



Seedling fate across different habitats: The effects of herbivory and soil fertility

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Abstract

The impact of extinction of predators and subsequent herbivore release on ecosystem functioning has been well studied in temperate ecosystems, yet we have very little information on threatened tropical rainforests. Herbivore overbrowsing can have profound effects on ecosystem processes through overconsumption or by altering organic inputs of leaves and roots as well as changing soil physical and chemical properties. We evaluated the fate of transplanted seedlings of four tropical tree species and nutrient availability in open control plots and enclosed plots that permitted free access by insects and excluded vertebrates and collected soil samples in old-fields, early secondary forests and old-growth forests. Seedling damage predominantly occurred in the dry season and produced an overall seedling mortality of 72%, with values of 43% and 86% in the plots that prohibited and permitted vertebrate access, respectively. Except for *Myrsine coriacea* in the old-fields and *Syagrus romanzoffiana* in the early secondary forest, seedlings suffered greater rates of damage and mortality in the open plots, showing that the aboveground large herbivores, such as capybaras (*Hydrochoerus hydrochaeris*), might prevent or at least delay plant recruitment in tropical areas supporting elevated densities. However, delayed deaths from disease by soil fertility-related factors were observed in late summer in the old-field seedlings, suggesting that previous activities in these areas had led to profound changes in the soil properties. Herbivores may have important consequences for tropical forest regeneration, as overconsumption may slow down nutrient cycling, promote cascading bottom-up effects on consumers, and ultimately lead to ecological meltdown. These consequences provide insight into the ecological effects of faunal change on human-altered tropical habitats.

Zusammenfassung

Die Auswirkungen des Aussterbens von Räubern und der anschließenden Entlastung von Herbivoren auf das Funktionieren von Ökosystemen wurden in gemäßigten Ökosystemen gut untersucht, aber wir haben wenige Informationen zu bedrohten tropischen Regenwäldern. Die Überbeweidung durch Herbivoren kann erhebliche Effekte auf Ökosystemprozesse haben und zwar durch Überkonsumption oder durch die Veränderung von organischen Einträgen durch Blätter und Wurzeln sowie geänderte

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physikalische und chemische Eigenschaften. Wir untersuchten das Schicksal transplantierte Sämlinge von vier tropischen Baumarten und die Nährstoffversorgung in offenen Kontroll-Plots und Ausschluss-Plots, die für Insekten zugänglich waren aber Wirbeltiere ausschlossen. Dazu nahmen wir Bodenproben auf alten Feldern, in jungem Sekundärwald und in alten Waldbeständen. Beschädigungen der Sämlinge traten hauptsächlich während der Trockenzeit ein und ergaben eine Gesamtmortalität von 72% mit 43% und 86% Mortalität auf Flächen ohne bzw. mit Zugang für Wirbeltiere. Mit Ausnahme von *Myrsine coriacea* auf den alten Feldern und *Syagrus romanzoffiana* im jungen Sekundärwald erlitten die Sämlinge auf den offenen Plots höhere Beschädigungs- und Mortalitätsraten, was zeigt, dass große oberirdische Herbivoren wie das Wasserschwein (*Hydrochoerus hydrochaeris*), den Neuaufwuchs in tropischen Gebieten, die höheren Besatz erlauben, verhindern oder zumindest verzögern könnten. Indessen wurde verzögertes Absterben durch Erkrankungen durch mit der Bodenfruchtbarkeit zusammenhängende Faktoren im Spätsommer bei Sämlingen auf den alten Feldern beobachtet, was nahelegt, dass frühere Aktivitäten zu grundlegenden Änderungen der Bodeneigenschaften auf diesen Flächen geführt hatten. Herbivore könnten wichtige Konsequenzen für die Regeneration von tropischen Wäldern haben, indem Überkonsumption den Nährstoffkreislauf verlangsamt, kaskadierende bottom-up-Effekte auf die Konsumenten befördert und schließlich zum ökologischen Zusammenbruch führt. Diese Konsequenzen gewähren einen Einblick in die ökologischen Effekte von Veränderungen der Fauna auf vom Menschen veränderte tropische Habitate.

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Introduction

The contemporary tropical extinction crisis is strictly allied to human activities, such as land-use change (forest destruction and fragmentation), invasive species, overexploitation, and climate change (MA 2005; Bradshaw, Sodhi, & Brook 2009). These degraded human-impacted “new forests” do not match the pristine forests in species richness and composition (Hobbs et al. 2006; Hobbs, Higgs, & Harris 2009), showing unpredictable forest recovery pathways owing to new interactions among organisms and between organisms and their environment (Suding & Hobbs 2009). Several of these forests are fading, exhibiting arrested development and/or are infested by invasive species (Chazdon 2008).

Human impacts on biodiversity can reduce the stability of ecological communities (Seddon, Griffiths, Soorae, & Armstrong 2014). Particularly, predator extinction or depletion can lead to herbivore release (Terborgh & Feeley 2010), impacting a wide variety of ecological functions (Ripple, Larsen, Renkin, & Smith 2001; Dirzo et al. 2014; Ripple et al. 2014). The potential role of predator loss in controlling ecosystem functioning is poorly known in tropical forests but appears to confirm the general trend of temperate ecosystems (see review by Ripple et al. 2014). As a major implication, the densities of canopy tree seedlings and saplings are severely reduced in predator-free areas supporting elevated densities of herbivores, confirmed by the tropical case study-based of Lago Guri in Venezuela (Terborgh et al. 2001; Lopez & Terborgh 2007).

The degree of herbivore impact depends on the timing and intensity of defoliation (Doak 1992), the incidence of past stresses (Cornelissen, Diez, & Hunt 1996), soil nutrient and moisture levels (Maschinski & Whitham 1989; Silla, Fleury, Mediavilla, & Escudero 2008), and herbivore abundance

(Côté, Rooney, Tremblay, Dussault, & Waller 2004). Thus, these aspects may have profound consequences for forest regeneration (Coley 1998; van der Heijden, Bardgett, & van Straalen 2008), particularly in tropical ecosystems, many of which already have nutrient-poor soils (Jordan & Herrera 1981) decreasing the probability of plant compensation for herbivory (Maschinski & Whitham 1989). Therefore, it is paramount to understand the effects of trophic cascades mediated by the absence of top predators and the overabundance of herbivores in plant regeneration in these areas.

