UNIVERSIDADE FEDERAL DE LAVRAS

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QUANTIFYING INVERTEBRATE-MEDIATED HERBIVORY ACROSS AN ANTHROPOGENIC DISTURBANCE GRADIENT IN AMAZONIAN FORESTS

LAVRAS – MG

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Prof. Dr. Jos Barlow

Orientador

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JÚLIA RODRIGUES BARRETO

QUANTIFICANDO HERBIVORIA MEDIADA POR INVERTEBRADOS AO LONGO DE UM GRADIENTE DE PERTURBAÇÃO ANTROPOGÊNICA EM FLORESTAS AMAZÔNICAS

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APROVADA em 31 de julho de 2017.

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À minha família, exemplos para tantas lições… Pelo suporte, amor e por tantas vezes que me faltou coragem, acreditarem no meu potencial e no êxito desta a qual dedico.

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> “No society that forgets the art of asking questions
> or allows this art to be forgotten, will ever find
> adequate solutions to the problems it faces”
>
> Zygmunt Bauman

RESUMO GERAL

A perturbação é uma ameaça generalizada para a biodiversidade, afetando indiretamente interações ecológicas com possíveis consequências de longo alcance para as florestas tropicais. Herbivoria é uma interação ecológica chave sendo um campo interessante para se explorar em florestas tropicais alteradas pelo ser humano, com o potencial de desvendar as críticas consequências para a comunidade e ecossistemas florestais. Demostramos em um estudo de larga escala que, apesar das taxas atuais de perturbação e efeitos negativos sobre a diversidade, esses impactos não necessariamente se estendem às interações ecológicas. Encontramos que níveis de herbivoria dominados por mastigadores seguido pelas duas outras formas de herbivoria mediada por invertebrados pesquisadas (minadores e galhadores), ambos com níveis relativamente baixos. Encontramos ausência de alteração níveis gerais de herbivoria ao longo de perturbações nas florestas amazônicas pesquisadas, com uma ligação também fraca entre herbivoria e variáveis de perturbação ambiental. Paisagens tropicais estão sofrendo taxas de perturbação sem precedentes e encontramos apenas um efeito sutil sobre a herbivoria em intensidades baixas de distúrbio. Atentamos para implicações em políticas de conservação, para que foquem na manutenção da funcionalidade encorajando o monitoramento de processos ecológicos, tais como a herbivoria. Herbivoria não só parece ser funcionalmente resistente a perturbações, mas também desempenha um papel crítico na regeneração da floresta, contribuindo de várias maneiras para a resiliência da floresta como um todo. Nossos resultados trazem informações sobre o funcionamento de florestas tropicais, uma vez que mudanças ambientais podem resultar em impactos a longo prazo do ecossistema.

Palavras-chave: Floresta amazônica. Biodiversidade. Funcionamento ecossistêmico. Gradiente ambiental. Perturbação florestal. Herbivoria. Dano foliar. Interações inseto-planta. Floresta primária. Floresta tropical.

ABSTRACT

Disturbance is a generalized threat to biodiversity, indirectly impacting ecological interactions with possible far-reaching consequences for tropical forests. Herbivory is a key ecological interaction being an interesting field to explore specially in human-altered tropical rainforests, with the potential to unravel critical consequences for both herbivores and forest ecosystems. We demonstrated in a large-scale study that, despite current rates of disturbance and negative effects on diversity, these impacts not necessarily extend to ecological interactions. We found these Amazonian forests herbivory levels to be dominated by chewing and the other two forms of invertebrate–mediated herbivory surveyed (mining and galling) followed both with relatively very low incidence dominated herbivory levels. No overall changes in herbivory levels along disturbance in Amazonian forests surveyed, with a weak link between herbivory and environmental disturbance variables. Tropical forest landscapes are suffering unprecedented rates of disturbance and we found evidences slight effect of light pressures of disturbance, we claim implications for conservation policies to focus on maintenance of functionality of ecological processes outcomes such as herbivory and encouraging monitoring of these. Herbivory not only seem to be functionally resistant to disturbance, but also play critical role on forest regeneration, contributing in several ways to forest resilience as a whole. Our results bring insights for tropical forest functioning since drivers of environmental change that affect biodiversity are likely to result on long-term ecosystem impacts.

