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Fire- and distance-dependent recruitment of the Brazil nut in the Peruvian Amazon

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ABSTRACT

The low natural regeneration of the Brazil nut (*Bertholletia excelsa*) in the Madre de Dios region of Peru is a major concern for the conservation and sustainable use of this species which sustains one of the cornerstone non-timber forest product economies in Amazonia. The Brazil nut is a gap-dependent, long-lived pioneer species that has been shown to regenerate more effectively in fallows than in mature forests. Aside from light and nutrient availability, recruitment success of the species might also be influenced by conspecific negative distance-dependent (CNDD) processes as shown for a myriad of other tropical tree species, but to date has not been studied in the Brazil nut. We measured Brazil nut recruitment in forty $150 \times 10\,m^2$ transects (totaling 6 ha), proportionally laid out in mature forest and fallow land. We found a higher likelihood of regeneration in fallows than in mature forest, which was mainly due to more successful transitioning from seedlings to saplings in fallows. Recruitment rates in fallows increased with the number of fire events occurring over the past 12 years, largely owing to the accumulation of resprouting individuals, but this positive correlation was only observed up to three fire events. We observed CNDD recruitment of the Brazil nut in fallows but not in mature forest, suggesting that pests and diseases might also condition Brazil nut recruitment. Our findings suggest that a better management of fallow land and more controlled use of fire in neighboring land uses could be a cost-effective manner to create Brazil nut rich forests through natural regeneration. On the other hand, the absence of high density Brazil nut stands in mature forests in Madre de Dios might mean that the impact of ancient humans there has been more limited than in other Amazonian regions.

1. Introduction

The Brazil nut (*Bertholletia excelsa* Bonpl.: Lecythidaceae) seed is one of the cornerstone non-timber forest products (NTFPs) in Amazonia, sustaining substantial extractive economies in Bolivia, Brazil and Peru (Guariguata et al., 2017). However, concern has been raised about low levels of juvenile recruitment putting at risk the maintenance of populations over the long term. Peres et al. (2003) attributed the recruitment bottlenecks observed in Brazil nut trees with diameter at breast height (DBH) ≥ 10 cm and < 60 cm in study sites across the Amazon to intensive exploitation over extended periods of time. This viewpoint has since been contested by a growing number of studies that also looked at regenerating Brazil nut trees with DBH < 10 cm and found no negative effect of intense harvesting on recruitment rates (Bertwell et al., 2018; Ribeiro et al., 2014; Scoles and Gribel, 2012; Wadt et al., 2008). In fact, there are increasing indications that extractive activities in natural Brazil nut stands may actually promote natural regeneration, possibly through modifications of the understory resulting in increased light regimes, along with other favorable effects of human disturbance (Scoles and Gribel, 2015, 2011).

The Brazil nut is a gap-dependent, long-lived pioneer species, implying that its natural regeneration is strongly favored by the availability of light through natural or anthropogenic gap creation (Moll-Rocek et al., 2014; Myers et al., 2000; Peña-Claros et al., 2002). The species is known to regenerate much more effectively in swiddens and fallows than under natural forest conditions (higher survival rates, stronger growth and higher densities) (Cotta et al., 2008; Guedes et al., 2014; Kainer et al., 1998; Scoles and Gribel, 2011). This finding has been attributed to a combination of (i) the preferential dispersion activities in swiddens and fallows of the tree's principal dispersal agent, the agouti (*Dasyprocta* spp), (ii) favorable growth conditions in cultivated fields (light and soil fertility) and (iii) the species' capacity to resprout after cutting (Guedes et al., 2014; Paiva et al., 2011; Scoles and Gribel, 2011). Seedling recruitment is likely to be additionally