Here, we evaluated the relative effect of aboveground herbivores (vertebrates and insects) and soil fertility on seedling fate across logging disturbance regimes in an Atlantic rainforest fragment with the highest density and biomass of vertebrate herbivores of the Atlantic forest (capybara 1112 kg km⁻², paca 97 kg km⁻², agouti 428 kg km⁻²) (see Bovendorp & Galetti 2007). Seedlings were transplanted into sites and soil samples were collected at three stages of habitat degradation (old field, early secondary and old-growth forests). These seedlings were planted in open control plots and in enclosed plots, which allowed free access to insects and excluded vertebrates. The seedlings were monitored over a year. We hypothesized that aboveground vertebrate herbivores are suppressing seedling establishment and, thus, that seedling survival would be higher in the plots from which vertebrates were excluded. However, we expected herbivore seasonal shifts as a result of changes in space use and foraging behavior over time (Quintana, Monge, & Malvarez 1994; Barreto & Herrera 1998; Giesel, Boff, & Boff 2013), resulting in habitat-specific damages to seedlings due to differences in plant species composition and structure among habitats. We predicted higher seedling damage in old field, where grasses are more common, as a result of more intensive grazing and trampling by vertebrates (Côté et al. 2004).

and leaf-cutter ant harvesting (Vasconcelos & Cherrett 1997), high to intermediate damage in early secondary forest due to abundant, high-quality forage (Coley 1983), and low damage in the low-production old-growth forest understory (Côté et al. 2004). We expected that soil properties would be unfavorable, inhibiting succession in the degraded old field and enhancing succession in early secondary and old-growth forest habitats as biomass accumulates (Chazdon 2003). An understanding of the mechanisms that shape human disturbed environments will help our ability to manage and conserve degraded, human-impacted “new forest” ecosystems.

Materials and methods

Study site

The study was conducted on Anchieta Island, a State Park covering an area of 806 ha, in southeastern Brazil (45°02' W–23°27' S). According to Köppen's climate classification system (Köppen 1948), the study site climate can be classified as Cwa. The total annual rainfall in the region is about 2100 mm, concentrated in the super-humid season from September to May (austral summer). The less-humid season, hereafter called as “dry season”, occurs from June to August (austral winter). There is no rainfall deficit in the study site (Genini, Galetti, & Morellato 2009). Although the island is approximately 400 m from the mainland – a surmountable obstacle for several animals and propagules (see review by Nogales, Heleno, Traveset, & Vargas 2012 and references therein) – and was left to regenerate naturally with no human intervention since 1977, it is largely covered with successional habitat types resulting from differential historic land-use intensity within the study area, which ranged from limited logging (old-growth forest) to extensive clearance (old-field). The island lacks top predators, such as jaguar, puma and ocelot, and the population of herbivores is significantly higher than the populations on the mainland or other tropical forests (capybara, red-rumped agouti, and paca) (see Bovendorp & Galetti 2007). Capybaras (*Hydrochaeris hydrochaeris*), with a weight of 50–60 kg, represent the highest herbivore biomass on the island with nearly 35 individuals km⁻² (Bovendorp & Galetti 2007).

Our surveys and experiments were conducted across the three Atlantic Forest habitats (old-fields, early secondary forests and old-growth forests) present on Anchieta, which comprise more than 93% of the area. The early secondary forest (409 ha, comprising 50.7% of the total land cover) contains predominantly small trees and is characterized by an open canopy with abundant anemochoric and pioneer species (Calderón-Miller 2008). In the 211 ha of old-growth forest (26.1%), palm trees – a key component of tropical forests (Svenning, Brorchsenius, Bjorholm, & Balsev 2008) – are more frequent, and this succession stage presenting a more stratified vegetation, including epiphytes, and a closed canopy layer. The 135 ha of old-field habitat (16.7%) contain patches of bare soil and herbaceous species with sparse shrubs largely dominated by *Miconia albicans*, *Myrsine coriacea*, *M. ferruginea* and fern species (*Gleichenella* spp.), which represent the lowest canopy layer (see Genini et al. 2009; Fleury, Rodrigues, do Couto, & Galetti 2014 for a full study site description).

Experimental design

Seedling survival

The seedling survival experimental stations ($n = 3$ per habitat) were randomly located along the trails, and we utilized a balanced split plot design to test the habitat and isolated effects of vertebrate herbivores on seedling survival. Each experimental station comprised a 24 m × 24 m parcel split into one open plot and an exclusion plot, which was enclosed using 2.5 cm welded wire fencing with a height of 1.5 m. Each experimental station contained ten 24 m rows with 6 transplanted seedlings per species, spaced 5 m apart, totaling 60 seedlings per species with two species per habitat.

We tested species with different environmental requirements and seed dispersal modes (Table 1). We used *M. coriacea* and *Schizolobium parahyba* in the old-fields and the palms *Syagrus romanzoffiana* and *Euterpe edulis* in the early secondary and old-growth forests. *M. coriacea* is one of the most common species in old-field areas, whereas *S. parahyba*, a fast-growing species and an important natural perch, is sparsely distributed. The palm species are considered keystone species (Terborgh 1986; Galetti et al. 2013)

Table 1. Seed and seedling characteristics of the four tree species tested in this study, listed in order of increasing shade tolerance. Mean values (\pm SE) for seedling height and number of leaves were obtained at the time of transplant to the field (March 2006).

Species	Family	Habitat ^a	Dispersal syndrome	Seed mass (g)	Seedling height ^b	Number of leaves
<i>Myrsine coriacea</i>	Primulaceae	Pioneer	Birds	0.02 \pm 0.004	17.62 \pm 4.45	9.15 \pm 2.45
<i>Schizolobium parahyba</i>	Leguminosae	Early secondary	Wind	1.74 \pm 0.25	17.95 \pm 3.74	2.00 \pm 0.67
<i>Syagrus romanzoffiana</i>	Arecaceae	Late secondary	Mammal	1.63 \pm 0.42	3.02 \pm 0.86	2.00 \pm 0.38
<i>Euterpe edulis</i>	Arecaceae	Climax	Birds	1.11 \pm 0.15	10.10 \pm 1.91	3.16 \pm 0.65

^asensu Budowski (1965).

^bMeasured in centimeters from the soil surface to the apical meristem of 180 or 360 individuals per species for *M. coriacea* and *S. parahyba* or *S. romanzoffiana* and *E. edulis*, respectively.

and play an important role at the study site, contributing more than 80% of the overall fruitfall biomass (Genini et al. 2009). Palm trees are absent in the old-fields, have few tree stands in the secondary forest and are more frequent in the old-growth forest. Although using different species for old-field sites than for the rest of the habitats could cause potential confounding factors, the early secondary forest and old-growth forest do not share woody species with the old-field site, most likely owing to contrasting abiotic conditions. Thus, we set up our experiments according to succession processes and the habitat requirements for the tested species. In addition, previous studies have shown that the phylogenetic relationship of plants is a weak predictor of the similarity of associated herbivore assemblages (Ødegaard, Diserud, & Østbye 2005).

