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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 transplantierter 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.

Keywords: Atlantic forest; Capybaras; Cascading effects; Herbivores; Seedling limitation

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)