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Original Research Article

Short term patterns of germination in response to litter clearing and exclosure of large terrestrial vertebrates along an Amazon forest regrowth gradient

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ABSTRACT

Efforts to restore tropical forest ecosystem services depend on understanding the barriers to germination of species of economic and cultural interest. Here we use two important non-timber forest product species (NTFP: *Inga capitata* Desv. – Fabaceae and *Euterpe oleracea* Mart. – Arecaeae) to compare germination across a forest regrowth gradient in the northeast Brazilian Amazon. Experimental treatments were used to examine the effects of mid to large-bodied vertebrates and litter cover on seed fate (germination, removal and invertebrate infestation) in 15 lowland sites within small-holder properties. Regrowth stage was classified into three groups, with five sites each of: late second-regrowth forest, early second-regrowth forest and abandoned pasture. We conducted a paired split-plot experiment using experimental plots composed of a vertebrate exclosure versus an open treatment and subplots with and without litter. We used Generalized Linear Mixed-Effects Models (GLMMs) to compare additive and interaction effects of treatments across regrowth stages compared with 15 paired control sites. We found that the effects of regrowth stage and exclosure were species specific and these effects differed between responses (germination, removal and invertebrate infestation). Clearing litter generated a significant effect only for invertebrate infestation, which increased in the cleared plots. Our findings show that seed removal limits germination success for both species across forest regrowth stages, with invertebrate infestation also having important but secondary effects. Increased removal and unfavorable abiotic conditions make direct seeding unviable in pasture sites. We suggest that direct seeding is a viable alternative for the establishment of these widely available NTFP species in late and early regrowth forests.

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1. Introduction

One option to revert tropical forest loss is the restoration of degraded forests and deforested landscapes (Chazdon and Guariguata, 2016; Holl, 2017). However, restoration actions are often considered to be economically expensive, especially

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in developing nations. Faced with limited resources there is increasing interest in accelerating natural regeneration within restoration actions (Chazdon and Guariguata, 2016; Holl, 2017; Meli et al., 2017).

Effective restoration relies on overcoming barriers to native plant regeneration that predominate in the earliest stages of succession (Chazdon and Guariguata, 2016; Holl, 2017). Barriers to regeneration differ with successional stage (Aide et al., 2000; Martínez-Garza and Howe, 2003; Shoo et al., 2016) and common interventions include varied strategies to suppress herbaceous vegetation (e.g. cutting or herbicide treatment), and measures to bolster propagule supply (e.g. direct seeding and artificial bird perches (Shoo and Catterall, 2013; Holl, 2017; Holl et al., 2017)). Direct seeding may be an effective and economic path for regeneration/restoration at both large and local spatial scales (Shoo and Catterall, 2013; Holl, 2017) but is potentially limited in tropical regions by factors such as predators and litter cover (Ganade and Brown, 2002; Shoo and Catterall, 2013; Palma and Laurance, 2015; Chazdon and Guariguata, 2016).

Direct seeding has been used as part of restoration actions with non-timber forest products (NTFPs) that are an important source of income to millions of people world-wide (Poffenberger and Singh, 1992; He et al., 2009). Non-timber forest products can potentially contribute towards sustainable development across rural Amazon regions (Richards, 1993). For example, the açai palm (*Euterpe oleracea*) is an important component of local and regional economies across the Amazon (Brondizio et al., 2002). The management and conservation of these important tropical NTFPs depends on a detailed understanding of plant recruitment. The processes that influence recruitment are strongly affected by myriad abiotic (i.e. habitat type, light, soil and nutrients (Guariguata and Ostertag, 2001)) and biotic (i.e. predation (Nepstad et al., 1996; Piironen et al., 2017), fungal infection (Bagchi et al., 2014) and litter effect (Xiong and Nilsson, 1999; Ganade and Brown, 2002)) factors. Therefore, it is necessary to understand how these limiting factors act along a successional gradient and in response to different levels of human disturbance to improve natural regeneration, restoration and agroforestry strategies (Richards, 1993; Shoo and Catterall, 2013; Palma and Laurance, 2015; Chazdon and Guariguata, 2016; Holl, 2017).

The diversity of Amazon forests means it is hard to separate the complex interactions driving recruitment (Guariguata and Ostertag, 2001; Camargo et al., 2002; Chazdon and Guariguata, 2016; Holl, 2017), yet previous studies clearly show how different animal groups can generate important impacts on plant recruitment. Seeds can be preyed upon by both vertebrates and invertebrates (Stoner et al., 2007; Griffiths et al., 2016), which may play key roles in limiting germination and subsequent recruitment. Exclosure experiments have revealed the impact of vertebrates on seed and seedling survival, especially in tropical forests to elucidate how this group contributes to the community structure of tropical forest trees (Asquith et al., 1997; Beck et al., 2013; Paine et al., 2016). Litter effect, is another factor affecting recruitment, and may also contribute to influence different processes by reducing erosion, evapotranspiration, thereby improving microclimatic conditions for seed germination and seedling establishment (Facelli and Pickett, 1991; Xiong and Nilsson, 1999; Ganade and Brown, 2002).

In this study, we evaluated the effects of mid to large-bodied vertebrates and litter cover on seed fate along a forest regrowth gradient of two important NTFPs species (*Euterpe oleracea* and *Inga capitata*). To quantify the effects of these different factors we experimentally assessed short term seed fate (germination, removal and invertebrate infestation) in three forest regrowth stages (late second-regrowth forest, early second-regrowth, and abandoned pasture).

2. Material and methods

2.1. Study area and sampling units

The study was conducted in 15 private properties surrounding the Amapá National Forest (Floresta Nacional Amapá—hereafter ANF). ANF is a sustainable-use protected area, of approximately 460,000 ha (ICMBIO, 2014), located on the pre-Cambrian Guianan shield craton at the base of the Tumucumaque Uplands, in the northeast Brazilian Amazon (0°55'29"N, 51°35'45"W, Fig. 1). The regional phytophysionomies consist of evergreen tropical rainforest vegetation (Gond et al., 2011), predominantly never flooded “*terra-firme*” forest, with some areas of flooded forest, bamboo and rocky outcrops (ICMBIO, 2014). The regional climate is classified by Köppen-Geiger as Am (Equatorial monsoon (Kottek et al., 2006)) with annual rainfall ranging from 2200 mm to 2500 mm during the last five years (2012–2016, (ANA, 2017), S1 Fig). During the months with highest precipitation levels (February to April), rainfall may reach 500 mm/month. The dry season (September to November) is characterized by total precipitation below 150 mm/month ((ANA, 2017), S1 Fig).

Data collection was conducted in 15 *terra-firme* sites located in private small-holder properties that were selected on the basis of differences in land-use histories (Norris and Michalski, 2013) and forest regrowth/regeneration stage (Fig. 1). All sites were close (110–554 m) to rivers (100–200 m wide) that are navigable by motorized boats, but due to riverbank formation the sites are never flooded.

Based on the land-use history the 15 sites were grouped into three regrowth stage classes: 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 abandoned pasture (N = 5, pasture areas dominated by grasses and herbs but that had never been used to raise livestock i.e. forest was cleared and grass planted in anticipation of cattle that were never bought). Each of the 15 sites was paired with a nearby (60–150 m) control site i.e. 20–30 m tall *terra-firme* forest without a history of mechanized timber extraction. To reduce the possible confounding influence of edge effects, all regrowth and control sites were established at 30 m from the nearest control-regrowth habitat edge (S2 Fig).

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