, among other processes, forest succession, seed dispersal, and disturbance. Many of the ecological processes associated with plant-animal interactions are simulated in VMs, but the effects of animals are not modelled explicitly. The VMs platform remains largely unexploited and only a few studies have used VMs to explore feedbacks between megafauna and vegetation (Pachzelt et al., 2013, 2015; Scheiter and Higgins, 2012). We suggest that VMs could be used to study plant-animal interactions in tropical ecosystems. In this context, the first aim of the present review is to synthesise the current knowledge concerning the role of large animals in tropical forests, particularly with respect to long-term changes and carbon cycling. Specifically, we provide an overview of the most relevant published studies and highlight shortcomings and strengths of three main subjects: (1) Contemporary megafauna (1.1) Effects on vegetation and forests dynamics; (1.2) the role of megafauna in carbon cycling; and past megafauna (2) the consequences of the late quaternary megafauna extinction and parallels with present day ecology. The second overall goal is to propose novel modelling approaches to increase links in the vegetation-megafauna-biogeochemistry framework. Increased interdisciplinarity could help to quantify the role of megafauna in vegetation dynamics and predict the consequences of their disappearance. Long-term predictions are necessary to evaluate future scenarios of ecosystem management and global change (climate changes, hunting pressure etc.). We thus provide (3) an overview of VMs that are relevant for tropical ecosystems and explain how these models can integrate data from different disciplines and field-studies. Specifically, we classify plant-animal interactions and associate each class to VMs processes and parameters. We then present (3.1) examples on how these processes and parameters could be used to explicitly simulate plant-animals interactions in VMs. The ultimate goal is to study feedbacks between megafauna and vegetation and how these interactions influence tropical ecosystems.

3.1.3 Contemporary megafauna

Effects on vegetation and forest dynamics

The ecological role of megafauna is often investigated by comparing forest areas with different faunal population densities (as a consequences of hunting and/or habitat fragmentation), or alternatively through animal exclosures. Most reviews on the effects of defaunation have focused on seed dispersal and predation (Kurten, 2013; McConkey and O'Farrill, 2016; Rosin, 2014; Stoner et al., 2007b, 2007a; Wright, 2003). Another review discussed other processes such as herbivory and carbon cycling but was not focused on megafauna (Dirzo et al., 2014). Therefore, here we only provide a brief overview of seed dispersal studies, and focus instead on research gaps and research questions that have received less attention in relation to large animals (but see Ripple et al., 2015).

Uncertainty in the outcomes of defaunation

In defaunation ecology, seed dispersal has received the most attention because the majority of tropical woody plant species are animal-dispersed. Large animals affect seed and seedling life stages and might contribute to the "Janzen-Connell effect" (i.e. increased seed and seedling survival as a function of distance from the parent tree facilitated by animal dispersal (Comita et al., 2014; Levi and Peres, 2013)), a process that enhances and maintains tree diversity in tropical forests. The lack of large mammals may therefore increase the likelihood of extinction for some large-seeded tree species (Beaune et al., 2013; Caughlin et al., 2015), however in certain cases smaller animals might act as alternative dispersers (Kurten, 2013). While there seems to be a consensus that plant species composition is affected by mammal community composition, results vary among studies because mammals can impact seedlings-saplings diversity and density with different outcomes (Beckman and Muller-Landau, 2007; Roldán and Simonetti, 2001; Wright et al., 2000, 2007b). For example, some studies show how the absence of primates can significantly change plant species composition (Nuñez-Iturri and Howe, 2007) while others show negligible effects on seedling recruitment (Chaves et al., 2015) or that rodents can be alternative dispersers for large seeds (Jansen et al., 2012). The issue is complex due to many interacting factors: i) hunting and fragmentation can differentially alter seed predation/dispersal and herbivory (Culot et al., 2015; Wright et al., 2000) and may or may not involve trophic release (Brodie and Giordano, 2013; Wright, 2003) through reduction in carnivore populations. For instance, Wright et al. (Wright et al., 2000) found that when poachers targeted rodents, seed predation decreased and seedling regeneration increased.

Simultaneously, however, seed predation by bruchid beetles increased (because rodents consumed less beetle eggs) and seed dispersal decreased reducing seedling regeneration. The net observed effect was an increase in palm seedling densities as poaching intensity increased. ii) Variation in micro-environments and light availability complicates discerning differences in recruitment and succession among study plots. As plots can be under different canopy covers, the impacts can differ for light-demanding and shade-tolerant plants. Chaves et al. (Chaves et al., 2015) stress that diversity and composition of adult trees and fragment spatial metrics are confounding effects rarely considered in such studies. In fact, contrary to other studies, when Chaves et al. (2015) accounted for these variables, no correlation was found between presence/absence of primates and seedling recruitment.

Overall, the wide range of results in these studies are likely the effect of a myriad of factors ranging from micro-habitat variability and fragment size (Laurance et al., 2006) to different degrees of defaunation and interannual variability in plant recruitment, concepts well explained by (Harrison et al., 2013). Furthermore, large animals disperse both small and large seeds (Chen and Moles, 2015) so the current hypothesis that defaunation penalizes mostly large-seeded species might be more nuanced than previously thought. Overall, the variety of environmental settings, faunal assemblages, and focal plant species increases the uncertainty when synthesising how changes in faunal assemblages will affect tropical ecosystem function.

The problem of time

The limited duration of field-studies also increases the uncertainty in their results. There is a lack of long-term tropical forest inventories, except for a few notable sites (such as Kibale NP in Uganda and Barro Colorado Island in Panama (Omeja et al., 2014; Wright et al., 2000)), where long-term data for multiple decades are available. Also, it is difficult to find comparable regions (similar adult tree composition, limited logging, etc.) with different defaunation histories, and to regularly monitor forest regeneration. These limitations are forcing forest ecology studies to rely on limited vegetation time-series. This severely constrains our ability to predict trends in future tree populations and to understand their long-term dynamics. Even the authors of one of the longest studies to date (15 years) admit that their period only covers the initial response phase post-defaunation (Harrison et al., 2013). Long-term data can produce significantly different results than short-term data. For example, two long-term studies on forest elephants (Hawthorne and Parren, 2000; Omeja et al., 2014) with respectively 25 and 15 years of vegetation data, did not detect any discernible impact on the composition of old growth

forests after a few decades without elephants. Conversely, some short-term studies concluded that elephants removal could have significant impacts on forests (Beaune et al., 2013; Campos-Arceiz and Blake, 2011).

Research is still far from providing insights at a timescale relevant for tropical tree generations (50-200 years) and we lack long-term projections on species composition and forest structure. Muller-Landau (Muller-Landau, 2007) presented a theoretical approach to predict changes across many tree generations. She used a pseudo-spatial lottery model that considers feedbacks between food availability and consumers and accounts for the dynamics between seed predation and dispersal. Her model showed that shorter dispersal distances lead to lower plant abundances and that plant abundance in future generations is highly dependent on the relative abundance of seed predators and seed dispersers. However, this study has remained a rather isolated case of evaluating long-term effects of changes in dispersal patterns.

Beyond seed dispersal: herbivory, disturbance, and nutrient cycling

Overall, within the defaunation literature, we have identified a bias towards seed dispersal processes and early plant life stages. The next challenge would be evaluating changes in future adult community composition, the effects of herbivory and disturbance, and the cascading effects on other forest processes. In particular, there is a research gap concerning the physical impacts (ecosystem engineering) of megafauna in tropical forests. Some processes such as trampling and uprooting have only been studied sporadically (Ganas et al., 2009; Kurten, 2013; Omeja et al., 2014), while others like the impacts on soil and the transport of biomass have not been evaluated (Wing and Buss, 1970). For example, (Wing and Buss, 1970) estimated that 413 forest elephants in Kibale could move roughly 22,612 t of material per year, and that trampling of herbaceous vegetation could protect the soil and reduce runoff. Given that forest elephant populations have declined by more than 80% (Maisels et al., 2013), today we are only seeing a small fraction of their potential effect as ecosystem engineers. Another important process is herbivory by vertebrates and invertebrates, which can affect forest regeneration and plant mortality (Kurten, 2013; Leal et al., 2014). For example, Chapman et al. (Chapman et al., 2012) have shown that folivorous primates can act as ecosystem engineers by killing or reducing growth of some tree species and increasing the productivity and abundance of other species. As well, large terrestrial herbivores such as duikers, tapirs, bush pigs, and peccaries can affect seedling/sapling mortality (Terborgh and Wright, 1994). Yet, studies on this are scarce (Piiroinen et al., 2016). Herbivory is also strictly connected to nutrient

transport which can influences tree growth (Feeley and Terborgh, 2005). Nutrient transport can also happen through seed dispersal (Stevenson and Guzmán-Caro, 2010). However, only a few studies investigate the effects of large herbivores on nutrient cycling in tropical forest. Lastly, a side effect of hunting is the proliferation of wind-dispersed lianas in the Neotropics when animal-dispersed trees lose their dispersers (Wright et al., 2007b). Lianas can affect the forest carbon cycle (van der Heijden et al., 2015), thus defaunation might as such modify vegetation composition and the carbon cycle.

3.1.4 The role of megafauna in carbon cycling

Megafauna and above ground carbon stocks in models and field studies

The potential correlation between plant biodiversity, species composition, and carbon storage remains unclear (Poorter et al., 2015; Sullivan et al., 2017). Bunker et al. (Bunker et al., 2005) proposed the first statistical modelling approach to highlight possible changes in carbon storage associated with changes in forest composition. Their methodology assumed constant basal area and simulated extinction by replacing trees of extinct species with species drawn randomly from the remaining species pool. However, this shift in species composition did not account for processes associated with forest dynamics (i.e., tree fall, succession, growth, etc.). Additionally, not accounting for changes in basal area and height might also influence the model prediction of changes in carbon stocks (Chave et al., 2014). The extinction scenarios simulated by Bunker et al. (2005) were not aiming to test the effects of animals. Nevertheless, their study is relevant to the hypothesis that defaunation might affect tropical carbon stocks. This hypothesis states that the disappearance of larger animals might lead to lower recruitment of large-seeded plants (Wright et al., 2007a), and because large-seeded plants have on average a slightly higher wood density than small-seeded ones (Queenborough et al., 2009), a forest with less large-seeded species will have lower carbon stocks. This hypothesis has been tested to evaluate changes in carbon stocks in different tropical regions under different defaunation scenarios. Three separate studies (Bello et al., 2015; Osuri et al., 2016; Peres et al., 2016) have combined tree inventories with plant trait data and used the statistical model of Bunker et. al (2005). The South American studies (Bello et al., 2015; Peres et al., 2016) have found a reduction in carbon storage following defaunation, while Osuri et Al.(2016) report divergent effects across the tropics. As already mentioned, these studies rely on a methodology that has limitations and does not provide any indication on the temporal rate of change. Notably, by

assuming constant basal area and not representing actual forest dynamics, the results are controlled only by the scenarios describing which tree species will disappear from the species pool. Additionally, trees are replaced by selecting randomly from the remaining species pool, so the ecological importance of wood density is not taken into consideration, despite its role throughout tree life stages (Chave et al., 2006). Thus, insights from modelling approaches are limited to only these few studies. There is also a lack of field-based studies measuring changes in biomass in response to defaunation, with the exception of Poulsen et al. (Poulsen et al., 2013) who show that in their study sites, hunted forests had lower aboveground biomass (AGB) than undisturbed forests. The authors are careful about these results due to various limitations of their methodology. This study is an isolated case, because differences in sapling communities AGB after defaunation are subtle (Harrison et al., 2013) and require long-term observations to be detected.

Carbon-animal feedbacks in the literature

The connection between animals and the carbon cycle has generally not been central in the defaunation debate (Galetti and Dirzo, 2013). The few articles discussing (in)direct effects of fauna on the tropical carbon cycle either only considered invertebrates (Dirzo et al., 2014; Metcalfe et al., 2014; Strickland et al., 2013) or underestimated the effects of fauna on carbon cycling (Tanentzap and Coomes, 2012). Tanentzap and Coomes (2012) offer the most complete review on the connection between carbon storage and herbivores covering several vegetation types. For tropical forests, Tanentzap and Coomes (2012) suggest that herbivores have minimal impacts on carbon storage, and discuss the role of elephants as herbivores but do not consider their indirect impacts as seed-dispersers and as ecosystem engineers (Beaune et al., 2013; Campos-Arceiz and Blake, 2011; Terborgh et al., 2016). Yet, a direct link between carbon stocks and the structural modification by large animal has not been shown. For example, forest elephants can stop regeneration and increase tree mortality (Omeja et al., 2014), but their long-term effect on carbon stocks at the landscape scale remains unresolved (Lewis et al., 2009). Furthermore, while scant, there is some evidence that nutrient cycling is an important service provided by megafauna that could also affect biomass (see paleoecology section below). Studies examining the impact of primate latrines on the distribution of nutrients in topsoil profiles have found higher levels of carbon below the top two centimetres compared to control sites (up to 6 centimetres) (Dos Santos Neves et al., 2010). Combined with evidence suggesting increased branching of tree roots in organic-matter-rich microsites, this suggests potentially higher belowground carbon storage in areas with functionally intact primate populations.

Uncertainties in the effects of megafauna on carbon cycling

In the present review, we considered both the direct and indirect impacts of large animals on carbon stocks by focusing on long-term changes in plant succession and forest structure. We found that analyses have focused either on dispersal services or herbivory, but rarely on the combined effects of both. Thus, we can only partially evaluate the relation between carbon stocks in tropical forests and vertebrate herbivores of any size. We suggest that future defaunation studies should consider the growing literature we presented in this section and evaluate if changes in fauna communities are also affecting carbon stocks. Similarly, we have noticed a lack of consideration of the role of fauna in research focused on carbon cycling and modelling. Perhaps this reflects a negative feedback - as field based studies do not investigate the fauna-carbon linkage there is little incentive and empirical basis for modelling studies. On the other hand, modelling approaches have not tried to elucidate the role of megafauna in tropical forest carbon cycling and thus provide explanations to guide field-studies. We conclude that the scientific community currently does not have a clear understanding of how herbivores (browsers, folivores, frugivores, etc.) influence the carbon cycle in tropical forests. It is possible that the contribution of fauna to the carbon cycle has been systematically underestimated (Schmitz et al., 2013) and in the future we should consider all the plant processes influenced by large animals. The available evidence suggests that the disruption of trophic dynamics resulting from the loss of megafauna will have consequences of unknown magnitude on the carbon cycle of tropical forests.

3.1.5 Paleoecology - past megafauna extinctions & parallels with present day ecology

The contemporary decline of large animals has parallels with the massive late Quaternary Megafaunal Extinction (LQME) when terrestrial vertebrate assemblages were disproportionately impoverished by the extinction of all their largest species including megaherbivores and their predators (Doughty, 2013; Gill, 2014). A branch of paleoecology has recently engaged in the understanding of the evolutionary and ecological consequences of these extinctions (Doughty, 2013). This research has major implications for interpreting modern ecosystems and designing conservation strategies (Donlan, 2005), because the LQME had large consequences for the functioning of ecosystems due to the loss of many ecosystem processes. This parallel raises the question if paleoecology can provide insights on how ecosystems might respond to the current megafauna extinction. For example, the recent use of fossil spores of dung fungi as a proxy allows to quantify megafaunal population fluctuations (larger fungi

biomass is associated with larger herbivore biomass, (Baker et al., 2013)). This technique has allowed the establishment of high resolution correlations between megaherbivore collapse and structural changes in vegetation in different continents including Australia, Madagascar and America (Burney et al., 2003; Davis and Shafer, 2006; Rule et al., 2012). Furthermore, a growing number of studies support the hypothesis that human-driven LQME had devastating cascading effects on lower size vertebrates, on plant community biodiversity and ecosystem function resulting in ecosystem shifts comparable in magnitude to those generated by climatic fluctuations (Burney et al., 2003; Doughty, 2013; Rule et al., 2012).

Megafauna and biosphere feedbacks were reviewed in two recent articles. (Gill, 2014) presented case studies on how megafauna extinctions changed fire regimes, created novel plant associations, altered forest composition, and disrupted terrestrial biogeochemistry. While (Bakker et al., 2015) discussed both modern and paleo megafauna but focused mostly on savannah ecosystems. While both reviews confirm the ecosystem wide effects of megafauna, they do not cover tropical forests indicating a research gap in this biome. In fact, megafauna may have a different role in savannah ecosystems, where they tend to remove woody cover (Asner and Levick, 2012) compared to tropical forests, where their impact is still unclear. For instance, mean AGB is 396 Mg ha^{-1} in Africa (with more megafauna) versus 289 Mg ha^{-1} in the Amazon (with less megafauna) and a marked difference in structure with more larger trees and lower stem density in Africa (Lewis et al., 2013; Malhi et al., 2013). The reason of this difference in forest structure is unclear but this may be a result of the impact of megafauna on forest dynamics. Elephants reduce the understory of the forest, increase smaller trees mortality, and reduce competition among plants for resources (Terborgh et al., 2016).

Carbon and nutrient cycling during LQME

To gather more information on the role of contemporary megafauna in forest dynamics and biogeochemistry we can examine how the Pleistocene megafauna extinctions may have impacted these variables. There is substantial isotopic evidence that extinct megafaunal herbivores in certain regions of South America had a highly C3 diet of trees (leaves or fruit) (França et al., 2015). Guimarães et al. (Guimarães et al., 2008) recently suggested that there were 103 possible Neotropical megafaunal-dispersed species that likely have co-evolved with South American now extinct megafauna species. A relevant question is then how the disappearance of the South American megafauna impacted Amazonian forest dynamics and carbon content. A recent study found that megafauna-distributed fruits on average have smaller

size ranges than other animal-dispersed tree species and used a simple model to suggest that this is due to decreased seed dispersal distance following the megafauna extinctions (Doughty et al., 2015a). Large-seeded fruits tend to have denser wood and the study estimated that the decline of the megafauna distributed species decreased mean carbon content in the Amazon by 1.5%. This decline in Amazonian carbon content is similar to the percent caused by the recent loss of seed dispersers suggested by Peres et al. (Peres et al., 2016).

Megafauna could also play an important role in the distribution of nutrients across landscapes because their consumption rates, gut passage times and day ranges are greater than that of smaller animals. Certain nutrients such as phosphorus clearly impact forest growth rates and it has been estimated that forest growth (woody NPP) is greater in the Western Amazon than the Eastern Amazon due to higher soil phosphorus content in the Western Amazon basin (Quesada et al., 2010). Fertility constraints may also impact species composition and there can be a strong shift in species composition across a region of change in soil fertility (Higgins et al., 2011). For instance, two recent studies compiled size relationship data for terrestrial mammals and found that the distribution of nutrients away from a concentration gradient is size dependent, with larger animals having disproportionately greater impact on this flow than smaller animals (Doughty et al., 2013; Wolf et al., 2013). It has been hypothesized that the ability of all animals to move nutrients away from concentration patches on land following the megafauna extinctions, decreased to ~8% of the pre-extinction value (Doughty et al., 2015b). Hence, if nutrients are now less evenly distributed compared to periods when megafauna were abundant, forest growth and carbon uptake may also have been impacted by megafauna extinctions.

Paleoecological datasets and limited coverage in tropical ecosystems

We found that the paleoecological literature contains many parallel hypotheses to the ones formulated in defaunation ecology. In fact, paleoecological datasets can inform current VMs. A key problem of finding datasets to inform the impact of megafauna on vegetation are the great timescales necessary to see an impact. However, there are increasing numbers of paleoecological datasets, such as pollen records with corresponding Sporormiella spore data that act as a proxy for megaherbivore populations (Burney et al. 2003, Davis and Shafer 2006, Rule et al. 2012), which can be used to quantify the impact of megaherbivore loss on vegetation. These datasets can be a first step to parameterize and test how loss or gain of

megafauna might affect vegetation over time. Much can be learned both empirically and theoretically from increased interactions between modern and paleoecology. Thus, we reiterate the call of Gill (Gill, 2014), and highlight the limited coverage of tropical ecosystems in paleoecology. Lastly, megafauna/carbon cycling interactions are an emerging topic in paleoecology, similarly to their contemporary ecology counterpart.

