Big trees drive forest structure patterns across a lowland Amazon regrowth gradient

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Abstract

Degraded Amazonian forests can take decades to recover and the ecological results of natural regeneration are still uncertain. Here we use field data collected across 15 lowland Amazon smallholder properties to examine the relationships between forest structure, mammal diversity, regrowth type, regrowth age, topography and hydrography. Forest structure was quantified together with mammal diversity in 30 paired regrowth-control plots. Forest regrowth stage was classified into three groups: late second-regrowth, early second-regrowth and abandoned pasture. Basal area in regrowth plots remained less than half that recorded in control plots even after 20-25 years. Although basal area did increase in sequence from pasture, early to late-regrowth plots, there was a significant decline in basal area of late-regrowth control plots associated with a decline in the proportion of large trees. There was also contrasting support for different non-mutually exclusive hypotheses, with proportion of small trees (DBH <20cm) most strongly supported by topography (altitude and slope) whereas the proportion of large trees (DBH >60cm) supported by plot type and regrowth class. These findings support calls for increased efforts to actively conserve large trees to avoid retrogressive succession around edges of degraded Amazon forests.

Introduction

Healthy tropical forests provide goods and services to human populations. Yet tropical forests show worrying rates of forest loss with an elevated loss / gain ratio and a statistically significant trend in annual forest loss of 2101 km^2/year [1]. One option to revert tropical forest loss is the restoration of degraded forests and deforested landscapes [2,3]. Although the post-disturbance restoration of forest ecosystems often involves passive restoration strategies (i.e. natural regeneration), the ecological results of this type of restoration are still uncertain [2-4].

Continuing widespread forest losses across Amazonia compromises vital ecosystem services such as carbon storage, regulation of hydrological cycles and climate patterns [5-7]. Riverside forests are particularly threatened and suffer losses due to the conversion of forest cover to pastures, compromising the maintenance of water flows [8]. The recovery of degraded areas is necessary to recuperate the standing forest value and the Amazon offers an excellent recovery opportunity due to its natural potential for regeneration [9,10]. Yet, the regrowth rate of degraded Amazon forests can be slow, as abandoned areas are typically on compacted poor quality soils [11,12] and due to the high structural and biological diversity of the original forests[13].

Separating the complex interactions driving recruitment and recovery patterns of highly diverse Amazon forests is challenging [2,3,14,15] , yet we know that different faunal groups can modulate and generate key impacts[16-19]. Indeed, the successional trajectory of natural regeneration in degraded forests can depend strongly on the concomitant recovery of faunal diversity and associated ecosystem services (e.g. seed dispersal) [20-22]. For example, seed predation by both vertebrates and invertebrates [23,24] can limit germination and subsequent recruitment[22]. Long-term experiments have demonstrated the impact of vertebrates on recruitment, showing how this group contributes to the maintenance of tropical forest species and structural diversity [25-28].

Amazon mammals are important component of forest diversity [25,29] including carbon [28] and biomass cycles [18]. Mammals can also play an important role in the successional trajectory and recovery of degraded areas as dispersers and predators of both seeds and seedlings [23]. Mid- and large-bodied mammals (weight> 1 kg) can disperse a large numbers of seeds over long distances [23,30]. For example, lowland tapirs can travel over 4 kilometers in a day [31] and disperse seeds of more than 70 tree species [32]. The loss of mid- to large-bodied mammals may release some plant species from herbivory and increase their dominance, which subsequently decreases tropical forest biodiversity[33,34].

Given the need to understand the patterns of forest structure in Amazonian forests, here we aim to identify how biotic and abiotic factors (Table 1) can explain patterns in forest structure across a successional gradient.

Table 1. Explanatory variables.

Working Hypothesis/Model	Variables	Source	Description/Ecological relevance	Supporting references
	Plot type	In situ.	Categorical factor with two levels: control and regrowth. Included in all models.	
Topography	Altitude	SRTM-DEM	Altitude is a driver and modulator of species distribution patterns from microhabitat to biogeographic scales. Altitude not only affects soil, water availability, climate and a myriad of other abiotic and biotic variables	10,13,35,36
	Slope	SRTM-DEM	Slope affects soil, water availability and tree mortality rates.	
Hydrography	TWI	SRTM-DEM	Topographic wetness index accounts for the topographic control of water movement in sloped landscapes and the associated control on soil moisture.	37
	Drainage proximity	SRTM-DEM	Combination of water gravitational potential (Height above the nearest drainage (HAND)) and soil drainage (Horizontal distance from nearest drainage (HDND)).	38-40
Regrowth class	Regrowth class	In situ: interview	Land-use history has a strong influence on rates of forest recovery. Categorical factor with three levels of regrowth class derived from the land-use history: late second-regrowth forest, early second-regrowth and pasture.	10,16,41,42
Time	Years since last use	In situ: interview	Time is a major determinant of forest succession.	
	Years since initial clearing	In situ: interview		
Mammals	Species richness	In situ: camera-trap images	Mammal diversity is positively related to tree biomass.	17,18,28,43
	Functional diversity	In situ: camera-trap images		

Table 2. Summary of survey locations. Characteristics of 15 sites used to study forest structure. Values are means with ranges in parentheses.

Regrowth class	Sites/ Plots	Size (ha)	Distance		Forest cover (%)		Tree BA (m^2/ha)		Large tree BA (m^2/ha)	
			River (m)	Town (km)	1 km	5 km	Reg.	Cont.	Reg.	Cont.
Late	5/10	5.8 (2.0–12.0)	288.15 (110–554)	40.4 (35.0–45.0	91.5 (87.4–95.4)	97.4 (96.4–98.5)	17.6 (11.5–25.3)	35.8 (21.7–47.4)	1.5 (0.0–7.7)	11.4 (0.0–22.3)
Early	5/10	2.4 (1.0–4.5)	348.5 (150–554)	38.2 (30.0–43.7)	90.7 (87.1–96.0)	97.2 (96.4–98.4)	11.1 (4.7–19.2)	49.3 (34.6–76.5)	0.0 (0.0–0.0)	20.8 (0.0–44.2)
Pasture	5/10	8.7 (6.8–9.9)	266.8 (170–461)	32.8 (26.8–40.8)	88.8 (85.7–91.1)	96.9 (95.5–98.5)	5.8 (0.0–15.9)	47.1 (32.6–64.8)	0.0 (0.0–0.0)	24.0 (12.0–41.2)
Totals	15/30	5.6 (1.0–12.0)	301.1 (110–554)	37.1 (26.8–45.0)	90.4 (85.7–96.0)	97.2 (95.5–98.5)	11.5 (0.0–25.3)	44.1 (21.7–76.4)	0.5 (0.0–7.7)	18.8 (0.0–44.2)

Results

Variation in stand structure variables

There were clear differences in forest structure between control and regrowth plots (Figure 1). On average control plots had increased basal area and increased proportion of large trees (Figure 1). In contrast regrowth plots tended to have increased proportion of small trees (<20 cm DBH).