Key words: Amazon Forest. Biodiversity. Ecosystem functioning. Environmental Gradient. Forest Disturbance. Herbivory. Leaf Damage. Plant-Herbivore Interactions. Primary Forest. Tropical Forest.

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SUMÁRIO

FIRST PART

1 INTRODUCTION

Herbivory is a fundamental and important ecosystem process across the world. Most tropical forests are disturbed to some degree, and any changes in herbivory could have big impacts on our understanding of globally relevant nutrient pathways.

One chapter containing one manuscript to be submitted to Journal of Ecology composes the present thesis.

We undertook an extensive survey of herbivory levels from canopy leaves collected at 20 sites (and 1100 individual stems) in eastern Amazonia along a disturbance gradient that goes from undisturbed forests to, selectively logged, selectively logged-and-burnt to secondary forests. We found that chewing incidence was the highest between forms of herbivory, followed by mining and galling. No overall change in herbivory levels was found along disturbance classes, except for chewing. Mean chewed area peaked at logged class (7.82%). Chewers' intensity of damage was positively influenced biomass but this effect was lost when variable was weighted by plant species dominance, displaying negative effect of landscape configuration instead. Mining and galling remains with comparatively lower levels with no response to disturbance gradients, being best explained by null models.

We measured herbivory levels in 1102 trees of 268 species. We demonstrated in a large-scale study that overall process of herbivory is being maintained across disturbed and recovering forests despite results of slight variance in chewing. Studies worldwide evidence impacts of disturbance on biodiversity however these effects had not yet reached herbivory as an outcome of tropical forest functioning. We claim for conservation strategies focusing on maintaining functionality of forests despite anthropogenic interests, these actions may sustain ecosystem functioning and contribute to forest resilience.

2 THEORETICAL FRAMEWORK

2.1 Overall Rationale

Herbivory has crucial effects on community structure and ecological functions, and is an important pathway for energy flows from plants to upper trophic levels (COLEY & BARONE, 1996; AGRAWAL, 2007; HEMPSON *et al*., 2015). Interactions between plants and herbivores are among the most intensively studied biotic interactions (TYLIANAKIS *et al*., 2008, JAMIESON *et al*., 2012). Herbivory is a key ecosystem process that reduces the biomass and density of plants materials, transfers mass and nutrients and affects habitat and resource conditions for other organisms. It involves over half of all terrestrial species and plays a critical role in determining community structure and ecosystem function (ZANGERL *et al.*, 2002).

Invertebrates, in particular insects, are the most diverse terrestrial group and are responsible for important ecosystem functions (reviewed in WEISSER & SIEMANN, 2004), at a global scale, the largest part of herbivory attributed to them (WILSON, 1987). Herbivorous insects are classified into a few functional groups (e.g. feeding guilds), including: sap-suckers, that siphon plant fluids affecting its flow and nutrients within the plant; miners and borers, that feed under plant surfaces; seed predators and frugivores that consume the reproductive parts of plants; gall-formers, that induce abnormal growth reactions by plant tissues due to feeding and sheltering within the plant tissue; chewers, species that chew foliage directly reducing photosynthetic tissue area; root-feeders, reduce plant capacity to acquire nutrients or remain upright (SCHOWALTER, 2011).