3.1.6 Integrating current knowledge in vegetation models

Each research area we touched upon contributes crucial information to reconstruct the role of megafauna in tropical ecosystems. Field studies do not capture long-term changes in forest succession, but they provide detailed assessments of how animals affect recruitment, dispersal, mortality, and germination. Paleoecology offers an alternative perspective, particularly with regard to processes over large spatiotemporal scales. Additionally, the carbon cycle has been extensively studied in several disciplines (Le Quéré et al., 2016) but the effects of animals on carbon cycling in VMs has not yet been implemented. Within this framework, VMs offer the potential to synthesize complementary knowledge across fields to address current shortcomings. Some VMs were developed specifically for tropical forests (TROLL (Marechaux and Chave, 2017), ED (Moorcroft et al., 2001), and FORMIND (Fischer et al., 2016)), while others were developed for more global applications but have been used in tropical studies at different scales (LPJ-GUESS (Sitch et al., 2003) and ORCHIDEE (Krinner et al., 2005; Verbeeck et al., 2011)). VMs are biogeophysical process-based models reproducing vegetation dynamics by simulating establishment, growth, dispersal, competition for resources, etc., over many tree generations. Although some of these processes might be overly simplified or not implemented (i.e., dispersal, establishment), most of them are simulated through time (hourly to yearly) and space (individual tree to the global level), depending on model resolution. VMs perform simulations using climate data (e.g. temperature, radiation, precipitation), in addition to soil and forest parameters. VMs can be validated or initialized with forest inventories, flux-tower data, and remote sensing products and can be parameterized with regional allometric equations, when these are available. Plant species in these models are often grouped in Plant Functional Types (PFTs) with similar biophysical and ecological properties (e.g.,. wood density, growth rate, mortality, allometry), but in some cases single-species models are implemented (i.e., TROLL). Examples of tropical PFTs are early/mid/late successional trees (e.g., in the ED2 model), or semi-deciduous and evergreen trees (e.g. in LPJ-GUESS). We distinguish between three model types: Dynamic Global Vegetation Models

(DGVM), Cohort-Based Models (CBM), and Individual-Based Models (IBM). DGVMs are more focused on large-scale patterns and biosphere-atmosphere feedbacks, while IBM tend to be used for small-scale ecological studies. CBM are somewhat in between, they represent forest structure in greater detail than DGVM but instead of tracking individual trees they use cohorts to reduce computation time. In table 1 we provide a quick comparison of relevant features and processes of five VMs, which were selected to illustrate the variety of existing models, for a more detailed description and classification of VMs refer to (Snell et al., 2014). Thus, VMs reproduce processes such as mortality, dispersal, establishment, etc., that are of interest to plant-animal interaction ecology and offer powerful scalability in time and space. In Figure 1, we show how plant processes simulated in VMs relate to animal guilds and processes.

Vegetation models	ORCHIDEE	LPJ-GUESS	ED 2	FORMIND	TROLL
Model type	DGVM	CBM	CBM	IBM	IBM
Number of tropical PFT (only evergreen trees)	1	2	4	5,13,22	163 species
Spatially explicit (gaps/cohorts/trees position in space is known)	No	No*	No	Yes	Yes
Seed parameters	No	Total seed biomass per cohort	- Seed bank - Total seed biomass per cohort	- Seed bank - Total seed biomass per tree	- Seed bank - Total seed biomass per tree
Dispersal	No	LPJ-DISP	No* - perfect dispersal	Yes – dispersal kernels	Yes - dispersal kernels
Size structure (cohorts/trees size is known within patch/gap)	No*	Yes	Yes	Yes	Yes
New recruit minimum height/DBH	/	/	Height 0.5m	DBH 10cm	DBH 1cm Height 1m
Nutrient cycling	*Nitrogen- *Phosphorous	*Nitrogen	Nitrogen		

Table 1. Overview of five vegetation models with processes and features that are relevant to the implementation of plant-animal interactions. * Indicates that the feature might be partly implemented or is implemented in a branch of the main model.

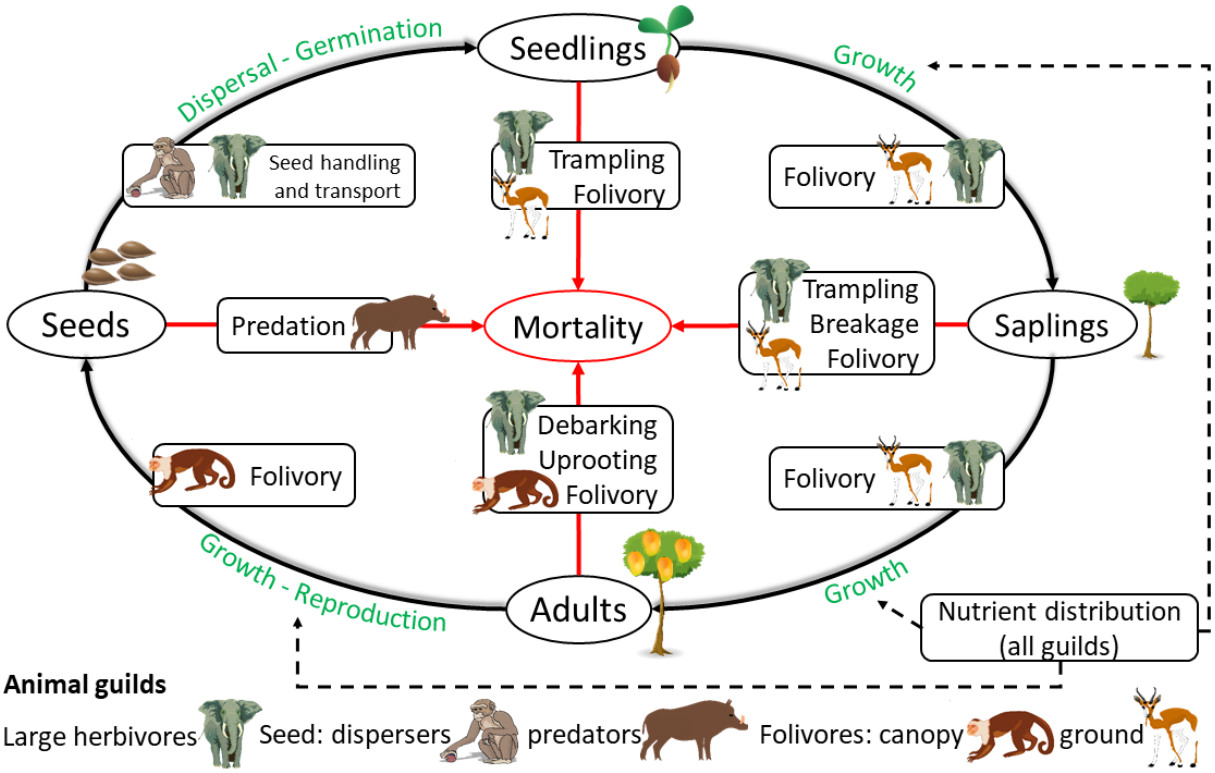

Figure 1. Progression of life stages and animal/plant processes associated with each progression. Black ovals represent life stages, the red oval is a terminal stage, rounded boxes indicate animal processes influencing life stage transitions. Solid black arrows indicate progression between life stages and green labels show plant process influenced by the pictured guilds. Dashed arrows show the indirect effect of nutrition transport on growth, and red arrows represent transitions to a terminal stage. Some animals might be in more than one guild and the icons are purely illustrative.

While VMs have been used for tropical ecology and carbon cycling studies, they have never been used to study plant-animal interactions in tropical forests. Yet, VMs have been employed to simulate plant-animal interactions in other ecosystems. This includes the effects of browsers in temperate forests (Holm et al., 2013; Rammig et al., 2007) and the impacts of savannah elephants (Scheiter and Higgins, 2012) and grazers (Pachzelt et al., 2013, 2015) in Africa. The latter studies are particularly interesting as they couple a VM with a physiological grazer population model. Additionally, these studies introduce Herbivore Functional Types (HFTs) that, similarly to PFTs, are groups of herbivores with common functional traits (body mass, diet, gut type, etc.). Pachzelt et al. (2015) defined four HFTs, each containing a single herbivore species. Hempson et. al (Hempson et al., 2015) have gone further and expanded the classification to include 92 medium-large African herbivores clustered in five HFTs. This

grouping of animal species based on traits suggests that HFTs could be associated with specific plant-animal interactions, PFTs, or plant traits, offering the potential to further implement herbivores in VMs. However, the PFT classification alone is currently limiting, as it does usually not consider plant traits that are relevant to animal-plant interactions. The next challenge is to expand the PFT concept to include plant properties that can describe such interactions. For example, seed size is relevant to the role of megafauna in the dispersal process, but if plant species affected by the absence of their dispersal vector are randomly distributed among PFTs, we cannot reproduce this interaction with more detail. Also, models based on PFTs might have difficulties capturing some key carbon dynamics such as drought (Powell et al., 2013), and there is a growing interest in trait-based approaches (Bodegom et al., 2014; Enquist et al., 2015). Trait-based modelling could provide greater flexibility, a more realistic representation of plants than PFT-based models, and enable large-scale simulations by reducing computational requirements (an advantage over IBMs). Another limitation is that so far VMs do not account for the effects of animals, partly because including animals in VMs might require simulating the complexity of animal movements. Movement would require some VMs processes to be spatially-explicit and tracking animal position and numbers. However other models that capture animal ecology and movement, such as the Madingley model (Harfoot et al., 2014), could be paired with the next generation trait-based VMs to simulate in detail both vegetation and animal ecology. Aside from these limitations, we argue that current VMs can already be used to explore plant-animal interactions and future development of trait-based VMs should consider these interactions.

3.1.7 How to model megafauna-vegetation interactions?

Following the Overview, Design concepts, and Detail protocol (ODD, (Grimm et al., 2010), we propose five case studies, plus a design concept for a coupled animal-vegetation model, on how to simulate the role of megafauna in VMs by combining data from field-studies and animal species life history (diet, body size, metabolic rate, etc.). Please note that in the ODD protocol we describe only the processes and variables that are relevant to each implementation and not the complete VM. Furthermore, we make these examples as general as possible, so they can be applied to different VMs. Some plant-animal interactions can be simulated explicitly in VMs, we refer to these cases as direct implementations. These can be accomplished through existing model Processes, Variables, or plant/PFT Parameters, for brevity will refer to these as PVPs. Examples of PVPs are mortality (process), leaf biomass (variable), and dispersal kernel (species/PFT specific parameter). In case of a direct implementation the plant-animal interaction measurement units could either match the PVP units, or be easily converted. For instance, kg of biomass consumed per day per animal can be related to a model variable such as leaf turnover rate (leaves shed over time). When a direct implementation is not possible because there is no matching PVP, we can encapsulate the effect of a plant-animal interaction within an existing PVP, we refer to this as indirect implementation. For example, bark is not explicitly modelled, thus to simulate debarking, which might increase tree mortality, we could change intrinsic adult tree mortality based on field studies measuring the effect of debarking. A summary of ecological interactions and their related PVPs is presented in Table 2. The list of processes in Table 2 is non exhaustive but covers the most studied ecological processes and some intuitive implementations.

Ecological process	Field measurement (units)	Direct implementation	Indirect implementation	DGVM	CBM	IBM
Folivory	Leaf intake (kg/day)	Leaf turnover rate		D	D	D
Flower consumption	Percentage of flowers or flower buds consumed		Net primary productivity allocation	I	I	I
Seed dispersal	Dispersal distance (meters)	Dispersal kernel function			D*	D
Seed predation or seed mortality	Proportion of killed seeds	- Removal from seed bank - Seed mortality			D	D
Seed ingestion or pulp removal	- Days to germination - Proportion of germinating seeds	Germination rate	Recruitment rate		I	I
Debarking	Proportion of trees killed		PFT/species-specific mortality rate	I	I	I
Trampling Uprooting Damage	Proportion of trees/seedlings killed or damaged	- Size/height-dependent mortality - Seedling mortality	Recruitment rate		D	D
Nutrients redistribution or increased lability	Soil carbon/nitrogen/phosphorus content (g/kg) - Concentration & lability	Soil carbon/nitrogen/phosphorus pools	- Gross primary productivity - Growth rate - Establishment rate	D*	D/I*	I

Table 2. Plant-animal interaction ecological processes and examples of field measurements. Examples of (D) direct and (I) indirect model implementations through existing PVPs and suggestion on model types more suited for implementing the process. *Indicates that the implementation might rely on a feature present in a branch of the model.

Example key process 1: Folivory - life stages: seedling, sapling, and adult

Leaf consumption happens both on the ground through browsing and grazing, and in the canopy. Terrestrial folivores can affect saplings and seedlings while canopy folivores target mostly adult trees. Folivory can affect various processes such as establishment, productivity, and growth (Fig. 1), and is also connected to nutrient cycling.

Purpose: Implement the impact of folivory (canopy and/or terrestrial) with either fixed rates of leaf consumption or variable rates calculated by a coupled animal population model. Leaf

turnover rates can be directly related to leaf consumption rates. Thus, by increasing the rate at which plants targeted by folivores shed their leaves, we can simulate this interaction.

Entities: Individual trees/cohorts/big leaf, represented by species or PFTs; folivores (not explicitly represented in the VM)

Scale: stand, hectare, grid cell (determined by homogeneous environmental data)

Entities	Variable	Description	Unit
Plants	*Folivore plants*	List of *entities* impacted by folivores	
	Non-folivore plants	List of *entities not* impacted by folivores	
	Bltr	Baseline leaf turnover rate	shed leaves $time^{-1}$
	Fltr	Folivory driven leaf turnover rate	shed leaves $time^{-1}$
	LeafBiom-fol plants	Leaf biomass of plants consumed by folivores	kg ha^{-1}
Animals	*Ad*	Animal density, can be the density of one species or multiple species in the same functional group	Individuals ha^{-1}
	Icr	Individual consumption rate, if more species are present it can be a weighted average based on *Ad*	kg day^{-1}
	Pcr	Population consumption rate	kg ha^{-1} day^{-1}
	Food preferences	Parameter/information to classify folivore and non-folivore plants (height, species, PFT, leaf N content, …)	

Table 3. Variables relevant to the implementation of folivory

Process overview and scheduling

At each time step (daily, monthly, annually) the VM calls the appropriate 'shed leaves function' following the algorithm shown in Figure 2. If there is no folivory within the spatial unit (stand, grid cell, etc.) then a baseline leaf turnover rate is applied to all plants. In the presence of folivory, a function determines which plants are targeted by folivores based on food preference (e.g., preferred canopy trees for folivorous primates or plants < 2 m for terrestrial folivores). If an animal model is coupled with the VM, then *Pcr* is recalculated at each time step, otherwise *Pcr* is fixed. Then, the leaf turnover rate of folivore plants is calculated based on their leaf biomass and the *Pcr* at the current time step. The last step is to shed leaves of both folivore and non-folivore plants, each at their own leaf turnover rate.

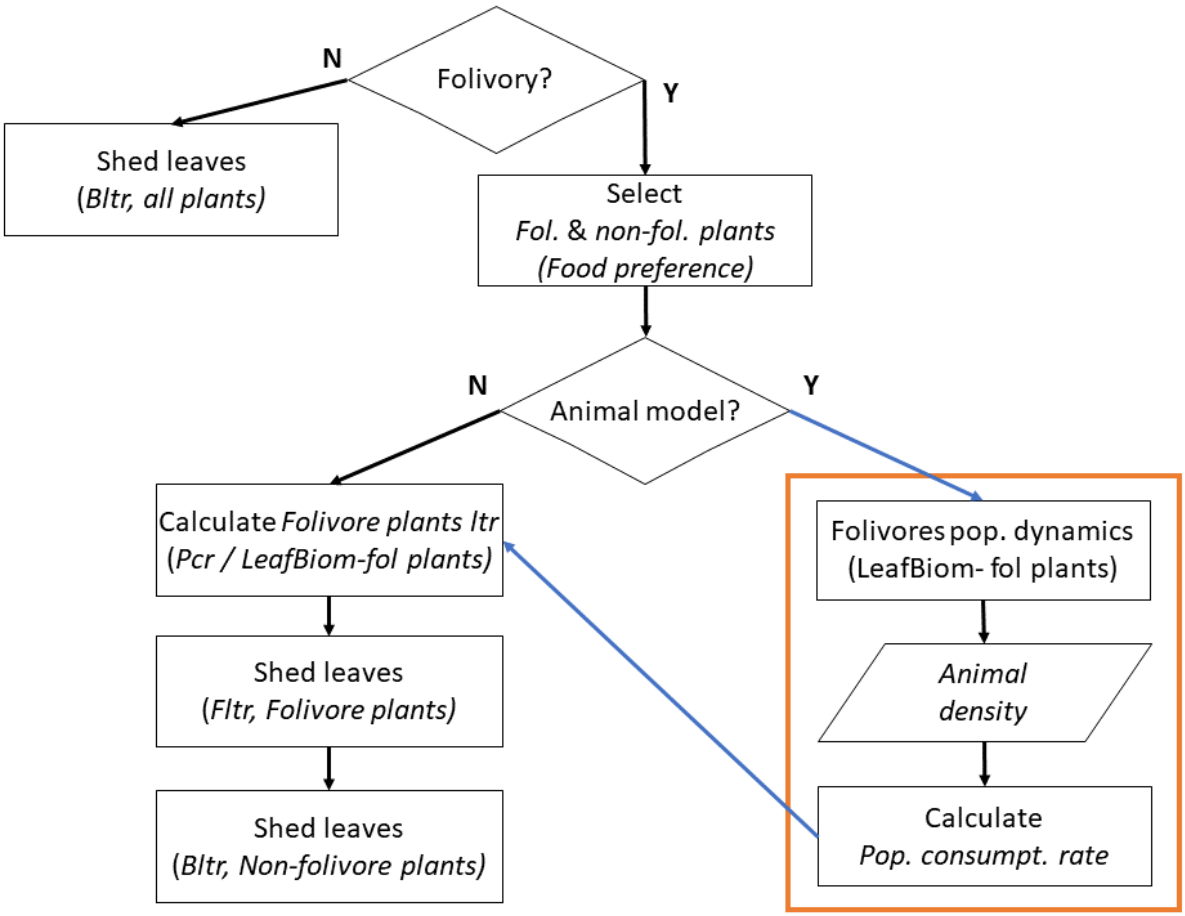

Figure 2. Flowchart of folivory submodel. Orange box delimits the animal model. Blue arrows show data exchange between models, black arrows show transitions within model time states. Rectangles are functions, diamonds are selections, and parallelograms are data input/output.

Design concepts

Basic principles: Leaf turnover rate has the advantage of being a parameter or state variable that is used to calculate leaf related processes (functioning, production, and destruction). Thus, implementing folivory requires only minor modifications to the VM.

Emergence: Folivory will reduce the total leaf area and as such the canopy photosynthetic capacity and thus gross primary productivity, however it might also increase net primary productivity as more fallen leaves will increase soil carbon and nitrogen in areas where there are preferred plant species (Feeley and Terborgh, 2005). Also, the effect of terrestrial folivory can impact seedling and saplings life stages and change plant species composition. However, for a better representation on the impacts of productivity, a more detailed representation of nutrient cycling is needed.

Assumptions and additional implementations: In this example, we assume that all consumed leaf biomass returns to the soil/litter. However, we could also set a percentage aside to simulate the conversion of leaf biomass into animal body mass. As well, we did not specify at which height folivory is implemented (e.g., bottom versus top crown), which might have a different feedback on NPP if the leaves consumed are sun-exposed or not. Models like ED2 that track the canopy vertical structure could be used simulate leaf consumption at specific canopy heights.

Initialization

The VM can be initialized based on real world data (forest plot data and/or remote-sensing) or from bare ground until the forest state of interest is reached (primary or secondary succession, or old-growth).

The *animal variables* can be initialized based on field data or based on the animal population model, if such model is capable of generating these variables. Even without a coupled animal model, it might be interesting to test the effect of folivory at different consumption rates.

Input data

Folivore species densities, individual consumption rates, and food preferences can be found in the literature (e.g., red colobus (Chapman et al., 2010; Struhsaker, 2010), red howler monkey (Julliot and Sabatier, 1993), Amazonian brocket deer (Gayot et al., 2004), mammals spp. (Leigh, 1999)). In particular, Leigh (1999) has a section on folivorous primates and estimates their yearly consumption. If individual consumption rates are not found, daily consumption rates can be estimated using allometric equations (Nagy, 1987). For non-strict folivores these estimations can be more challenging as the percentage of leaf in the diet can vary through time.