To mitigate the probability that morphological variation could influence seedling performance, a total of 1080 nursery-grown seedlings of the four study species were obtained in similar sizes within species (Table 1) and maintained for 45 days at intermediate site conditions before being transplanted to the field. In March 2006, the seedlings were simultaneously transplanted to the field to avoid bias from temporal variation in mortality risk (Hurlbert 1984). The seedlings were examined bimonthly in the first half of the year-long experiment, and at 3-month intervals thereafter; hence, five sets of measurements were conducted. At each census, all seedlings were examined for particular types and intensity of damage and classified as dead or alive. A seedling was considered dead when it was dried, uprooted, severed at the stem or completely missing. The intensity of damage was classified as in Massey, Massey, Press, and Hartley (2006): 1, no defoliation; 2, up to 5% defoliation; 3, 5–20% defoliation; 4, 20–50% defoliation; 5, 50–90% defoliation; and 6, 90–100% defoliation; corresponding to the extent of damage by observing the aerial part of transplanted seedlings. The vertebrate activity, subdivided into consumption-related and trampling, was scored as positive when the seedlings were uprooted, flattened, or had damaged, broken, or chewed stems or leaves. The damage by litterfall was noted when a seedling had a bent, damaged, or broken stem or leaves and there was direct evidence of debris on the seedling. Invertebrate herbivory included defoliation or severing by leaf-cutter ants, indicated by the stem fiber patterns without chew marks; cricket herbivory was indicated by random defoliation and egg-laying; and leafhopper herbivory was indicated by round holes on leaves. Because some leafhoppers are vectors of pathogens (Webb 1987), we considered the insect-pathogen association when observed. The seedlings were characterized as diseased when they exhibited necrotic tissue. When two or more agents affected the same seedling, the associations were evaluated and considered in statistical analyses (see Supplementary Materials).

Soil fertility

Surface soil samples were collected within the old-fields, early secondary forest and old-growth forest. For each

habitat, soil samples were obtained at 10 stations established at 100 m intervals along the trails at two soil depths, 0–5 cm and 5–10 cm, collected using a 10 cm × 10 cm × 5 cm soil corer. Chemical analyses of pH, organic matter (OM), P, K, Ca, Mg, and Al were conducted as they potentially exert a stronger influence in tropical ecosystems (Vitousek 1984). The cation exchange capacity (CEC) and base saturation (BS) were obtained by calculation. The full methodology is described by van Raij, Cantarella, Quaggio, and Furlani (1997). See Supplementary Materials for details on the statistical analysis.

Results

Intensity of damage on seedlings and agents of damage

Considering all the seedling species and habitats combined, seedlings transplanted into the open plots accessible to vertebrates suffered higher intensities of damage than those in the enclosed plots (General Linear Mixed Model, $F = 200.2$, $P < 0.0001$). Only 15 (1.4%) of the 1080 seedlings remained intact, damage varied among plant species ($F = 157.58$, $P < 0.0001$), over time ($F = 1071$, $P < 0.0001$), and among habitats ($F = 15.2$, $P < 0.0001$). However, the intensity of damage on seedlings exposed to the same vertebrate herbivore regimes (within open or enclosed plots) did differ among the habitats ($F = 26.8$, $P < 0.0001$). Damage was highest in the old-growth forest, intermediate in the early secondary forest, and lowest in the old field. In old-growth and early secondary forests, significant interactions between species (*E. edulis* and *S. romanzoffiana*) and treatments (exclosure-open) were shown ($F = 10.7$, $P = 0.001$ and $F = 5.5$, $P = 0.02$, respectively), but exerted no effects between *M. coriacea* and *S. parahyba* in old-field sites ($F = 3.51$, $P = 0.062$).

Based on Tukey's HSD test, the three main causes of damage in order of severity were vertebrate activity (both consumption and trampling), litter deposition, and disease, as the extent of damage caused by these sources was significantly higher than by invertebrates. For a detailed summary of seedling damage incidence, please see Table 2 and Fig. 1.

Seedling survival

The results reveal that seedling survival depends heavily on protection from vertebrate herbivores. Consumption and trampling by vertebrates resulted in significantly higher and earlier seedling mortality in the control than in the enclosed plots. After four months, 45% of the total transplanted seedlings were lethally damaged, and by the end of the 1-year period, 76% of the seedlings were dead (Fig. 1). Overall, the seedlings protected from vertebrate damage experienced lower mortality, with 35% survival compared with 18% in the

