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Selective logging effects on 'brown world' faecal-detritus pathway in tropical forests: A case study from Amazonia using dung beetles

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ABSTRACT

While a significant effort has been made to understand how human activities influence biodiversity, less attention has been given to the consequences of tropical forest disturbance on belowground functional processes and its linkages with environmental drivers. Here, we demonstrate how selective logging influenced dung beetle communities and two associated ecological processes – namely, dung consumption and incidental soil bioturbation – in the eastern Brazilian Amazon, using a robust before-and-after control-impact design. We tested hypotheses about logging-induced changes on environmental condition (canopy cover, leaf litter and soil texture), community metrics (e.g. dung beetle species richness and biomass) and beetle-mediated faecal-detritus processing; and on the importance of the environment for beetle communities and functional processes. We show that post-logging changes in canopy openness do not necessarily mediate logging impacts on dung beetle diversity and biomass, which were directly influenced by reduced impact logging (RIL) operations. Although neither environmental condition (leaf litter or soil sand content) nor faecal consumption and incidental soil bioturbation were directly affected by RIL, the relationships between environmental condition and biological components were. By showing that selective logging alters the linkages among belowground ecological processes and environmental drivers, we provide support that logged forests can retain some important functioning processes, in particular faecal consumption, even when the dung beetle diversity and biomass are impoverished. These results provide support for the resistance of functional processes to logging-induced changes in biodiversity.

1. Introduction

Forest degradation poses a major threat to natural forests and, because it takes place over much larger spatial scales, can result in just as much biodiversity loss as deforestation (Barlow et al., 2016). Millions of hectares of tropical forests have been allocated for timber production (Guariguata et al., 2010) and selective logging is considered a primary driver of tropical forest degradation (Gatti et al., 2015; Pearson et al., 2017). Given the increased global demand for low-cost timber (Blaser et al., 2011), understanding the ecological consequences from logging operations is a key challenge for reconciling timber production and tropical forest conservation.

Despite progress made to comprehend the logging consequences on forest structure and canopy (Asner et al., 2006, 2004b; Gatti et al., 2015), biodiversity (Edwards et al., 2014a, 2014b; Richardson and Peres, 2016), ecosystem values such as carbon stocks (Berenguer et al., 2014; Griscom et al., 2017), soil characteristics (Negrete-Yankelevich et al., 2007) and other environmental aspects of tropical forests (Osazuwa-Peters et al., 2015), the impact of logging on important ecosystem processes remains underrepresented in the literature. This is important, as the sustainability of selective logging could be strongly linked to the extent to which affected forests can maintain the ecosystem processes found in pristine forests (Edwards et al., 2014c; Ewers et al., 2015). Moreover, where effort has been given to understand the impacts of selective logging on biodiversity and ecosystem functioning, studies normally focus on aboveground components and comparatively little is known about logging consequences on belowground biodiversity and brown world ecological processes (but see Slade et al., 2011). In particular, faecal-detritus interactions and decomposition processes are critically important in terrestrial environments and form

Abbreviations: BACI, before-and-after control-impact experimental design; DBH, diameter at breast height; FSC, Forest Stewardship Council; FAO, Food and Agriculture Organization of the United Nations; GLM, generalised linear model; RIL, Reduced-Impact Logging

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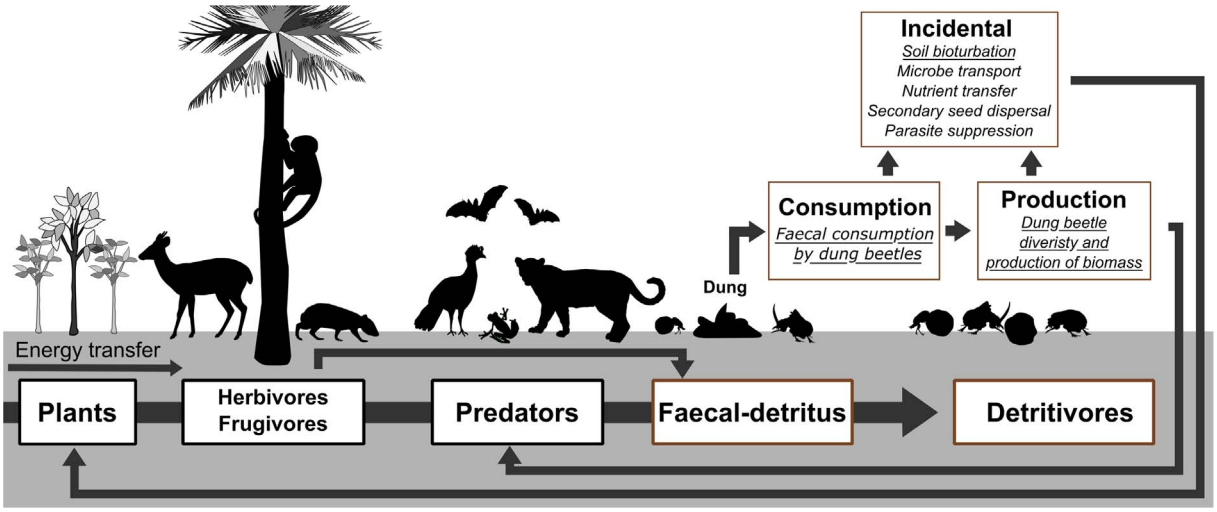