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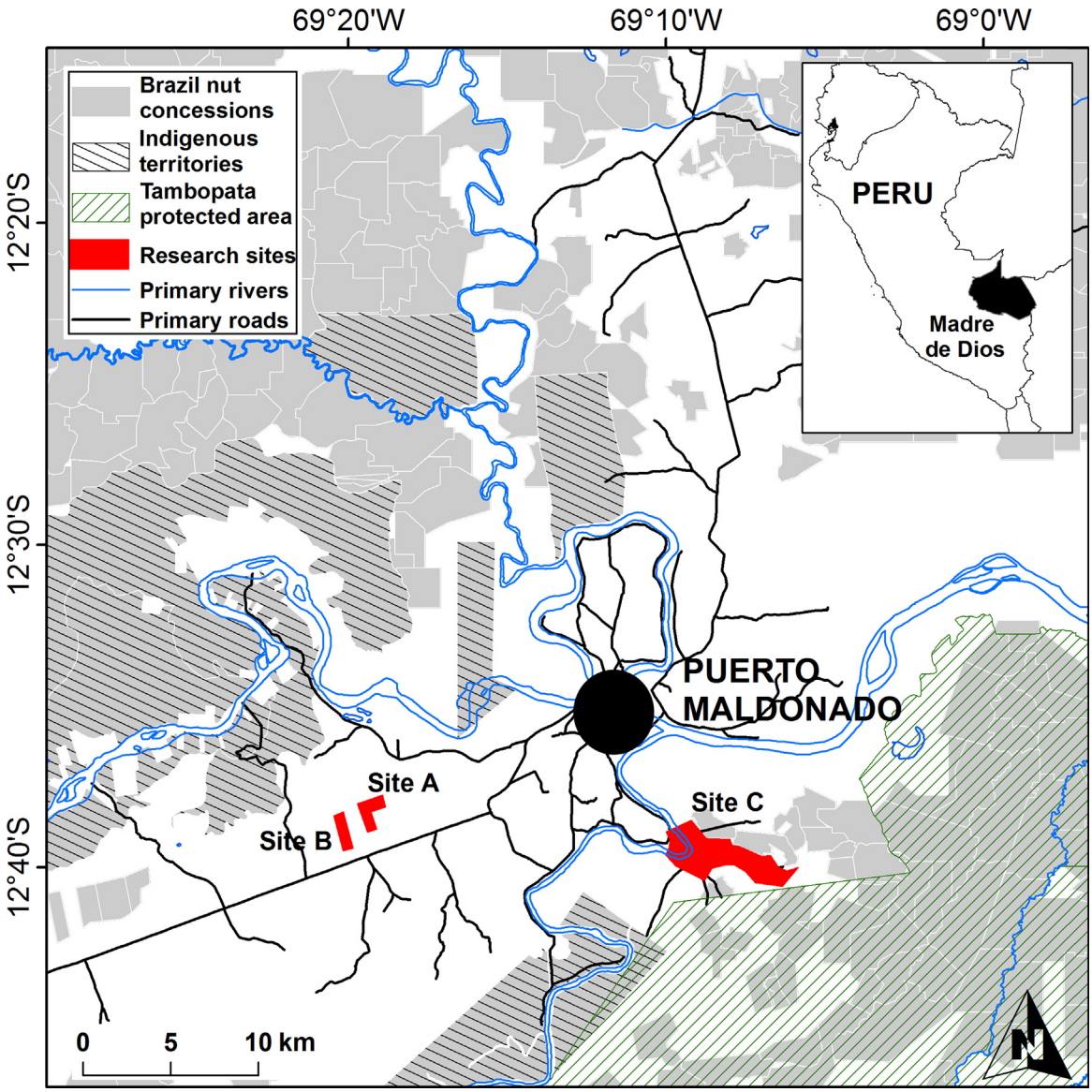

Fig. 1. Location of the research sites in Madre de Dios, Peru. Sites A and B correspond with Brazil nut rich mature forest concessions of the IIAP (Instituto de Investigaciones de la Amazonia Peruana); site C is characterized by fallow lands in the buffer zone of the Tambopata national park.

promoted by hunting of agoutis in swiddens and fallows, thus freeing more abandoned scatter hoards for germination (Ribeiro et al., 2014; Shepard and Ramirez, 2011). Interestingly, Paiva et al. (2011) showed that the positive effects of repeated slash-and-burn events on Brazil nut regeneration are cumulative. In a study in Amapa, eastern Amazonia, they found that Brazil nut densities increased from approximately 9 to 14 and 27 trees ha^{-1} after one, two and three or more shifting cultivation cycles, respectively, owing to the high resprouting capacity of recruits after vegetation cutting and burning.

The positive effect on Brazil nut recruitment of longstanding practices of swidden agriculture used since pre-Columbian times is believed to explain, at least partly, the aggregated distribution pattern of Brazil nut observed in many areas across the species' distribution range (Thomas et al., 2014; Thomas et al., 2015). Especially in central and eastern Amazonia, the Brazil nut tends to occur in high-density groves, commonly referred to as 'manchales', 'castanhais' or 'bolas', with densities ranging from 10 to 20 trees (≥10 cm DBH) per hectare, interspersed with vast areas of forest (up to thousands of hectares) with little to no Brazil nut trees (Mori et al., 1990; Peres and Baider, 1997; Salomão, 2009). By contrast, in southwestern Amazonia, the Brazil nut has a more continuous occurrence in the forest and tree densities are much lower (~1–2 trees ≥10 cm DBH per hectare). Thomas et al. (2015) hypothesized that the absence, or much reduced salience, of high-density Brazil nut groves in southwestern Amazonia might be partly due to different ecological conditions in this region, compared to central and eastern Amazonia. Notably, differences in the incidence of pests and diseases might influence Brazil nut recruitment rates. For example, Shepard and Ramirez (2011) found exceptionally high Brazil nut densities (50 individuals per hectare, mostly in the size class of 10–60 cm DBH) in a small, fire-impacted grove in Alter do Chão, Pará, with most of the trees being multi-trunked. They attributed these observations to positive influences on recruitment from anthropogenic disturbance combined with the site's drier climate, resulting in lower rates of Brazil nut recruits succumbing to fungus.

Negative impacts of pests and diseases on tree recruitment rates are well known in the tropics. Seeding mortality of tropical trees in shaded areas has been shown to be mainly due to the higher presence of undergrowth pests and pathogens in conspecific aggregates (Augspurger, 1984a,b), generating conspecific distance- and/or density-dependent mortality. This process is known as the Janzen (1970) – Connell (1971)