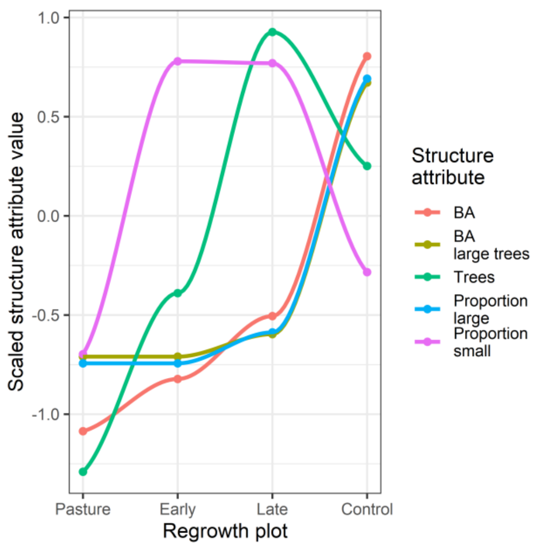

Figure 1: Forest structure changes across a lowland forest regrowth gradient. Showing mean values of five forest structure attributes recorded in 30 plots (15 control and 15 regrowth). Regrowth plot shows differences between control, late second-regrowth, early second-regrowth and pasture plots. Values are scaled (centered

and scaled by the standard deviation) to enable simultaneous visual comparison of the different attributes. The lines are from LOESS smoothing as guides to aid visual interpretation.

The number and basal area of living trees tended to increase with altitude and this relationship was stronger in regrowth areas (Figure 2). The relationship with altitude was strongly affected by low lying (90 masl) pasture plots with no trees that generated significant leverage on the linear relationship (Figure 2).

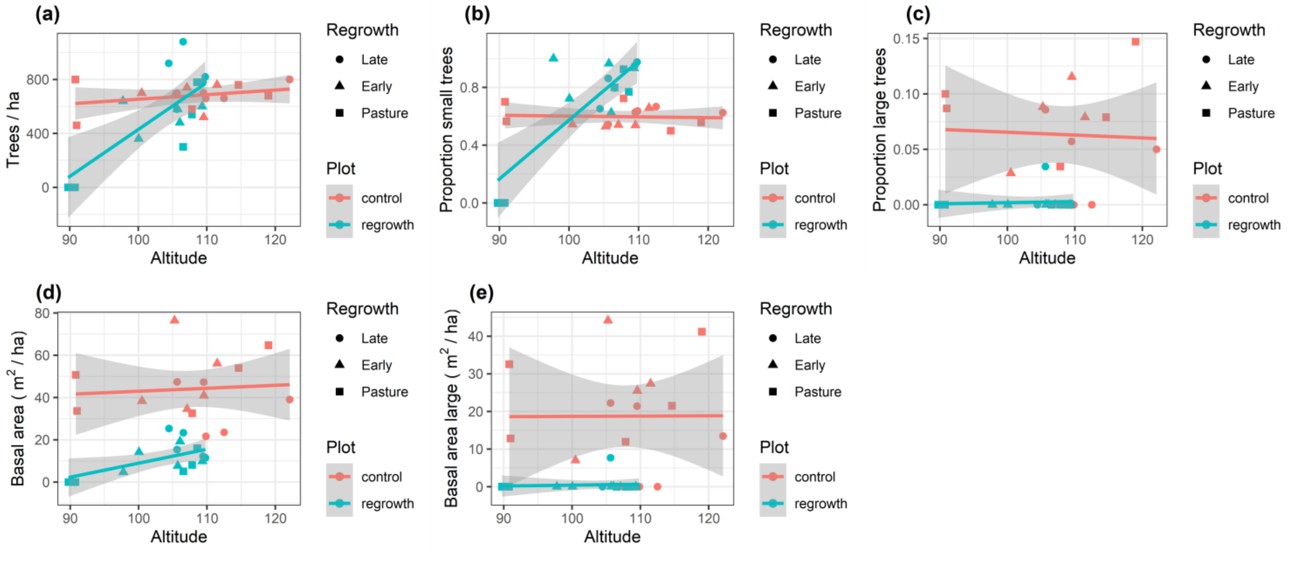

Figure 2: Forest structure along a lowland Amazon regrowth gradient. Showing trends in (a) number of trees (> 10 cm DBH) per ha, (b) proportion of small trees (10 – 20 cm DBH), (c) proportion of large (> 60 cm DBH) trees, (d) basal area and (e) basal area of large (>60 cm DBH) tree in 30 plots (15 control and 15 regrowth). Lines and shaded areas are mean values and 95% confidence intervals from linear models illustrating trends in basal area with increasing altitude (masl). Points with different shapes represent different regrowth classes.

Basal area ranged from 0 to 76.4 m^2/ha across the 30 survey plots (Table 2), with control plots showing an average fourfold increase in basal area compared with regrowth plots (mean basal area 44.1 and 11.5 m^2/ha, control and regrowth respectively, Figure 2). The patterns in plot basal area also differed between regrowth classes (Figure 3, Supplementary Table S1). There was a significant interaction between plot type (control/regrowth) and regrowth stage, with basal area increasing across pasture, early and late regrowth plots but control plots showing the opposite trend, with basal area decreasing significantly in late-regrowth control plots (Figure 3).

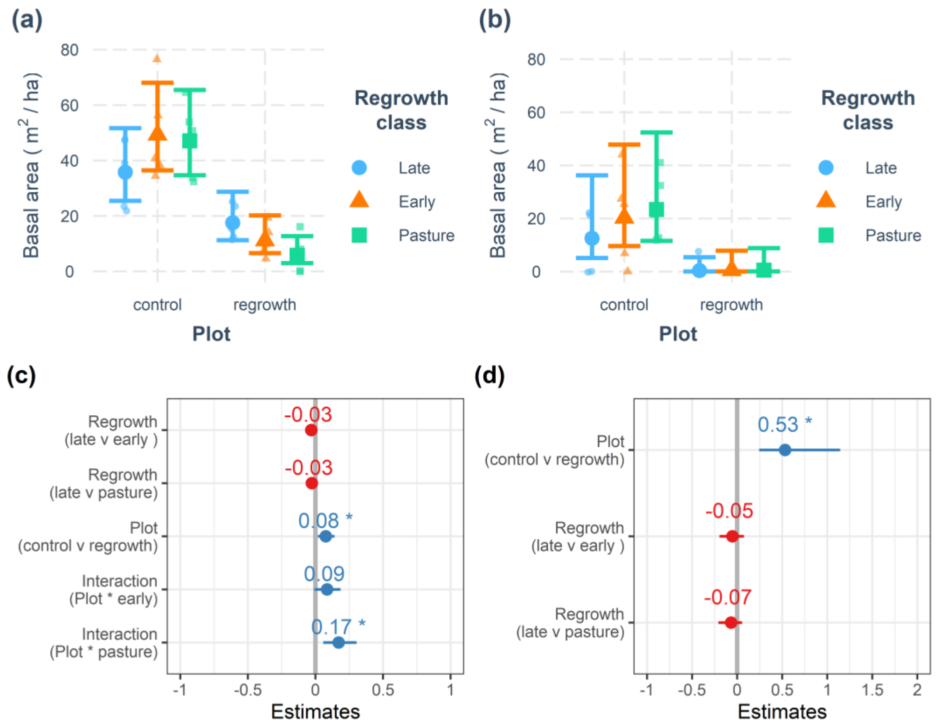

Figure 3: Basal area changes across a lowland forest regrowth gradient. The basal area of all (a and c) and large (b and d) living trees were recorded in 30 plots (15 control and 15 regrowth). Regrowth class shows differences between late second-regrowth, early second-regrowth and pasture plots contrasted with control forest plots. Top row shows Generalized Linear Model (GLM) predictions (mean and 95% confidence intervals) for basal area of (a) all and (b) large trees. Bottom row is the associated Forest-plot of the most parsimonious GLMs testing for interactions between regrowth class, plot type and years since last use in the basal area of (c) all and (d) large trees. Forest-plots show coefficient estimates and standard errors.