Fig. 1. Dung beetle-mediated faecal detritus-pathway. The energy flow comes from Sun and other key soil elements (e.g. N and P), being assimilated by plants. Plants are consumed by herbivores and frugivorous, which in turn are consumed by predators. These animals, through defecating, produce the resources for the faecal-detritus pathway. Dung beetles mediate many incidental detritus-processing such as soil bioturbation, seed dispersal and nutrient transfer from detritus to the soil, therefore providing a positive feedback for plants. They also consume faeces directly, leading to secondary beetle biomass production, and are consumed by their own predators. Processes investigated in this study are underlined.

intricate connections between below and aboveground sub-systems (Moore et al., 2004). Although these interactions do not necessarily involve direct trophic interactions, their decline or loss are expected to instigate a downstream cascade of impacts on ecosystem processes, with dramatic implications for both 'green' and 'brown' worlds (Wu et al., 2011).

Dung beetles (Coleoptera: Scarabaeinae) are a focal group of detritivores that are frequently used in ecological research linking biodiversity to ecosystem functioning under changing environmental conditions (e.g. Braga et al., 2013; Slade et al., 2011). Through dung manipulation for feeding and nesting purposes (Hanski and Cambefort, 1991), dung beetles play a vital role in facilitating the transfer of energy and matter through dung-based pathways (Nichols and Gardner, 2011). They influence a range of specific detritus processes (Fig. 1), such as faecal consumption and soil bioturbation (Nichols et al., 2007), dung beetle biomass production for predators (Young, 2015), secondary seed dispersal (Griffiths et al., 2016, 2015) and microbial transport across the soil-surface (Slade et al., 2016). Although previous investigation has shown that impacts of human activities in tropical forests on dung beetles are mediated by habitat type and via body-size-dependent responses (Nichols et al., 2013b), conclusions were based on a space-for-time design which may underestimate the impacts from human disturbance (França et al. 2016a). Moreover, despite evidence highlighting the importance of environmental context to predict dung beetle-mediated ecological processes within undisturbed forests (Griffiths et al., 2015), we are not aware of any empirical study exploring the extent to which an anthropogenic forest disturbance, such as selective logging, alters the importance of environmental drivers for dung beetle-mediated faecal-detritus processes.

In this paper, we address these gaps by using a BACI experimental design to explore the impacts from selective logging in the eastern Brazilian Amazonia. Specifically, we examine (1) how environmental conditions, dung beetle communities and associated ecological processes at different stages of the dung-detrital pathway are affected by logging operations, and (2) how potential logging-induced changes in environmental drivers are reflected in ecosystem functional processes provided by dung beetles. We predict that forest disturbance induced by selective logging (1) has negative consequences on forest structure (Asner et al., 2004a), dung beetle communities and associated detrital processes (Slade et al., 2011); and (2) alters the relative importance of the environmental context for dung beetle communities and associated functional processes. We expect that, first because disturbance tends to alter both environmental heterogeneity and diversity/productivity relationships (Cardinale et al., 2000). Second, because previous research has shown that forest disturbance alters the importance of habitat variables for arthropod communities (Oliver et al., 2000), and dung beetles and associated ecological functions are greatly influenced by environmental context (Davis et al., 2001; Griffiths et al., 2015). Our findings are not only important for understanding how forest disturbance shapes environmental drivers and belowground ecosystem functioning in tropical forests, but also provide new insights into the ecological value of selectively logged tropical forests and how environmental context mediates the biological consequences of human activities.

2. Material and methods

2.1. Study site

The study was carried out within a logging concession area of 1.7 Mha located in the state of Pará in north-eastern Brazilian Amazonia (0°53S, 52°W; Appendix A, Fig. A1). This area comprises a mosaic of *Eucalyptus* plantations and regenerating secondary forests embedded within a large matrix of evergreen dense tropical rainforest (Souza, 2009) subjected to low levels of disturbance (Barlow et al., 2010; Parry et al., 2009). This region is within the equatorial/tropical rainforest climate (Af, Köppen's classification), with annual rainfall and average temperature of 2115 mm and 26 °C, respectively (Souza, 2009).

This logging concession is certified by the Forest Stewardship Council (FSC) and follows the FAO model code with reduced-impact logging (RIL) on a 30-year rotation (FSC, 2014). Main activities under RIL include pre-harvest mapping, measurement and identification of all commercially viable trees with DBH ≥ 45 cm within 10 ha (250 × 400 m) logging management units planned to be logged with a specific logging intensity ($m^3\,ha^{-1}$). Moreover, harvest incorporates methods that aim to minimize residual stand damage, such as vine cutting, directional felling, and planning of roads, skid trails and log decks (Dykstra and Heinrich, 1996).

2.2. Experimental design

We used the company's pre-harvest inventory to select 34 management units (hereafter sample units). These included 29 'logging' units destined to be logged along a gradient of planned logging