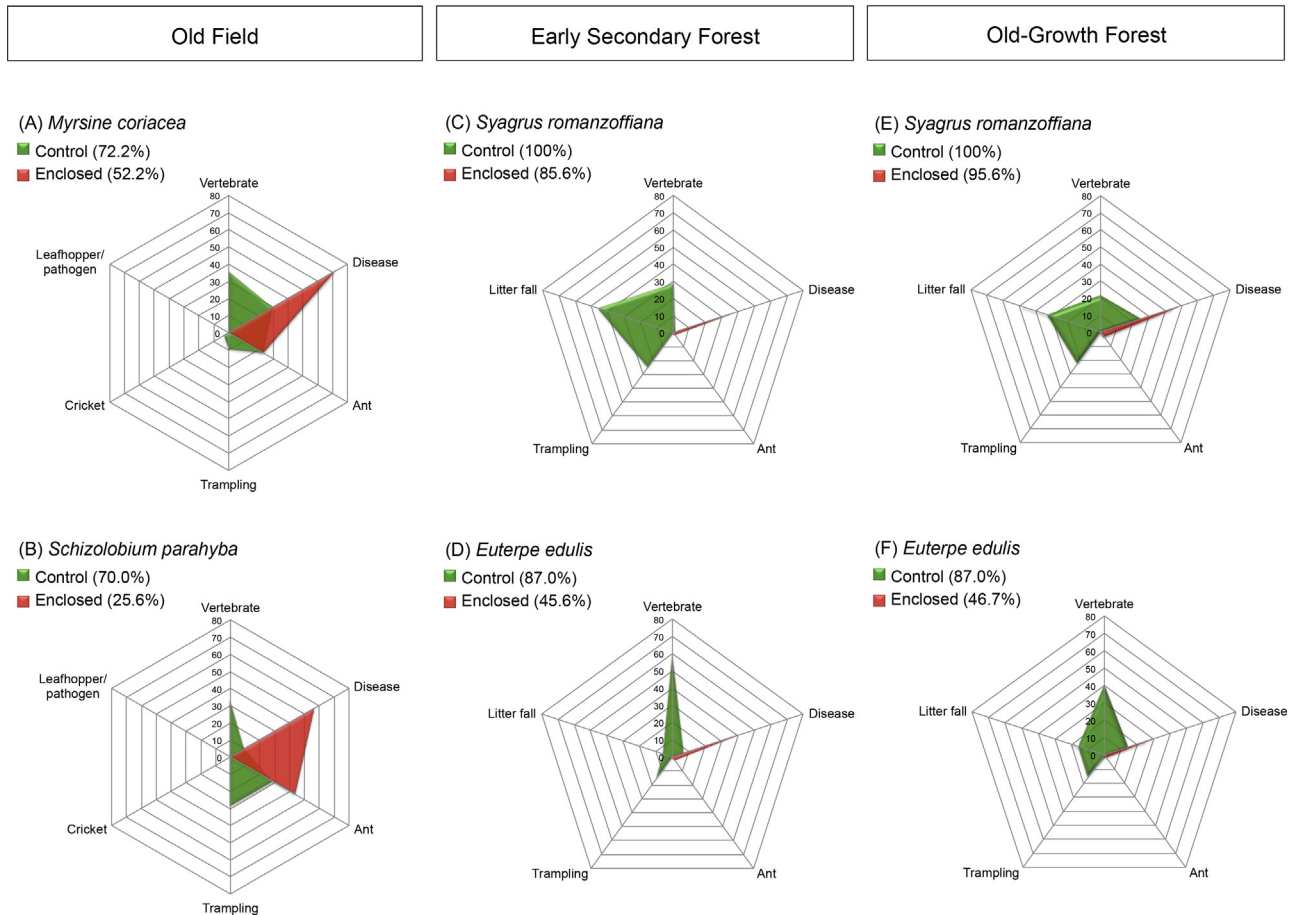


Fig. 1. Total and relative injury-specific percent mortality after a 1-year period in control and enclosed treatment plots for seedlings of four tree species transplanted on Anchieta Island.

open plots by the end of the study year (GLMM, $F = 169.3$, $P < 0.001$; Figs. 1 and 2).

Regardless of seedling species and habitat type, the time course of the probability of remaining unaffected differed significantly between the open and enclosed plots (log-rank $\chi^2 = 45.89$, $P < 0.0001$), with earlier deaths in the open plots (Table 3 and Fig. 2A). Seedlings exposed to the same vertebrate herbivore regimes, i.e., within open or enclosed plots, did vary among habitat type ($F = 19.5$, $P < 0.0001$) and species ($F = 530.4$, $P < 0.0001$; Figs. 1 and 2). Except for *M. coriacea* in the old-fields ($\chi^2 = 1.42$, $P = 0.23$) and *S. romanzoffiana* in the early secondary forest ($\chi^2 = 1.65$, $P = 0.20$), the seedling survival functions were significantly higher in the vertebrate exclusion plots than in the open plots (Fig. 2).

Damage from vertebrates, litterfall and soil-borne disease were the major causes of seedling mortality ($P < 0.05$, Fig. 1). Except for the lethal vertebrate damage, seedlings often died only after injury by two or more agents. The invertebrate injuries – mainly by leaf-cutter ants, *Atta sexdens* – were more intense in the old field than in the forests and caused 15% of seedling deaths when considering all old-field seedlings (Fig. 1). In early secondary and old-growth forests,

defoliation by ants was responsible for less than 2% of all seedling deaths (Fig. 1).

Soil fertility

The values for the chemical parameters were similar for the two soil depths (GLM, $F \geq 3.99$, $P > 0.05$ for all parameters; Fig. 3; Fig. S1; Table S1). Using pooled data from both depths, the PCA-biplot projection allowed simultaneous visualization of the relationships between the habitats and the variables: organic matter, P, base saturation and acid saturation were more or less closely correlated with PCA axis 1 (Fig. 3). Acid saturation was negatively related to axis one, while the other three variables were positively correlated to PCA axis 1. PCA axis 2 was determined by cation exchange capacity (CEC), whereas aluminum concentrations and pH were not particularly closely related to any of the two axes (Fig. 3).

Old-growth forests soils scored above average for organic matter, P, base saturation and pH, but below average for Al and acid saturation. These differences separated samples from old-growth forest and old field. Although early secondary

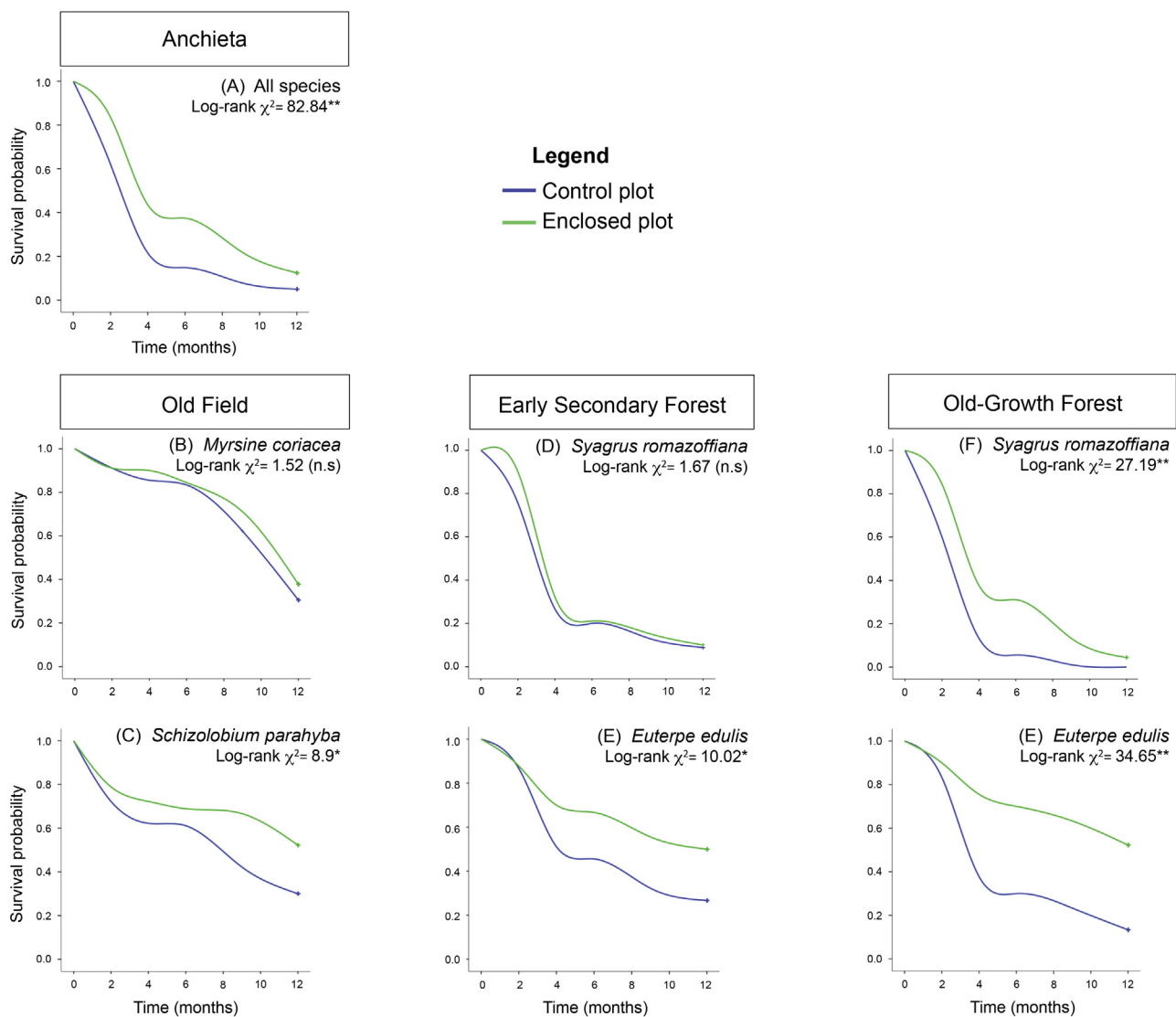


Fig. 2. The functions were calculated for a 12-month study period to compare seedling survival in open and enclosed treatment plots after pooling data from all seedling species and three habitat types (A). Functions for individual species and habitat types were also calculated (B–G). One and two asterisks indicate significance at the $\alpha=0.05$ and $\alpha=0.001$ level, respectively.

