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Defaunation impacts on seed survival and its effect on the biomass of future tropical forests

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Abstract

Large animal species, which provide important ecological functions such as dispersal of seeds or top–down control of seed predators, are very vulnerable in fragmented forests, being unable to survive in small fragments, and facing increasing hunting pressure. The loss of large animals affects two main ecological processes crucial for the tree reproductive cycle: seed dispersal of large seeds (e.g. provided by tapirs) and control of seed predator population (e.g. provided by large cats). The changes in both processes are expected to increase seed mortality since seeds are not dispersed away from conspecifics (causing increased pre-dispersal mortality due to negative density dependent effects) and/or face increased predation after a dispersal event (post-dispersal mortality). Although an extensive body of empirical knowledge exists on seed predation, the link between seed loss and adult tree community composition and structure is not well established, as well as the temporal scale seed changes affect adults. Using an individual-based forest model (FORMIND), we evaluate the long-term consequences of increased pre and post-dispersal seed mortality on the future forest biomass retention of a Brazilian Northeastern Atlantic forest. Our results show that forest biomass is significantly affected after 80–93% pre-dispersal loss of large seeds, or post-dispersal predation densities of 20–25 predators per parent tree. Large-seeded tree species are at increased risk of local extinction causing up to 26.2% loss of forest biomass when both pre and post-dispersal processes are combined. However, these changes can last up to 100 years after the occurrence of defaunation. In summary we conclude that large animal loss has the potential to reduce future forest biomass and tree species-richness by impacting seed survival, and should be considered in the planning of biodiversity friendly landscapes as well as in calculations of the global carbon budget.

Keywords: biomass, carbon stocks, defaunation, deforestation, forest modelling, fragmentation, plant population, community dynamics, seed dispersal, seed predation, tropical forest ecology

INTRODUCTION

Animals play a crucial role in the reproductive cycle of plants in tropical forests, as the main agents of pollination and seed dispersal (Janzen 1969, Janzen 1970). However, hunting and habitat loss due to deforestation, and the resulting ecological cascades due to changes of predator/prey abundances, are major threats to animal communities, especially to animals larger than 1 kg (Chiarello 1999). In the heavily deforested Atlantic Forest of Brazil for example, only fragments larger than 20,000 ha can sustain viable populations of large mammal species (>1kg) that are commonly abundant in undisturbed areas (Chiarello 2000). Due to plant-animal mutualisms, changes in the animal community (defaunation, i.e. population reduction and eventual local extinction) may significantly affect tree community composition and structure (Silva and Tabarelli 2000, Tabarelli et al. 2004, Bello et al. 2015, Peres et al. 2016). For example, the disappearance of large birds with large beak sizes, may result in extinction of 33.9% of Atlantic Rainforest tree species with seeds larger than 15 mm if they are not dispersed by other agents (Silva and Tabarelli 2000).

Seeds have a higher chance of surviving if they are not attacked by predators, which can occur before dispersal (i.e. pre-dispersal predation) or after (post-dispersal predation) (Forget et al. 2006). Since reproducing trees (parents) are known to attract predators (Janzen 1969, Nathan and Casagrandi 2004), poor dispersal away from conspecifics leads to reduced tree recruitment (Jordano et al. (2011), but see Peters (2003)) due to negative density dependent effects (Janzen 1970, Nathan and Casagrandi 2004, Bagchi et al. 2010). Tree species with large seeds depend on large animals for their dispersal (Moran et al. 2004), and can therefore become especially vulnerable in areas where these animals are absent (Mendes Pontes et al. 2016, Pfeifer et al. 2017). Up to 77% of undispersed seeds, or seeds which are dispersed to the vicinity of conspecifics, face high predation pressure by beetles (Fragoso 1997) and rodents (Visser et al. 2011). In areas with mammal poaching, up to 97% less seeds are dispersed and 30% to 50% more seeds were predated by beetles in comparison to protected areas (Wright et al. 2000). In addition, the extirpation of large carnivores is known to cause increases in herbivore populations (Terborgh et al. 2001), with indirect negative effects on plant reproductive tissue such as seeds (Schmitz et al. 2000). Also, seed dispersal by gut passage, a dispersal process restricted to larger animals for larger seeds, can increase seed germination rates by killing existing larvae of bruchid beetles which infested the seed in the pre-dispersal phase (Miller 1994).

Increases in seed predation can thus lead to additional seed mortality, and affect the density and composition of future germinated seedlings (Galetti et al. 2006, Vanthomme et al. 2010). Besides seed predation, lack of seed movement through dispersal can cause a shift in seedling composition simply because these propagules do not arrive in certain areas such as forest edges or isolated forest fragments (Melo et al. 2006, Costa et al. 2012). In the defaunated and fragmented landscape of Northeast Brazil for example, a shift in the assemblage of large seeded tree seedlings has been observed in small forest fragments (up to 91 ha), which contain only 2.5% of large seeded species instead of around 14% in larger forest areas (Santo-Silva et al. 2012). Large seeded seedlings are also greatly reduced in abundance, representing only 0.27% of all seedlings in edge habitats in comparison to around 8% in undisturbed areas. These findings lead us to expect that altered fragmented and overhunted landscapes, which do not support populations of large animal species are or will become impoverished in large seeded tree species (Melo et al. 2007). In addition the shift in community structure and composition, reduction in large seeded species may also change ecosystem functions. This is expected because seed size is positively correlated to maximum adult tree height and wood density. Significant relationships between seed size and maximum adult tree height and wood density have been reported across Neotropical forests (although the significance may vary for individual sites (Wright et al. 2006, Wright et al. 2010)). Therefore the impoverishment of the large seeded tree species group would negatively impact the carbon retention ability of forests, as already shown by Bello et al. (2015) and Peres et al. (2016).

However, some important points remain unknown: How much loss in seed abundance of large seeds due to increased seed predation, is needed to influence the future tree community? How will a reduction in seed abundance affect tree structure and composition? What is the time lag between seed abundance reduction and tree population change? To address these knowledge gaps forest models are a useful tool to upscale local empirical observations (Fischer et al. 2016). One of these forest models, FORMIND, has a 20 year long history of successful representation of forest dynamics (Fischer et al. 2016) also under several disturbance scenarios including logging (Huth and Ditzer 2001, Huth et al. 2004), climate change (Fischer et al. 2014, Hiltner et al. 2016), landslides (Dislich and Huth 2012), and fragmentation (Groeneveld et al. 2009, Pütz et al. 2011, Dantas de Paula et al. 2015). With regards to defaunation, two recent studies using statistical models have related defaunation to biomass loss in fragmented forests, by substituting large seeded trees for others from the community, and estimating future carbon stocks (Bello et al. 2015, Peres et al. 2016). In contrast, by using individual based forest models such as FORMIND, it becomes possible to generate projections of forest states emerging from the influence of increased seed predation on various ecological processes, also considering large time scales.