Submodel

The animal model simulates folivores population dynamics based on the available leaf biomass of their preferred plant species. This model can be a Lotka-Volterra predator-prey model or a more complex spatially explicit individual based model.

The “shed leaves” function takes two inputs: a list of entities and their leaf turnover rate.

The other functions calculate (see Table 3 for variables definition):

Pcr = Ad x *Icr (eq. 1). In eq. 1, Ad* can be either fixed or calculated by the animal model.

Fltr = Pcr/*LeafBiom-fol plants (eq. 2)*

Example key process 2: Flower consumption and debarking – life stage: adult

We found limited information on flower consumption and debarking, additionally neither flowers nor bark are simulated in VMs. Nonetheless, we want to mention briefly two indirect implementations.

Flower consumption: Primates can significantly impact tree reproduction (fig. 1) by reducing both pollination and seed production (Riba-Hernández and Stoner, 2005). Let us assume that when flowers are removed from a tree, the leftover carbon not used to produce fruits is redirected to other pools. We could then change the proportion of NPP assigned to reproduction based on the intensity of flower consumption. However, we could not find information on how tropical trees allocate carbon when fruits do not set.

Debarking: Debarking increases tree mortality (fig. 1) by increasing the chance of fungal and invertebrate attacks (Höft and Höft, 1995). Most field studies are on savannah elephants, and usually measure changes in tree mortality rates due to debarking. However, a debarked tree might take many years to die, thus determining the precise cause of death is often difficult. Tree mortality is a PVP that could be used to indirectly include this process In VMs. Specific PFT/species and larger trees have a higher change of being debarked, thus this could be a species and size dependent mortality.

Example key process 3: Seed processes - life stages: seed and seedling

Frugivores and granivores affect dispersal, germination, and recruitment through dispersal, predation, pulp removal, fertilization, and scarification (Fig. 1). Seed dispersal is a heavily studied subject and data abound, but compared to other processes, dispersal is less developed in VMs. However, there is an increasing interest to develop more realistic dispersal in VMs (Snell et al., 2014). VMs that are spatially explicit, such as LPJ-DISP (Snell, 2014), FORMIND and TROLL, already offer the ability to implement different dispersal kernel functions that can be associated with distinctive dispersal modes observed in tropical trees

(Harrison et al., 2013; Seidler and Plotkin, 2006). Here we present one way of implementing seed related processes.

Purpose: Implement the impact of seed dispersal and seed predation

*Entities***:** Individual trees/cohorts, represented by species or PFTs; frugivores and granivores (not explicitly represented in the VM)

Scale: stand, hectare, grid cell (determined by homogeneous environmental data)

Entities	Variable	Description	Unit
Plants	*Dk*	Seed dispersal kernel	meters
	S&F-Biom	Seed and fruit biomass	Kg ha^{-1}
	Gs	Germination statistics (time and/or probability to germinate) based on seed handling	
Animals	*Ad, Icr, Pcr*	Same as Folivory example	
	Food preferences	List of plant species dispersed or predated by a species or functional group	

Table 4. Variables relevant to the implementation of seed processes

Process overview and scheduling

At each time step (daily, monthly, annually), after seed production (Fig. 3), seed fate is determined for each plant entity. Seeds can be flagged as predated, dispersed, or non-dispersed. Predated seeds are then destroyed. Dispersed seeds are moved according to a dispersal kernel function. Non-dispersed seeds fall under the parent tree. In the last step, the function 'Germination rate' is applied to both dispersed and non-dispersed seeds.

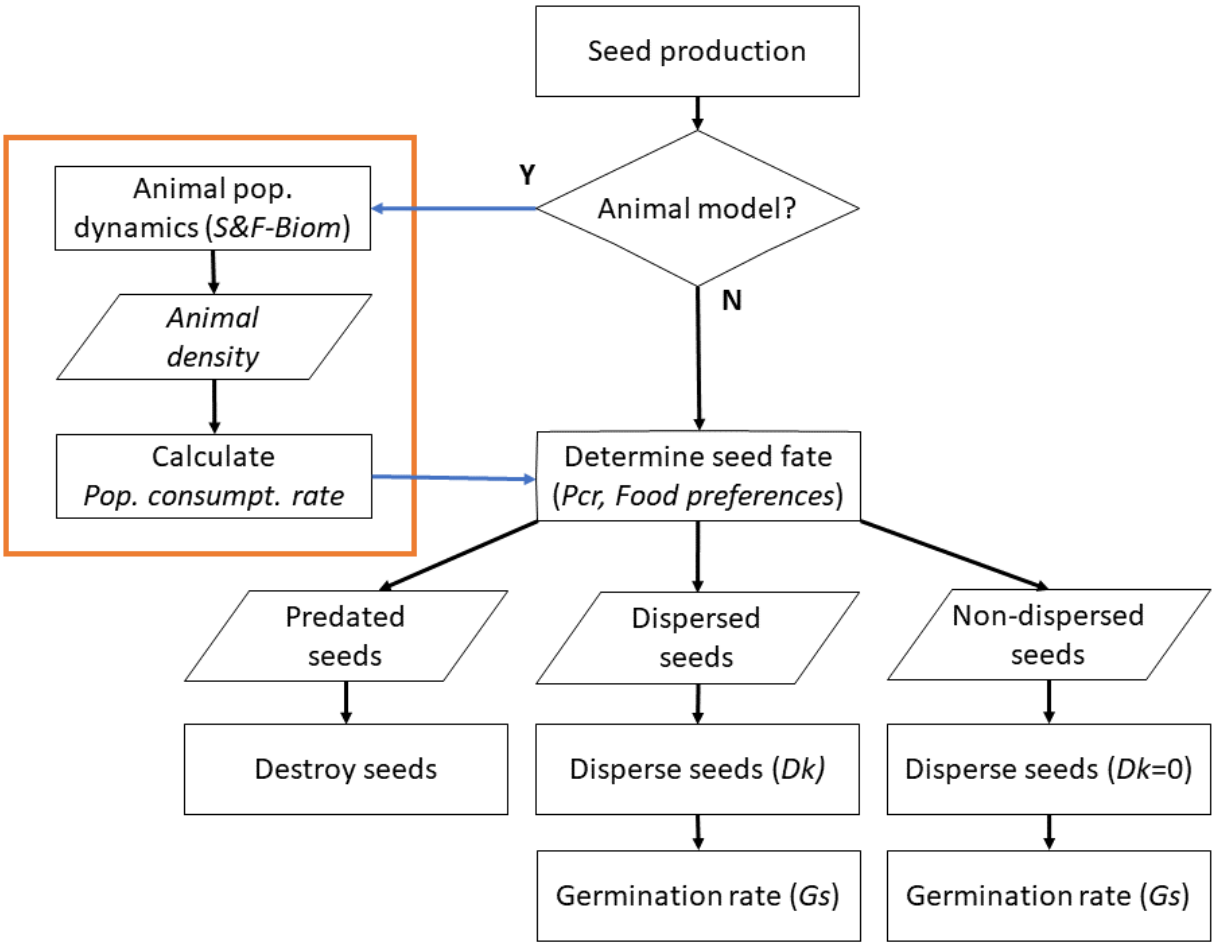

Figure 3. Flowchart of seed processes submodel. Orange box delimits the animal model. Blue arrows show data exchange between models, black arrows show transitions within model time states. Rectangles are functions, diamonds are selections, and parallelograms are data input/output.

Design concepts

Basic principles: This seed dispersal module allows to simulate a range of seed-animal interactions observed in the field. It describes seed fate from seed production to germination. The effect of seed handling (ingestion, pulp removal, scarification, etc) is also considered, as it can either damage seeds or promote germination. We should also note that seedlings are influenced by density-dependent mortality, edge effect, and fragment size, which are inevitably connected to seed processes and animal densities. Seedling mortality should be determined by the VM based on environmental conditions and other mortality factors, thus allowing to study edge effects. Additionally, the effect of fragment size is related to animal densities, which are here considered.

Emergence: Seed predation and dispersal can interact in complex ways (Wright et al., 2000). Plant recruitment will likely be influenced by animal densities and their food preferences. Thus, different animal community compositions will lead to different forest regeneration patterns and plant species composition (Muller-Landau, 2007). Density dependence (Lebrija-Trejos et al., 2016; Muller-Landau, 2007) and shade tolerance (Kelly and Purvis, 1993) increase the uncertainty of the outcome, both in terms of forest composition and carbon stocks. Density dependent processes are associated with seed predators, herbivores, plant niche-partitioning, and host-specific pathogens (Comita et al., 2014). While the latter two are out of our scope, we discuss the former two. Furthermore, distance- and density-dependent mortality relate to plant biodiversity and can be species specific (Comita et al., 2014). Thus, it is difficult to implement both processes in PFT-based models, and in species-based models because only a few species have been studied. Nonetheless, we still expect that seedling recruitment patterns affected by density dependence might emerge from implementing folivory and seed dispersal. Edge effect and forest fragment size are also important factors influencing regeneration, particularly at the seedling stage (Melo et al., 2007; Santo-Silva et al., 2013). Finally, interspecies difference in plant traits (e.g., leaf toughness, growth rate, allocation patterns) can also affect seedling mortality. However, as most VMs do not work at the species level, it is difficult at this time to evaluate the sensitivity of model output to interspecies variation.

Assumptions and indirect implementations: In this example, we assume that all consumed seed biomass returns to the soil/litter. We also assume that the VM is spatially explicit and that has a seed bank. However, some VMs do not have a seed bank or seed germination rate, and new recruits are created based on recruitment rates and NPP. In these cases, we would have to encapsulate the effect of seed fate and germination through recruitment rate. It such case, we have to be careful about how the VM transitions between seed and new recruit, including minimum size for new recruits. Because germination and establishment are separate processes driven by different biotic and abiotic factors (Snell et al., 2014).

Initialization

Same as the Folivory example.

Even without a coupled animal model, it might be interesting to test the effect of different densities of frugivores and granivores.

A challenge to overcome in PFT-based models is to group plant species based on their dispersal syndrome, as the current PFTs grouping might not be well suited for this task. Traits relevant to seed dispersal and predation should be included while maintaining some typical PFT trade-offs (e.g., growth-rate vs shade tolerance). An approach adopted in FORMIND was to group species in six PFTs based on shade tolerance, seed size, and dispersal syndrome (Dantas de Paula, 2017).

Input data

Complete animal-seed interaction observation networks are still scarce, and mostly biased towards seed dispersers. However, particularly for South America, there is a good amount of data that can be used to estimate seed fate and dispersal distance (Bello et al., 2017; Hammond and Brown, 1995; Muller-Landau et al., 2008). In the absence of specific animal-seed interaction data, seed morphology can be used to estimate dispersal syndrome (Forget et al., 2007). Animal densities and individual consumption rates data can be found in the literature as already described in the Folivory example. For example, Leigh (1999) estimates how fruit production is partitioned among different animal guilds. This example could be used to estimate the quantity of predated and dispersed seeds. Germination data on the effects of gut passage (Fuzessy et al., 2016; Hawthorne and Parren, 2000) and pulp removal (Silvius and Fragoso, 2002) is available. However, germination studies cover only a few selected species, so germination is probably the most difficult process to parameterize with current data. If germination data are limited, we could use other plant traits to determine germination probability such as seed size and successional stage (Hopfensperger, 2007).

Submodels

The animal model is similar to the one we described in the Folivory example. However, in this case it would use seed and fruit biomass to simulate animal population dynamics.

For each plant entity, the “Determine seed fate” function assigns seeds to different pools (predated, dispersed, and non-dispersed). It takes two inputs: *Pcr* and *Food preferences* for each animal entity that interacts with the plant entity (species or PFT).

The “Destroy seeds” function returns the seed biomass to the soil carbon pool.

"Disperse seeds" uses the dispersal kernel function associated to the plant entity to determine dispersal distance. Seeds will then be added to the seed bank. Note that non-dispersed seeds will be deposited under the parent tree, we indicate this as *Dk=0* in Fig. 3.

"Germination rate" assigns to seeds a probability of germination and a germination time based on seed handling.

***Example key process 4: Vegetation disturbance* - life stages: seedling, sapling, adult**

Under this category we group all the structural effects of megafauna not related to biomass consumption. For example, trampling, tree damage, tree uprooting, and soil disturbance. We discuss this implementation and a few key details through a simplified ODD.

Purpose: Implement the structural effects of megafauna

*Entities***:** Individual trees/cohorts/big leaf, represented by species or PFTs; megafauna (not explicitly represented in the VM)

Variables

We define four variables to characterize megafauna disturbance types:
Rate represents the frequency at which the disturbance is applied to the landscape.
Scale is the percentage of the landscape that is disturbed.
Intensity is an index indicating the magnitude of the disturbance.
Target describes which entities are modified by the disturbance.

Rate, *scale*, and *intensity* depend on animal density and movement (home range and resource selection). *Target* is related to animal physiology, behavior, and resource selection.

Process overview and scheduling

Megafauna disturbance is applied at a time step matching the *rate* of disturbance and to an area defined in *scale*. The disturbance function will modify plant or environmental entities according to *intensity* and *target*. If available, a coupled animal model updates animal density according to the location and availability of resources provided by the VM (see *Two-way plant-animal feedbacks* section). Lastly, *rate, scale,* and *intensity* are updated according to the new animal density.

Design concepts

Basic principles: Similarly to other disturbances (e.g., fire and tree fall), megafauna disturbance should modify the structure and function of the forest and create new environmental conditions.

Input data

Data needed to parameterize the structural damage of megafauna will have to include animal species density, an estimate of the fraction of the study area utilized over a time period, and habitat/vegetation type preferences (height/size/species of targeted plants, closed forest or gaps, forest edge, etc.). These data allow to estimate *rate, scale,* and *target*. Additionally, a measure of the effect of such disturbance is needed. For example, vegetation disturbance might be measured with plant mortality rates. Soil compaction could be measured with soil properties (porosity and airflow) or plant growth rates. Ideally, the effect of disturbance should be measured at different species densities, which would allow to estimate various levels of *intensity*. We provide some examples of available data to estimate the disturbance variables for forest elephants, the relevant variables are within parentheses. Terborgh et. al (2016) have measured structural damages to small trees at different elephant densities (*intensity*, and *target*). Another study has quantified the mortality rate of trees larger than 10 cm DBH (*rate, scale*, and *target*) (Omeja et al., 2014). Furthermore, as we already mentioned, Wing & Buss offer insights and data on the ecosystem engineering role of forest elephants. We recognize that finding studies that provide data for all four disturbance variables might be challenging, in such cases the missing variables will have to be estimated.

Emergence: Megafauna disturbance could impact a series of processes such as plant growth rate, regeneration, and competition among plants. Fast-growing plants that can quickly escape trampling might be favored. Additionally, regeneration in forest gaps might be hampered. Thus, we expect changes in community composition and forest structure. The magnitude of these changes will be dependent on the sensitivity of the model to the four disturbance variables.

Example key process 5: Nutrient redistribution and availability **- life stages: from seed to adult**

Megafauna can impact nutrients in different ways: by redistributing nutrients across concentration gradients and by accelerating nutrient cycling and making nutrients readily available (labile nutrients). Nutrient cycling in VMs is an area of recent development, particularly nitrogen and phosphorus. (Goll et al., 2017; Smith et al., 2014; Trugman et al., 2016; Zaehle et al., 2010). So far, these models have been run at the global scale or for non-tropical ecosystems. Thus, they require re-validation and perhaps re-parametrization to simulate tropical forests N and P cycles. Furthermore, a direct implementation of the influence of large animals on these processes would benefit from having lability and concentration level of nutrients, a missing feature in current VMs. Given the scarcity of studies covering this topic and the current modelling limitations, we only provide a short overview of possible implementations. Let us assume that one of the current VMs can reliably simulate nutrient cycling in a tropical ecosystem. Inevitably, nutrient cycling is connected to by biomass consumption, we could reuse and expand the Folivory and Seed processes submodels. We have to simulate two processes: nutrient distribution and modification of nutrients concentrations and lability. The former requires a spatially-explicit animal model that can reproduce animal movement, which is discussed in the next section. Furthermore, the Folivory and Seed processes submodels could be used to estimate the amount of biomass consumed and translocated by herbivores. Regarding nutrient mineralization, we could use the functions "Shed leaves" and "Disperse seeds" to modify nutrients concentration and lability when plant biomass is digested.

In the absence of nutrient cycling in a VM, the effects of large animals could be simulated indirectly via existing PVPs such as growth rate, gross primary productivity, and establishment rate. This implementation, while less dynamic than a direct one, could use data from field studies (Feeley and Terborgh, 2005) to relate animal densities to growth and establishment rates. Additionally, estimates of the amount of nutrient transported can be obtained with mathematical models (Wolf et al., 2013). These information should allow to test some hypothesis on how different patterns of nutrient cycling can affect forest productivity and community composition.

3.1.8 Coupled animal-vegetation models - two-way plant-animal feedbacks

The design concepts we provided include a basic implementation of an animal population model that updates animal densities according to the availability of a certain resource. A similar concept has been used to couple a VM with an animal demographic model (Pachzelt et al., 2013). However, the extended home ranges of megafauna are a key ecological component playing a critical role in plant-animal feedbacks. In particular, seed dispersal and nutrient distribution require spatially-explicit mechanics that are currently lacking in VMs. A more detailed and spatially explicit animal model (i.e., Madingley model) could provide the level of detail needed in terms of animal dispersal, consumption, and population dynamics. We have already pointed to relevant literature useful to parameterize animal models, in addition to the HFT concept, which reduces the complexity of simulating single species. The basic principle of simulating two-way feedbacks between vegetation and animals is to have a mutual exchange of data between two coupled models (fig. 4). The VM will provide to the animal model a landscape map containing the location and state of plants, and any relevant environmental variables (e.g., temperature, water sources). The animal model will update the landscape map according to animal movements and resource utilization. The landscape map will then be returned to the VM which will update its state and resume the simulation until the next time step of data exchange (fig. 4). This approach would allow to test hypotheses not only on the effects of animals on plants but also on how animal populations might react to changes in plant communities. Ideally, this framework could be employed to study the repercussions of changes in animal biodiversity and climate on megafauna-plant feedbacks and forest functioning. The biggest challenge may be to harmonize the spatio-temporal scales of the coupled models. Doing so requires evaluating at which scales animal species influence vegetation processes and how these are represented in VMs. Additionally, correlating the effect of a species over a certain time and area requires measurement of this effect at different animal densities. Such data are not always available and are usually measured only over short periods. Thus, extrapolating the effect of animals over long periods and at different densities might be a source of uncertainty in simulations.