and old-growth forests scored similarly for organic matter, P and base saturation, they differed in pH, Al and acid saturation, with early secondary forest being more acidic. PCA axis 2, strictly correlated with CEC, separated early secondary forests from old field and old-growth forest. Old field and old-growth forest scored negatively for CEC in most cases, but early secondary forests scored highly positive. Generally, soil chemistry in the early secondary forests was spatially more heterogeneous than in the other habitats.

Discussion

We found that time and habitat influence the intensity of seedling injury by the different damage-causing agents, creating a complex spatiotemporal pattern of seedling survival.

The intricate effects of seedling mortality factors act predominantly during the dry season and vary over time among the species and habitats with different logging regimes.

Seedling injury and mortality were more intense during the dry season. During the dry season, vegetation is scarcer and offers reduced nutritional levels (Barreto & Herrera 1998). As a response, herbivores (vertebrates and invertebrates) normally experience physiological and morphological seasonal adjustments, changing not only their diet composition but also expanding their home-range (Corriale, Muschetto, & Herrera 2013), foraging time allocation, quantity and searching movements (van Schaik, Terborgh, & Wright 1993; Wirth, Beyschlag, Ryel, & Hölldobler 1997; Barreto & Herrera 1998), which leads to increased seedling mortality.

Seedling survival depends heavily on escaping vertebrate herbivory on Anchieta. An adult capybara, undoubtedly the

Table 2. Count of damaged seedlings (N), mean of damage (intensity \pm SE) and total percent of affected seedlings by an agent of damage. The intensity of damage corresponds to the mean scale of damage (from 1 to 6, Massey et al. 2006) per seedling species and habitat type after a one-year period. The damage-causing agents are not mutually exclusive. Multiple damage agents may affect a given seedling, and all injury types were considered.

Agent of damage	Old field			Early secondary forest			Old-growth forest											
	<i>Myrsine coriacea</i>		<i>Schizolobium parahyba</i>		<i>Syagrus romanzoffiana</i>		<i>Euterpe edulis</i>		<i>Euterpe edulis</i>									
	N	Intensity %	N	Intensity %	N	Intensity %	N	Intensity %	N	Intensity %								
Vertebrate activity ^a	37	5.73 \pm 0.80	41.1	51	5.63 \pm 0.87	56.6	46	5.6 \pm 1.08	51.1	58	5.89 \pm 0.70	64.50	38	6.00 \pm 0.00	42.2	50	6.00 \pm 0.00	55.5
Litter fall	0	0	0	0	0	0	86	5.94 \pm 0.54	47.7	16	5.69 \pm 0.70	8.90	73	5.96 \pm 0.35	40.5	34	5.85 \pm 0.61	18.8
Disease	24	5.92 \pm 0.41	13.3	19	5.95 \pm 0.23	10.5	31	6.00 \pm 0.00	17.2	40	5.95 \pm 0.22	22.22	63	6.00 \pm 0.00	35.0	38	5.97 \pm 0.16	21.1
Invertebrate activity	134	5.36 \pm 1.23	74.4	121	4.84 \pm 1.52	67.2	16	2.94 \pm 1.57	8.9	79	3.41 \pm 1.45	43.88	9	4.89 \pm 1.69	5.0	65	3.55 \pm 1.48	36.1

^aCounted only in open control plots (90 individuals per habitat).

major threat to seedlings, consumes 690 g dry weight of food per day (Ojasti 1973). Under optimal conditions where resources are extremely abundant, capybaras preferably feed on Poaceae and Cyperaceae species (Quintana, Monge, & Malvarez 1998; Forero-Montana, Betencur, & Cavelier 2003; Desbiez, Santos, Alvarez, & Tomas 2011) and selectively eat available C3 grasses (Santos, Costa, Souza, Arrigoni, & Moraes 2002), thus adjusting their diet to cope with differences in food abundance and quality (Barreto & Herrera 1998; Quintana 2002; Borges & Colares 2007; Desbiez et al. 2011). Nevertheless, the limited herbivore carrying capacity caused by the grass shortage on Anchieta, which is even scarcer in the dry season, alters capybara habitat use by intensifying movement, reducing selectivity, and increasing intake rates of several C3 and CAM plant species (K. Ferraz, unpubl. data). This feeding strategy results in indiscriminate damage and mortality by trampling and defoliation of seedlings with permitted vertebrate access across all habitat types. Nevertheless, seedling damage by vertebrates varies over time. As opposed to our prediction, it is higher in the dry season and in more dense forest given heterogeneous and spatially distributed food (Fleury et al. 2014). Ninety-two percent of seedling mortality due to trampling and vertebrate intake occurred during the dry season.

Although vertebrates undoubtedly exert a pronounced influence on seedling fate across all habitats of Anchieta Island, ants were responsible for 15% of the seedling deaths in the old-field but had negligible effects on seedling survival in both secondary and old-growth stands. It has been documented that ants are dominant herbivores in the Neotropics and are able to harvest large quantities of the leaf crop (Urbas, Araújo, Leal, & Wirth 2007; Costa, Vasconcelos, Vieira-Neto, & Bruna 2008), but the lethal defoliation by ants in this study was more restricted to those seedlings transplanted on or close to *Atta* nest sites, as observed in the old-field site. Browsing pressure had no significant effect on *M. coriacea* seedling survival due to its resprouting ability after defoliation (Hermann, Haug, Pillar, & Pfadenhauer 2012). However, late deaths in *M. coriacea* and *S. parahyba* from soil-borne diseases were observed in late summer in the old-field site. Although the tested species planted in the old-field site tolerate full sunlight, several seedlings were dried up after the summer. Browsing by mammals reduces ectomycorrhizal infections (Rossow, Bryant, & Kielland 1997), and trampling leads to periods of soil anoxia, especially under wet conditions as in austral summer, which reduces the decomposition of soil organic matter because of unfavorable abiotic conditions for mineralization (Schrama et al. 2013).