Here we simulated the effects of increased seed predation scenarios, considering levels typically found in defaunated forests to answer the question: How does increased pre- and post- dispersal seed mortality of large seeded tree species affect the forest biomass and functional composition of future defaunated forests?

We investigate this question by parameterizing the individual-based forest model FORMIND using field data from a large undisturbed area, and by simulating changes in pre- and post- dispersal seed mortality due to predation.

2. MATERIALS AND METHODS

2.1 Modelled tree growth and reproduction

FORMIND is an individual- and process-based forest model that simulates the growth of single trees based on an individual tree carbon balance (Fischer et al. 2016). Trees are described based on their stem diameter (DBH) using allometric equations to determine tree height, crown size, leaf area index and tree biomass. Forest dynamics emerge from basic processes, such as light competition, seed dispersal, establishment of tree seedlings and tree mortality. Tree species are classified into plant functional types (PFTs), according to life history characteristics. In FORMIND, the simulation area is divided into 20 m x 20 m plots (i.e. 1 ha simulation area is composed of 25 plots) in which trees interact – the only between-plot processes are seed dispersal and falling tree damage. Environmental conditions such as light environment, temperature and disturbances influence individual tree growth and survival (Köhler and Huth 1998).

For the simulations carried out in this work, the local seed dispersal module was used in FORMIND (in contrast to the global seed rain module in which a constant seed number is updated every time step). In the local seed rain module, seeds are dispersed from parent trees, defined as trees larger than a diameter threshold. This threshold was defined and averaged for each PFT (Table A1) according to species-specific maturity thresholds in which 60% of all individuals are parent trees (Muller-Landau et al. 2002, Wright et al. 2005). Parent trees disperse individual seeds using a dispersal kernel described by a negative exponential function, with average and maximum dispersal distances defined for each PFT, and seed number per parent tree calibrated in order to reproduce the seed rain observed in the field for each PFT in an undisturbed forest (Melo et al. 2006). Seeds falling via the local seed rain germinate according to their PFT minimum germination PAR (Photosynthetically Active Radiation) levels, or if not germinated in the immediate time step, are included in the plot's seed bank. The seeds remain in the plot seed bank until PAR levels are adequate or the seed is eliminated by the seed bank mortality, which represents non-predation seed loss such as deep burial. Larger seeds germinate at lower light levels than small seeds, and have higher seed bank mortality rates. Germinated seeds become seedlings with a height of 0.5 m in order to reproduce the seedling definitions from field studies. Maximum seedling density (parameter $T_{seedlingmax}$ from table S1) is limited to 8 seedlings.m^{-2}, of which 7.8% are large seeded seedlings and the rest small seeded seedlings (Melo et al. 2007). Seedlings that survive the next time step become juveniles (non-reproducing trees) and then adults, and are subjected to a total mortality rate that is a sum of the background mortality rate (fixed value) and the diameter-dependent mortality rate, both PFT-specific.

The existence of these basic seed dispersal and germination processes allows FORMIND to simulate the effects of seed number change in tree community dynamics. The effects of tree size on its seed crop, carbon allocation to reproduction and pollination processes were not included for simplicity, and were not considered to have a major effect for this experimental setup.

In this study, defaunation effects (changes in pre- and post-dispersal seed mortality) were implemented into FORMIND as drivers of seed number change. In the following we will present these changes which enabled us to carry out the current experiment on defaunation. A detailed model description can be found in Fischer et al. (2016), and a full list of FORMIND parameter values used in this study can be found in the Appendix (Table A1).

2.2 Modelled seed dispersal and predation

In our experiment, we assume that the loss of large animals will affect the dispersal of large seeds, increasing their density and their vulnerability to pre- and post-dispersal predation. Pre-dispersal is defined as mortality either before the seed has left the tree, or after it has left the tree but before its first transportation event. In tropical forests, the most significant seed predators are rodents (in particular squirrels, agoutis and spiny rats) and insects (in particular bruchid beetles) (Forget et al. 1994, Visser et al. 2011). While the former group feeds directly on the seeds by consuming its endocarp, the latter predates by laying eggs on the seeds, with the larvae consuming the endocarp. The relative importance of each may depend on species, site (e.g. in the Amazon, bruchids (Fragoso 1997), in Panama, rodents (Gálvez and Jansen 2007)), and seed production season (Forget et al. 1994). In this study pre-dispersal mortality represents the loss of large seeds due to increased predation by bruchids and rodents (with the former also predating the seed before it leaves the tree), and post-dispersal predation caused by bruchids (Visser et al. 2011).

We define large seed pre-dispersal mortality (M_{pre}) in the simulation as a percentage reduction in seed output of large seeds, assuming that non-dispersed seeds will be lost (Janzen 1969). This simplification is based on two field-based assumptions: 1. between 60% and 97% of seeds fall near to fruiting conspecifics in defaunated environments (Wright et al. 2000); and 2. More than 70% of all seeds within 30 m of a parent tree are infested by bruchids (fragoso 1997). Therefore we modelled pre-dispersal predation to be density independent, but also due to the rodent component being density independent (Visser et al. 2011).