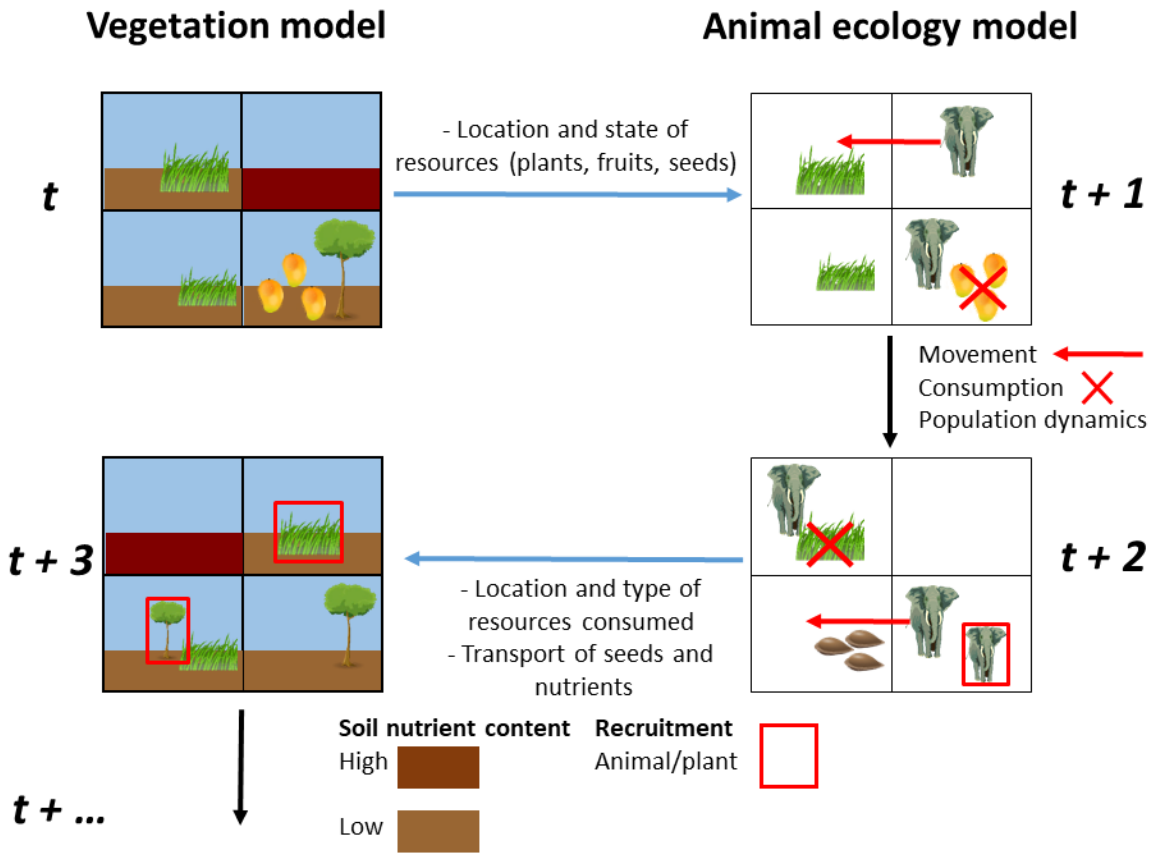

Figure 4. Conceptual scheme of a coupled vegetation–animal model. Time step t could be either an initial state or an intermediate state. Ecological interactions: elephants transport nutrients, consume shrubs, and transport seeds promoting tree recruitment. Blue arrows show data exchange between models, black arrows show transitions within model time states.

3.1.9 Future modelling perspectives

The many empirical studies on megafauna-plant interactions will enable different approaches: (I) simulations in VMs could help identify ecosystem tipping points in a more realistic fashion than pure theoretical models. For example, when does an animal population cease to be a functional disperser for a plant species? We could test this by implementing the effect of dispersal by a particular animal with different population sizes and measure the outcome in terms of number of plants and spatial distribution. (II) In complex systems, VMs offer a controlled environment where confounding factors can be teased apart and complexity can be reduced. For example, what is the role of the microenvironment compared to ingestion of seeds in the recruitment process? This hypothesis can be tested in VMs that have a detailed representation of the microenvironment such as ED2 and experimental studies on the effects

of seed ingestion. An important question is whether data relative to a specific taxon/site can be used to parameterize models for a different site or a similar species. Also, the lack of regular forest inventories with information on disturbance history (hunting, logging, degradation) reduces our ability to constrain model parameters and validate the model output. This limits our analysis to relative changes in the effects of animal-plant interactions. The benefits of VMs are their large suite of processes and extensive output which enable the analysis of changes in short/long-term succession, forest function, and structure; whereas field-studies can only track a fraction of these processes. While we recognize that VMs output will never match 1:1 actual forest observations, they still allow studying relative changes in vegetation dynamics within realistic orders of magnitude. Hence, we suggest a mechanistic modelling approach as an additional, complementary, and integrative tool to evaluate the impact of megafauna, and particularly for long-term studies. Specific VMs should be chosen according to the research question focus (see our suggestions in Table 2). Overall, VMs provide a flexible and powerful tool to explore a range of research questions concerning the role of megafauna in tropical forests, and their potential has barely been explored.

3.1.10 Conclusion

The mechanisms linking megafauna to ecosystem functioning have just started to emerge. Our knowledge of these links is limited and hampers our ability to predict how ecosystems might respond to the rapid decline of megafauna, particularly in the long-term. A better understanding of megafauna ecology is crucial not only for preserving tropical forests and avoiding irreversible states, but also for local and global human populations that depend on tropical ecosystems and their services. The connection between tropical carbon cycle and megafauna needs further investigation and is particularly important in relation to its implications for atmospheric CO_2 concentrations and potentially for climate patterns. Carbon cycling research should therefore reconsider the role of fauna as more than just negligible.

In our review, we observed that field-based research related to megafauna and defaunation in tropical forests is prone to severe limitations in terms of predicting future shifts in species composition and forest structure beyond the early stages of defaunation. As well, we still have a limited knowledge of the role of megafauna in biogeochemical cycling and ecosystem engineering. We also observed, a strong bias in terms of taxonomic and functional groups, and tropical regions (Hawes et al., 2013; Kurten, 2013). For example, Neotropical primates and seed dispersers are overrepresented while African and Asian large ungulates,

elephants, and seed predators are the most understudied groups. This is particularly crucial given that these underrepresented groups might have a disproportionate effect on forest dynamics. We should also strive to build plant-animal databases (Bello et al., 2017) that could be used as input for different modelling approaches. These datasets should describe the role of each animal (seed disperser/predator, herbivore) and the intensity of each interaction, such effort would help establish functional thresholds of dispersal and the effects of herbivory and seed predation.

We have proposed VMs as an additional tool to further our knowledge on megafauna ecology and overcome some of the current methodological limitations. We have given an overview of methodological approaches on how to implement plant-animal interaction in VMs by integrating different types of data. When possible, we provided ideas to exploit existing VMs and PVPs with minimal model modifications. The processes that can be implemented more intuitively in VMs include folivory, disturbance, and seed related processes. Additionally, we proposed a coupled animal-vegetation model that can provide further opportunities to study processes that involve complex feedbacks and animal population dynamics and movements. One of the challenges of this approach is to consider the spatial scale at which megafauna processes are active and run these models at a spatial scale (resolution) that is relevant to the studied research question. Another challenge is to decide if the presence of fauna should be implemented directly or indirectly (see Table 2), particularly for spatially explicit processes such as nutrient cycling. Furthermore, we have discussed ideas and limitation in terms of data input and parametrization.

To study the role of megafauna we need an interdisciplinary approach involving modelling (vegetation and animal), defaunation ecology, and paleoecology. As animals also influence vegetation-climate feedbacks, we envision a modelling approach that encompasses and integrates all three components to generate new insights. To bridge this interdisciplinary gap, we suggest that future defaunation studies also consider AGB and components of nutrient cycling. For example, some defaunation studies are 10-15 years-old, these sites could be resurveyed to measure recruitment rates of mature trees and AGB. We could revisit already collected data to analyse forest properties that were previously overlooked. Furthermore, we could compare nutrient distribution in forests with different densities of large animals. In terms of data collection, some of the concepts we illustrated might provide ideas for field-ecologists when considering the type of data useful to modellers. Additionally, while the implementation

examples we provided were specific for tropical forests, similar strategies could possibly be adapted for other ecosystems.

Authors' contribution

F.B. coordinated the project, lead the writing, and created figures. All authors participated in writing the manuscript and gave final approval for publication.

Acknowledgments

Fabio Berzaghi was supported by University of Tuscia and University of Molise Doctoral School in Science, Technology and Biotechnology for Sustainability and by European Forest Institute project "Supporting the Global Implementation of REDD+ and FLEGT". Martin R. Nielsen was supported by FFU grant 13-08KU - "REDD+: -the Forest grab of all times?". We would like the anonymous reviewers for the comments and Alex Lowe for the help in editing the manuscript.

3.1.11 References

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3.2 The influence of megafauna on tropical forest structure and carbon cycling: forest elephants in the Congo Basin

3.2.1 Abstract

Very large herbivores, the megafauna (body mass > 45kg), can have a disproportionate effect on the functioning and structure of ecosystems. The majority of megafauna went extinct ~10,000 years before present and many of the extant megafauna species can be found in the tropical forests of Central Africa. Among tropical extant megafauna, the African forest elephant (*Loxodonta cyclotis* Matschie, 1900) is one of the largest terrestrial animals. The ecosystem-engineering role of forest elephants in African tropical forests has been studied mostly in relation to their function as seed dispersers. Much less is known on the processes of disturbance and nutrient distribution caused by this large species. When in closed canopy forests, forest elephants can increase small tree mortality, break stems, and clear the understory by browsing. This thinning effect might influence forest functioning, and might be responsible for the characteristic structure and higher carbon stocks of African tropical forests. I investigated the effect of forest elephant disturbance by combining two approaches. Firstly, I used the vegetation model Ecosystem Demography 2 to test the medium and long-term influence of elephant disturbance on vegetation dynamics, forest structure, and carbon stocks. Secondly, I analyzed forest inventories in areas with different elephant disturbance intensities and compared them with the model results. I present the first description of how changes in eco-environmental processes influenced by elephant disturbance lead to a shift in forest carbon stocks, functional composition, and productivity. I also provide the first projections of how various elephant densities at different time scales might affect Congo Basin forests. The results have implications for the conservation of a threatened species, for forest management, and for climate policy.

3.2.2 Introduction

Most megafauna, mammalian vertebrates with a body mass greater than 45kg, went extinct during the late Quaternary Megafauna Extinction between 50,000 and 10,000 years before present (Martin, 1984). The cause of this massive extinction might have been changes in climate or over hunting by humans (Araujo et al., 2017; Koch and Barnosky, 2006; Lorenzen et al., 2011). Regardless of what caused the LQME, the disappearance of megafauna might have had profound consequences for ecosystems (Gill, 2014) and climate (Doughty et al., 2010). The far-reaching influences of past megafauna on ecosystems in terms of functioning and structure might be relevant also today (Bakker et al., 2015; Brault et al., 2013; Malhi et al., 2016). The rapid disappearance of the remaining megafauna might have cascading effects for ecosystems with unknown long-term consequences (Estes et al., 2011; Ripple et al., 2015). Elephants (genera *Loxodonta* and *Elephas*), the largest extant megafauna living on land, are classified by the International Union for Conservation of Nature Red List as vulnerable (*Loxodonta*) or endangered (*Elephas*). While the ecosystem-engineering role of savanna elephants (*Loxodonta africana* (Blumenbach, 1797)) has been studied extensively (Guldemond and Van Aarde, 2008; Scheiter and Higgins, 2012; Shannon et al., 2008), forest elephants (*Loxodonta cyclotis* Matschie, 1900), who are primarily tropical forest dwellers, have received attention mostly for their role as seed dispersers (Beaune et al., 2013; Campos-Arceiz and Blake, 2011; Hawthorne and Parren, 2000). Lately, partly due to their population collapse and uncertain future (Maisels et al., 2013), research on forest elephants has increased and their influence on other vegetation processes has begun to emerge (Omeja et al., 2014; Terborgh et al., 2016a). A current hypothesis is that the presence of megafauna in African tropical forests, as opposed to Amazonia where fewer large herbivores species remain, might contribute to the differences in structure between the two regions (Lewis et al., 2013; Terborgh et al., 2016b). For example, Terborgh et al. (2016b) suggested that the presence of megafauna might account for some of the differences in structure and composition between Gabonese and Peruvian forests. Forest elephants, by clearing the understory and increasing tree mortality within certain size classes, might be partly responsible for the marked differences in size class distribution and the observed high number of very large trees in Gabon forests, and in Congo basin forests (Lewis et al., 2013). There are also some reports that the absence of forest elephants might favor lianas infestation, a process that might lead to lower carbon stocks (van der Heijden et al., 2015). Other studies have also speculated that a reduction in forest elephant disturbance following their population collapse, may partly contribute to an increase in above-ground

carbon storage in African tropical forest (Lewis et al., 2009, 2013). However, these studies did not test any hypothesis regarding the role of megafauna. To address this research gap, I tested the hypothesis that the disturbance caused by forest elephants has a clear impact on the forest structure and carbon cycling of Congo Basin forests. By reducing the number of stems, this thinning process might lower the competition for resources (light, water, and nutrients) among plants and allow larger and older trees to dominate (Lewis et al., 2013). I examined the effects of forest elephants at the landscape level and at the stand level to disentangle the mechanisms driving changes in the ecosystem. To do so I analyzed forest inventories in sites with different intensity of elephant disturbance. In parallel, I used a mechanistic vegetation model to simulate the influence of elephants on long-term forest structure and function. Finally, I evaluated how different elephant densities might affect forest structure and functioning to provide information that can be used for management and conservation of both forests and elephant populations. I provide the first estimate of the effects of forest elephants at different population densities on aboveground biomass (AGB), net primary productivity (NPP), and forest structure. I also provide an evaluation of the mortality rate of small plants (<10cm DBH) caused by elephants, as this estimate is not available from direct observations of elephant foraging in forests. My goal was not only to better describe the ecosystem-engineering role of forest elephants but also to shed light on the ecological importance of this megafauna species and the implications for its conservation.

3.2.3 Methods

Forest inventory data

I obtained forest inventory data from the Ndoki Forest (1.5-3° N, 16–17° E) near the Nouabalé-Ndoki National Park (NNNP), Republic of the Congo (DRC) and from LuiKotale research site (2°47'S, 20°21'E) at the southwestern edge of the Salonga National Park, Democratic Republic of the Congo (DRC), (see figure 1). Both sites are located in primary forests with very low human disturbance without permanent human settlements nearby. While in LuiKotale elephants have been absent for nearly 30 years (Beaune et al., 2013), Ndoki was until recently one of the last stronghold of forest elephants in the Congo Basin with a population density of 0.56 individuals/km^2 (Blake et al., 2007). Although in the last few years Ndoki has lost approximately 50% of its population (Maisels et al., 2013). Ndoki Forest covers a larger area and has a wide range of environmental conditions and vegetation cover and LuiKotale is a smaller site primarily within closed canopy forest. However, the forest inventory was

performed in both sites in lowland closed-canopy forest with some patches dominated by *Gilbertiodendron dewevrei*.

Figure 1. Location of forest inventory plots: Ndoki Forest in Republic of Congo and LuiKotale in Democratic Republic of Congo. Location of forest elephant studies used for parametrization of forest elephant disturbance: Kibale National Park in Uganda.

Annual precipitation in LuiKotale is higher (> 2000 mm) than Ndoki (1422 mm but this was measured at NNNP, might be slightly higher in Ndoki Forest) and both sites have a dry season. The forest data from LuiKotale comprises of 15 plots of 1-ha where all trees with DBH ≥ 10 cm were measured. All plots were chosen randomly from heterogeneous primary forest and are separated by distances between 250 m to 6 km (Beaune et al., 2013). The Ndoki data includes all trees ≥ 10 cm DBH surveyed in 115 paired plots of 200 m² along elephant trails. Each pair had one plot on an elephant trail intersection and the other off the trail at a distance between 50 and 100 m from the intersection plot in a direction chosen with a random compass bearing (see figure 2 and (Blake and Inkamba-Nkulu, 2004)).

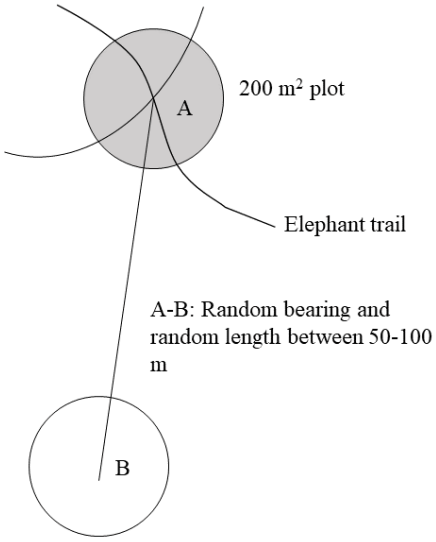

Figure 2. Ndoki Forest paired plots on elephant trail intersections (A) and off trail (B), adapted from Blake and Inkamba-Nkulu 2004.

Statistical analysis of forest inventory

Based on the intensity of elephant disturbance I classified the forest inventory data in three groups: no disturbance (LuiKotale plots), low disturbance (off trail Ndoki plots B), and high disturbance (on trail Ndoki plots A). Because the plots at Ndoki are smaller, I pooled all 230 Ndoki plots which gave a total area of 4.6 ha split equally between on-trail and off-trail. While this seems low compared to the 15 ha of LuiKotale, it is one of the few data sets available in pristine lowland Congo Basin forests with contrasting elephant disturbance intensities. For comparison, Omeja et. al (2014) surveyed 5 ha to estimate tree mortality due to elephant. To analyze the differences in forest structure along the elephant disturbance gradient I fitted a Weibull function on the distribution of tree sizes. The Weibull distribution parameters are shape and scale which determine the form of the distribution. The shape parameter (β) is equal to 1 when the distribution is exponential, when $\beta < 1$ there are more small trees relative to large trees, and it is the opposite when $\beta > 1$. The scale parameter (α) is a close approximation of the median of the distribution (Lima et al., 2016).

Vegetation model, input data, and model validation

I used the Ecosystem Demography 2 model (Medvigy et al., 2009; Moorcroft et al., 2001) to simulate the dynamics and properties of a tropical lowland forest in the same general area as LuiKotale, DRC. ED2 is a deterministic vegetation model that represents the heterogeneity of

a forest by simulating plant ecophysiological processes and competition for resources among plants. Instead of simulating individual trees, ED2 uses cohorts defined by a system of partial differential equations used to approximate the behavior of an individual-based gap model. The landscape is divided in grid cells with size determined by the resolution of the environmental data (climate and soil). It is important to note that any point simulated within a metrological grid cell will lead to the same results because it is driven by the same environmental data. ED2 is a deterministic model and given the same parameters and input, it provides the same results with no variability. Within a grid cell, climate and soil are the same but the microenvironment changes according to the horizontal and vertical structure of the vegetation in each patch. Within each cell, the heterogeneity of the vegetation is captured by dividing the area in patches, each with a different size and age structure. Patches do not have a geographical position within grid cells and each patch occupies a fraction of the simulated area. Because at the patch level there is no geographical information, the total area simulated accounts to one, but the forest properties are scaled to an actual area (hectares, m^2, etc.). Each patch is composed by a collection of cohorts with a dynamic vertical structure and a similar disturbance history. Each cohort is defined by plant density, size, plant functional type (PFT), and age while the other properties (leaf area index, biomass, etc.) are derived using allometric equations or defined by PFT-specific properties. Processes in ED2 are resolved at different time steps from minutes for biophysics processes to a year for patch dynamics (see Longo, 2014; Medvigy et al., 2009; Moorcroft et al., 2001 for further model details).

PFTs are commonly used in vegetation models to represent the functional diversity of plants present in a certain ecosystem or biome. In ED2 there are three tropical PFTs: early, mid, and late successional. Each PFT is defined by roughly 80 parameters that describe biomass and height allometry, leaf biophysical properties, mortality, growth rate, phenology, photosynthesis, etc. For tropical PFTs most of these parameters are similar, however some of the dissimilar parameters should be noted as they are important to interpret the results. In particular, wood density (g/cm^3) is one of the key parameters as it influences density-independent mortality (aging mortality) and DBH-leaf/stem biomass allometry (kg leaf biomass/plant). In addition, PFTs differ in leaf and root turnover rate, and maximum photosynthetic capacity. In brief, early successional are pioneer, fast growing plants that thrive in light gaps and have high turnover rates. Late successional are shade-tolerant, slow growing plants with high wood density and low turnover rates. Early successional also have a higher mortality due to aging compared to mid successional, while late successional are not subject to

aging mortality. Given trees of the same size, late successional will have higher leaf biomass than the other two PFTs. Mid successional are a compromise between the two but slightly closer to late successional. Table 1 contains a summary of these parameters.

PFT / Parameter	**early**	**mid**	**late**
Wood density (g/cm^3)	0.53	0.71	0.9
Density-independent mortality (%)	5	2.8	0*
Leaf & root turnover rate (% lost/year)	100	50	33
Specific leaf area (m² leaf/kgC)	16	11.6	9.6
Maximum photosynthetic capacity (µmol/m2/s)	18.75	12.5	6.25
DBH-leaf or stem dead biomass allometry (higher value= higher leaf/dead biomass given the same DBH)	0.42/0.17	0.56/0.22	0.71/0.28

Table 1. Summary of the main parameters responsible for the differences between the three tropical PFTs. *Late successional are still subject to other types of mortality (i.e., carbon starvation and treefall).