The past intense changes in the old-field sites, in particular, the soil compaction and soil organic matter and leaching losses, resulted in infertile acidic soils. The old-field sites showed an extremely high Al-saturation (Al³⁺), low concentrations of most mineral nutrients that are essential for plant development, a low organic matter content, which leads to a low CEC, and high P-fixation (Gullison et al. 2007). Old-growth forest soil low CEC was attributable to covariation

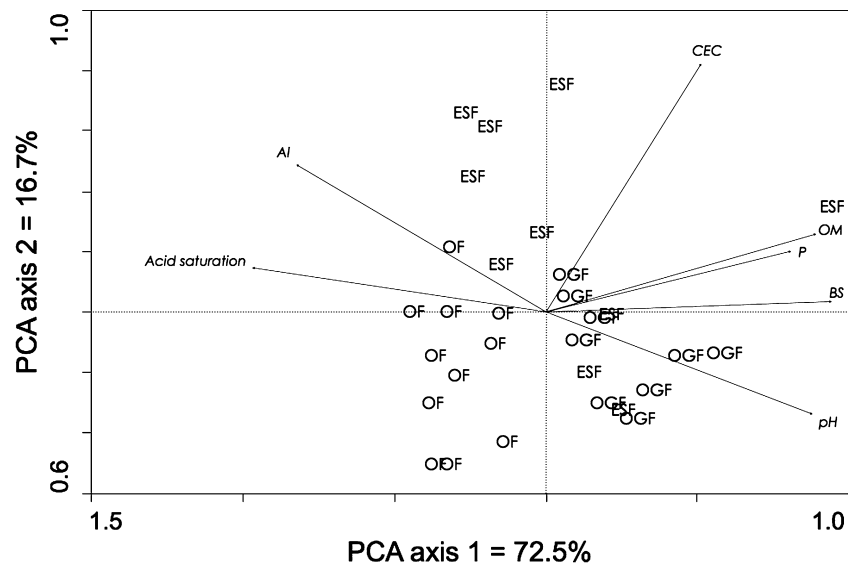


Fig. 3. PCA biplot of soil chemical parameters obtained for old-fields (OF), early secondary forest (ESF) and old-growth forest (OGF) on Anchieta Island at a depth of 0–5 cm, with Al = aluminum, OM = organic matter, CEC = cation exchange capacity, BS = base saturation and P = phosphorus.

with soil base saturation, while old field soil was found to be associated with a high concentration of aluminum occupying the soil colloids cation exchange. The tight stoichiometry of macronutrients linked to P-limitation indicates that P plays an important role in the net primary productivity of tropical forest ecosystems (McGroddy, Daufresne, & Hedin 2004), being largely dependent of the recycling of P through litter decomposition (McGroddy et al. 2004). Soil P-limitation is caused by changes in pH (Weand, Arthur, Lovett, Sikora, & Weathers 2010), affecting the release of inorganic P associated with Al (Lu et al. 2012) and influencing Al-toxicity (Weand et al. 2010). Soils with a pH below five and more than 60% Al saturation of the CEC, as recorded in the old-field, may suffer from Al-toxicity (Sawma & Mohler 2002). Extremely high Al-concentrations impede root development and reduce the uptake of other nutrients, especially calcium and magnesium, which are closely associated with root growth and plant development (Holl 2007) and likely caused the late but con-

siderable seedling mortality from disease in the old-fields. The high Al-toxicity is thus sufficient to hamper succession in the old-field (Sawma et al. 2002).

The concentrations of soil nutrients across the Anchieta habitats corroborate the previous hypothesis that soil fertility tends to increase as biomass accumulates (Chazdon 2003). The old-field site has a low but variable quantity of litterfall biomass (67.4 ± 110.6 g) and extremely acidic plant litter (pH 3.12 ± 0.53) entering the belowground subsystem (Fleury 2009). In this habitat, previous activities may have led to soil acidification and the substantial loss of soil nutrients, an amount that appeared to exceed the input sources; thus, a resupply might be necessary to reestablish the functioning of the decomposer subsystem (Wardle et al. 2004).

The intermediate and heterogeneous values for the fertility parameters in the early secondary forest suggest that the soil in this habitat is resilient. The litterfall nutrient inputs significantly increase and facilitate the recuperation of soil function

Table 3. Means (months \pm SD) of life expectancy by group of seedlings in open control plots and plots that excluded herbivores, as determined by Kaplan–Meier life table survival analysis at the 95% confidence level (Fig. 2).

Habitat	Species	Treatment	
		Control plots	Enclosure plots
All habitats	All species	4.35 \pm 0.12	6.33 \pm 0.16
Old field	<i>Myrsine coriacea</i>	9.90 \pm 0.35	10.29 \pm 0.33
	<i>Schizolobium parahyba</i>	7.79 \pm 0.46	9.09 \pm 0.46
Early secondary forest	<i>Syagrus romanzoffiana</i>	5.04 \pm 0.34	5.54 \pm 0.33
	<i>Euterpe edulis</i>	7.08 \pm 0.41	8.82 \pm 0.42
Old-growth forest	<i>Syagrus romanzoffiana</i>	3.60 \pm 0.20	5.78 \pm 0.30
	<i>Euterpe edulis</i>	6.02 \pm 0.39	9.31 \pm 0.40

in secondary stands (Houghton 2010), thus reestablishing the aboveground-belowground positive feedback (Wardle et al. 2004). Further, the greater litterfall deposition biomass increases mechanical damage on seedlings. In dry seasons, the increased drought stress (Lieberman & Li 1992), wind speed and mechanical turbulence (Lieberman et al. 1992) intensify the mechanical damage by litterfall (Barlow, Gardner, Ferreira, & Peres 2007), especially in the early secondary forest. In the early secondary forest, pioneer and early secondary trees characteristically have higher rates of growth and leaf turnover than late successional trees (Coley 1983), increasing mechanical damage to the transplanted seedlings, especially to *S. romanzoffiana*. The seedlings of this species are less likely to both receive and survive mechanical damage than those of *E. edulis*, which, with their stronger stems, commonly recover after mechanical damage.

In tropical forests, an increasingly human-dominated, fragmented and defaunated environment, overconsumption by the resilient herbivore community might decrease productivity and slow nutrient cycling (Côté et al. 2004) as the quantity and quality of litter available to underground decomposers declines (Weand et al. 2010). The contrasting plant species composition, seasonal resource availability for herbivores and soil nutrient availability to plants may lead to differences in type and intensity of herbivore damage among habitats due to variation in space use, abundance and foraging behavior of herbivores (Maher & Burger 2011). The combined effect of aboveground and soil components, despite their variation among the tested species and their considerable differential action through time and habitats, could be simultaneously affecting plant regeneration. Thus, the sensitivity of these vital linkages to perturbation may have important consequences for forest regeneration once producers impose regulation from the bottom-up, thus reducing the diversity and carrying capacity for consumers and potentially leading to ecological meltdown (Terborgh et al. 2001). In these habitats, population control of herbivores should be the first step before implementing artificial measures to accelerate natural regeneration to a point where conditions allow the recolonization and reconstruction of biotic communities.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2014.11.006>.