There was a highly significant positive linear relationship between overall basal area and large tree basal area ($F_{1,28} = 127.5$, $R^2 = 0.82$, $P < 0.0001$). The basal area of large trees decreased significantly in regrowth compared with control plots (Figure 3). On average large trees accounted for 42% of the basal area in control plots compared with only 4% in regrowth plots (Table 2). Indeed a single large tree (>60 cm DBH) was recorded only once in a late-regrowth plot. This relationship was also reflected in the decline in basal area of late-regrowth control plots (Figure 3), which was associated with a decline on the proportion of large trees that accounted for a reduced 31% of the basal area in late-regrowth control plots (Table 2).

Relationships between forest structure, mammal diversity and environmental variables

Mammal diversity varied considerably across the survey plots (Figure 4). There appeared to be a tendency for basal area to increase with mammal diversity in Late-regrowth plots, yet basal area was only weakly associated with mammal diversity within the different regrowth classes (Figure 4). Indeed, the diversity of mammals was found to be only weakly informative for explaining the basal area of trees across the 30 sample plots (Table 3).

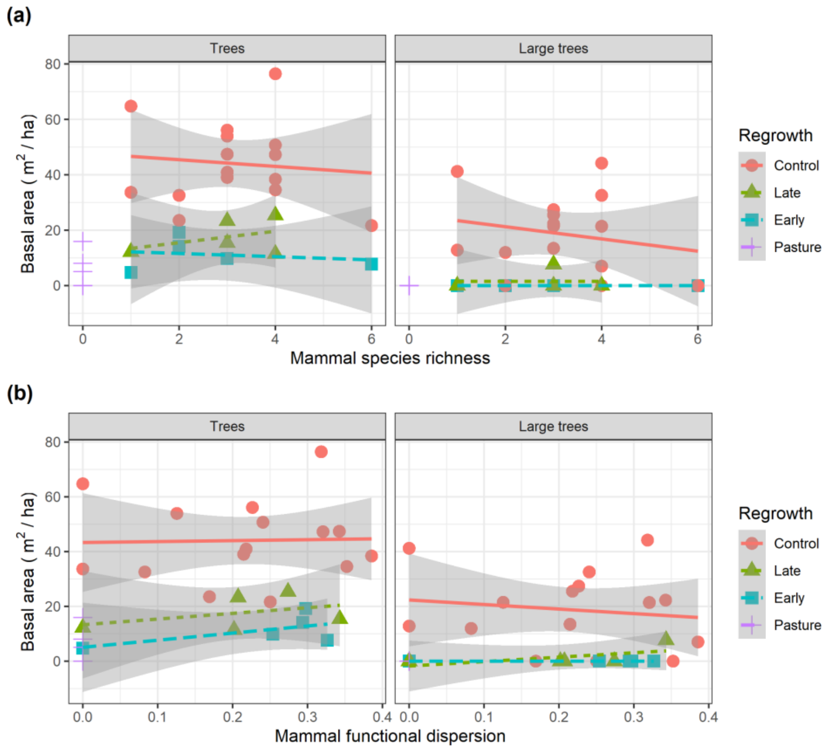

Figure 4. Mammal diversity and basal area across a lowland forest regrowth gradient. The basal area of (a) all and (b) large living trees were recorded together with the diversity (species richness and functional dispersion) of terrestrial mammals in 30 plots (15 control and 15 regrowth). Lines and shaded areas are mean values and 95% confidence intervals from linear models illustrating trends in basal area with increasing mammal diversity. Points with different shapes represent different regrowth plot types.

Comparison of the models representing the alternative hypothesizes showed that plot type (control v regrowth) and topography were the most important first ranked variables for the five forest structure attributes (Table 3). The most simple model including only plot type explained more than 50% of model deviance for all forest structure attributes except for the number of trees (DBH>10 cm). Plot type and regrowth class were both included in the 95% confidence set of models for the basal area of large trees (Table 3). In contrast Topography was the most important (first ranked) model for the number of trees, proportion of small trees and tree basal area (Table 3). Mammal diversity, Time and Hydrography models were not well supported and were not included in the 95% confidence set of models for any of the forest structure attributes (Table 3).

Table 3. Summary of the Generalized Linear Models created to explain forest structure in 30 plots (15 control and 15 regrowth). Models ordered by decreasing AIC (Akaike Information Criterion) values.

Forest structure	Model[a]	Dev. Exp	Loglik	BIC	AIC	Δ AIC	W_i AIC[b]
Trees							
	Topography	60.5	-100.6	231.9	219.3	0.0	0.91
	Regrowth class	49.8	-105.1	234.1	224.3	5.0	0.07
	Mammals	51.3	-104.7	240.0	227.3	8.1	0.02
	Hydrography	45.8	-106.3	243.1	230.5	11.3	0.00
	Time	42.9	-107.0	244.7	232.1	12.8	0.00
	Plot	6.5	-114.4	239.1	234.9	15.6	0.00
Proportion small trees							
	Topography	75.2	-64.3	155.7	144.5	0.0	0.96
	Hydrography	70.4	-67.5	162.2	151.0	6.5	0.04
	Mammals	66.4	-70.2	167.6	156.4	11.9	0.00
	Time	65.1	-71.0	169.3	158.1	13.6	0.00
	Plot	53.7	-78.7	164.3	161.5	17.0	0.00
	Regrowth class	55.4	-77.6	175.6	167.2	22.7	0.00
Proportion large trees							
	Plot	54.9	-30.5	67.8	65.0	0.0	0.88
	Regrowth class	60.6	-28.9	78.2	69.8	4.8	0.08
	Mammals	62.9	-28.3	83.7	72.5	2.8	0.02
	Time	62.8	-28.3	83.8	72.5	2.8	0.02
	Topography	54.7	-30.6	88.5	77.3	7.5	0.00
	Hydrography	52.8	-31.1	89.5	78.3	8.5	0.00
BA all trees							
	Topography	80.7	-100.9	232.3	220.4	0.0	0.89
	Regrowth class	72.9	-105.8	235.4	225.6	5.2	0.06
	Plot	62.9	-110.4	231.0	226.8	6.4	0.04
	Mammals	71.7	-106.4	243.4	230.8	10.4	0.01
	Time	69.3	-107.6	245.8	233.2	12.8	0.00
	Hydrography	66.0	-109.1	248.8	236.2	15.9	0.00
BA large trees							
	Plot	58.3	-61.5	133.1	128.9	0.0	0.87
	Regrowth class	67.1	-59.9	143.5	133.7	4.8	0.08
	Hydrography	70.9	-59.0	148.7	136.1	7.1	0.02
	Mammals	70.4	-59.2	148.9	136.3	7.4	0.02
	Time	65.7	-60.1	150.9	138.3	9.4	0.01
	Topography	60.8	-61.0	152.7	140.1	11.2	0.00

[a] Models used to explain forest structure. All models contained plot type (control/regrowth) as categorical factor. Variables and associated estimates in the different models can be found as Supplementary Information Table S2 online.