Disturbance is a critical process related to the effect of elephant and ED2 has a disturbance module that allows to characterize different disturbance types. Disturbance events in ED2 are treefall, fire, logging, and land use change. Disturbances are applied yearly and trigger the creation of new patches, similarly to gap creation in individual-based models, to represent the new vegetation structure after the disturbance. Each year new patches are created and patches with similar disturbance history and similar cumulative leaf area index at different height levels are merged otherwise the number of patches would become very large. Typically, 20-25 patches are enough to capture the heterogeneity of the vegetation. The survivorship rate of plants affected by a disturbance is defined by the equation:

$$s = 1 - (1 - \exp(-\mu))/A \quad \text{(eq. 1)}$$

Where μ is the instantaneous mortality rate because is integrated over time using ordinary differential equations and can vary between zero and infinity. A is the fraction of the simulated area which is disturbed each year. The rate at which disturbance is applied to the landscape is defined by:

$$\lambda = \ln(1 - A) \quad \text{(eq. 2)}$$

In addition to disturbance rate and survivorship, disturbances are defined by the type and size of plants that are affected depending by the disturbance type. For example, in ED2 the mortality caused by a treefall event is dependent on the size of the fallen tree and by the size of the trees within the patch where the treefall event happens. When trees smaller than 10 m fall they do not cause mortality to other trees and this event does not trigger the creation of a new patch. Instead, a tree taller than 10 m falling causes a higher mortality for tall trees and lower mortality for small trees. Mortality can be set as size-dependent, which is useful to simulate the effect of elephant disturbance.

As input data for the model I used meteorological forcings from the NCEP/NCAR reanalysis I (Kalnay et al., 1996). I have used time series at 6-hour intervals of the variables: air temperature, wind, relative humidity, pressure, precipitation, and radiation. I have selected data from 1979 until 2015 because from 1979 reanalysis data have become more reliable thanks to the integration of more accurate satellite data (Kalnay et al., 1996). I also considered two other reanalysis data sets (ERA-Interim and Princeton Global Forcings) but discarded them as they had unusually high values of humidity and radiation in the Congo Basin, these values were out of the model boundary conditions. In particular, the Princeton Global Forcings had relative humidity above 100%. Soil data came from the United Nations Food and Agriculture Organization global soil database (Fischer et al., 2008). The geographic extent of the simulation is determined by the resolution of the meteorological forcings which for NCEP Reanalysis I is 1.8°x1.8°, roughly a square of 90km^2 per side. Inside this area climate is homogeneous and ED2 provides an average of forest properties per unit area across this grid cell. This is important to consider when validating and evaluating the model output against ground data. The main reason why I only simulated one area is that the meteorological data coverage in the Congo Basin is poor. This leads to very homogeneous climatic data across the Basin that would lead to very similar simulation results. Finer scale soil and climate data would be necessary to simulate vegetation differences that are more site-specific.

I ran an initial spin-up simulation from bare ground (just seeds and a few seedlings for each PFT) for 500 years to reach a close-to-equilibrium state in which number of plants, biomass, basal area, etc. have minimal year-to-year variation. I then validated the model by comparing the average of the last 100 years of the model output with forest inventory from LuiKotale. The forest properties I have used for the validation include AGB, basal area, stems per hectare, and the distribution of class size. I calculated AGB following (Chave et al., 2014) but instead of

using the height allometry proposed by (Chave et al., 2014), which tends to overestimate AGB in Congo Basin forests, I used a region specific height allometry proposed by Kearsley et al. (2013).

Implementation and parametrization elephant disturbance

I reviewed the literature exclusively related to *Loxodonta cyclotis* and that provided quantitative measurements of plant mortality caused by elephant foraging or movement. After excluding all studies on *Loxodonta africana* and *Elephas maximus*, and the studies on *Loxodonta cyclotis* focused on other aspects of its ecology (diet, seed dispersal, etc.), only a few articles provided quantitative measurements of the effects of forest elephant foraging (Blake, 2003; Inogwabini et al., 2013; Omeja et al., 2014; Ssali et al., 2013; Terborgh et al., 2016a; Wing and Buss, 1970). It is important to restrict the analysis because *Loxodonta cyclotis* foraging behavior is very different from *Loxodonta africana and Elephas maximus* (Terborgh et al., 2017). Living in forests, *Loxodonta cyclotis* have access to more foliage at lower heights than their savanna counterparts, so *Loxodonta cyclotis* feed mostly on herbaceous vegetation and tree saplings and have less need to break branches and uproot trees to reach foliage (Blake, 2003; Wing and Buss, 1970). Most studies agree that forest elephants feed and interact with trees of size < 10cm DBH (referred to small trees from now on) in more than 90% of the cases and up to 97% (Blake, 2003; Ssali et al., 2013; Wing and Buss, 1970). The effect of elephants on small tree mortality rate and their specific feeding behavior is currently unknown in closed canopy forests (Blake, 2003; Terborgh et al., 2016a). Further, Terborgh et. al (2016a) and Omeja et. al (2014) reported that stem breaks often do not lead to tree mortality. A rough estimate of small tree survivorship due to foraging of highly destructive herbivores is reported from a *Sus scrofa* nesting area in Malaysian forests where 93.4% of saplings had resprouted after breakage (Terborgh et al., 2017). This finding might suggest that survival rate of dicot plants, the main diet of elephants in closed canopy African forests, might be higher than 80% as dicots can resprout after elephant disturbance (J. Terborgh *personal communication*). In addition to small trees, forest elephants have a direct effect on trees of size between 10-30cm DBH that are uprooted or pushed over. The mortality in this size class has been estimated with more precision and has been reported to be between 1-1.4% (Omeja et al., 2014; Wing and Buss, 1970). Trees >30 cm are mostly subject to debarking and no correlation has been found between debarking and tree mortality (Struhsaker et al., 1989). As explained previously, three critical information are needed to define a disturbance in ED2: the area affected by the disturbance (*A*) within a specified time period, which is used to calculate the disturbance rate;

the survivorship of plants (*s*) when such disturbance takes place, which can be calculated from the mortality rate; and the type of plants that are affected by the disturbance. To model elephant disturbance I considered two separate class sizes: 0-10 cm and 10-30 cm with separate survivorship rates, which I estimated from literature. I implemented a new disturbance type in ED2 and defined a size-dependent and PFT-independent survivorship with two parameters:

sst : survivorship of small trees (<10 cm DBH)

slt : survivorship of large trees (≥10 and <30 cm DBH)

I also defined the elephant disturbance rate λf which depends on the fraction of the simulated area disturbed by elephants annually *Af* (see eq. 2). A large study by Wing and Buss (1970) is the only source of information that helps estimate *Af* as a function of elephant densities. Wing and Buss estimated that the elephant population in Kibale at a density of 0.75 individual/km^2 during one year interacts with 14.31% of all forest stems within the area available to elephants. From this number I assumed that *Af*= 14% because 97.54% of stems used by elephants are less than 10 cm DBH and 75% are less than 2.5 cm DBH. Since the vast majority of stems in a forest are smaller than 10 cm DBH and with no other data available, 14% is a first approximation of the fraction of the area annually disturbed by elephants at the given population density. Not knowing the exact mortality rate for plants <10 cm, *sst* was set conservatively at 90%, calculated using a 1.4% annual mortality rate. In comparison, treefall in ED2 has a similar mortality rate of 1.25%, and is applied over a much smaller area 1.26% but has a survivorship of 0% for trees taller than 10 m and 10% for trees smaller than 10 m. Hence, a 1.4% mortality applied only to small trees is reasonable considering the destructive nature of elephant foraging. Similarly, *slt* was calculated using the 1.4% annual mortality reported by Omeja et. al 2014 for the same Kibale population studied by Wing and Buss. Omeja et al. datum was used because Wing and Buss did not report an exact figure of mortality rate. However, Wing and Buss reported that 1.08% of trees were pushed over which is close to the finding of Omeja et al., assuming that a tree is killed when pushed over. More evidence that the mortality rates I have chosen might be conservative are given by another study. Ssali et. al documented the fraction of trees toppled in 20x4m plots: 41% of trees in between 2-10 cm DBH and 7% of trees >10 cm DBH, but they do not specify if these trees were killed. Due to the uncertainty in the estimation of mortality of small trees, I performed a sensitivity analysis in which I evaluated the effect of various small tree survivorship rate on the model results.

Modeling protocol and scenarios of elephant densities

Initially, a 500 years spin-up period from bare soil was used to create a forest state at equilibrium in which forest properties have minimal year-to-year variation. This equilibrium state was used to set the initial conditions for the second phase that ran for another 1000 years. The second phase included the control simulation without any modification and a set of simulations in which I introduced the disturbance of elephants at different densities. I chose to simulate 1000 years because the time needed to reach equilibrium depends on the disturbance rate and the simulations included a wide range of disturbance rates. I defined density scenarios starting from a density of 0.75 elephants/km² associated with a disturbed area of 14% and assumed a constant ratio between *Af* and Ephd. This assumption implies that at a change in density, elephants will disturb a higher (or lower) fraction of the landscape but the intensity of disturbance (*sst* and *slt*) will remain constant. In other words, at any Ephd, the local effect will be the same (90% survivorship) but the disturbance will be applied to an area proportional to the density. This is a reasonable assumption given that forest elephant group size is usually small, between 2-4 individuals (White et al., 1993), with minimal overlap between individuals (Schuttler et al., 2012), and that groups are solitary unless when they gather in forest clearings. Although, it should be mentioned that different groups might move through the forest using the same trails (Blake and Inkamba-Nkulu, 2004). In line with this assumption, I estimated the disturbed area as a function of elephant density through a range of previously reported densities across central Africa (see table 2). I have divided the simulated scenarios in low density (0.25,0.5,0.75, and 1) and high density (2,3,4, and 5) for several reasons. Low densities are more common, at least in recent times. When poaching is limited or absent densities over large areas could be between 0.5-1.0/km^2 (Maisels et al., 2013). However, we do not know what historical densities of forest elephants could have been before human intervention. High densities have been documented less frequently than low densities. Still, elephant densities of 2-3/km^2 , and in some periods up to 4/km², are some of the highest to appear in the literature in different parts of central Africa (Carroll, 1986; Morgan, 2007; White, 1994). Further, given the assumption concerning the *Af*-density ratio, values farther away from the baseline (*Af*=14% at a density of 0.75) should be taken more carefully as at higher densities the effect over a large area might deviate from the baseline assumption. Lastly, I included 5 individuals/km^2 as it represents an elephant disturbed area of 95% and could represent a limit scenario where a population is constrained within a protected area. Table 2 shows a summary of the scenarios. Because the area simulated in ED2 is not tied to a specific geographic extension, the results can be interpreted in terms of elephant density and extrapolated to any area (from 1 ha to a

national park, to a region), obviously an area with similar environmental conditions and forest properties. However, elephant disturbance is not modelled in a spatially explicit fashion, so the simulations are more representative of the local effects of this disturbance. In reality, elephant movement in closed-canopy forests is along trails and is influenced by water and fruit availability (Blake and Inkamba-Nkulu, 2004). To address this model limitation and contrast the results in terms of local versus global effect, I use *Af* values shown in table 2 to calculate continent-wide estimates of AGB using a weighted average. AGBcontinent = AGBelephant x (*Af*) + AGBcontrol x (1-*Af*). It is important to test the effect of different elephant densities on vegetation not only to better understand the species ecology but also for conservation and management purposes.

Elephant density (individuals/km^2)	***Af* (% of area disturbed by elephants)**
0	0
0.25	4.7
0.5	9.5
0.75	**14**
1	19
2	38
3	57
4	76
5.3	95

Table 2. Simulations of elephant density scenarios. *Sst* and *slt* refer to the survivorship of plants within the area disturbed by elephants. In bold the base scenario based directly on the data found in literature.

Sensitivity analysis

I performed a sensitivity analysis on the parameter *sst*, which represents the intensity of disturbance, to evaluate its effect on model output. The analysis was also useful to test plausible ranges of small tree mortality, as this was the parameter estimated with the highest uncertainty. The effect of λf is already shown through the density scenarios and the sensitivity analysis was performed including these scenarios. The sensitivity analysis was run for 500 years and for each scenario three values of *sst* were tested: the baseline of 90%, one at 80%, and a third at 70%. Table 3 shows a summary of all the sensitivity analysis simulations. A consideration regarding the *sst* parameter and the intensity of elephant disturbance. In the control simulation

small trees total biomass and leaf biomass are approximately 9 Mg/ha and 3Mg/ha respectively. A survivorship of 90% corresponds roughly to 0.13 Mg/ha lost due to elephant disturbance. Forest elephants annual consumption at a density of 0.75 is roughly 0.47 Mg/ha (calculated with a gross assimilation efficiency of 22% (Rees, 1982) and estimates of biomass droppings from Wing and Buss 1970). Considering that the majority of the biomass is not consumed in closed-canopy forest, 0.13Mg/ha lost due to elephant is reasonable since it might include some biomass lost to consumption and some from death of small trees. A lower survivorship of small trees thus implies that the intensity of the disturbance is higher, transferring more biomass to the soil. Since in the model I introduced elephant disturbance instantaneously and kept a constant elephant density, I assumed a zero-sum game between plant biomass and elephant biomass, as the carbon assimilated by elephants would eventually return to the soil carbon pool.

Elephant density (individuals/km^2)	***sst* (survivorship after elephant disturbance)**
all densities	**90% - high survivorship**
all densities	80% - medium survivorship
all densities	70% - low survivorship

Table 3. Sensitivity analysis simulations. Values of survivorship of small trees. In bold the simulation based on the baseline parametrization.

Analysis of model results

I compared the results of the scenarios against the control simulation (no elephant disturbance). I divided the results in medium-term effects (250 year) and long-term effects (up to 1000 years). I evaluated the results both in terms of trend (through time series), time to reach equilibrium, and the average of forest properties at equilibrium. When an evident state of equilibrium was difficult to identify I used a moving standard deviation to identify periods of stability when the moving standard deviation was lowest throughout the time series. A moving standard deviation was necessary because vegetation changes through time. Lastly, I disentangled how possible alterations in forest processes at the stand level contribute to variations in forest structure and function.

3.2.4 Results

Forest inventory and model validation

The analysis of the forest inventory data from LuiKotale and Ndoki Forest shows a clear difference in the density distribution of class sizes (Weibull distribution) between the plots under high elephant disturbance intensity and the low and no disturbance plots (figure 3). The Weibull shape and scale are statistically different among the three forest types. High intensity plots have higher median DBH (higher scale) and a lower proportion of small trees compared to large trees (smaller shape). The difference is more subtle between the plots with no elephants and the ones under low disturbance. The plots with no elephant disturbance have the highest number of trees smaller than 15 cm DBH and as disturbance increases so does the frequency of trees larger than 40 cm DBH. A similar pattern is observed in the number of stems >10 cm and basal area (table 4).

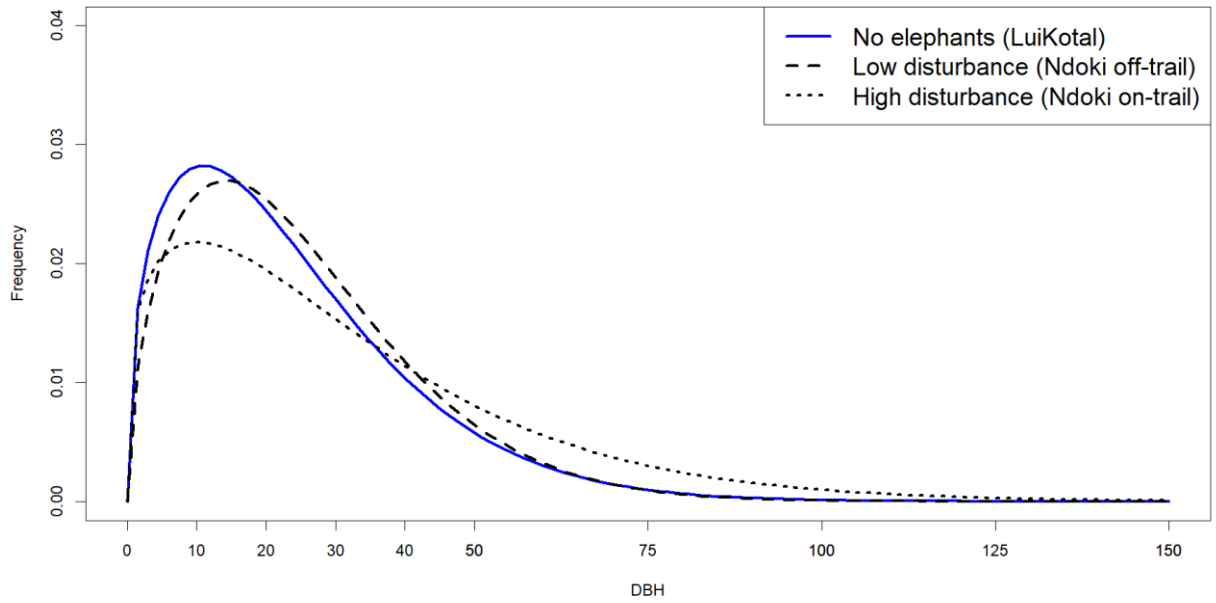

Figure 3. Weibull distribution of forests under different elephant disturbance intensities. Note that the function is fitted with data starting from 10cm DBH.

Data source	Stems/ha	Mean tree size (m^2)	Basal area (m^2/ha)	AGB (Mg/ha)	Shape	Scale
Model	411 (11)	0.088	36 (0.5)	388 (7)	1.71 (0.02)	31.46 (0.59)
No elephants (LuiKotale)	438 (52)	0.075	33 (7)	432 (122)	1.41 (0.01)	26.09 (0.24)
Low disturbance (Ndoki off-trail)	335	0.075	25	370*	1.54 (0.03)	27.85 (0.69)
High disturbance (Ndoki on-trail)	399	0.148	59	1015*	1.26 (0.02)	33.87 (0.93)
Central Africa (Lewis et. al 2013)	425	0.074	31.5	429		

Table 4. Stems per hectare, mean tree size, basal area, AGB, Weibull shape and scale. Standard deviation across years or plots is indicated within parentheses. Model results are from the average of the last 50 years of the spin up simulation. Mean tree size refers to the stem size. LuiKotale average is calculated across 15 1-ha plots. Ndoki plots, 200 m² each, have been aggregated and standard deviation could not be calculated. * Calculate considering a mean density of 0.65 provided by Lewis et. al 2013 and height allometry for Central Africa by (Feldpausch et al., 2011).

The model output compared reasonably well to the LuiKotale data in terms of stems/ha, basal area, and AGB (table 3). There are differences in the distribution of size classes (figure 4) with the simulated forest having a higher frequency of trees between 20 cm and 75 cm and less trees in the smaller size classes. It should be noted that the forest inventory is only a snapshot in time of a small fraction of the landscape while the model simulates transient vegetation and presents an average over a large area. The functional composition has a good mix of early, mid, and late successional, with late and early successional occupying a similar basal area (see figures 5 and 6). NPP is ~33 Mg/ha per year also compares reasonably well with recent field measurement in tropical Africa of roughly 30 Mg/ha per year (Moore et. al 2017).

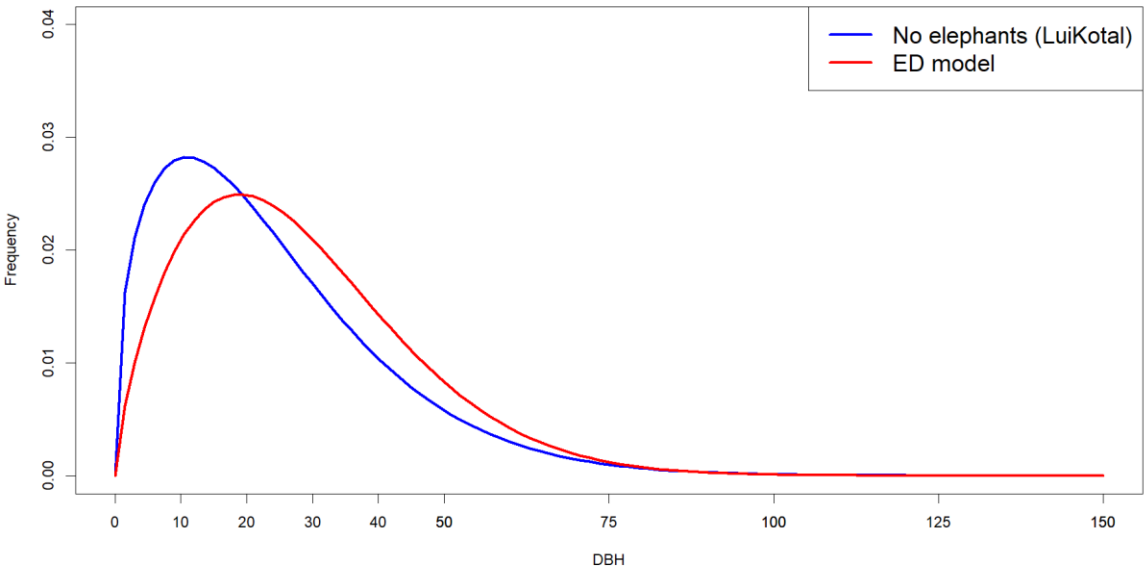

Figure 4. Weibull distribution of forest simulated by ED2 and LuiKotale forest.