References

- Barlow, J., Gardner, T. A., Ferreira, L. V., & Peres, C. A. (2007). Litter fall and decomposition in primary, secondary and plantation forests in the Brazilian Amazon. *Forest Ecology and Management*, 247, 91–97.
- Barreto, G. R., & Herrera, E. A. (1998). Foraging patterns of capybaras in a seasonally flooded savanna of Venezuela. *Journal of Tropical Ecology*, 14, 87–98.
- Borges, L. V., & Colares, I. G. (2007). Feeding habits of capybaras (*Hydrochoerus hydrochaeris*, Linnaeus 1766), in the Ecological Reserve of Taim (ESEC – Taim) – south of Brazil. *Brazilian Archives of Biology and Technology*, 50, 409–416.
- Bovendorp, R., & Galetti, M. (2007). Density and population size of mammals introduced on a land-bridge island in southeastern Brazil. *Biological Invasions*, 9, 353–357.
- Bradshaw, C. J. A., Sodhi, N. S., & Brook, B. W. (2009). Tropical turmoil: A biodiversity tragedy in progress. *Frontiers in Ecology and the Environment*, 7, 79–87.
- Budowski, G. (1965). Distribution of tropical American rain forest species in the light of successional process. *Turrialba*, 15, 40–42.
- Calderón-Miller, L. (2008). Chuva de sementes e limitação ao recrutamento em diferentes fisionomias da Ilha Anchieta. In *Ciências Biológicas (Biologia Vegetal)*. Rio Claro, SP: UNESP.
- Chazdon, R. L. (2003). Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspectives in Plant Ecology Evolutions and Systematics*, 6, 51–71.
- Chazdon, R. L. (2008). Beyond deforestation: Restoring forests and ecosystem services on degraded land. *Science*, 320, 1458–1460.
- Coley, P. D. (1983). Herbivory and defensive characteristics if tree species in a lowland tropical forest. *Ecological Monographs*, 53, 209–233.
- Coley, P. D. (1998). Possible effects of climate change on plant/herbivore interactions in moist tropical forests. *Climatic Change*, 39, 455–472.
- Cornelissen, J. H. C., Diez, P. C., & Hunt, R. (1996). Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology*, 84, 755–765.
- Corriale, M. J., Muschetto, E., & Herrera, E. A. (2013). Influence of group sizes and food resources in home-range sizes of capybaras from Argentina. *Journal of Mammalogy*, 94, 19–28.
- Costa, A. N., Vasconcelos, H. L., Vieira-Neto, E. H. M., & Bruna, E. M. (2008). Do herbivores exert top-down effects in Neotropical savannas? Estimates of biomass consumption by leaf-cutter ants. *Journal of Vegetation Science*, 19, 849–854.

- Côté, S. D., Rooney, T. P., Tremblay, J. P., Dussault, C., & Waller, D. M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology and Systematics*, *35*, 113–147.
- Desbiez, A. L. J., Santos, S. A., Alvarez, J. M., & Tomas, W. M. (2011). Forage use in domestic cattle (*Bos indicus*), capybara (*Hydrochoerus hydrochaeris*) and pampas deer (*Ozotoceros bezoarticus*) in a seasonal Neotropical wetland. *Mammalian Biology*, *76*, 351–357.
- Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, *345*, 401–406.
- Doak, D. F. (1992). Lifetime impacts of herbivory for a perennial plant. *Ecology*, *73*, 2086–2099.
- Fleury, M. (2009). Interações ecológicas entre plantas e animais: implicações para a conservação e restauração de uma ilha pluvial Atlântica. In *Ecologia Aplicada*. Piracicaba: Universidade de São Paulo.
- Fleury, M., Rodrigues, R. R., do Couto, H. T. Z., & Galetti, M. (2014). Seasonal variation in the fate of seeds under contrasting logging regimes. *PLOS ONE*, *9*, 8.
- Forero-Montana, J., Betencur, J., & Cavelier, J. (2003). Dieta del capibara *Hydrochoerus hydrochaeris* (Rodentia: Hydrochaeridae) en Caño Limón, Arauca, Colombia. *Revista de Biología Tropical*, *51*, 579–590.
- Galetti, M., Guevara, R., Cortes, M. C., Fadini, R., Von Matter, S., Leite, A. B., et al. (2013). Functional extinction of birds drives rapid evolutionary changes in seed size. *Science*, *340*, 1086–1090.
- Genini, J., Galetti, M., & Morellato, L. P. C. (2009). Fruiting phenology of palms and trees in an Atlantic rainforest land-bridge island. *Flora*, *204*, 131–145.
- Giesel, A., Boff, M. I. C., & Boff, P. (2013). Seasonal activity and foraging preferences of the leaf-cutting ant *Atta sexdens piriventris* (Santschi) (Hymenoptera: Formicidae). *Neotropical Entomology*, *42*, 552–557.
- Gullison, R. E., Frumhoff, P. C., Canadell, J. G., Field, C. B., Nepstad, D. C., Hayhoe, K., et al. (2007). Tropical forests and climate policy. *Science*, *316*, 985–986.
- Hermann, J. M., Haug, S., Pillar, V. D., & Pfadenhauer, J. (2012). Shrubs versus ‘gullivers’: Woody species coping with disturbance in grasslands. *Plant Ecology*, *213*, 1757–1768.
- Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., et al. (2006). Novel ecosystems: Theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, *15*, 1–7.
- Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: Implications for conservation and restoration. *Trends in Ecology & Evolution*, *24*, 599–605.
- Holl, K. D. (2007). Oldfield vegetation succession in the neotropics. In V. A. Cramer, & R. J. Hobbs (Eds.), *Old fields: Dynamic and restoration of abandoned farmland* (pp. 93–117). Washington, DC: Island Press.
- Houghton, R. A. (2010). How well do we know the flux of CO₂ from land-use change? *Tellus B*, *62*, 337–351.
- Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, *54*, 187–211.
- Jordan, C. F., & Herrera, R. (1981). Tropical rain forests: Are nutrients really critical? *American Naturalist*, *117*, 167–180.
- Köppen, W. (1948). *Climatología: con un estudio de los climas de la tierra*. México: Fondo de Cultura Económica.
- Lieberman, D., & Li, M. (1992). Seedling recruitment patterns in a tropical dry forest in Ghana. *Journal of Vegetation Science*, *3*, 375–382.
- Lopez, L., & Terborgh, J. (2007). Seed predation and seedling herbivory as factors in tree recruitment failure on predator-free forested islands. *Journal of Tropical Ecology*, *21*, 129–137.
- Lu, X., Mo, J., Gilliam, F. S., Fang, H., Zhu, F., Fang, Y., et al. (2012). Nitrogen addition shapes soil phosphorus availability in two reforested tropical forests in southern China. *Biotropica*, *44*, 302–311.
- MA. (2005). Ecosystems and human well-being. In *Synthesis*. Washington, DC, US: Millennium Ecosystem Assessment.
- Maher, C. R., & Burger, J. R. (2011). Intraspecific variation in space use, group size, and mating system of caviomorph rodents. *Journal of Mammalogy*, *92*, 54–64.
- Maschinski, J., & Whitham, T. G. (1989). The continuum of plant-responses to herbivory: The influence of plant-association, nutrient availability, and timing. *American Naturalist*, *134*, 1–19.
- Massey, F. P., Massey, K., Press, M. C., & Hartley, S. E. (2006). Neighbourhood composition determines growth, architecture and herbivory in tropical rain forest tree seedlings. *Journal of Ecology*, *94*, 646–655.
- McGroddy, M. E., Daufresne, T., & Hedin, L. O. (2004). Scaling of C:N:P stoichiometry in forests worldwide: Implications of terrestrial Redfield-type ratios. *Ecology*, *85*, 2390–2401.
- Nogales, M., Heleno, R., Traveset, A., & Vargas, P. (2012). Evidence for overlooked mechanisms of long-distance seed dispersal to and between oceanic islands. *New Phytologist*, *194*, 313–317.
- Ødegaard, F., Diserud, O. H., & Østbye, K. (2005). The importance of plant relatedness for host utilization among phytophagous insects. *Ecology Letters*, *8*, 612–617.
- Ojasti, J. (1973). *Estudio biológico del chigüire o capibara*. Caracas, Venezuela: Fondo Nacional de Investigaciones Agropecuarias.
- Quintana, R. D. (2002). Influence of livestock grazing on the capybara's trophic niche and forage preferences. *Acta Theriologica*, *47*, 175–183.
- Quintana, R. D., Monge, S., & Malvarez, A. I. (1994). Feeding habits of capybara (*Hydrochaeris hydrochaeris*) in afforestation areas of the Lower Delta of the Paraná River, Argentina. *Mammalia*, *58*, 569–580.
- Quintana, R. D., Monge, S., & Malvarez, A. I. (1998). Feeding patterns of capybara *Hydrochaeris hydrochaeris* (Rodentia, Hydrochaeridae) and cattle in the non-insular area of the lower delta of the Paraná River, Argentina. *Mammalia*, *62*, 37–52.
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., et al. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*, 151.
- Ripple, W. J., Larsen, E. J., Renkin, R. A., & Smith, D. W. (2001). Trophic cascades among wolves, elk, and aspen on Yellowstone National Park's northern range. *Biological Conservation*, *102*, 227–234.
- Rossow, L. J., Bryant, J. P., & Kielland, K. (1997). Effects of above-ground browsing by mammals on mycorrhizal infection in an early successional taiga ecosystem. *Oecologia*, *110*, 94–98.
- Santos, S. A., Costa, C., Souza, G. S. E., Arrigoni, M., & Moraes, A. (2002). Qualidade da dieta selecionada por bovinos na sub-região de Nhecolândia, Pantanal. *Revista Brasileira de Zootecnia*, *31*, 1663–1673.