[b] Akaike weights (W_i) from largest to smallest.

Discussion

We integrate field and remotely sensed data to establish support for multiple non-mutually exclusive hypotheses explaining patterns in forest structure across a lowland Amazon regrowth gradient. We establish that different hypotheses are supported for different structure attributes. Here we discuss these findings in terms of prospects for the passive restoration of degraded Amazon forests.

The mean basal area value from our 15 control plots (44.1 m^2/ha) was close to the mean from 42 Guyana Shield forest plots (43.4 m^2/ha, range 10 – 65 m^2/ha) in French Guiana [35]. The results from Molto, et al. [35] were obtained from an extensive survey of 0.5 – 1 ha plots. Although our plot size was smaller compared to Molto, et al. [35], the similarity in mean values suggests that our plots do provide a representative sample of forest structure in the regrowth areas. The basal areas obtained from our regrowth plots followed a similar trajectory to those reported from abandoned pasture in Costa Rica [10], where the most recently abandoned pasture plots (<14 year) had mean basal area of 13.5 m^2/ha, with basal area increasing to 26.1 m^2/ha after 21 – 30 year [10].compared with 11.1 and 17.6 m^2/ha respectively in our Early (1-5 year) and Late (20 – 25 year) regrowth plots. This also follows a similar pattern to values reported from 370 successional forest plots in the Brazilian Amazon, with basal area values typically < 10 m^2/ha in early stages (< 5 year) and reaching 25 m^2/ha after 15 years [44].

Although results from lowland forest sites in Costa Rica suggest rapid recovery of pasture areas [10] this could be related to the substantially lower basal area in the seven old growth reference plots (26.1 m^2/ha, range 19.3 – 32.2 m^2/ha) compared with those in our study area. Our results are similar to those reported from the central Amazon, where 25 y of regrowth restored half of the mature-forest biomass [41]. A recent analysis of 45 Neotropical secondary forest study sites found that secondary forests in the lowland tropics reach 90 percent of old growth biomass in a median time of 66 yr [13]. Our findings do suggest nuanced difference in successional trajectories. Basal area increased rapidly in early regrowth stages and this could be explained by the less intensive land use (i.e. lack of pasture) and the proximity to large areas of intact forest. In contrast basal area of late-regrowth areas was less than those reported from other areas [10,44]. This could be related to soil productivity, as previous studies show that highly diverse Guyana Shield wet forests can take longer to establish [13]. With basal area of control plots dominated by large trees it seems likely that many decades will be necessary for forest structure (total basal area, proportion of large trees) to return to pre-disturbance values.

The success of active and passive restoration can depend on ecological conditions [45]. We found topography was the most informative model for explaining patterns in number of tress, tree basal area and proportion of small trees (Table 3, Figure 2). Differences in altitude and slope have been shown to affect floristic structure of tropical forests from local to regional scales [16,35,42,46-48]. Indeed, even relatively small variations in topography can generate changes in local-scale soil chemistry, hydrology and microclimate [46,49]. The effects of topography do not operate in isolation from hydrology and the increased numbers of small trees and tree biomass with increasing altitude (Figure 3) agree with previous studies that show trees grow more slowly in more low lying (and often more waterlogged) terrain [42].

We found a weak association between mammal diversity and regrowth forest structure. Previous studies in a nearby protected area show that this group of mammals (mid– to large–bodied Artiodactyla, Perissodactyla and Rodentia) are more strongly associated with factors such as access to water [50] and altitude [50,51]. A recent study also showed that mammal abundances were more strongly associated with phenology (fruit fall) than basal area along 10 km of forest in the western Guyana Shied [52]. Additionally, regrowth class was found to be the primary driver of mammal species encountered independent of forest cover [53]. For example the number of species detected in control and regrowth plots (all with forest cover >87%) varied between 1 and 6 (Figure 4). Mid- to large-bodied seed dispersers are a critical component of Amazon forests [18,19,25] and are also widespread and ubiquitous across myriad Amazonian forest types [54-56]. The eight species are therefore not strictly dependent on the quality of forest habitat compared with other more specialist groups such as primates [57]. The lack of a strong relationship between diversity of these eight mammal seed dispersers and forest structure attributes (i.e. overall basal area and proportion of small trees) is therefore to be expected.

Decades of research show that myriad edge effects can extend up to 150 m in fragmented Amazon forests [58,59]. Considering the range of expect edge-effects it is highly probable that the natural regeneration and/or restoration of regrowth habitats in Amazon small-holdings (typically < 100 ha) will strongly depend on species ecological responses to habitat edges [60]. Previous studies show that edge effects increase mortality of large trees, which in turn has major impacts on forest ecosystems [61]. In highly fragmented areas edge-effects can drive tree communities through a process of "retrogressive succession"[62] and toward an early successional state that may persist indefinitely. This early successional state can be characterized by functional and structural differences in that larger slower-growing tree species with high wood density tend to decline whereas faster-growing tree and liana species with lower wood density increase[62,63]. The decline in the number and basal area of large trees from our control plots along 20-25 year old edges suggest that retrogressive succession may establish even in relatively un-fragmented areas surrounded by extensive forest cover.

Our findings provide an early warning that even under a best case scenario there is potential for "retrogressive succession". We found not only a lack of large trees in regrowth plots but also that large tree basal declined in older late-regrowth control plots. We suggest that this decline in large tress may be the primary driver of differences between regrowth and old growth forest and as such represent an unquantified component of resilience and time to recovery of Neotropical secondary forests. We also suggest that the continued presence of mid- and large bodied mammal seed dispersers in the study area are likely to be vital in order to avoid such "retrogressive succession".

Methods

Ethics Statement

All methods were carried out in accordance with relevant guidelines and regulations. Fieldwork and data collection was conducted under research permit numbers SISBIO 40355–1, 47859-1 and 47859-2 to DN, issued by the Brazilian Ministério do Meio Ambiente ("MMA"). Data collection used non-invasive, remotely activated camera traps and did not involve direct contact or interaction with animals, thus no ethical approval was required. Interviews with local residents were approved by Brazilian Ministério do Meio Ambiente (SISBIO permits 45034-1, 45034-2, 45034-3) and the Ethics Committee in Research from the Federal University of Amapá (UNIFAP) (CAAE 42064815.5.0000.0003, Permit number 1.013.843). Interviews were conducted with residents that were both (1) willing to be interviewed (written informed consent was obtained from all interviewees) and (2) aware of the site history.