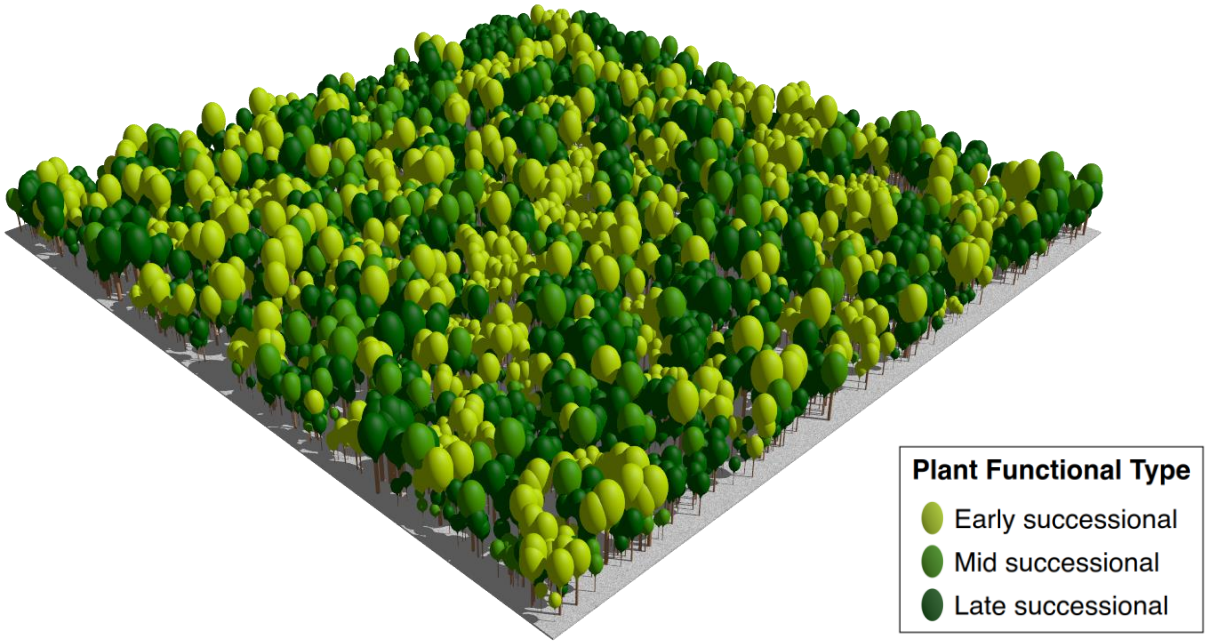

Figure 5. Three dimensional representation of functional composition after 500 years spin-up period at LuiKotale.

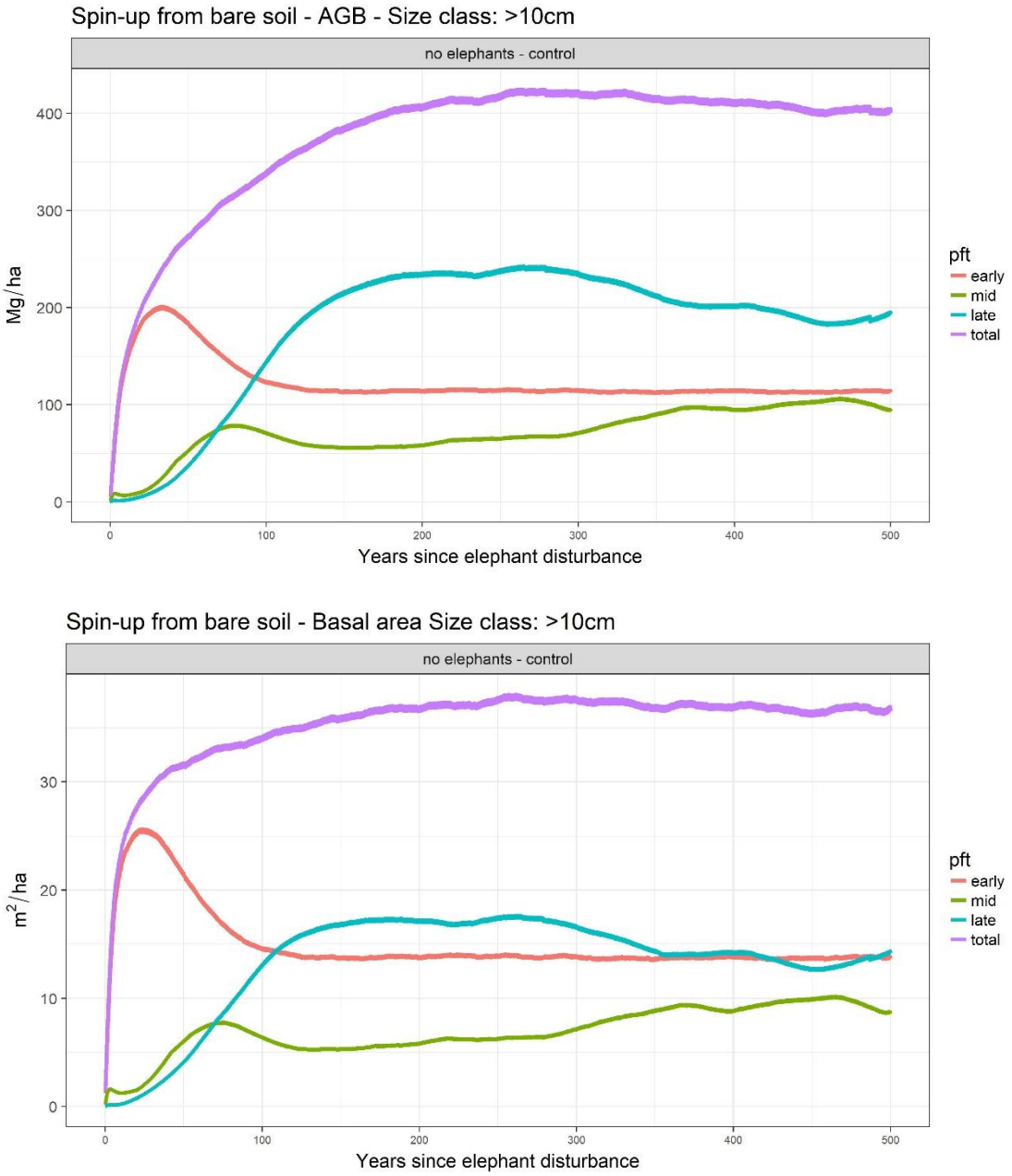

Figure 6. AGB and BA during the 500 years spin-up period at LuiKotale.

Model results from the elephant density scenarios

Local medium-term effects after elephant introduction (0-250 years)

Two separate trends can be observed in terms of AGB (figure 7). At densities 0.25-2 a small initial decline is followed by an increase (~1 Mg/ha/year) leading to a rather stable state with AGB higher than control. AGB gains are between 10%-38% (39-146 Mg/ha) with the highest gains at intermediate densities 0.5-1. At densities 3-5 a sharp decline (~2.5 Mg/ha/year) is followed by a highly variable state where AGB is between -3% and -29% (13-113 Mg/ha) lower than control. BA declines initially at all densities, but while at densities 0.25-1 it returns to levels pre-disturbance, at high densities 2-5 BA is reduced up to ~40% (20 m^2/ha) compared to the control (36 m^2/ha). In terms of functional composition, the disturbance causes a heavy loss of early successional PFT and an increase in late and mid successionals (figure 8). At very high densities 4&5 mid successionals start to decline but only after 150-200 years. Mean tree size increases (figure 9) which along a mostly steady BA indicates a change in structure with less stems/ha but of larger size compared to the control.

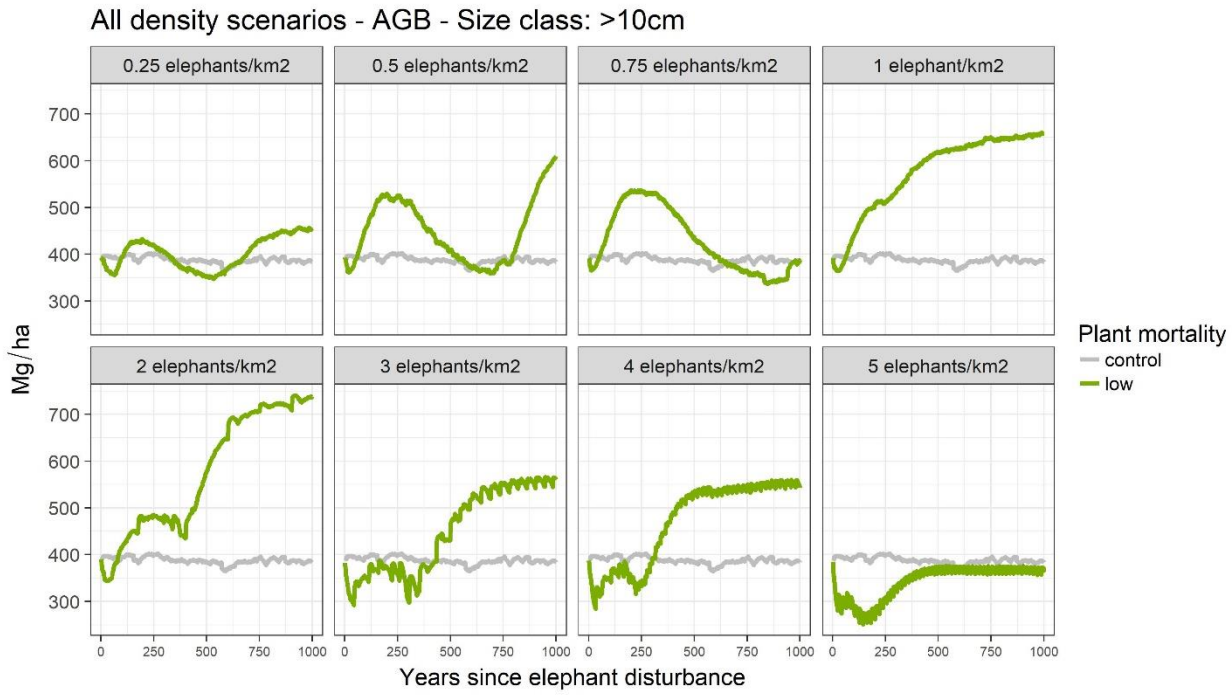

Figure 7. Aboveground biomass of trees >10 cm DBH in low elephant density simulations until 1000 years post elephant introduction.

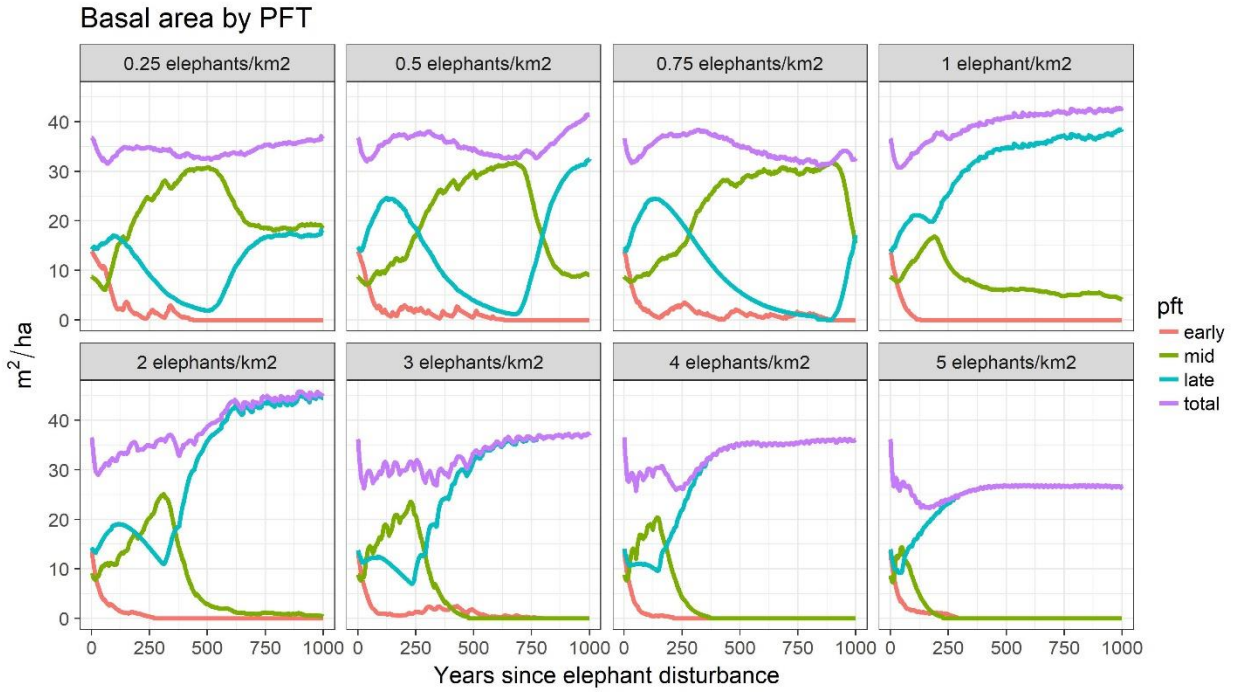

Figure 8. Basal area by PFT and total for trees >10 cm DBH in low elephant density simulations from 0 until 1000 years post elephant introduction.

Long-term effects after elephant introduction (250-1000 years)

At all elephant densities, aside from 5 and 0.75, this type of continuous disturbance leads to an equilibrium forest with higher AGB compared to control. The higher the elephant density the shorter time it takes to reach equilibrium but the trajectory can be oscillatory (densities 0.25-0.75) or more direct (1-5) (figure 7). At lower densities 0.5-0.75 there is still not a clear equilibrium, but the trajectories of BA functional composition show a trend towards a forest dominated by late successional, like most of the other simulations. Thus, functional diversity is lost only after 500 years at high elephant densities (3-5), while at the other densities mid and late successional PFTs, and in some cases early successionals, persist even after 1000 years. The oscillations between high and low AGB states are due to competition between mid and late successionals and AGB always increases faster (~1 Mg/ha) than it declines (~0.4 Mg/ha). Only at the highest density the equilibrium AGB is lower than control, although only by 1-2%.

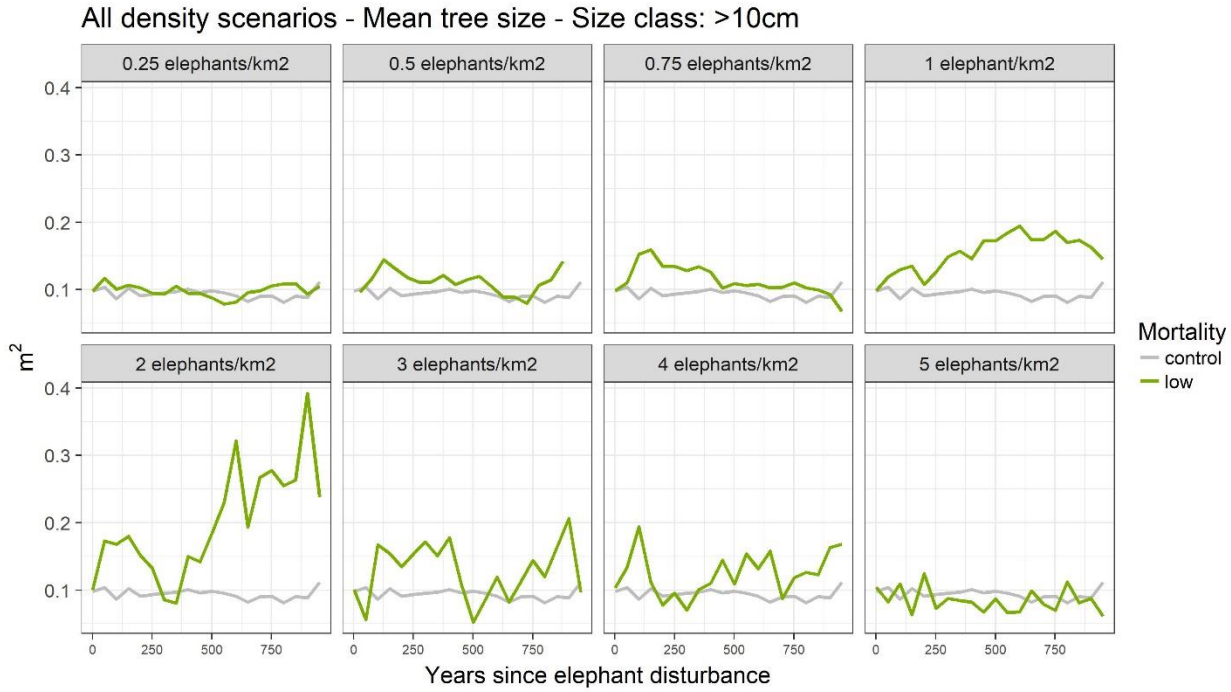

Figure 9. Mean tree size of trees >10 cm DBH for all elephant densities scenarios. The jitter is due to the division in size classes and only one value being plotted every 50 years to increase readability.

Elephant density (individuals/km^2)	AGB (Mg/ha)	% change in AGB from control	Functional diversity (order of dominance)	Years to equilibrium/ peak
0	388 (7)	-	late, early, mid	300*
0.25	450 (4)	+19	late=mid	800
0.5	600 (6)	+54	late, mid	1000 [(a)]
0.75	**532 (2) / 343 (3)**	**+37 / -12**	**late=mid, early (low)**	**200 / 830**
1	650 (8)	+67	late, mid	770
2	730 (4)	+88	late, mid (low)	930
3	550 (20)	+41	late	800
4	550 (6)	+41	late	600
5.3	360 (10)	- 5	late	500

Table 5. Summary of results for density scenarios with AGB at equilibrium or at low and high peaks of temporary stability. Standard deviation across years is indicated within parentheses. Functional diversity is reported at end of simulation. * Spin-up from bare ground. (a) Might be approaching equilibrium

Plant productivity, macro and micro processes driven by elephant disturbance

NPP is lower in elephant disturbed forests and is negatively correlated with AGB. Much of this is related to the functional composition of disturbed forests because they have a higher density of late successional cohorts that are less productive than early and mid successional (figure 10). However, late successional have higher wood density and lower mortality and even though their annual NPP is lower, over time the standing biomass of disturbed forests increases and in certain cases remains higher than the control. It is interesting to note that in elephant disturbed forests per plant annual NPP is overall lower than in the control with the exception of very large (>50 cm DBH) late successional trees (figure 11). These large trees in some cases can produce up to 100-110 Kg of carbon per year compared to 60-70 Kg in forest non-disturbed by elephants.