- Sawma, J. T., & Mohler, C. L. (2002). Evaluating seed viability by an unimbibed seed crush test in comparison with the tetrazolium test. *Weed Technology*, *16*, 781–786.
- Schrama, M., Heijning, P., Bakker, J. P., van Wijnen, H. J., Berg, M. P., & Olf, H. (2013). Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. *Oecologia*, *172*, 231–243.
- Seddon, P. J., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: Restoring species in a changing world. *Science*, *345*, 406–412.
- Silla, F., Fleury, M., Mediavilla, S., & Escudero, A. (2008). Effects of simulated herbivory on photosynthesis and N resorption efficiency in *Quercus pyrenaica* Willd. saplings. *Trees: Structure and Function*, *22*, 785–793.
- Suding, K. N., & Hobbs, R. J. (2009). Threshold models in restoration and conservation: A developing framework. *Trends in Ecology & Evolution*, *24*, 271–279.
- Svenning, J.-C., Brorchenius, F., Bjorholm, S., & Balsev, H. (2008). High tropical net diversification drives the New World latitudinal gradient in palm (Arecaceae) species richness. *Journal of Biogeography*, *35*, 394–406.
- Terborgh, J. (1986). Keystone plant resources in the tropical forest. In M. E. Soulé (Ed.), *Conservation biology* (pp. 330–334). Massachusetts: Sinauer.
- Terborgh, J., & Feeley, K. (2010). Propagation of trophic cascades by multiple pathways in tropical forests. In J. Terborgh, & J. A. Estes (Eds.), *Trophic cascades: Predators, prey, and the changing dynamics of nature* (pp. 125–140). Washington: Island Press.
- Terborgh, J., Lopez, L., Nuñez, V. P., Rao, M., Shahabuddin, G., Orihuela, G., et al. (2001). Ecological meltdown in predator-free forest fragments. *Science*, *294*, 1923–1926.
- Urbas, P., Araújo, M. V., Leal, I. R., & Wirth, R. (2007). Cutting more from cut forests: Edge effects on foraging and herbivory of leaf-cutting ants in Brazil. *Biotropica*, *39*, 489–495.
- van der Heijden, M. G. A., Bardgett, R. D., & van Straalen, N. M. (2008). The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters*, *11*, 296–310.
- van Raij, B., Cantarella, H., Quaggio, J. A., & Furlani, A. M. C. (1997). *Recomendações de adubação e calagem para o Estado de São Paulo*. Campinas: Instituto Agrônomo de Campinas, Fundação IAC.
- van Schaik, C. P., Terborgh, J., & Wright, S. J. (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, *24*, 353–377.
- Vasconcelos, H. L., & Cherrett, J. M. (1997). Leaf-cutting ants and early forest regeneration in central Amazonia: Effects of herbivory on tree seedling establishment. *Journal of Tropical Ecology*, *13*, 357–370.
- Vitousek, P. M. (1984). Litterfall, nutrient cycling and nutrient limitation in tropical forest. *Ecology*, *65*, 285–298.
- Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., van der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, *304*, 1629–1634.
- Weand, M. P., Arthur, M. A., Lovett, G. M., Sikora, F., & Weathers, K. C. (2010). The phosphorus status of northern hardwoods differs by species but is unaffected by nitrogen fertilization. *Biogeochemistry*, *97*, 159–181.
- Webb, M. D. (1987). Species recognition in *Cicadulina* leafhoppers (Hemiptera: Cicadellidae), vectors of pathogens of Gramineae. *Bulletin of Entomological Research*, *77*, 683–712.
- Wirth, R., Beyschlag, W., Ryel, R. J., & Hölldobler, B. (1997). Annual foraging of the leaf-cutting ant *Atta colombica* in a semideciduous rain forest in Panama. *Journal of Tropical Ecology*, *13*, 741–757.

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