We modelled post-dispersal seed mortality (M_{post}) as the density dependent component of seed predation, caused by female bruchid oviposition. Strictly speaking, in M_{post} seed predation should be interpreted as seed parasitism, but we keep predation for simplicity. M_{post} is calculated for each 20 m x 20 m plot in the simulation, using the Holling's disc equation (Holling 1959, Nathan and Casagrandi 2004), and is dependent on both seed and parent tree number. We use Holling's disc type II functional response since it is the most frequently observed (Jeschke et al. 2002), and used to model seed predation and host-parasitoid systems (Rogers 1972). The effect of parent trees was included because bruchids are known to be attracted to the neighborhood of food sources (Janzen 1970, Fragoso 1997, Visser et al. 2011), increasing proportionally to adult tree density (Wright 1983, Visser et al. 2011). The Holling's disc predator type II response accounts for the "predation satiation" effect when faced with higher seed numbers. M_{post} is therefore modelled as:

$$M_{post} = \frac{S_{pred}}{S_{total}}$$

with

$$S_{pred} = N_{pred} \cdot S_{total} \cdot \Psi$$

and

$$N_{pred} = T_{parent} \cdot I$$

$$\Psi = \frac{a}{1 + a \cdot T_h \cdot S_{total}}$$

Where S_{total} is the total number of seeds in the plot's seed pool for a particular PFT, and S_{pred} is the number of seeds lost due to post-dispersal predation. S_{pred} is calculated multiplying the total number of predators N_{pred} by S_{pred} and the predator seed consumption rate Ψ. N_{pred} is a function of the number of parent trees T_{parent} for a particular PFT and the number of predators per parent tree I (the infestation rate). This number represents in our model the number of visiting female bruchids for each parent tree per year, with oviposition (i.e. predation) representing eventual consumption by the larvae. The seed consumption rate of one individual bruchid, Ψ in relation to the total number of seeds in the plot is the Holling's disc equation, with parameters a (predator efficiency) and T_h (handling time). I, a and T_h are the parameters in our model, and which are applied independently for each PFT. We increase I in order to test the effects of possible bruchid predator numbers, and observe the effects of changing M_{post} in forest biomass. The Ψ parameters a and T_h are kept constant, and at the range of values observed for host-parasite insect systems (Rogers 1972). These are important parameters that depend on the predator species, and can determine the rate in which seeds are lost. Although rodents can also cause damage to seeds after they are dispersed, post dispersal predation by rodents was not included since parameters on rodent attack efficiency and handling time could not be found from empirical data. We have considered the predator consumption parameters from Ψ (a, predator efficiency and T_h, handling time) to be equal among seed size groups, as concerning undisturbed areas, no differences in pre- and post-dispersal seed mortality of seeds with different sizes was found in a review study (Moles et al. 2003).

2.3 Field data and plant functional types

We parameterized the FORMIND forest model using field data from a large undisturbed forest fragment in the Brazilian Northeastern Atlantic Forest (BNAF). This landscape is located in the Serra Grande sugar mill property, which comprises approximately 9,000 ha of forest fragments entirely surrounded by a uniform landscape of sugar-cane monoculture. The property is located in a low-altitude plateau (300 – 400 m a.s.l.) covered by remnants of the lowland "*terra firme*" tropical forest. Some of the forest fragments are evergreen while others are semi-deciduous, containing altogether 219 species distributed among five main families: Leguminosae, Lauraceae, Sapotaceae, Chrysobalanaceae and Lecythidaceae. Over the last 200 years the Serra Grande landscape has largely remained under the same land use configuration - it has been therefore considered a long term fragmented landscape, and used as reference for future effects of fragmentation in several studies (Tabarelli et al. 2004, Melo et al. 2006, Melo et al. 2007, Oliveira et al. 2008, Santos et al. 2008, Tabarelli and Lopes 2008, Santo-Silva et al. 2012, Tabarelli et al. 2014).

The study site is home to a large 3,500 ha forest fragment, namely Coimbra forest. It is frequently used as a control area representing undisturbed conditions (Oliveira et al. 2008, Santos et al. 2008). Although Coimbra is smaller than the suggested minimum value for the survival of large animals (20,000 ha), the forest still contains a large proportion of large seeded trees in the community. Since the Coimbra forest is located within the long term fragmented landscape, we assume it is not expected to undergo further changes due to defaunation.

The field data consists of two datasets obtained in the interior of Coimbra forest:

1. Seed rain assessments during a 1-year period using 100 seed plots of 1m² (total sampling effort of 200 m²) comprised of 50 ground plots, and 50 seed traps placed 1.2 m above the ground (Melo et al. 2006, Costa et al. 2012).
2. Adult tree inventory consisting of twenty 0.1 ha plots (total area of 2 ha) located in mature forest (> 200 m from the edge of Coimbra forest).The inventory included all trees larger than 10 cm in stem diameter

at breast height (DBH), for which DBH, tree height and lowest taxonomic level were recorded (Oliveira et al. 2008).

We grouped tree species into six PFTs. The PFTs were defined according to two light tolerance levels, shade-tolerant and shade-intolerant, and three seed classes: non-animal dispersed seeds, small seeds (<15 mm) dispersed by animals, and large seeds (>15 mm) dispersed by animals. This PFT grouping is the most relevant to capture the effects (negative or positive) of defaunation, as shown by studies in Serra Grande (Silva and Tabarelli 2000, Melo et al. 2006, Melo et al. 2007, Oliveira et al. 2008, Santos et al. 2008, Tabarelli and Lopes 2008). By analyzing the field data, we observed that larger seeded tree species have significantly higher adult wood density than smaller seeded species ($F_{(1,217)} = 5.993$; $p = 0.0152$, Fig. S1).

The field data on seed rain was used to parameterize the dispersal kernels (negative exponential, equation S1) of the six PFT (Table 1). In order to calculate seed dispersal distances, we used the *dispeRsal* R package (Tamme et al. 2014). This method uses a statistical approach (linear regression with cross validations) to determine how well various plant traits (dispersal syndrome, seed mass, seed release height and terminal velocity) predict dispersal distances. We estimated maximum dispersal distance (R_{max}) for each tree species using dispersal syndrome (categories grouped into biotic and abiotic dispersal) and maximum seed release height (i.e., average of the maximum measured height for each species). We averaged species-specific maximum dispersal distances for the corresponding PFT. Mean dispersal distances (R_{mean}) were estimated from the maximum distance using the maximum-mean dispersal relationships provided by Thomson et al. (2011), with $R^2 = 0.90$; n = 220 species; slope = 0.836 ± 0.031 SE; $P < 0.001$. The calculated maximum dispersal distances per PFT produced an expected large variation, ranging from short dispersal distance in non-animal dispersed tree species (e.g., PFT4 with R_{max} of 67 m and R_{mean} of 10 m) to animal dispersed tree species (e.g., PFT5 with R_{max} of 1,327 m and R_{mean} dispersal of 37 m).

