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Biodiversity consequences of land-use change and forest disturbance in the Amazon: A multi-scale assessment using ant communities

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ABSTRACT

Quantifying and understanding the main drivers of biodiversity responses to human disturbances at multiple scales is key to foster effective conservation plans and management systems. Here we report on a detailed regional assessment of the response of ant communities to land-use change and forest disturbance in the Brazilian Amazon. We aimed to explore the effects of land-use intensification at both site and landscape scales, examining variation in ant species richness and composition, and asking which set of environmental variables best predict observed patterns of diversity. We sampled 192 sites distributed across 18 landscapes (each 50 km^2) in Paragominas, eastern Brazilian Amazon, covering ca. 20,000 km^2. We sampled from undisturbed primary forest through varyingly disturbed primary forests, secondary forests, pastures and mechanised agriculture, following a gradient of decreasing total aboveground biomass. Irrespective of forest disturbance class, ant species richness was almost twice as high in forests when compared to production areas. In contrast, ant species composition showed continuous variation from primary forest to intensive agriculture, following a gradient of aboveground biomass. Ant species richness at all spatial scales increased with primary forest cover in the surrounding landscapes. We highlight the limited value of species richness as an indicator of changes in habitat quality, reinforcing calls to consider species composition in assessments of forest disturbance. Taken together, our results reveal the unique biodiversity value of undisturbed primary forests, but also show that disturbed primary forests and secondary forests have high conservation value, and thus play an important role in regional conservation planning.

1. Introduction

Human-induced changes to the biosphere have led to widespread biodiversity loss across the planet (Gibson et al., 2011; Newbold et al., 2015). Tropical forests are at the forefront of conservation concerns as, despite harbouring two-thirds of global terrestrial biodiversity (Slik et al., 2015), they remain subject to high levels of deforestation, fragmentation, and selective logging, among other impacts (Malhi et al., 2014). As a result, much of the remaining areas of tropical forests are embedded within human-modified landscapes containing different land-use systems, including a variety of agricultural lands and areas of standing forests that have experienced different levels of anthropogenic disturbance (Gardner et al., 2009). Despite extensive research on the impacts of particular land-use changes on biodiversity (e.g. Coronado et al., 2009; Karp et al., 2012), we still know very little about biodiversity persistence within such heterogeneous landscapes.

Our current understanding of biodiversity responses to and forest disturbance change in tropical forests regions is limited by some methodological limitations of past studies. First, many studies have examined only highly contrasting land uses — e.g. forests versus agriculture (e.g. Azevedo-Ramos et al., 2006; Dexter et al., 2012). Second, few studies comprehensively document environmental variables that could be used to understand factors promoting biodiversity persistence in different land-use systems (but see Carrara et al., 2015). Third, despite growing indications that landscape-level attributes (e.g. area of remaining forest cover) can have an important influence on local patterns of

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biodiversity (Solar et al., 2015), most studies continue to only be conducted at the local (site) scale without appropriate reference to broader landscape conditions (Tabarelli et al., 2012). Finally, the vast preponderance of biodiversity studies in human-modified tropical forests have focused on plants and vertebrates (e.g. Antongiovanni and Metzger, 2005; Dexter et al., 2012), yet we know that invertebrates comprise most species and they often respond differently to human-induced disturbances (Andersen and Majer, 2004; Barlow et al., 2007a; Solar et al., 2015).

Arthropods are by far the most numerically dominant faunal group in tropical environments, and play critically important roles in ecosystem functioning (Hamilton et al., 2010). Among the arthropods, ants are a ubiquitous group, dominating faunal biomass in many forests (Hölldobler and Wilson, 2009; Basset et al., 2015), occupying all forest strata (Blüthgen and Feldhaar, 2010), and playing a wide variety of key functional roles relating to soil health, nutrient cycling, energy flow, herbivory and seed dispersal (Del Toro et al., 2012). Moreover, ants have been widely used as bioindicators of human disturbance (Andersen and Majer, 2004). Yet despite their importance, very few studies have assessed responses of tropical forest ant communities to human disturbance at large spatial scales, such as those comprising several hundreds of kilometres (but see Vasconcelos et al., 2006; Vasconcelos et al., 2010; Leal et al., 2012 for exceptions), and, to our knowledge, none across multiple-use human-modified landscapes.

Here we examine the implications of human-modified tropical forests and land-use change for Amazonian ant assemblages, focussing on the importance of forest habitats for the conservation of species at local and regional scales. We report on an assessment of ant communities sampled from 192 transects distributed across eighteen 50-km^2 catchments in a large (ca. 20,000 km^2) human-modified region of the eastern Brazilian Amazon. We address two specific questions. First, how does ant species richness and composition vary with land-use change and forest disturbance (from undisturbed forest, through varying degrees of forest disturbance and production areas) at site and landscape scales? Second, what set of environmental variables best predict observed patterns of species richness and composition at both site and landscape scales? We also identify ant species that are strongly associated with different land-uses and therefore could be used as valuable indicators of the ecological consequences of human disturbance. Taken together, these analyses provide a quantitative understanding of the environmental drivers of maintenance and loss of ant communities in one of the most species-rich areas of the planet, and can help provide a basis for predicting the biodiversity consequences of future land-use change and forest disturbance.