Herbivorous insects' ecological roles are complex. At the individual level, they alter plant growth, affecting water and nutrient fluxes (SCHOWALTER & LOWMAN, 1999; SCHOWALTER *et al.*, 1986; TRUMBLE *et al.,* 1993). At the community scale, herbivory affects composition through its impact on the relative competitive abilities of the species present and can even alter the rate of succession (BROWN & ALLEN, 1989). Reducing vegetation cover, herbivory greatly influences conditions experienced by understory and soil communities; reduces vegetation biomass or litter accumulation, affecting the abundance of fuel to support fire, soil water-holding capacity, and vegetation demand for water during drought (SCHOWALTER 2011). By doing so, herbivory can have a substantial impact on the structure and function of ecological communities even influence an ecosystem's stability (HEMPSON *et al.*, 2015). Thus, further than just a simple loss of leaf tissue, herbivory is an ecosystem regulator and variation in herbivory can cascade to lower and upper trophic levels (CHEW, 1974; MATTSON & ADDY, 1975; LEEN & INMAN, 1975; KITCHELL *et al.*, 1979).

2.2 Herbivory and Human Disturbance

High rates of disturbance and deforestation in tropical forests, due to the expansion of agriculture, are complemented by events that disturb the remaining forests, including defaunation, selective logging, the spread of wildfire, and landscape fragmentation (FAO, 2006; MALHI *et al.*, 2014; KAREIVA *et al.*, 2007). Protecting this refuge of two-thirds of all the world's species (BRADSHAW *et al*., 2009) becomes even more difficult when such drivers interact, with species losses resulting in redesigned communities and altered ecological interactions (DE SASSI *et al*., 2012; MENÉNDEZ *et al*., 2008; LEAL *et al*., 2014) causing further loss of tropical forest diversity (TYLIANAKIS *et al*., 2008; FAHRIG, 2013; MORANTE- FILHO *et al*., 2015). We do not yet understand how this cascade of effects will result in changes of biodiversity and ecosystem functioning (TSCHARNTKE *et al*., 2005, MITCHELL *et al*., 2015), therefore it is important to understand how ecological processes and regulation of terrestrial ecosystems are affected (MORANTE-FILHO, 2016).

Effects on biodiversity result in novel combinations of species and shifts in communities' structure (MCKINNEY & LOCKWOOD, 1999; TABARELLI *et al*., 2010), disrupting ecological interactions with potential ecosystem effects (CARDINALE *et al*., 2012; DE COSTER *et al*., 2015; MITCHELL *et al*., 2015; VALIENTE-BANUET *et al*., 2015). Anthropogenic changes are affecting species survival more than changes in average conditions (GUTSCHICK & BASSIRIRAD, 2010, Jentsch et al. 2007, Kaushal et al. 2010, Reusch et al. 2005) and contemporary biodiversity declines are among main drivers of changes in ecosystem functioning (TILMAN *et al*., 2012). Biodiversity effects had been suggested to depend on trophic interactions (BRUNO *et al*., 2008; DUFFY *et al*., 2005), herbivory and disturbance along with biodiversity are long known to affect ecosystem functioning (TILMAN *et al*., 2012). Changes in plant diversity in response to anthropogenic drivers were also before noticed to be positively associated with changes in temporal stability of productivity (HAUTIER *et al*., 2015). Hautier and colleagues (2015) evaluated variance in herbivory and other factors such as N, CO2, fire and water; also suggesting that biodiversity-mediated effects on stability were independent of drivers.

Although forest disturbance may intensify herbivory pressure due to increased density of insect herbivores, there is much uncertainty as the link between herbivores and plants is complex. In particular, invertebrates are sensitive to small changes in microclimate (WALLIS DE VRIES & RAEMAKERS, 2001) and environmental conditions can affect dynamic and effects of herbivory (BROWN & ALLEN, 1989). Disturbance was noticed to increase herbivory at the edge (COLEY, 1982) and at burnt areas (KNIGHT & HOLT, 2005), but also reported to decrease through increased control of host plant on insect herbivores (MCEVOY & COOMBS, 1999). Plants exposed to the sun are prone to higher levels of herbivory, however when accessing effect of light gradients, mining pressure was unusually found to decrease in shade (COLLINGE & LOUDA, 1988). Chewers and leaf-miners' pressure increased with exposure to light (Lincoln and Mooney, 1984; Louda and Rodman, 1996).