2.4 *Simulation scenarios*

The unknown parameters baseline mortality (M_b), small tree mortality (M_d) and seeds per parent tree (N_{seed}) were calibrated using 4 ha, 1,000 year simulations in order to identify the parameter values that reproduced the field observed total seed rain, seedling density, stem number and aboveground biomass per PFT. This field-calibrated parameterization is considered the "undisturbed scenario". Since we also do not have field values for bruchid densities for parent tree, we consider a baseline value of 0 bruchid predators per parent tree per year and increase the value in the scenarios. Therefore, our "undisturbed" scenario is defined by the deactivation of M_{pre} and M_{post}, with seed mortality occurring only due to seed bank loss (i.e. yearly mortality rate of non-germinated seeds as defined by the parameter $M_{seebank}$ in Table A1). The value S_{total}, used to calculate post-dispersal seed mortality, is equal to the seed rain of each PFT in each plot.

In order to observe the effects of M_{pre} and M_{post} on community structure and forest biomass at the study region, FORMIND was run varying both variables within a broad range and considered their individual and combined effects. In detail, we explore M_{pre} from 0 – 100% in the large seed functional group, and M_{post} considering increases in the number of seed predators per parent tree (infestation), by varying the I parameter of N_{pred}, until significant differences were detected. For each M_{pre} and I value, FORMIND was run in an area of 4 ha for 1,000 years (starting from an undisturbed forest inventory) and the last 100 years were averaged for analysis. We kept the I parameters equal for all PFT, since we do not have field data to support differential predation rates.

Finally, we analyzed the changes in the long-term dynamics of biomass for key values of M_{pre} (i.e. in which significant effects were observed). For this we simulated the forest for 10 runs of 1,500 years under low I conditions (5 $N_{pred}{\cdot}T_{parent}^{-1}$), activating M_{pre} after the first 750 years with values of 0%, 90%, 95% and 100%. We aim here to observe how changes in the regeneration patterns (seedling numbers per PFT) affect future forests, and especially the lag between changes in seed dispersal and the effect on adult tree communities.

3. RESULTS

3.1. Model Calibration

The calibrated model for the undisturbed scenario showed a reasonable fit for the forest properties, with most averages from the last 200 years of the 1000 year simulations falling within standard deviation ranges for field observed values (Fig. 1). Seedling values were somehow underestimated, and stem numbers overestimated, with biomass values providing the best fit. The actual simulation runs can be seen in Fig. S2.

3.2. Biomass changes and Community shifts

The activation of both seed predation processes resulted in scenarios where total biomass was reduced. The highest reduction was 26.2% in the extreme scenario that was tested (total biomass with M_{pre} + M_{post}: 240.36 t organic dry matter [ODM]·ha^{-1} ±2.88 SD, with M_{pre} of 98% and M_{post} of 50 $N_{pred}.N_{Trees}^{-1}$) in relation to the undisturbed scenario where both mortality processes were deactivated (undisturbed forest biomass: biomass of 325.73 t (ODM·ha^{-1} ±2.45 SD). When activated independently, M_{pre} reduced total biomass up to 22.57% (total biomass only M_{pre} activated: 252.19 t ODM ·ha^{-1} ±3.55 SD) and up to 20.63% in the case of M_{post} (total biomass only M_{post} activated: 258.54 t ODM·ha^{-1} ±3.80 SD). Critical thresholds for significant effects on total biomass in relation to the undisturbed scenario occurred between 80% and 93% for M_{pre} and 20 – 25 $N_{pred}·T_{parent}^{-1}$ for M_{post} (Fig. 2A). Beyond these thresholds, the tree community becomes dominated by light demanding shade-intolerant species (i.e. pioneer), which due to their lower wood density push the community to lower average biomass values.

Both predation processes promote increase in the proportion of biomass contributed by pioneer species, which after the critical M_{pre} and M_{post} values become the most significant retainers of biomass in the community, being responsible for over 60% of total community biomass (Fig. 2A and 2B). This occurred since groups such as the shade-tolerant, small-seeded, animal-dispersed trees (PFT5) and both small-seeded pioneer groups (PFT1 and PFT2) faced indirect negative and positive effects respectively due to the increased space and light resources resulting from the loss of the large-seeded PFT3 and PFT6. Similarly, increases in the density dependent M_{post} (directly applied to all PFTs) disproportionally the large-seeded groups (Fig. 3), but also PFT4 and PFT5 negatively (shade-tolerant) and PFT1 and PFT2 positively (small-seeded, shade-intolerant). In conclusion, both predation processes resulted in a similar pattern: the shift of the forest's biomass partition from the shade-tolerant, animal-dispersed PFTs to a pioneer PFT-dominated community.

3.3. Temporal dynamics

The temporal dynamics experiment was carried out considering the M_{pre} values that had an effect on the forest community (Fig. 4). The simulations of 95% and 100% M_{pre} had a significant effect on the number of large-seeded seedlings, shifting the regeneration community. However, the effect on total biomass of adult trees only became evident 100 years after the activation of dispersal failure. This suggests an important lag between changes in tree regeneration and future tree communities.

4. DISCUSSION

Our findings confirm the conclusions of other studies that highlight the role of defaunation in affecting the large seeded tree community, and their reproductive failure resulting in total forest biomass losses. Forest models such as FORMIND can provide useful insights into this process, and projections for future forests. A limitation of this study is that the simulation is parameterized using data collected from only one study site in the Atlantic Forest. Although the exact extent of defaunation impact on biomass in other forests will depend on the relevance of the large seeded group for total community biomass, we believe that the main trends found here are generally applicable, since the proportion of large seeded trees in light-limited environments such as tropical rainforests are known to be high, and similar (Westoby et al. 1996).

4.1. How much seed loss is needed to cause impacts to the adult tree biomass?

In terms of impacts on total aboveground forest biomass, we found a maximum reduction of up to 26.2% loss due to large animal defaunation effects. Two recent studies by (Peres et al. 2016) and (Bello et al. 2015) considering the entire Atlantic and Amazon Forests in Brazil found 2.5% to 37% biomass loss in defaunated forest areas, a range within which our results fall. By using empirical studies alone, however, it is not possible to establish how tree communities react to reproductive collapses such as seed loss. Using a process- and individual-based forest model, we observed significant effects on biomass only above a threshold of more than 80% pre-dispersal loss of large seeds and an infestation rate of 20 predators per parent tree. This means that large-seeded trees produce more seeds than required for the maintenance of the reference undisturbed population, suggesting resistance of large-seeded tropical tree species to increased seed loss at our study site. This excess seed production, as evidenced by the seed data used to parameterize the model, may function as a buffer for biotic (e.g. escape from predation (Nathan and Muller-Landau 2000, Nathan and Casagrandi 2004)) or abiotic (e.g. climate variability (Nicotra et al. 2010)) factors.