Study area

Our study took place in 15 areas of regrowth on small holder properties[53,64] in the center of the State of Amapá (Figure 5). The regional climate is classified by Koppen-Geiger as Am (Equatorial monsoon) [65], with annual rainfall greater than 2500 mm [66]. The driest months are September to November (total monthly rainfall < 150 mm) and the wettest months from February to April (total monthly rainfall > 300 mm) [66]. The State of Amapá has the lowest deforestation rate in Brazil and > 70% of the Amapá receives some form of legal protection. There is no large scale agricultural developments or monocultures along the waterways and properties retain typically small (< 1000 ha) areas of opened land, which are cleared for small scale family agriculture, which focuses on acai, small scale production of fruits and vegetables for sustenance and limited commercial sale of regional produce (e.g. manioc flour) in local markets. There are some 54 properties upstream of the nearest town (Porto Grande [67]). There has never been any expansive clearcutting in the region and there are no monocultures (e.g. soy) or cattle production. All sites were at least 26 km from the nearest town by river, and all sites are surrounded by matrix of continuous closed canopy forest cover (Table 2). Pesticides and/or herbicides had never been used at any of the sites.

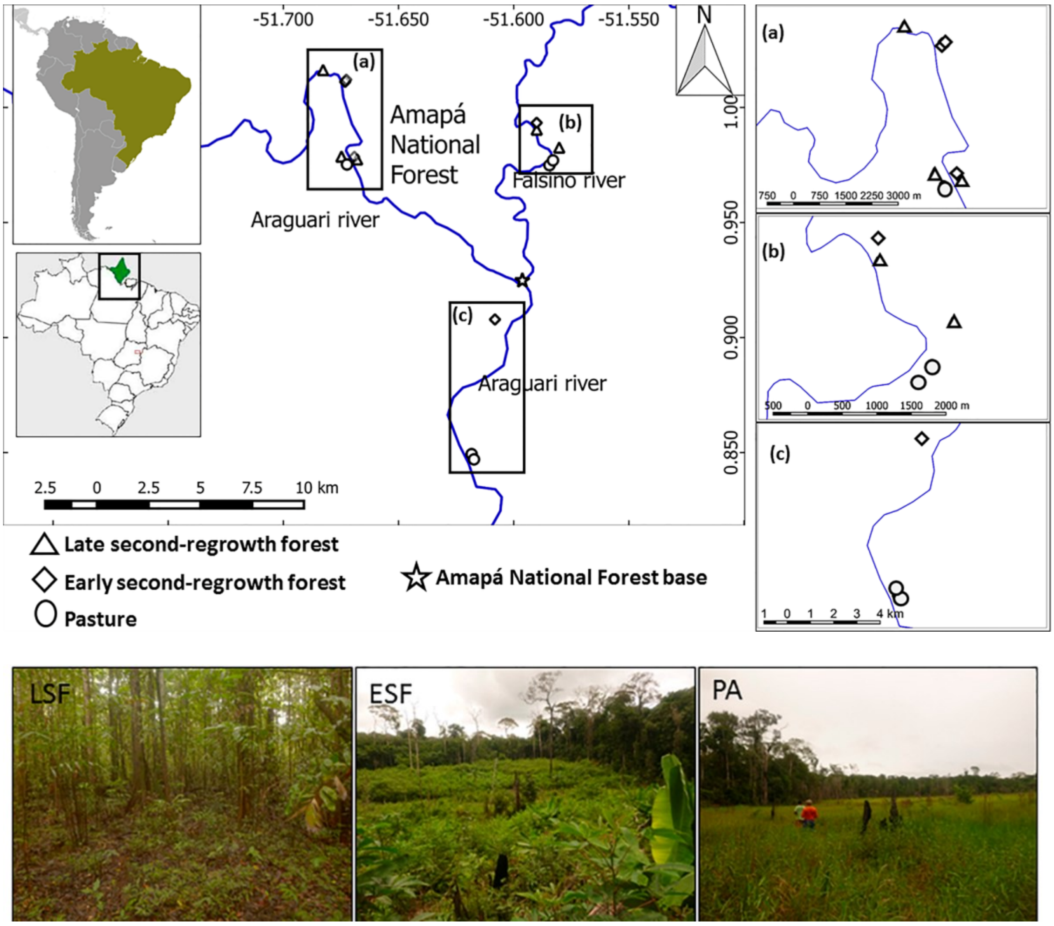

Fig. 5. Map of the study area in the eastern Amazon. Showing the location of 15 study sites, grouped into three regrowth stages in the small holder properties close to rivers (solid blue lines): late second-regrowth forest (LSF, triangles), early second-regrowth forest (ESF, squares) and pasture (PA, circles).

A described previously[53,64] the 15 small-holder properties were selected based on differences in land-use histories and forest succession/regrowth stage. All sites were close (110 – 554m, Table 2) to 100 – 200 m wide rivers that are navigable by motorized boats, but due to riverbank formation the sites are never flooded. These 15 sites were grouped into three regrowth classes based on the land-use history: late second-regrowth forest (N = 5, most recent human disturbance between 20 and 25 years), early second-regrowth (N = 5, most recent human disturbance between 1 and 5 years), and pasture (N = 5, recently cleared and abandoned pasture areas dominated by grasses/herbs but that had never been used to raise livestock, with the most recent disturbance between 1 and 17 years). Each of the 15 regrowth sites was paired with a nearby (60 to 150 m) control site i.e. 20 – 30 m tall *terra-firme* forest site without a history of mechanized timber extraction. To reduce the possible confounding influence of edge effects that are known to strongly influence the distribution of trees in Neotropical forests, all regrowth and control sites were established at a standardized distance (approximately 30 m) from the nearest control-regrowth habitat edge.

Forest structure

Data were collected from May to August 2016. Forest structure data (i.e., number of trees and basal area) were obtained from plots measuring 50 x 10 m (500 m^2), at each of the 30 points, totaling 1.5 hectare. This plot size was selected as it has been widely used to examine structural changes in tropical forests [19,41,42,68] and several of the regrowth areas were too small (Table 2) to enable the establishment of larger spatially independent plots. We obtained five measures (responses) to characterize the forest structure in each plot. These were selected based on previous studies that show their appropriateness to distinguish attributes of regrowth/successional stages related to biodiversity of Amazon forests [13,44,69,70]. The number of all trees ≥ 10 cm DBH (diameter at breast height at a standard 1.3 m above ground, or above tallest root buttress) was used to quantify the number of trees per area in each plot (m^2). This count included all trees which had at least half of their basal trunk inside the plot. The proportion of small (10 – 20 cm DBH) trees was calculated to represent the expected increase of younger trees in regrowth areas. The proportion of large (>60 cm DBH) trees was calculated as this is known as an important characteristic of mature/late succession areas [44,70]. We also calculated the basal area of all and large trees as this is known to be strongly correlated with tree biomass [71]. For example basal area and biomass were > 99% correlated in 23 plots from lowland Costa Rica [10].