Temperature and climate gradients found overall herbivory increase in North America (LOUDA & COLLINGE, 1988, Australia (LANDSBERG &GILLIESON, 1995) and even in constant latitude (BALE *et al.*, 2002).

Moreover, although a body of evidence suggests that secondary metabolites are not predictive of herbivory (KUROKAWA *et al.*, 2010; CARMONA *et al.*, 2011; PEARSE, 2011; LORANGER *et al.*, 2012; SCHULDT *et al.*, 2012), plant physical and chemical defences can also change along disturbance gradients (COLEY, 1987; MCINTYRE *et al.*, 1999). Many secondary compounds, morphological and life-history traits have been attributed to chemical and physical defence against herbivores (COLEY & BARONE, 1996; JONES & LAWTON, 1991; POORTER *et al.*, 2004). Compounds were found to co-vary in a non-random pattern along successional stages (CHAI *et al.*, 2016) and influence herbivore levels, yet the magnitude of this effect is still subject to debate, particularly in tropical rain forests (MOLES *et al.*, 2011; CÁRDENAS *et al.*, 2014). Disturbance is also expected to affect generalists and specialist herbivores in different manners, changes in plant species composition are likely to trigger specialists' restriction in host or even local extinction because of lower availability some specific resources/habitats, being also possible that the generalists could be more abundant in disturbed sites (GUIMARÃES *et al.*, 2014).

Anthropogenic habitat modification can cause shifts in herbivorous insects species composition through the replacement of specialists by generalist herbivores (KAARTINEN & ROSLIN, 2011), thus novels combination of resources might favour generalists, known to display better resilience (HARVEY *et al.*, 2010). Understanding the role of plant-herbivores interactions along gradients of disturbance pressure is crucial to understand the shape of this relationship so that improvements can be made on predicting impact of a changing environment on biodiversity.

2.3 Herbivory in the Canopy

Some effort had been directed to exploring tropical forests canopies, while climate change threatens plant-animal interactions, multidisciplinary research has expanded concepts of global species richness, physiological processes and the provision of ecosystem services (OZANE *et al.*, 2003). Despite evidence that leaf damage rates in tropical forests are relatively high and that tropical herbivory is dominated by insects (COLEY & BARONE, 1996), given the impracticality of accessing tropical forest canopies, only a few studies have surveyed herbivory there. Schowalter (1995) and Schowalter & Ganio (1999) comparing herbivore abundances and folivory in replicated disturbed and undisturbed patches of tropical evergreen forests found that disturbance increased abundances of herbivorous insects on abundant, rapidly-growing early successional plant species such as *Jacaranda copaia, Cecropia sciadophylla*. Continued measurement of herbivory over long time periods would be able to relate changes in the intensity of herbivory to environmental changes and to effects on ecosystem processes (SCHOWALTER, 2011).

2.4 Methodological issues related to herbivory assessments

Assessing herbivory have its difficulties especially for some plant parts and forest canopies, for that reason, measurements had not been standardized (SCHOWALTER, 2011). Within tropical evergreen forests, a variety of studies have assessed herbivory rates through different and often not comparable methods (ODUM & RUIZ-REYES, 1970; BENEDICT, 1976; SCHOWALTER, 1994; SCHOWALTER & GANIO, 1999; WINT 1983; LOWMAN *et al*., 1993). Estimates of herbivory based on long-term monitoring of leaves are often 3–5 times the estimates based on discrete measurement of leaf area loss (LOWMAN, 1995). Measure of proportion of missing leaf area at a point in time does not represent the rate of consumption or removal of plant material but, due to inaccessibility of the canopy, is a suitable method for measuring porosity, photosynthetic capacity and canopy interactions with soil or atmosphere interactions (SCHOWALTER, 2011).