2. Materials and methods

2.1. Study region

We conducted our study in Paragominas, a municipality located in the eastern Brazilian Amazon, in the state of Pará (Fig. 1). Paragominas was originally covered with evergreen tropical forest, but has experienced circa 35% forest loss and widespread degradation of remaining forests in recent decades, especially due to forest conversion to pastures and mechanised agriculture, and degradation by selective logging, fragmentation and understory fires (for more details, see Gardner et al., 2013; Viana et al., 2016).

We sampled two major land-use categories, divided into seven classes: production areas (3 classes) and forests (4 classes). Production areas comprised mechanised agriculture (N = 14), cattle pastures (N = 50), and silviculture (monocultures of *Eucalyptus* spp. and *Schyzolobium parahyba* var. *amazonicum*, N = 12). Forest classes comprised secondary forests (N = 20), logged and burnt primary forests (N = 44), logged primary forests (N = 43) and undisturbed primary forests (N = 9). Forest classification was based on systematic field observations of evidence of past human disturbance, such as charcoal and logged stumps, combined with a visual analysis of a 20-year chronosequence of satellite images (Gardner et al., 2013).

2.2. Sampling design

We used ArcGIS 10 to divide Paragominas into 182 roughly evenly sized third- or fourth-order catchments (ca. 50 km^2 each — landscape scale), from which we selected 18 for biodiversity surveys that were distributed across a gradient of remaining forest cover (6–100%). Within each landscape, we allocated 8–12 transects (each 300 m — site scale) at a standard density of 1 transect/4 km^2, separated by at least 1.5 km. The number of sites allocated to each land-use class was proportional to the overall area occupied by either production areas or forests within a catchment. In total, we sampled 192 transects over an area of approximately 20,000 km^2 (Fig. 1; detailed information can be found in Gardner et al., 2013).

Along each site we installed six epigaeic baited pitfall traps spaced by 50 m that operated for a 48-h period. Traps consisted of plastic containers (10 cm diam.) half filled with a solution of water, salt (5%) and soap (5%), and baited with sardine and honey, which were placed in a cup hanging above the plastic containers that was unreachable to the ants. After sampling, we identified the ants using available taxonomic keys (e.g. Fernández, 2003; Baccaro et al., 2015) and the reference collection of the Community Ecology Lab, Federal University of Viçosa. Species nomenclature was checked and revised against Bolton's online catalogue (Bolton; http://antcat.org, accessed in Feb/2016). Morphospecies were assigned number codes that apply only to this study. A full collection of voucher specimens is housed at Community Ecology Lab, Universidade Federal de Viçosa.

2.3. Environmental variables

We sampled a range of environmental variables that represent important resources and habitat conditions for tropical ants (Carvalho and Vasconcelos, 1999; Blüthgen and Feldhaar, 2010), and are known to vary both within and between the different land-use classes surveyed (Table 1). Sampled variables included total aboveground biomass (AGB), biomass of fine woody debris (FWD), litter biomass (LB), tree species richness (TSR), canopy cover (CC), soil bulk density (SBD), clay percentage in the soil (CP), percentage of primary forest within a 500 m buffer around the site (PFP_S), percentage of primary forest in the entire landscape (PFP_L) and deforestation trajectory curvature profile, which is a metric that characterises whether deforestation has been conducted more in the past or more recently (FCCP, Ferraz et al., 2009). Data for forest structure, tree species richness, and soil were obtained from measurements made within transects (for more details, see Berenguer et al., 2014). Both PFP and FCCP were calculated at site and landscape scale by analysing time-series of satellite images (see Gardner et al., 2013 for more details). Canopy cover and tree species richness were highly correlated with percentage of primary forest cover at both transect and catchment scales (Pearson $\rho > 0.73$), and therefore they were removed from analyses (Zuur et al., 2010).

2.4. Statistical analyses

We adopted total aboveground biomass (see Table 1) as a proxy for characterising a continuous gradient of land-use intensification and forest disturbance (Grime, 1979). Aboveground biomass is sensitive to multiple human impacts on forests in our sites (Berenguer et al., 2014), and is therefore a measure of their combined impact. All forest classes were significantly different with regard to AGB at the site scale ($\chi^2_{6,11} = 513.2$, $P < 0.001$, $R^2 = 0.93$, Fig. S1), but pasture and mechanised agriculture were indistinguishable from each other because of either the scarcity or total lack of trees.

To assess the relationship between ant species richness and land-use class at the site scale, we used Generalized Linear Mixed Model (GLMM,