Explanatory variables

We investigated predictions from multiple non-mutually exclusive hypotheses to explain patterns in basal area (Table 1). A total of 10 variables were used to form models to represent 5 working hypotheses (topography, hydrography, regrowth class, time and mammal diversity) that based on the findings from previous studies were likely to explain the observed patterns [10,13,28,40,41,72]. We chose to work with mainstream, widely available environmental variables. Four of these (the topographic and hydrographic model variables) were computed from remotely sensed digital terrain model (SRTM-DTM): altitude (masl), slope, TWI (Topographic wetness index), DND (Distance to Network Drainage) calculated from the interaction between HAND (Height above network drainage) and HDND (Horizontal distance to network drainage). The time model included years since the regrowth site was opened and years since last use, both of which were obtained from interviews with local landowners.

Mammal functional diversity was obtained from a camera-trap survey conducted at the same time (May to September 2016) and in the same plots as forest structure was sampled [53]. Camera traps equipped with infrared triggers (Bushnell Trophy Cam, 8MP, Overland Park, KS, USA) were installed in each of the 30 plots following standardized protocols [50,51,73]. This camera trap survey [full details provide in [53]] including a sampling effort of 827 camera-trap days (450 and 377 camera-trap days, control and regrowth sites respectively) was used to estimate functional diversity of eight terrestrial mammal seed dispersers (*Cuniculus paca*, *Dasyprocta leporina*, *Myoprocta acouchy*, *Mazama americana*, *M. nemorivaga*, *Pecari tajacu*, *Tayassu pecari* and *Tapirus terrestris*).

Data analysis

Tree Basal Area in each plot was obtained as the sum of the basal area value for each individual tree derived from the DBH of each tree following the formula BA (basal area in m^2)=

0.00007854 X DBH^2 (constant obtained by solving the following equation to obtain BA in m^2 from the DBH measured in cm [69]):

$$BA = \frac{\pi \times (DBH/2)^2}{10000}$$

We calculated basal area of all and large (>60cm DBH) living trees [69,70,72]. We also calculated the proportion of small stems (10 – 20 cm DBH trees) as this has been shown to be an important measure of stand structure in forest regrowth areas [35,69].

To represent diversity of terrestrial mammal seed dispersers we calculated a richness and functional diversity (FD) value for each of the 30 plots [53]. Richness was calculated as the observed number of species (hereafter “species richness”) at each plot. Although there are many diversity metrics, we chose species richness as it is widely used and clearly interpretable [74,75] and with relatively few (eight) species and 30 plots there were strong correlations between species richness values and alternative diversity metrics such as Shannon and Simpson diversity (Spearman rho > 0.89). We used Functional Dispersion (FDis) [76] as an index of functional diversity as it is not strongly influenced by outliers, accounts for relative abundances, is unaffected by species richness and can be calculated from any distance/dissimilarity measure [76,77]. Functional Dispersion was estimated with the dbFD function [77] using default settings.

To examine patterns in forest structure attributes we used Generalized Linear Models. We used an information theoretic model averaging framework [78] to examine the support for five models representing the five non-mutually exclusive hypotheses – topography, hydrography, regrowth class, time and mammal diversity (see Table 1 for variable description and ecological relevance). We evaluated models based on their information content, as measured by AIC – Akaike Information Criterion. The relative importance of the models was measured by the models Akaike weights (Burnham & Anderson 2002 pp. 75-77, 167-172), which is a scaled measure of the likelihood ratio that ranges between 0 (least important) and 1 (most important). None of the unexplained variation (model residuals) was related to the geographic distance among plots so we did not need to control for spatial dependence. All analysis were conducted using the R language and environment for statistical computing [79], with base functions and functions available in the following packages: vegan [80], ggplot2 [81], MuMIn [82], and tweedie [83].

Data Availability Statement

The raw forest structure and environmental data used in the analysis of this study have been deposited in the OSF - Center for Open Science at DOI: 10.17605/OSF.IO/MC27U.

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Author Contributions

D.N. conceived of the project; V.J.U.CR and A.A.S collected data. V.J.U.CR, A.A.S and D.N. performed data analysis and interpretation. A.A.S prepared figure 1. D.N. prepared figures 2-5. T.M.F.C and D.N. wrote the main manuscript text. All authors reviewed and revised the manuscript.

Competing Interests Statement

The authors declare that they have no competing interests as defined by Nature Research, or other interests that might be perceived to influence the results and/or discussion reported in this paper.

Supporting Information

Big trees drive forest structure patterns across a lowland Amazon regrowth gradient

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Supplementary Table S1

Table S1: Generalized Linear Model values.

	All trees						Large trees					
	Full			Best			Full			Best		
Predictors	*Est.*	*CI*	*p*	*Est.*	*CI*	*p*	*Est.*	*CI*	*p*	*Est.*	*CI*	*p*
(Intercept)	0.46	0.40–0.53	**<0.001**	0.46	0.43–0.50	**<0.001**	0.66	0.50–0.81	**<0.001**	0.64	0.55–0.76	**<0.001**
Last use	0.00	-0.00–0.00	0.933				-0.00	-0.01–0.01	0.896			
Regrowth (late v early)	-0.01	-0.10–0.07	0.826	-0.03	-0.08–0.01	0.176	-0.04	-0.24–0.17	0.710	-0.05	-0.20–0.08	0.441
Regrowth (late v pasture)	-0.00	-0.09–0.08	0.966	-0.03	-0.07–0.02	0.245	-0.08	-0.27–0.10	0.355	-0.07	-0.21–0.06	0.311
Plot (control v regrowth)	0.14	0.02–0.28	**0.050**	0.08	0.02–0.14	**0.022**	0.02	-0.40–0.44	0.917	0.53	0.24–1.14	**0.016**
Interaction (Last use * early)	-0.01	-0.02–0.01	0.467				-0.01	-0.05–0.03	0.525			
Interaction (Last use * pasture)	-0.00	-0.01–0.00	0.386				-0.00	-0.01–0.01	0.986			
Interaction (Last use * Plot)	-0.00	-0.01–0.00	0.280				0.03	-0.04–0.10	0.339			
Interaction (Plot * early)	0.03	-0.11–0.17	0.624	0.09	-0.01–0.19	0.090	46.73		0.999			
Interaction (Plot * pasture)	0.15	0.02–0.29	**0.040**	0.17	0.06–0.30	**0.011**	42.03		0.999			
Observations	30			30			30			30		
R^2 Nagelkerke	0.83			0.80			0.81			0.74		
AIC	229.40			225.62			140.45			132.02		

Supplementary Table S2

Generalized Linear Models created to explain forest structure in 30 plots (15 control and 15 regrowth). Model summaries for responses of five structural attributes: (a) The number of all trees ≥ 10 cm DBH ; (b) Proportion of small (DBH 10 – 20 cm) trees; (c) Proportion of large (DBH >60 cm) trees; (d) Basal area of all trees; (e) Basal area of large trees. Showing slope estimates (“Est”) for 10 variables in 5 models (time, regrowth class, mammal diversity, hydrography and topography). “NE” denotes cases when values could not be reliably estimated. The time model included years since the regrowth site was opened and years since last use. The regrowth model included sites grouped into three regrowth classes (pasture, early-regrowth and late-regrowth). Topography included altitude (masl) and slope. Hydrography was modelled with TWI (Topographic wetness index), DND (Distance to Network Drainage) calculated from the interaction between HAND (Height above network drainage) and HDND (Horizontal distance to network drainage). Mammal diversity was obtained from camera-traps and quantified as species richness and Functional Dispersion (FDis).