Also, the pre-dispersal predation threshold of >80% seems realistic for defaunated environments, lying with the observed 60%-97% of seed dispersal failure (Wright et al. 2000) in defaunated environments (in mammal-abundant sites the failure is 1%-5%). The defaunation in this cited field study is represented by the poaching of three animals, Agouti, Coati and Deer, whose density was reduced from 1, 0.07 and 0.03 per ha in undisturbed areas to ~0.2, 0.01 and 0.005 per ha in defaunated areas).

In relation to post-dispersal predation, the threshold density of 20 seed predators per parent tree may appear small, but it must be considered that the time step of the model is one year, and that extremely low initial predation densities of bruchids (2 individuals per ton of stored seeds) can result in >50% of seeds damaged within 4-6 months (Bailey 2007). Beyond this threshold, and within our tested predator infestation range of 0-50, M_{post} reaches the maximum value of 1 for PFT with lower seed output number, meaning that seeds survive predation only in plots uninhabited by parent trees.

4.2. What is the community composition of a defaunated forest?

The empirical studies by Bello et al. (2015) and Peres et al. (2016) have estimated the effects of defaunation on forest biomass by considering the substitution of the lost large-seeded trees by other species taken randomly from the remaining species pool. According to our simulations, the loss of one functional group triggered nonrandom shifts in community composition. This suggests that some PFT benefit more than others from the loss of the large seeded tree species, and random substitutions may not be realistic. This is another point demonstrating the usefulness of process-based forest simulations for analysis of community changes.

For our simulated study site, defaunation had the community effect of transforming a late-successional forest stand, dominated by shade-tolerant trees, into a early successional stand dominated by pioneer, fast-growing trees (Figure 3). This is non-trivial since PFT5, which is shade tolerant and small seeded, was somehow indirectly affected by changes in the large seeded groups PFT3 and PFT6. In the defaunated community of the increased M_{pre} and M_{post} scenarios (individually and in conjuction) the PFT1 and PFT2 (small-seeded and shade-intolerant species) are overrepresented. Besides retaining less biomass, early succesional tree communities are composed by a lower number of species as well as more common tree species than their late successional counterparts, and this process is refered to as biotic homogeneization (Lôbo et al. 2011). Homogenization can occurr due to forest fragmentation, especially through microclimatic changes due to edge effects, recurrent fires and the collapse of animal-plant interactions such as those caused by defaunation, greatly impoverishing the biota of tropical landscapes (Tabarelli et al. 2004).

Since large seeded species produce less seeds than small seeded species, and large seeds are unlikely to accumulate in the soil seed bank, large seeded species adult populations are more susceptible to higher seed mortality rates (Moles et al. 2003). Considering seed size strategies, our modelling approach of predation indicates that higher seed predation rates benefit small seeded species, shifting the tree community towards dominance of small-seededed species (Figure 3). The high number of seeds produced by PFT 1 and PFT2 (within the small seeded shade intolerant group, Table 1) means that they are relatively unaffected even in extreme M_{post} scenarios (seed predator density of 50 ind/T_{parent}) due to the satiation effects that are included in the predation equation. Higher predator density values that would also affect pioneer species are theoretically possible, but this was not tested in this study. This confirms the expectation that fewer but larger seeds make for better competitors on the individual seed level (Turnbull et al. 1999, Leishman 2001), but smaller and more abundant seeds provide more surviving seeds under high seed predation environments (Bradford and Smith 1977). However, this advantage can be offset by other life history traits such as plant size, longevity, juvenile survival rate and reproductive size threshold. These traits are all included in the FORMIND model, and may become more or less relevant for the survival of a PFT when certain conditions such as light levels are considered. Furthermore, for other forest communities, the loss of a disperser and consequent aggregation of seeds may actually lead to increased survival and even to the emergence of monodominant stands (Peh et al. 2011, Kazmierczak et al. 2016).

4.3. After animal dispersers are lost, when can we expect changes to the tree community?

FORMIND allows a glimpse into the time scale of the defaunation process, from seed mortality to adult biomass and community shift. The simulations show a lag of 100 years between seed loss and adult mortality. Therefore, defaunated areas can potentially appear undisturbed for a long time after the animal dispersers are locally extinct, with many large seeded trees species composing “living-dead” communities (Janzen 1986). The consequent collapse of this living-dead community has been a long standing expectation from related empirical studies, but the time scale of this high mortality event remains elusive without the use of models such as those applied in this study. Finally, our time lag result has broad implications on the study of carbon balance of tropical forests, as a spike of emissions can occur one century after an area goes through the process of fragmentation or overhunting. This should be taken in account for global carbon budgets and risk assessments of local long-term carbon sequestration projects.

4.4. Conservation implications

This study provides support for the unique role of large animals in preserving the carbon retention services of tropical forests. The relevance of the effects of defaunation in human modified landscapes is growing, as tropical deforestation continues and more natural areas become fragmented (Hansen et al. 2013, Haddad et al. 2015). The tropics house more than 50 million forest fragments, with a mean area of 29 ha (Brinck et al. 2017). Such a low mean area per fragment represents bad news for large animals. In the Atlantic forests of Brazil, the amount of remaining forest contained in fragments smaller than 20,000 hectares, the threshold under which many large animals are thought not to survive (Chiarello 2000), corresponds to 79% of the total forest area (Ribeiro et al. 2009). As the present and other studies show (i.e. Bello et al. 2015, Peres et al. 2016), this means that large seeded species will suffer, causing long lasting effects on forest structure, composition and ecosystem services.