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SECOND PART - MANUSCRIPT:
HERBIVORY LEVELS ACROSS A DISTURBANCE GRADIENT IN AMAZONIA

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Abstract:

1. Herbivory is a fundamental and important ecosystem process across the world. Most tropical forests are disturbed to some degree, and any changes in herbivory could have big impacts on other trophic interactions, trophic levels and on our understanding of globally relevant nutrient pathways and ecosystem functioning.

2. We undertook an extensive survey of herbivory levels from canopy leaves collected at 20 sites (and 1100 individual stems) in eastern Amazonia along a disturbance gradient that goes from undisturbed forests to, selectively logged, selectively logged-and-burnt to secondary forests.

3. We measured herbivory levels in 1102 trees of 268 species. Chewing incidence was the highest between forms of herbivory, followed by mining and galling. No overall change in herbivory levels was found along disturbance classes, except for chewing. Mean chewed area peaked at logged class (7.82%). Chewers' intensity of damage was positively influenced biomass but this effect was lost when variable was weighted by plant species dominance, displaying negative effect of landscape configuration instead. Mining and galling remains with comparatively lower levels with no response to disturbance gradients, being best explained by null models.

4. We demonstrated in a large-scale study that overall process of herbivory is being maintained across disturbed and recovering forests despite results of slight variance in chewing. Studies worldwide evidence impacts of disturbance on biodiversity however these effects had not yet reached herbivory as an outcome of tropical forest functioning. We claim for conservation strategies focusing on maintaining functionality of forests despite anthropogenic interests, these actions may sustain ecosystem functioning and contribute to forest resilience.

Key words: Amazon Forest; Biodiversity and ecosystem functioning; Environmental Gradient; Forest Disturbance; Herbivory; Leaf Damage; Plant-Herbivore Interactions; Primary Forest; Tropical Forest.

Introduction

Tropical forests are very important as reservoirs of biodiversity (Bradshaw et al., 2009), and for their role in ecosystem functioning such as carbon sequestration and storage (Berenguer et al. 2014). It is therefore crucial to understand human impacts on these systems. Much effort has gone into understanding biodiversity or carbon dynamics (Li *et al.* 2013; Metcalfe *et al.* 2014; Berenguer *et al.* 2015; Robinson *et al.* 2015) but much less has been directed at changing ecosystem processes. Quantifying ecological interactions offers a way of understanding how ecosystem processes are being affected by current rates of degradation.

Herbivory is a fundamental and important ecosystem process across the world, involving over half of all terrestrial species and acting as an important pathway for energy flow from plants to upper trophic levels (Zangerl et al. 2002; Coley & Barone, 1996; Agrawal, 2007; Hempson et al. 2015), with crucial effects on quantity and quality of organic material transferred to the soil and nutrient cycling (Bardgett & Wardle 2003; Hartley & Jones 2004). Tropical ecosystems were for a long time believed to experience higher rates of herbivory than temperate ecosystems (Coley and Aide, 1991; Coley, Barone & Barone 1996) however such tendencies have not been confirmed (Springett, 1978; Landsberg and Ohmart, 1989; Adams & Zhang, 2009; Moles et al., 2011a,b; Rasmann & Agrawal, 2011), even in global surveys (Kozlov et al. 2015). Moreover, there is significant variation in attempts to quantify herbivory levels in tropical forest, with estimates of insect attack ranging in different systems all over the world (from 0.1% in Goley, 1977; 7-9% in Dirzo, 1987; to 17% reached through long-term measurements by Filip *et al.* 1995; and 48% among gap-specialist species in Coley *et al.*, 1996).