(a) The number of all trees DBH ≥ 10 cm

	Time			**Regrowth class**			**Mammals**			**Hydrography**			**Topography**		
Predictors	*Est*	*CI*	*p*	*Est*	*CI*	*p*	*Est*	*CI*	*p*	*Est*	*CI*	*p*	*Est*	*CI*	*p*
(Intercept)	35.4	15.9–55.0	**0.002**	35.2	27.3–43.1	**<0.001**	25.04	5.31–44.77	**0.021**	20.04	-25.26–65.35	0.395	33.66	-67.46–134.78	0.521
Plot type	-5.2	-32.9–22.4	0.714	6.6	-4.6–17.8	0.257	-8.48	-29.64–12.67	0.440	-95.06	-201.10–10.97	0.093	-402.66	-1045.25–239.93	0.232
Since first open	-0.2	-1.2–0.9	0.764												
Since last use	0.1	-2.7–2.8	0.954												
Plot *First	-0.4	-1.9–1.1	0.573												
Plot *Last	-0.8	-4.7–3.1	0.703												
First *Last	0.0	-0.1–0.1	0.963												
Plot *First *Last	0.1	-0.1–0.3	0.388												
Regrowth (Late v Early)				-1.2	-12.4–10.0	0.835									
Regrowth (Late v Pasture)				-2.4	-13.6–8.8	0.677									
Plot *Early				-14.0	-29.8–1.8	0.095									
Plot*Pasture				-23.2	-39.0–-7.4	**0.008**									
Species.richness							2.9	-7.0–12.8	0.571						
Functional.dispersion							41.7	-78.5–162.0	0.503						
Plot *Species.richness							15.1	1.6–28.5	**0.039**						
Plot *FDis							-37.0	-174.8–100.75	0.604						

	Time			Regrowth class			Mammals			Hydrography			Topography		
Richness *FDis							-11.6	-52.86–29.65	0.587						
Plot *Richness *FDis							-36.2	-88.80–16.5	0.192						
TWI										1.8	-4.2–7.8	0.561			
DND										-6.6	-42.1–29.0	0.722			
Plot * TWI										12.7	-2.0–27.3	0.105			
Plot * DND										-155.8	-285.0–-25.3	**0.029**			
TWI * DND										1.6	-4.6–7.7	0.623			
Plot * TWI* DND										20.4	0.9–39.9	0.053			
Altitude													-0.0	-1.0–1.0	0.980
Slope													-1.7	-16.9–13.8	0.845
Plot *Altitude													3.7	-2.4–9.7	0.250
Plot * Slope													37.9	-70.3–146.2	0.499
Altitude * Slope													0.0	-0.1–0.2	0.813
Plot *Altitude* Slope													-0.34	-1.4–0.7	0.522
Observations	30			30			30			30			30		
R^2 Nagelkerke	1.000			1.000			1.000			1.000			1.000		
Deviance	2206.473			1942.400			1883.533			2095.536			1438.744		
AIC	232.075			224.251			227.328			230.527			219.246		
log-Likelihood	-107.037			-105.125			-104.664			-106.264			-100.623		

(b) Proportion of small (DBH 10 – 20 cm) trees

	Time			**Regrowth class**			**Mammals**			**Hydrography**			**Topography**		
Predictors	*OddsRatios*	*CI*	*p*	*OddsRatios*	*CI*	*p*	*OddsRatios*	*CI*	*p*	*OddsRatios*	*CI*	*p*	*OddsRatios*	*CI*	*p*
(Intercept)	1.1	0.6–2.2	0.704	1.6	1.2–2.2	**0.002**	1.1	0.5–2.5	0.778	0.5	0.11–2.7	0.461	5.2	0.1–515.3	0.475
Plot type	38.4	8.6–236.0	**<0.001**	3.7	2.0–5.1	**<0.001**	5.7	2.1–15.3	**0.001**	0.4	0.00–66.8	0.713	126.0	0.0–313.0	0.713
Since first open	1.0	1.0–1.1	0.336												
Since last use	1.0	0.9–1.1	0.834												
Plot *First	0.9	0.8–1.0	**0.015**												
Plot *Last	0.8	0.7–1.0	**0.017**												
First *Last	1.0	1.0–1.0	0.841												
Plot *First *Last	1.0	1.0–1.0	**0.029**												
Regrowth (Late v Early)				0.8	0.5–1.2	0.302									
Regrowth (Late v Pasture)				1.0	0.6–1.5	0.856									
Plot *Early				1.7	0.8–3.6	0.190									
Plot*Pasture				1.0	0.4–2.2	0.938									
Species.richness							1.2	0.8–1.8	0.284						
Functional.dispersion							2.3	0.0–256.3	0.724						
Plot *Species.richness							1.3	0.7–2.5	0.415						
Plot *FDis							0.0	0.0–0.3	**0.020**						
Richness *FDis							0.5	0.1–2.4	0.389						
Plot *Richness *FDis							1.7	0.1–22.2	0.702						
TWI										1.1	1.0–1.4	0.210			
DND										0.4	0.1–1.5	0.200			
Plot * TWI										1.3	0.6–2.6	0.464			
Plot * DND										0.0	0.0–12.4	0.211			
TWI * DND										1.2	0.9–1.5	0.169			

	Time			Regrowth class			Mammals			Hydrography			Topography		
Plot * TWI* DND										1.5	0.6–3.8	0.411			
Altitude													1.0	1.0–1.0	0.775
Slope													0.6	0.3–1.2	0.153
Plot *Altitude													0.9	0.6–1.5	0.803
Plot * Slope													0.7	0.0–160.2	0.920
Altitude * Slope													1.0	1.0–1.0	0.190
Plot *Altitude* Slope													1.0	0.9–1.1	0.965
Observations	30			30			30			30			30		
R^2 Tjur	0.133			0.111			0.113			0.188			0.192		
Deviance	46.970			60.088			45.259			39.873			33.410		
AIC	158.064			167.181			156.352			150.967			144.503		
log-Likelihood	-71.032			-77.591			-70.176			-67.483			-64.252		

15 (c) Proportion of large (DBH >60 cm) trees

	Time			Regrowth class			Mammals			Hydrography			Topography		
Predictors	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*
(Intercept)	0.0	0.0–0.1	**<0.001**	0.0	0.0–0.1	**<0.001**	0.1	0.0–0.5	**0.004**	0.0	0.0–0.8	**0.032**	6.43	NE	0.647
Plot type	0.4	0.0–54.2	0.714	0.2	0.0–0.9	**0.042**	0.0	0.0–0.9	**0.040**	3.9	NE	0.887	NE	NE	0.830
Since first open	1.1	1.0–1.2	0.071												
Since last use	1.2	1.0–1.5	0.088												
Plot *First	1.0	0.7–1.2	0.685												
Plot *Last	0.8	0.4–1.6	0.492												
First *Last	1.0	1.0–1.0	0.060												
Plot *First *Last	1.0	1.0–1.0	0.505												
Regrowth (Late v Early)				1.5	0.6–3.8	0.417									
Regrowth (Late v Pasture)				2.4	1.0–5.8	0.060									
Plot *Early				0.3	0.0–9.6	0.526									
Plot*Pasture				0.3	0.0–9.7	0.530									
Species.richness							0.9	0.4–1.8	0.653						
Functional.dispersion							0.6	NE	0.921						
Plot *Species.richness							0.1	0.0–5.3	0.271						
Plot *FDis							165.7	NE	0.540						
Richness *FDis							0.9	0.0–17.0	0.936						
Plot *Richness *FDis							1114.3	NE	0.253						
TWI										1.1	0.7–1.6	0.659			
DND										0.6	0.1–4.9	0.593			
Plot * TWI										0.6	0.0–7.5	0.669			
Plot * DND										NE	NE	0.393			