One meta-analysis study was unable to find links between reduction in fragment size and loss of seed dispersal services, even though significant loss was observed for increased hunting and selective logging which in turn are fostered by fragmentation (Markl et al. 2012). In any case, efforts in reducing the distance between fragments (i.e. creating stepping stones, Barbosa et al. 2017), or forested corridors between fragments (Pardini et al. 2005), and controlling hunting can go a long way towards increasing the survival of large animals in fragmented landscapes, as well as preventing the effect of their loss on other biological groups. The creation of large-scale protection zones (such as the “Environmental protection areas” [APA] in the Brazilian national system of conservation units, or the Natura 2000 in Europe), where permeability of human modified habitats (i.e. biological flux among undisturbed natural areas) is increased through policy implementation, could potentially prevent even severely fragmented areas such as the Brazilian Atlantic forest from the consequences of defaunation. Finally, payment for environmental services (PES) schemes could prove crucial for the coexistence of large animals with humans, as important pilot programs for the protection of jaguars have shown (Dickman et al. 2011).

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AUTHOR'S CONTRIBUTIONS

M.D.P, J.G., V.M. and A.H. conceived the research and M.D.P. let the writing and carried out the simulation and analysis of the simulation results. All authors contributed extensively to the work presented in this paper.

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Figure Legends

Figure 1. Cross-validation plots for the reference undisturbed (non-defaunated) forest simulation, calibrated in relation to the field data. A. Seed rain; B. Seedlings; C. Stem number (larger than 10 cm diameter); D. Aboveground biomass.

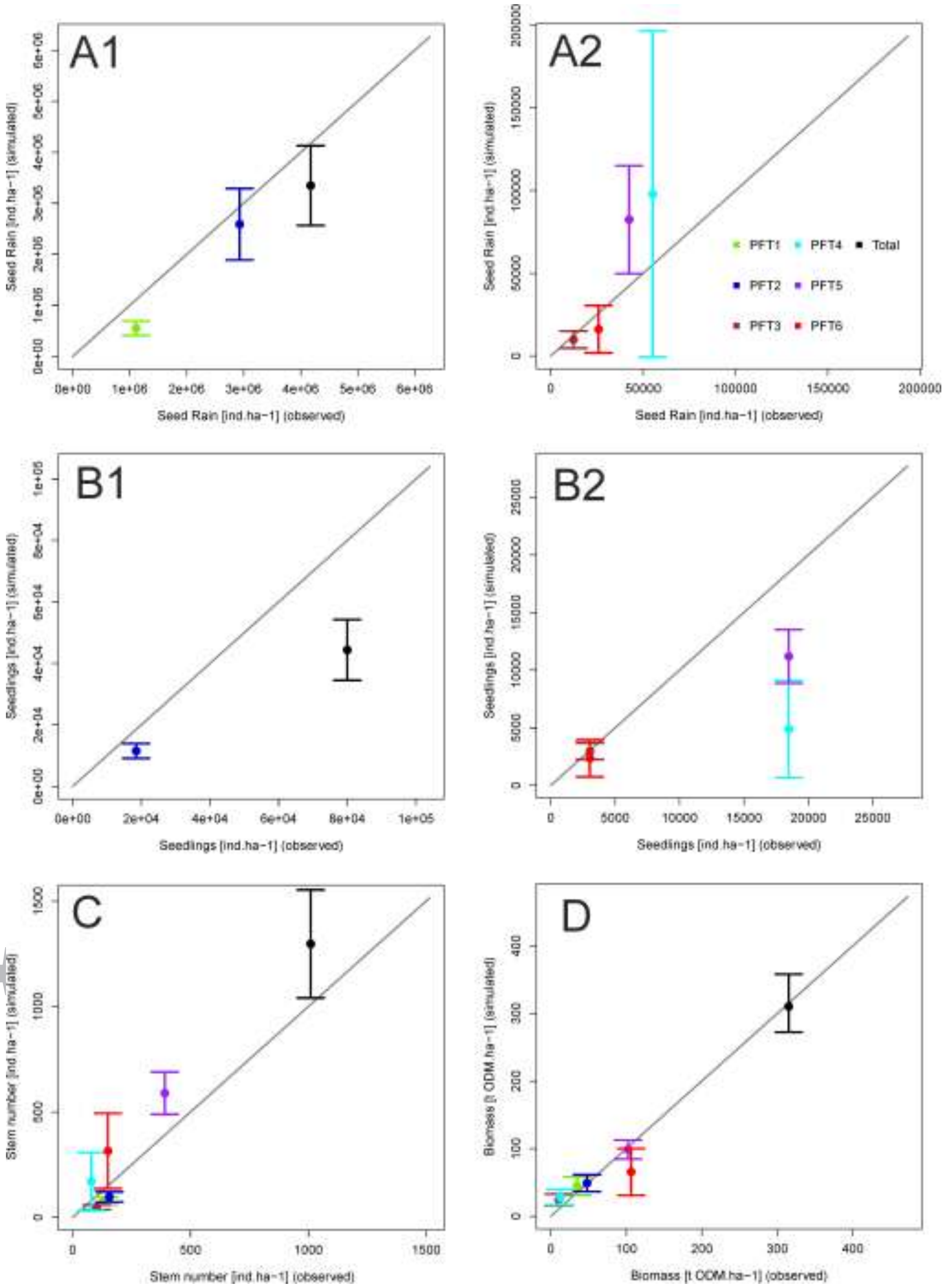

Figure 2. Simulation results for A. Combined effects of M_{pre} and M_{post} on the total forest biomass for selected values of M_{post}. B. Biomass partition of the total, showing community functional shift with varying pre-dispersal mortality (M_{pre} ranging from 0% to 98% for PFTs 3 and 6), and C. with varying post-dispersal mortality M_{post} (predator densities per parent tree varying from 0 to 50 $N_{pred}.T_{parent}^{-1}$). Forest biomass is averaged over the last 100 years of simulation (total run of 1,000 years).