At least some of this variation can be explained by methodological approach, as estimates of herbivory based on long-term monitoring often are 3–5 times the estimates based on discrete measurement of leaf area loss (Lowman, 1995). But there are three key additional knowledge gaps that limit our understanding. First, very few studies report the role of herbivores in tropical forest woody species canopies, due to the impracticality of accessing such heights. Second, no studies have examined the shape of this relationship in response to human disturbance pressures in tropical forests even though insect densities (Coley, 1982; Knight & Holt, 2005), resource quantity (McNaughton *et al.* 1989) and quality (Coley, Bryant & Chapin 1985), plant defences (Coley 1987; McIntyre *et al.* 1999) and predation levels (Elton, 1973: Maas et al. 2013, Mitchell et al. 2015; Morante-Filho *et al.* 2016) are all likely to change along these gradients. As well established in the literature, lack of bottom-up control may drive enhanced herbivory pressure in human-altered landscapes (Coley and Barone 1996, Wirth et al. 2008, Leal et al. 2014). Moreover, data from rainforest gaps suggests that herbivory levels should be much higher following disturbance (Coley et al. 1996), but we lack robust empirical data to test this. This is vital, as most remaining tropical forests are disturbed to some degree, and any changes in herbivory could have big impacts on our understanding of globally relevant nutrient pathways. Third, many studies focus on leaf loss from chewing invertebrates (e.g. Hodar & Zamora, 2004; Fagan *et al.* 2005; Unsicker *et al.* 2006; Pennings *et al.* 2007; Wolf *et al.* 2008; Balhom *et al.* 2011; Silva *et al.* 2012), but do not consider other forms of invertebrate-mediated herbivory that are prevalent in tropical forests, such as miners and gall-formers.

We address these three knowledge gaps by undertaking an extensive survey of herbivory levels in eastern Amazonian canopies along a disturbance gradient that includes undisturbed, selectively logged, selectively logged-and-burnt and secondary forests. We evaluate both incidence (proportion of leaves or leaflets affected) and leaf area inflicted by three invertebrate-mediated forms of herbivory - chewers, miners and gall-formers in 1102 trees of 268 species across 20 sites. Specifically, we ask: (i) Whether and how do the three different forms of invertebrate-mediated herbivory vary across four different classes of tropical forest disturbance?; (iii) Can plot-level herbivory levels (both naïve and weighted by species abundance) be predicted by environmental variables reflecting forest disturbance history, soil fertility and landscape configuration?

Methods

Study Area

This study was conducted during the dry season of 2015 in a region of eastern Amazonian the municipalities of Santarém, Belterra and Mojuí dos Campos, state of Pará, Brazil (Figure 1).