	Time			Regrowth class			Mammals			Hydrography			Topography		
TWI * DND										1.1	0.8–1.6	0.562			
Plot * TWI* DND										0.3	0.0–10.4	0.462			
Altitude													0.96	0.89–1.03	0.265
Slope													0.63	0.18–2.16	0.464
Plot *Altitude													0.81	0.13–5.00	0.821
Plot * Slope													0.12	NE	0.897
Altitude * Slope													1.00	0.99–1.01	0.406
Plot *Altitude* Slope													1.02	0.75–1.38	0.906
Observations	30			30			30			30			30		
R^2 Tjur	0.027			0.008			0.001			0.028			0.026		
Deviance	22.439			23.760			22.382			28.416			27.326		
AIC	72.554			69.778			72.532			78.313			77.272		
log-Likelihood	-28.277			-28.889			-28.266			-31.156			-30.636		

19 (d) Basal area of all trees

	Time			Regrowth class			Mammals			Hydrography			Topography		
Predictors	*Est*	*CI*	*p*	*Est*	*CI*	*p*	*Est*	*CI*	*p*	*Est*	*CI*	*p*	*Est*	*CI*	*p*
(Intercept)	0.45	0.39–0.52	**<0.001**	0.46	0.43–0.50	**<0.001**	0.43	0.36–0.51	**<0.001**	0.48	0.31–0.65	**<0.001**	0.48	0.10–0.90	**0.028**
Plot type	0.21	0.03–0.43	**0.046**	0.08	0.02–0.14	**0.022**	0.25	0.13–0.38	**0.001**	0.35	-0.59–1.47	0.500	4.85	-0.94–10.40	0.106
Since first open	-0.00	-0.00–0.00	0.956												
Since last use	-0.00	-0.01–0.00	0.341												
Plot *First	-0.00	-0.01–0.01	0.790												
Plot *Last	0.00	-0.02–0.02	0.998												
First *Last	0.00	-0.00–0.00	0.331												
Plot *First *Last	-0.00	-0.00–0.00	0.719												
Regrowth (Late v Early)				-0.03	-0.08–0.01	0.176									
Regrowth (Late v Pasture)				-0.03	-0.07–0.02	0.245									
Plot *Early				0.09	-0.01–0.19	0.090									
Plot*Pasture				0.17	0.06–0.30	**0.011**									
Species.richness							0.01	-0.03–0.05	0.624						
Functional.dispersion							-0.04	-0.53–0.42	0.855						
Plot *Species.richness							-0.06	-0.15–0.03	0.192						
Plot *FDis							-0.53	-1.28–0.22	0.178						
Richness *FDis							-0.01	-0.17–0.15	0.900						
Plot *Richness *FDis							0.22	-0.11–0.57	0.210						
TWI										-0.01	-0.03–0.02	0.634			
DND										0.05	-0.09–0.17	0.499			
Plot * TWI										-0.03	-0.18–0.10	0.679			
Plot * DND										0.46	-0.74–1.86	0.486			

TWI * DND										-0.01	-0.03–0.02	0.468			
Plot * TWI* DND										-0.06	-0.26–0.12	0.553			
Altitude													0.00	-0.00–0.00	0.994
Slope													-0.02	-0.08–0.03	0.412
Plot *Altitude													-0.04	-0.10–0.01	0.126
Plot * Slope													-0.48	-1.33–0.43	0.297
Altitude * Slope													0.00	-0.00–0.00	0.473
Plot *Altitude* Slope													0.00	-0.00–0.01	0.316
Observations	30			30			30			30			30		
R^2 Nagelkerke	0.997			0.998			0.997			0.996			0.999		
Deviance	74.501			65.927			68.631			82.585			47.959		
AIC	233.200			225.615			230.793			236.227			220.376		

22 (e) Basal area of large trees

	Time			Regrowth class			Mammals			Hydrography			Topography		
Predictors	*Est*	*CI*	*p*	*Est*	*CI*	*p*	*Est*	*CI*	*p*	*Est*	*CI*	*p*	*Est*	*CI*	*p*
(Intercept)	0.7	0.5–0.9	**<0.001**	0.7	0.6–0.7	**<0.001**	0.7	0.4–0.7	**<0.001**	0.7	0.4–1.0	**<0.001**	0.5	-0.53–1.71	0.406
Plot type	535.7	NE	0.998	0.3	-0.0–0.6	0.051	62.9	NE	0.999	NE	NE	0.823	-31.5	-204.4–39.4	0.552
Since first open	-0.0	-0.0–0.0	0.303												
Since last use	-0.0	-0.0–0.0	0.186												
Plot *First	-26.7	NE	0.998												
Plot *Last	-27.4	NE	0.998												
First *Last	0.0	-0.0–0.0	0.159												
Plot *First *Last	1.4	-1447.1–1449.9	0.998												
Regrowth (Late v Early)				-0.1	-0.2–0.0	0.189									
Regrowth (Late v Pasture)				-0.1	-0.2–0.0	0.103									
Plot *Early				39.5	NE	0.998									
Plot*Pasture				39.5	NE	0.998									
Species.richness							0.0	-0.1–0.1	0.762						
Functional.dispersion							-0.1	-1.0–0.8	0.811						
Plot *Species.richness							89.8	NE	0.999						
Plot *FDis							-212.3	NE	0.999						
Richness *FDis							0.0	-0.3–0.3	0.859						
Plot *Richness *FDis							-252.1	NE	0.999						
TWI										-0.02	-0.1–0.0	0.392			
DND										0.11	-0.1–0.3	0.273			
Plot * TWI										-63173.6	NE	0.823			
Plot * DND										976655.4	NE	0.823			

	Time			Regrowth class			Mammals			Hydrography			Topography		
TWI * DND										-0.02	-0.1–0.0	0.239			
Plot * TWI* DND										-96752.4	NE	0.823			
Altitude													0.0	-0.0–0.0	0.765
Slope													-0.0	-0.2–0.1	0.861
Plot *Altitude													0.3	-0.4–1.9	0.550
Plot * Slope													5.7	-6.2–36.0	0.536
Altitude * Slope													0.0	-0.0–0.0	0.913
Plot *Altitude* Slope													-0.1	-0.3–0.1	0.538
Observations	30			30			30			30			30		
R^2 Nagelkerke	1.000			1.000			1.000			1.000			1.000		
Deviance	140.557			134.847			121.384			119.165			161.409		
AIC	138.281			133.726			136.303			136.050			140.145		