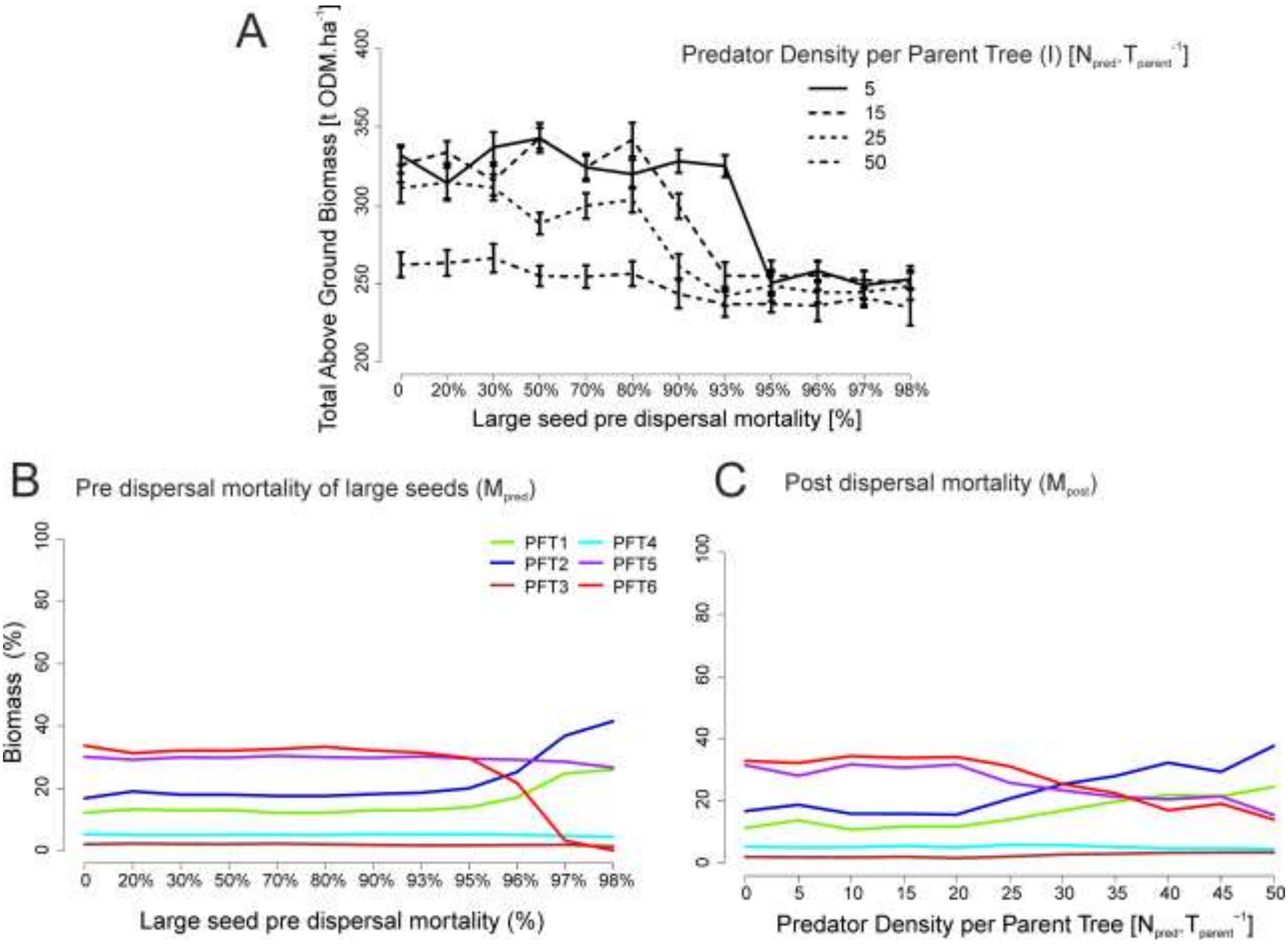

Figure 3. Simulation results for relative changes in biomass for seed size and shade tolerance functional types. A. Pre-dipersal mortality variation and B. Post-dispersal mortality variation. Biomass change is given in percentage in relation to 0% M_{pre} or 0 M_{post} (0 predators per parent tree).