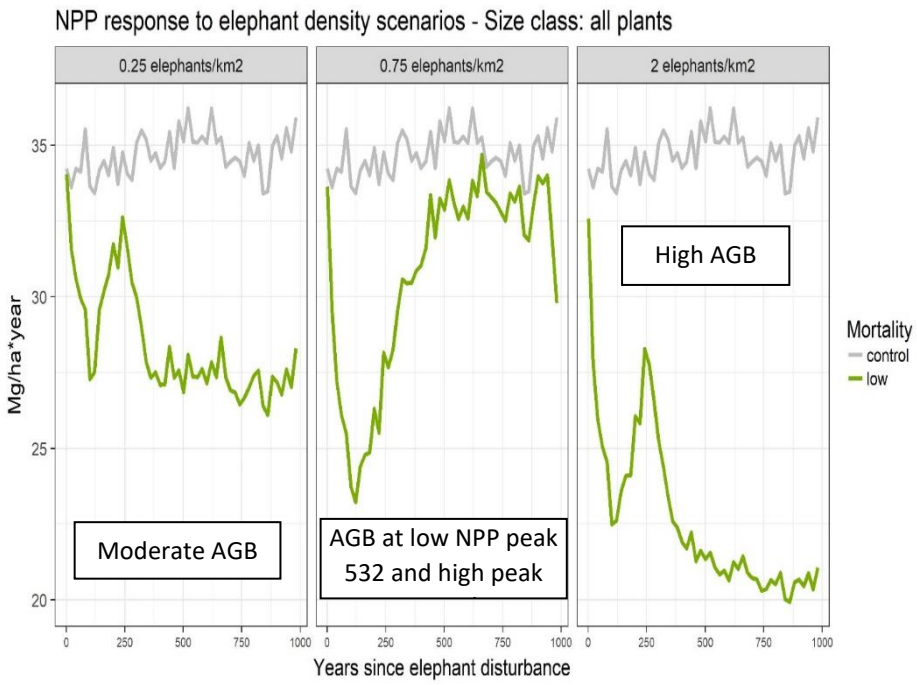

Figure 10. Typical response of NPP in three elephant density scenarios. The 0.25 scenario are is mostly dominated by late successional but still has some early successional. The 0.75 scenario has a mix of mid and late successional. The 2 scenarios has a complete dominance of late successional.

Figure 11. Typical response of NPP per plant in three elephant density scenarios. The scenarios are the same as described in figure 10.

Competition for light and water is also modified as the mortality in the lower class sizes (1-30 cm DBH) changes plant density and the microenvironment. These changes increase or decrease competition for resources among and between class sizes. Similar effects are observed across all densities scenarios. Leaf area index (LAI) increases in the 50+ cm DBH size class and the result is less light reaching the lower size classes (figure 12 and 13).

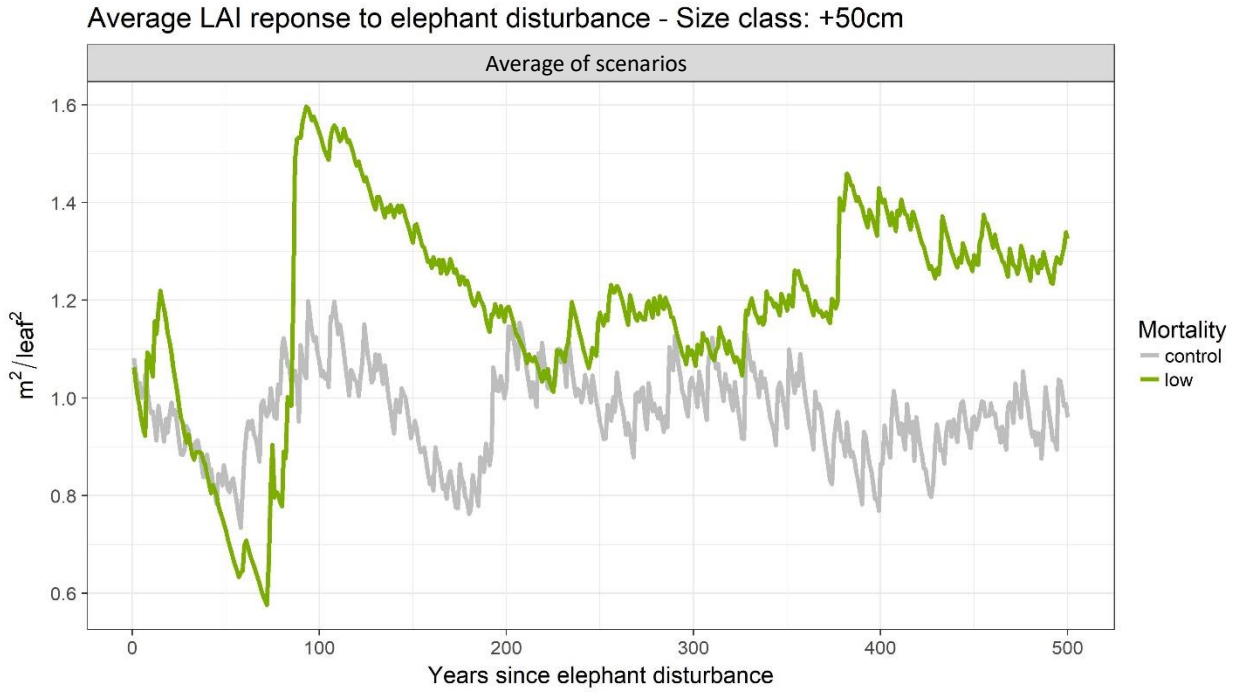

Figure 12. Average LAI across all densities for trees with DBH >50 cm.

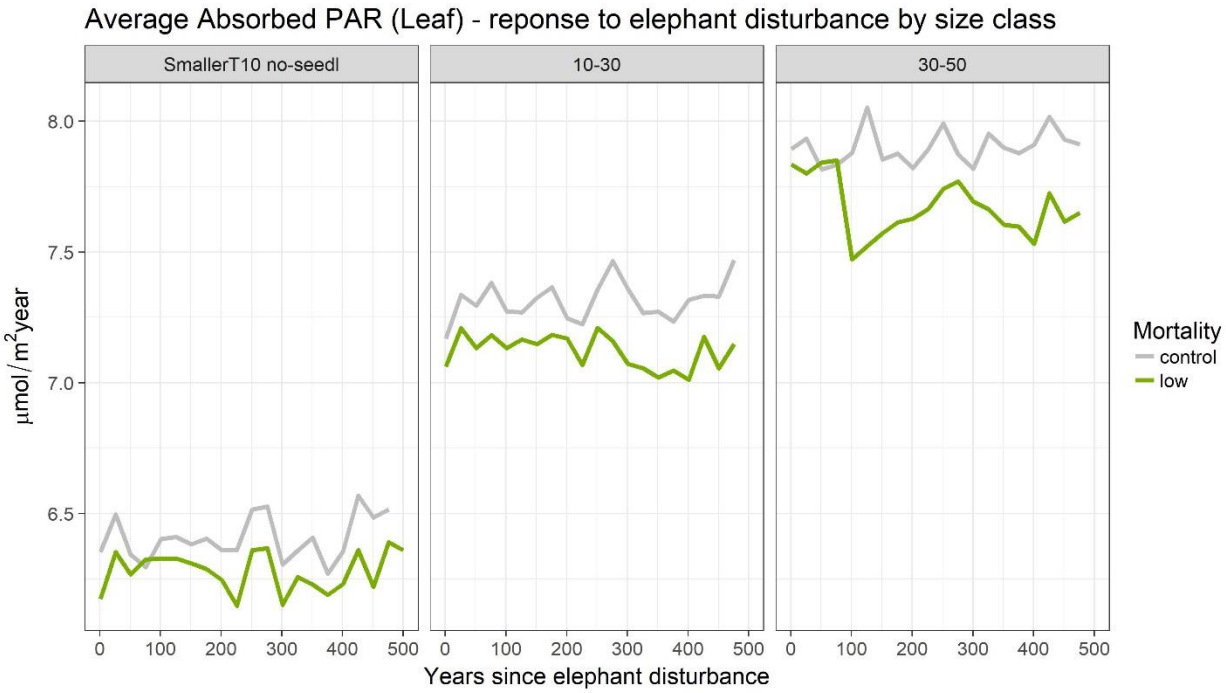

Figure 13. Average absorbed PAR (log scale) in different size classes.

Water availability also changes in elephant disturbed forests compared to the control. Seedling (<0.5 m height) are subject to higher water stress even though they are less abundant, and water stress of trees >10 cm is lower (2-4%) (figure 14).

Overall, these conditions create a more hostile understory microenvironment favoring shade-tolerant late successional cohorts that can survive longer periods of negative carbon balance. Seed production is also affected, in ED2 cohorts start producing seeds once they reach a height of 18m (~27cm DBH) and the thinning effect of elephants reduces gradually the number of mature trees. Hence, the higher mortality of mature early and mid successional cohorts compared to late successional cohorts changes the proportion of seed biomass among functional types (figure 15). Water stress and light availability differences are small between control and disturbed forests, within a few point % a year. Conversely, the reduction in seed biomass is more significant and decreases from ~1.5 kgC/m^2*year to 1-0.5 kgC/m^2*year in the first 15-25 years. A significant change considering that the external seed rain, the seed immigration from outside the simulated area, is 0.01 kgC/m^2*year.

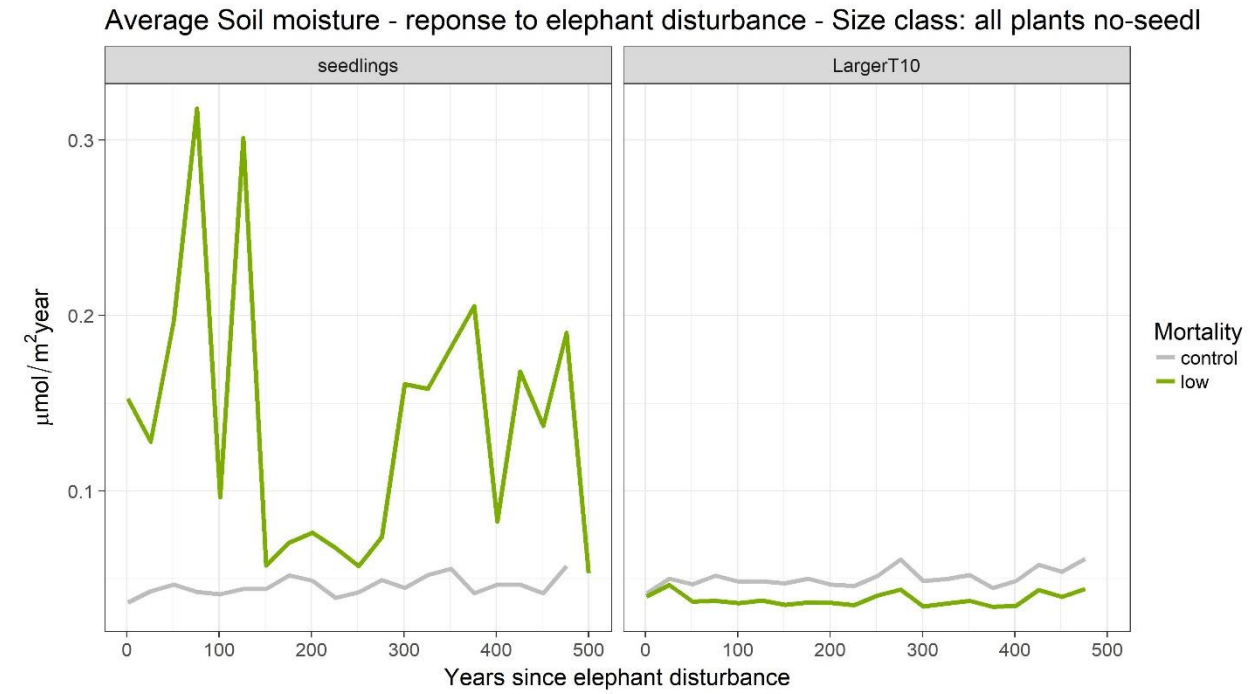

Figure 14. Soil moisture stress factor for different size classes. Seedlings are all plants shorter than 0.5m .Soil moisture stress factor goes from 0 to 1. Higher values indicate higher stress. Jittering in the seedlings plot is due to the high number of plants recruited each year and by the division in size classes.

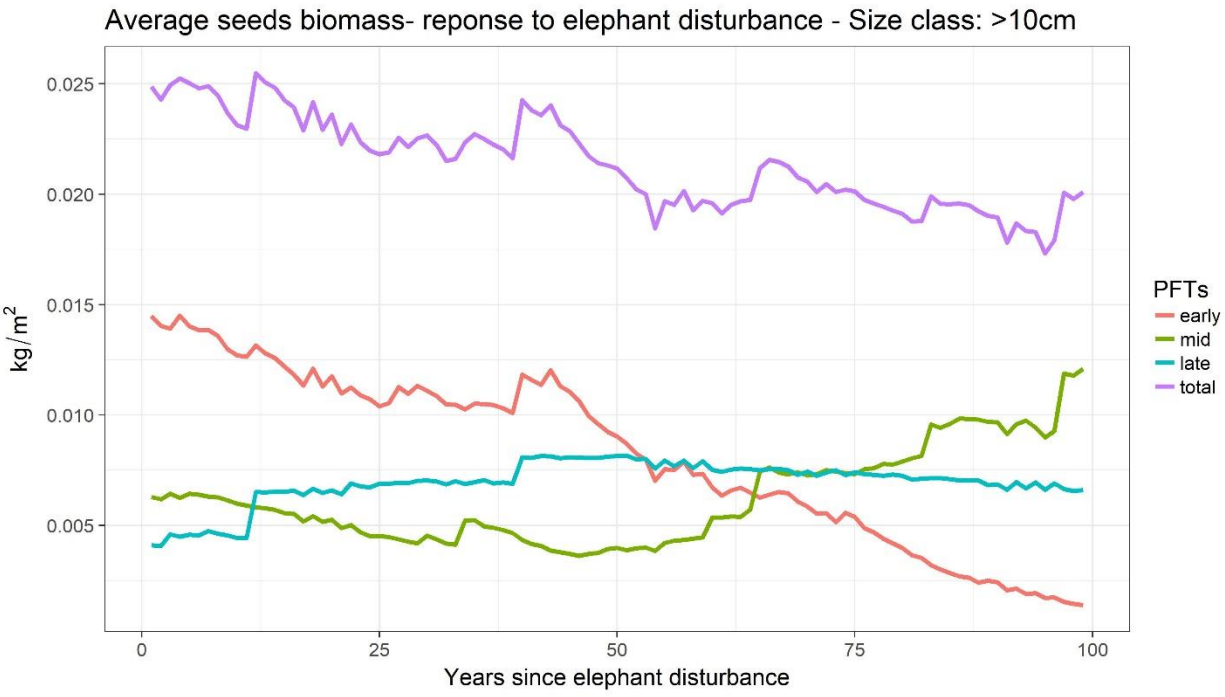

Figure 15. Average seed biomass per PFT in the first 100 years post disturbance. The average is representative of the average response across all density scenarios.

Global effect on Central African forests

The presence of forest elephants across their potential range has large impacts on Central Africa carbon stocks (figure 4). Elephant range reduction leads to heavy carbon losses, ranging from 0.91 Pg of C (s.d. 0.11) up to 1.98 Pg (+/- 0.24) considering a potential range of 2,200,000 km² and a density 0.5/km². The current losses are also high 1.89 Pg of C (+/- 0.24) because both range (24%) and density (0.25/km^2) have decreased. Elephant introduction would have the opposite effect. The rate of change depends on different factors: the forest state, tree mortality, elephant density at introduction/extinction, and range. In elephant disturbed areas carbon gains are faster (~1 Mg/ha) than losses (~0.5 Mg/ha) because the disturbance rate of elephants is higher and more pervasive than treefall.

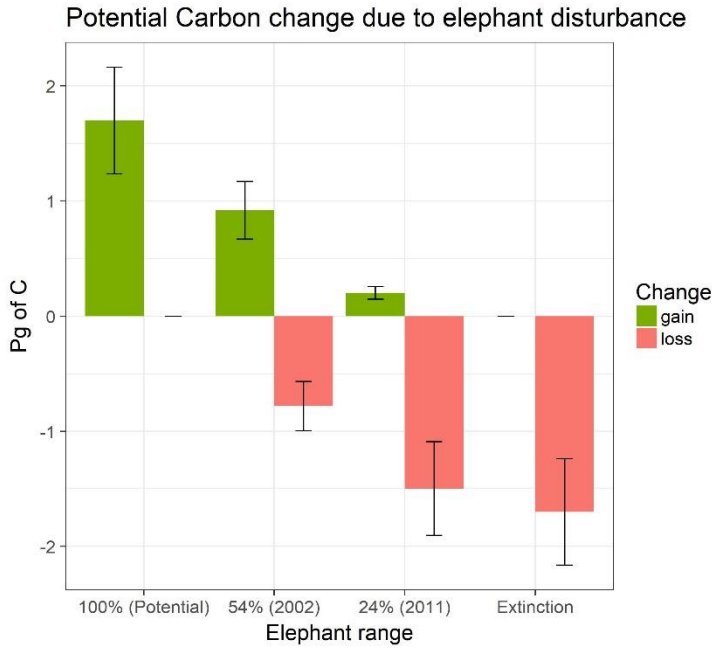

Figure 16. Changes in above ground carbon stocks due to elephant presence (gain) or absence (loss). Ranges 100% and 54% are calculated with a density of 0.5, 24% is calculated with a density of 0.25 (Maisels et al., 2013).

Sensitivity analysis

The sensitivity analysis reveals that the model sensitivity to changes in small trees mortality varies based on the elephant density scenarios. Higher mortality rates can affect the path to equilibrium, the magnitude of changes in forest properties, and the system state (at equilibrium or oscillating). Overall, the differences affect mostly long-term trends and start to appear only after 150 to 300 years, which indicates that long-term projections results are more sensitive to different mortality rates than medium-term results (figure 17).

Low density scenarios: At the two lowest densities (0.25 and 0.5) the effect on AGB is mostly on the path taken but the results are similar, with the exception of the intermediate mortality rate at density 0.25 leading to lower AGB. At densities of 0.75 and 1, the trend in higher mortality simulations is towards a state of higher AGB than the low mortality. This is similar to what is observed in higher density simulations that reach equilibrium. The difference is that, at low densities, the increase in AGB is slower. Also, at higher mortality rates mid successional are more penalized compared to low mortality simulation. The difference between low mortality and medium-high is significant in the long-term.

High density scenarios: Parameter-wise, as the elephant density increases along with the disturbed area, the differences in *sst* become smaller. The results of this can be observed in how the low and medium mortality simulations tend to have increasingly similar trajectories as density increases. The response to high mortality is markedly different with a peak and a decline in AGB. At density 5 high mortality dampens and delays AGB growth. At density 3, the effect of higher mortalities is minimal within the first 500 years.

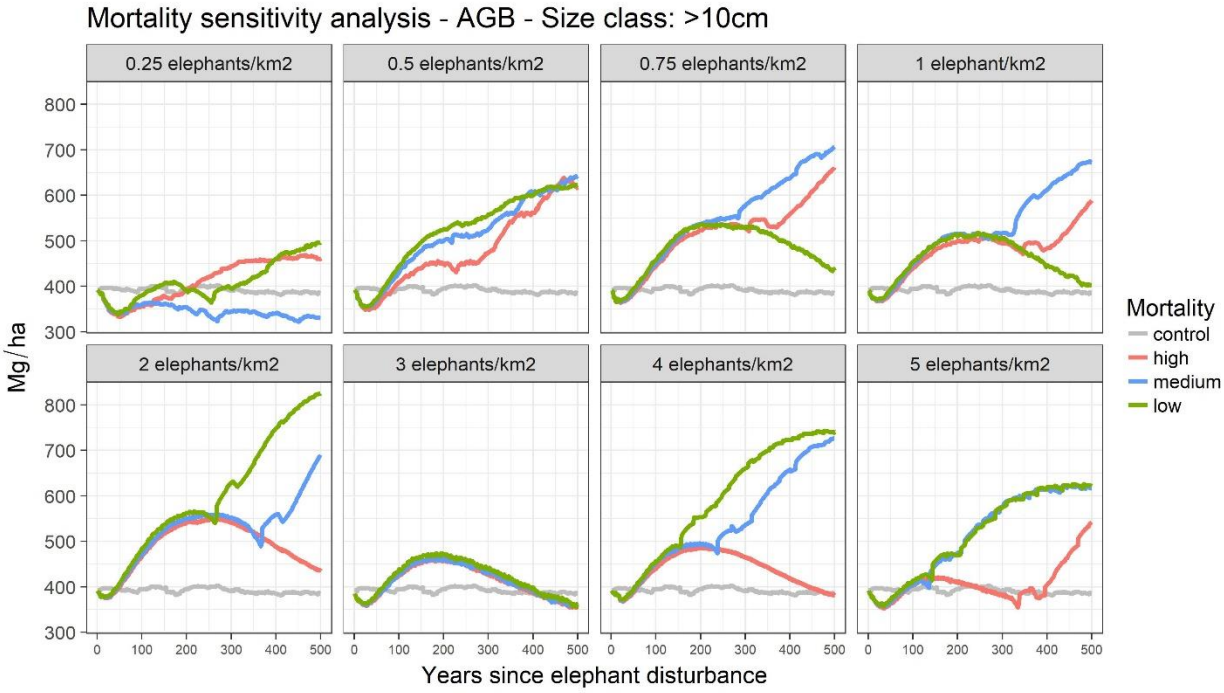

Figure 17. AGB of trees >10 cm DBH for all density scenarios, until 500 post elephant disturbance introduction.

3.2.5 Discussion

The simulation results show that elephant disturbance, even at the lowest density, has a significant influence on forest structure and function. In 7 out of 8 simulations, the hypothesis is confirmed that elephant disturbance might shift forest structure to a forest dominated by a higher number of large trees and less small trees. The hypothesis that this effect might also lead to a forest with a higher carbon content was also confirmed in 6 out of 8 eight scenarios. In some cases, and particularly in the first phase after elephant disturbance was applied, AGB decreased because elephant increased the turnover rate of smaller trees. The hypothesis that, by clearing the understory, elephants would reduce competition among plants and increase plant productivity was only partially confirmed. Instead, I have found a more nuanced mechanism. Clearing the understory filters the number of plants reaching size classes above 30cm DBH and it allows trees >50 cm DBH to become more dominant. These very large trees reduce the available light for the lower size classes, and increase water stress of seedlings. These conditions shift the functional composition to a forest dominated by shade-tolerant, slow growing species. Even though per plant NPP is overall lower, over time very large late successional trees become more productive and dominant taking advantage also of their lower mortality rate. The dominance of these late successional large trees is driven by several processes that are triggered and maintained by the disturbance of elephants. The analysis of the forest inventory data, even though limited to a small area, seem to suggest a similar conclusion. However, field data do not provide any insight on the processes that might be at the root of the observed differences in structure.

The results of the thinning performed by elephants is in line with what has been described in ecological theory has the self-thinning rule, which relates an increase in biomass to a decrease in plant density (Westoby, 1984). Thinning is also a practice used in tropical forest plantations which can lead to much higher annual AGB accumulation rates (6-15 Mg/ha, (Lugo et al., 1988)) compared to what can be observed in my simulations (~1 Mg/ha). For example, a plantation of *Terminalia ivorensis*, a fast-growing pioneer species, when thinned to a density of 192 stems/ha produced 7.9 Mg/ha (Norgrove and Hauser, 2002). This plantation was in Cameroon with similar precipitation averages to the simulated forest. Even though forest plantations are young productive forests of fast growing species and under intense thinning, the structural modification is similar to the one performed by elephants, whereas disturbance by treefall has the opposite effect. Treefall creates forest gaps that promote the recruitment of

light-demanding species that on average have lower wood density, in the end reducing AGB (Ferry et al., 2010). Thus, megafauna disturbance might cause an increase in carbon stocks and a change in plant density. This process might partly contribute to the reported differences between African tropical forests and other tropical forests, in particular Amazonian (Lewis et al., 2013; Terborgh et al., 2016b). The time scale of changes associated to this disturbance should also be considered because the effects can be more subtle compared to forest thinning and less destructive than treefall but more ubiquitous. Short-term (10-30 years) and year-to-year variations are small and difficult to detect at the landscape level because initially only small trees are affected. In the medium-term (50-150) the effects become evident, however there are also transitions between high and low AGB states depending on the extent and intensity of the disturbance. The long-term trends (250-500) are more difficult to evaluate because there is an increased uncertainty with long-term projections and other factors can influence the magnitude and direction of change (elephant population dynamics, human disturbance, environmental conditions). Further, the modeling approach has its limitations. I had to make some assumptions and simplifications on the ecology and the effects of elephants in closed-canopy forests because the literature on the subject is very limited. In fact, I found that most of the reported results cannot be used to parametrize elephant disturbance in a vegetation model. Data are very scarce to parametrize this process and limit our ability to better characterize and describe elephant disturbance in a model. Additionally, my study only addresses the effect of elephants in closed canopy forests. However, elephants interact with plants and the environment through other processes and in other habitats. For example, forest elephants play an important role as seed dispersers which might lead to changes in future plant species compositions (Blake et al., 2009), although the importance of seed dispersal might be site dependent (Campos-Arceiz and Blake, 2011; Hawthorne and Parren, 2000). Another important and poorly known process is the transport of nutrients through consumption and defecation of high quantities of biomass which might affect plants primary productivity (Doughty et al., 2015). Lastly, while there are some indications on habitat preferences and movement of forest elephants (Blake, 2003; Blake and Inkamba-Nkulu, 2004; Schuttler et al., 2012; Wing and Buss, 1970), little is known about their behavior and movements in closed forests (Blake, 2003; Terborgh et al., 2016a). Due to the lack of this information, and partly because ED2 is not spatially explicit, I had to assume that the intensity of elephant disturbance is homogeneous within the area utilized by elephants. I partly accounted for this but more information on the frequency and area disturbed is needed. In reality, elephants move through the forest along trails and go off trail to feed on herbaceous vegetation, bark, and fruits. Instead

of being homogeneous, the highest disturbance intensity is on and near the trail and tapers off away from it (Inogwabini et al., 2013). Perhaps the on-trail forest data from Ndoki represent a very high intensity of elephant disturbance, because these are areas of more frequent elephant passage.

3.5.6 Conclusions

The role of megafauna in terrestrial ecosystems is becoming more evident but their influence on many ecological processes is still unknown (Malhi et al., 2016). Forest elephants are one of the last remaining megafauna species but they are threatened by poaching and habitat loss. Vegetation disturbance in closed canopy forests is an important ecosystem-engineering activity performed by forest elephants but it is difficult to study in the field. Lately, the long-term effects of this activity has been proposed as one of the drivers of the higher AGB and particular structure found in Central African forests (Lewis et al., 2013; Terborgh et al., 2016b). However, the processes that might be responsible for these differences are highly debated. This study is the first attempt to use a vegetation model to simulate the disturbance effect of forest elephants in Congo Basin closed-canopy forests. I provided the first estimates of the effects of elephant disturbance on forest structure and functional composition over different time scales and at various elephant densities. In addition, I described the eco-environmental mechanisms triggered by elephants that might be responsible for the observed changes in forest structure and carbon stocks. I also included in my analysis forest inventory data from sites subject to different intensities of elephant disturbance. Both the simulation results and the field data suggest that the thinning operated by forest elephants could in most cases increase AGB, and at very high densities reduce plant functional diversity. The magnitude and rate of change of forest properties in elephant disturbed forest depend on the intensity of disturbance and the density of elephants. At the most commonly observed elephant densities (0.5-1 elephants/km^2) this type of disturbance has a clear influence on forest dynamics and function. However, as the year-to-year changes can be subtle and the timescale leading to significant changes is long, it might be difficult to detect such effect during short-term field studies. In this regard, this study was useful to better define data gaps and to pinpoint processes and forest properties that require further investigation. Field measurements or remote sensing products could help verify the effect of megafauna on tropical forests. To improve model accuracy we would require fieldwork monitoring elephant activities and plant mortality before and after elephant visitation at regular intervals. Furthermore, LIDAR might allow to measure forest properties (i.e.,

functional diversity and structure) at large scales in areas with different elephant densities or to estimate the total area disturbed by elephants during a given period. Since many areas are now devoid of forest elephants, monitoring changes in the understory could help verify if after elephant disturbance ceases we observe the reverse process described in this study. However, in areas where forest elephants are missing there are often other types of disturbances (i.e., logging and forest degradation). Modeling and field studies are also needed on the distribution of nutrients by elephants, a process that has not been investigated. For future modeling improvements, better data are needed in regards to the mortality of plants caused by elephants, and more estimates of the correlation between area disturbed and elephant density. Even with the limitations of the ED2 model (i.e., AGB overestimation, extinction of early successional and over dominance of late successional), the relative differences between the control simulation and the elephant scenarios are showing that elephant disturbance can have a large effect in the medium to long term. These results have implications for forest elephant conservation and for forest management. It appears that the forest elephant, and other megafauna in tropical forests, could play an important role in maintaining or increasing carbon stocks in tropical forests. Furthermore, even at very high densities, forest elephants do not seem to threaten a transition from closed canopy forests into a more open woodland, and could perhaps be useful in forestry as a natural thinning agent. Thus, even if at the moment a population rebound is unlikely (Turkalo et al., 2017), an increase in the current forest elephant populations does not seem to be as problematic as it has been with savanna elephant populations kept in restricted areas (Scheiter and Higgins, 2012). The effect of loss of functional diversity should be further evaluated in the field and in the ED2 model, where the lack of a mechanistic seed dispersal processes and a limited seed immigration rate might cause the demise of early successional in the high density scenarios. In particular, the high-density scenarios should be interpreted with caution, as well as the long-term projections. As any modeling exercise, the results are tied to the choice of parameters that are chosen based on the available data. The lack of data on the effects of forest elephants underlines the limited knowledge we have on this species and the many ecosystem-engineering processes it performs. This study provides new evidence that the role of megafauna in terrestrial ecosystems can have wide-reaching influences. The results indicate that at commonly observed elephant densities (0.5-1/km^2) this disturbance has a clear influence on forest dynamics and function and across Central Africa can account for ~2 Pg of C, roughly 4% of C in African tropical forest (Lewis et al., 2009). The collapse of elephant populations could reduce Central African carbon stocks by 1.89 Pg of C (+/- 0.24), almost as much as the combined loss of carbon in tropical America

and Africa due to defaunation (Osuri et al., 2016). The economic cost would be US$ 9.5 billion at a carbon stock price of US$ 5/Mg C. It should also be considered that the area disturbed by elephants and their density were chosen conservatively. Higher carbon and economic impacts would increase if any of these parameters would be higher. If megafauna can modify tropical forests carbon cycling, one of the largest world carbon sinks, then indirectly megafauna might also influence climate, which is a significant implication also in terms of carbon stock and climate policy. In this perspective, the value of the ecosystem services provided by the forest elephant and the other megafauna should be evaluated carefully by local and international policy makers and conservation managers.

Acknowledgments

I would like to thank Stephen Blake, Francoise Bretagnolle, and David Beaune for sharing their forest inventory data. Thanks to Marcos Scaranello for the statistics and to Christopher Doughty for the initial ideas that generated this study. Thanks to Marcos Longo for the support with the model. Thanks to Simone Vieira for hosting me in her lab. Also thanks to my internal PhD committee for the feedback on my initial results that helped improve the study. Thanks to the Centre de Calcul et Messageries, Pôle des Systèmes d'Information et des Usages du Numérique Université de Bourgogne for the use of their cluster.

3.2.7 References

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4 Conclusions and future perspectives

In the first part of this dissertation I highlighted the research gaps concerning the ecology of tropical megafauna and detailed all plant-megafauna and environment-megafauna interactions that have been reported in the literature. An outstanding majority of studies has focused on seed dispersal and consequently there is very limited knowledge on all other types of interactions. It is surprising that very little is known on the effects of herbivory and nutrient distribution considering that megafauna consume large quantities of biomass and as a result relocate high amounts of nutrients across the landscape. Additionally, I have found that the vast majority of the current knowledge of tropical megafauna ecology is based on short-term field studies. While these studies provide excellent information on fine scale processes, they fall short of giving insights on the influence of megafauna on tropical ecosystems over large-scales and long periods. To overcome some of the current limitations, the first major contribution of my thesis is the development of methodologies to implement plant-animal interactions in vegetation models. The approach I have proposed allows the integration in vegetation models of information on fine-scale processes gathered in field studies. With the implementation of animal processes, vegetation models would allow to evaluate the role of megafauna at large spatio-temporal scales. Even though the examples I provide are on tropical megafauna, these methodologies are broadly applicable to many ecosystems and animal-plant interactions, and are not specific to any vegetation model. As the role of animals in influencing ecosystems and the atmosphere is becoming more evident, these methodologies will become increasingly useful to study these feedbacks.

In the second part of this thesis I have shown how one of the methodologies I have developed can be used to further our knowledge on the role of megafauna in tropical ecosystems. In particular, I investigated the role of forest elephants in Central African tropical forests. The second major contribution of my thesis is to have shown that the disturbance by forest elephants can have important effects on the structure and function of tropical forests in the Congo Basin. Forest elephants can influence carbon cycling by changing the size class distribution of trees and the forest functional composition. I also provide the first explanation on the mechanisms driving changes in carbon cycling due to the influence of megafauna, namely the competition for resources among plants. The results have implications for the conservation of a species on the edge of extinction, for forest management, and for carbon stock policy.

The modeling approach has its limitations because it oversimplifies a very complex system. Models are limited by the data that is needed to formalize ecological processes into mathematical equations and assign values to the parameters in these equations. However, the development of models should not be hampered by the lack of data because modeling results could identify data gaps or highlight ecological mechanisms that might have been overlooked. This should be an iterative process with continuous feedbacks between ecological modeling, experimental work, and observations. Vegetation models still have intrinsic limitations such as simplification of plant biodiversity, high uncertainty to the responses of plants to carbon dioxide increase, and no plant trait variability. Aside from these limitations, there has been very little consideration for the role of animals on vegetation dynamics, from invertebrates to elephants. It is not surprising, as these models were conceived for forest ecology and climate studies. However, by not including animal processes we might be missing an important driver of ecosystem change. The effect of animals becomes more and more relevant in light of global changes in ecosystems such as invasive species (Lowe S. et al., 2000), animal extinction (Brodie et al., 2014), and climate change (Root et al., 2003). Some examples are the bark beetle invasion in Europe (R. Kirkendall and Faccoli, 2010), the disappearance of large animals in tropical forests (Laurance et al., 2012) , and the consequences of climate change on pest attacks (Rosenzweig et al., 2001). Thus, the first step for future development would be to identify animal processes with a greater potential impact on ecosystems and prioritize the implementation of those processes in vegetation models. This endeavor requires increased collaborations between zoology, botany, ecological modeling, ecosystem ecology, and environmental sciences. In regards to specific future directions for better understanding the ecology of megafauna and their influence on ecosystems, I propose to focus on the following processes: nutrient distribution, a better characterization of disturbance including herbivory, and coupling an explicit animal model with a vegetation model. Nutrient distribution by large animals has been shown to influence plant productivity (Doughty et al., 2015; Wolf et al., 2013). Hence, any modeling study addressing questions regarding the effect of nutrient distribution should consider the dynamic feedback between nutrient availability and plant productivity. Animal movement and home range should also be considered as they are an important aspect of megafauna ecology. For this reason, coupling a vegetation model with a dedicated animal model like the Madingley model might be a first approach (Harfoot et al., 2014). Also, the effect of herbivory and disturbance should be further considered, not only for terrestrial herbivores but also for canopy dwellers. The effects of disturbance also include indirect and direct modification to soil properties through compaction and changes in

vegetation cover. These changes might affect soil water hydrology, respiration and decomposition rates, temperature and optical properties. Soil processes and its characteristics are rarely studied in relation to the potential effect of large animals; in this case, experimental studies should be prioritized to gather preliminary data for future modeling work.

In conclusion, the lack of knowledge on the ecology of megafauna is worrisome considering that many megafauna populations are in rapid decline, not only in tropical forests. Furthermore, the emerging evidence on the wide reaching influence of megafauna on ecosystems urges a more thorough investigation of their ecology to evaluate their role and the possible consequences of their decline or introduction (Donlan, 2005). The latest developments in methodology and tools, in particular vegetation models and remote-sensing products, offer increased opportunities for novel approaches to study the megafauna.

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5 Acknowledgements

Sometime in 2010, after some soul searching, I decided to change my life and switch career from computer science to ecology. It followed a long meandering journey and for this reason the list of acknowledgments is just as long as the years it has taken and the places I have been to reach this point. I will try to remember all the key people that have guided or helped me through this journey. I will try to do so in their native language, because if there is one thing that people appreciate is trying to speak their language (sorry I have not managed to learn Dutch or German yet).

Vorrei ringraziare la mia famiglia e i miei amici per avermi seguito in questo tortuoso percorso del dottorato, e in particolare vorrei ringraziare mia madre, grazie per i manicaretti! Merci Elsa pour ton soutien et la patience!

Grazie ai prof. Scarascia-Mugnozza e prof. Marchetti per avermi permesso di sviluppare il mio progetto di dottorato, mi ritengo fortunato per aver avuto questa opportunità. Grazie ai miei colleghi di Viterbo: Daniela, Guido, Dario L., Claudia, Diego, Giacomo, Domenico, e Andrea, per avermi fatto sentire a mio agio e soprattutto per gli aiuti fuori dal lavoro. Un ringraziamento in particolare a Simone e Carlo che in più di un'occasione mi hanno tolto le castagne dal fuoco, e non so come avrei fatto senza di voi! Grazie a Carlo, Alessio, e Manfredo per le chiacchierate sui modelli e l'ecologia. Grazie ai membri della mia commissione interna, i prof. Dario Papale, Marzio Zapparoli, e Luigi Portoghesi. In particolare Dario che mi ha sempre dedicato tempo pur senza nessuna obbligazione (aspetto con impazienza quell'accessorio dell'elefante!). Grazie al prof. Mauro Moresi per avermi guidato tra i meandri burocratici e per essersi fatto piacere gli elefanti nonostante i dubbi iniziali, ha visto prof. che in qualche modo ce l'ho fatta!? Grazie a Daniele Melaragni per la pazienza con i miei rimborsi spese machiavellici! E grazie all' Ufficio Mobilità e Cooperazione Internazionale per avere finanziato il mio soggiorno in Brasile.

Thanks to all my scientific collaborators who have helped me in different ways: Hans Verbeeck, Chris Doughty, Martin Nielsen, and Stephen Blake. Thanks to Hans for the hospitality in Gent and at the conference in Montpellier and for the time he has dedicated to me. Thanks to Chris for inviting me to Oxford and for all our interesting science discussions. Thanks to Martin for hosting me at DTU. Thank you Stephen for allowing me to use your precious data!

Thanks to Christopher Reyer, Giorgio Vacchiano, and the COST Association that have allowed me to join PROFOUND from which I have benefitted tremendously through conferences, task groups, and short-term scientific missions. My PhD would have not been the same without this opportunity.

Merci à Jérôme Chave et François Bretagnolle pour le temps qu'ils ont dédié à mon travail. Un remerciement particulier à François pour l'hospitalité de son appartement, pour ses conseils et pour sa gentilesse. Merci également à Isabelle pour la collaboration, pour son amitié et pour son appartement. Merci aux amis du laboratoire de Toulouse. Merci à Pierre-Michelle Forget pour notre collaboration scientifique. Merci à Julien Pergaud pour la patience avec le cluster ! Merci beaucoup à la famille Dost pour m'avoir offert un second foyer et un beau bureau avec une belle vue et une piscine!

Muito obrigado a Simone Vieira por me convidar no laboratório dele e pelo seu tempo. Graças a Marquinho e Maiza por o ajudo com a ambientação e para as aulas de português. Muito obrigado a Marcos pela hospitalidade na sua casa, o ajudo para procurar casa e a introdução a cultura e língua brasileira, e pelo suo tempo e amizade e pela assistência com o modelo EPH.

Thanks to John Bates for giving me the first opportunity for doing research in a very special institution and for the mentoring throughout my search for a PhD. Thanks to Mary Wisz for the opportunity to work with her, the mentoring, and the friendship. Thanks to Jesper Harbo Andersen for the opportunity to work with him. Muchas gracias a el prof. José Luis Rangel Salazar para la oportunidad de trabajar con el. Thanks to Kurt Leslie for being such an inspiring teacher and to be the first guidance into ecology. Thanks to Joseph Oyugi for supporting my independent study and introducing me to John. Thanks to Liliana Marin for teaching me GIS which has opened the doors of research. Thanks to Julian Kerbis for his support at the Field Museum. Thanks to my Seattle friends: Foen, Itzue, Kumar, Alex, Carolyn, and anyone else I might have forgotten. Thanks to Sam Wasser for the opportunity to see how conservation biology is done.

6 List of publications

Berzaghi, F., Verbeeck, H., Nielsen, M.R., Doughty, C. E., Bretagnolle, F., Marchetti, M., Scarascia-Mugnozza, G. (2017). Assessing the role of megafauna in tropical forest ecosystems and biogeochemical cycles - the potential of vegetation models. Ecography. Accepted (pending revision)