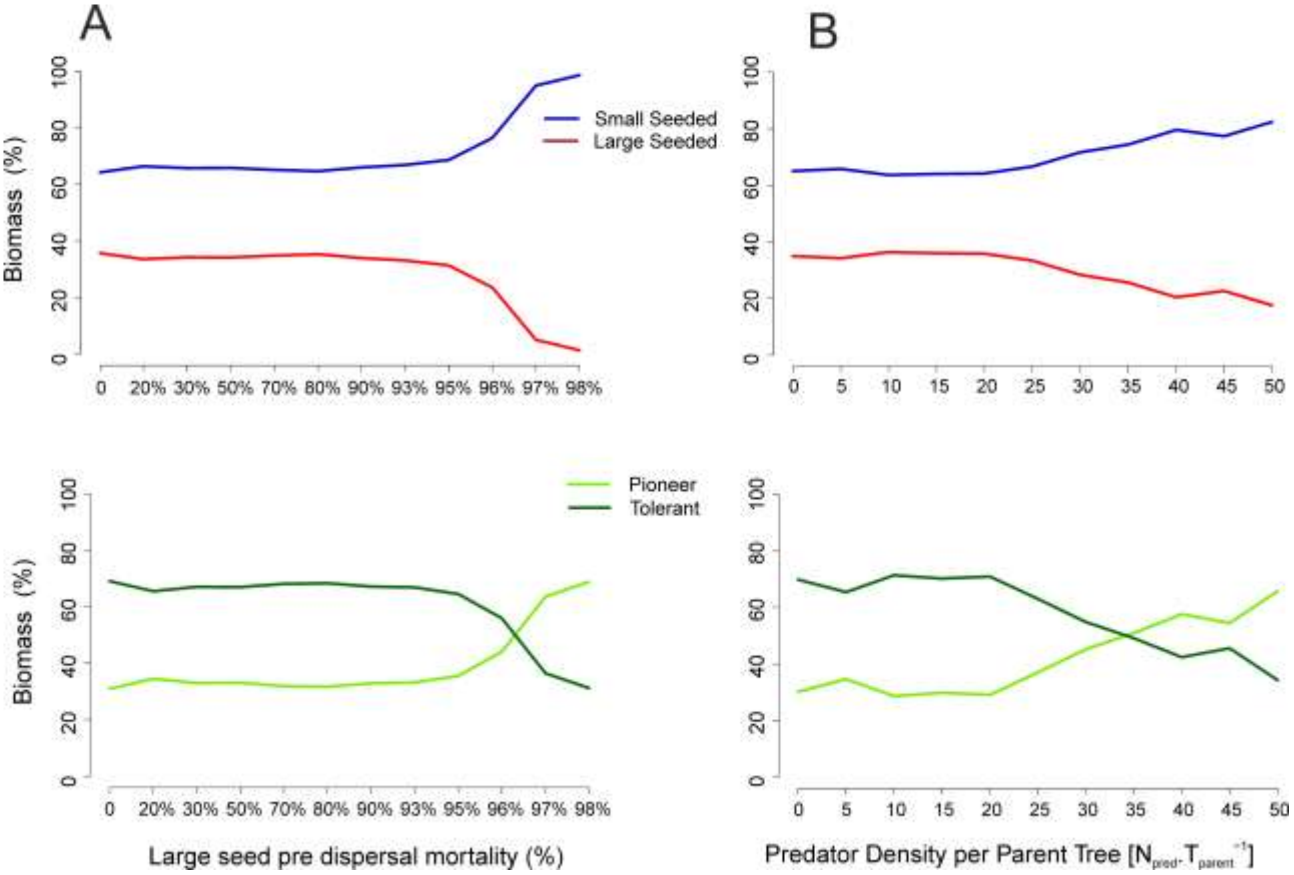

Figure 4. Simulation results on A. aboveground forest biomass and B. number of seedlings from large seeded species (shown here after a spinup period of 400 years), considering four M_{pre} conditions (0%, 90%, 95% and 100%). The I parameter of M_{post} (predators per parent tree) was fixed at 5 $N_{pred}.T_{parent}^{-1}$ and lines represent the average of 10 simulations of 1500 years each, on an area of 4 ha. M_{pre} effects were activated after 750 years (dashed purple line) and significant effects on biomass were observed after 100 years (dashed black line). The black point in A. represents the field measured average biomass value.

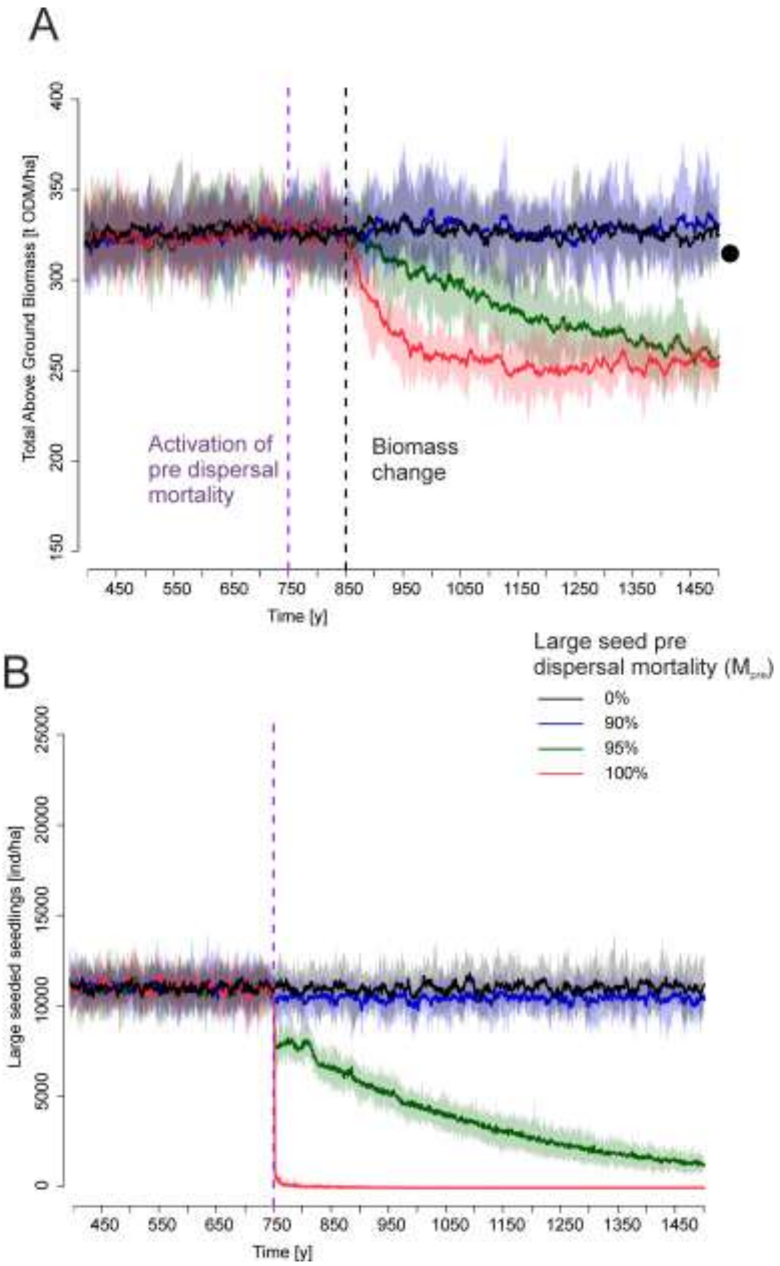

Table Legends

Table 1. Field data for mature forest plots of Brazilian Atlantic Forest in NE Brazil (Coimbra forest). Tree species are grouped according to six plant functional types (PFT). Data values include trees larger than 10 cm in stem diameter and are averaged per hectare. Classifications for shade-tolerance were obtained from literature (Santos et al. 2008). Non-animal seed dispersal includes wind or ballistic dispersal. Size threshold between small and large seeds is 15 mm. Species richness, stem number and basal area values were taken from Oliveira et al. (2008). Data on seeds per year were based on Melo et al. (2006). The maximum increment of stem diameter was based on data from Santos et al. (2008).

Coimbra (Mature Forest)									
PFT	**Shade Tolerance**	**Seed Dispersal Category**	**Species Richness**	**Number of Stems ha-1**	**Biomass (Mg/ha)**	**Basal Area (m^2/ ha)**	**Seeds per year/ha**	**Max. Dispersal Distance (m)**	**Max. Increment of Stem Diameter per Year (mm)**
1	Intolerant	Non-Animal	55	133.5	34.94	8.77	1,110,666	115.41	30.00
2	Intolerant	Small Seeds	103	155.5	47.99	8.48	2,926,997	1139.48	43.25
3	Intolerant	Large Seeds	23	102	10.66	3.46	12,333	1120.15	15.89
4	Tolerant	Non-Animal	16	78.5	12.65	2.12	55,222	67.31	19.79
5	Tolerant	Small Seeds	49	391	102.39	14.8	42,444	1327.87	16.84
6	Tolerant	Large Seeds	29	149.5	106.39	12.26	25,889	1142.61	19.21
Total	-	-	275	1010	315.02	49.89	4,173,551	-	-