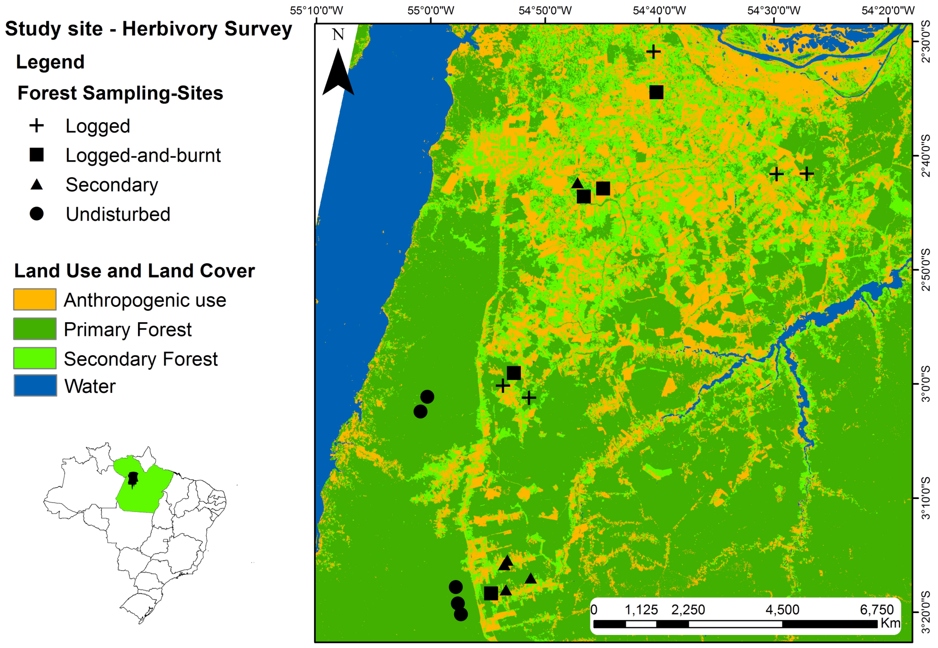

Figure 1 Location of the study region in Santarém-Belterra-Mojuí dos Campos (abbreviated to Santarém), plots distribution on 20 study catchments.

The region accounts for 41% of all forest loss in the Brazilian Amazon between 2000-2016 (PRODES 2016) and is still marked by a high rate of forest and land use changes along the past 40 years, now presenting a mosaic of agricultural and forested lands (Gardner *et al.* 2013). Location has suffered both kinds of human-driven pressures, degradation and deforestation. These differ on rates of disturbance, deforestation being the complete removal of forest cover, changing land use; and degradation being the deterioration of remaining forests, reducing its provision of goods and services (Parrotta, Wildburger & Mansourian 2012). From 2007 to 2013 the Brazilian Amazon experienced 102,924 Km^2 of degraded forests, being the state of Pará the second most impacted, with 26,374 Km^2 (INPE, 2014).

Data was sampled across 20 plots (10x250 m, 0.25 ha) distributed along the following four forest classes classified by Gardner et al. (2013): undisturbed primary forests (n=5); logged primary forests (n=5); logged-and-burned primary forests (n=5); and secondary forests recovering after agricultural abandonment (n = 5). The disturbance gradient was defined using a combination of field assessments and an analysis of canopy disturbance, deforestation and regrowth in a 20-years chronosequence of satellite images (for more information about land use classification and forest structure see Gardner et al. 2013, Berenguer et al. 2014, Barlow et al. 2016). Plots were located in evergreen non-flooded forests and were placed at least 1500 m from each other and at least 100 m from forest edges.

Herbivory sampling

To assess levels of foliar herbivory (i.e. losses measured at a single point in space and time), we sampled fully sunlight leaves of three individuals of all trees and palms species ≥ 10 cm DBH that contributed to 80% of the basal area of each plot. This criterion was based on Grime's "mass-ratio hypothesis" which suggests that ecosystem properties are determined by the characteristics of dominant plants (Grime 1998). All individuals were identified to species level by experienced and local parabotanists. Herbivory was sampled across all leaves of a fully sunlight branch collected by a tree climber. We classified herbivory into two different surveys, incidence and severity of herbivory. Incidence as the number of leaves affected by each form of herbivory (i.e. chewers, miners, and gall-formers) divided by the total number of leaves collected in that branch. It is therefore expressed as the proportion of affected leaves. We called severity the average prevalence of damage per stems, expressed as average proportion of damaged leaf area. For chewing damage, this was based on measurements of leaf area affected; for galls and mines we based this on the estimated area affected, recognising that simple area estimates may underestimate physiological consequences for the plant. When not specifying between incidence and severity, we refer to "herbivory levels" solely.

For individuals with simple leaves, to sample miners and gall-formers' severity, each leaf was assigned to one of the damage classes according to the percentage of the area of the leaf lamina that was damaged: intact leaves, 0.01–1, 1–5, 5–25, 25–50, 50–75 and 75–100% (see methods of Alliende 1989). To measure the severity of damage caused by chewers, we randomly selected 30 chewed leaves per individual and scanned them (example on appendix). Using a graphics software, we manually drew the outline of all leaves with damaged edges, so we could recreate the initial leaf area (i.e. prior to damage). Using an imagery software (ImageJ, NIH, MD, USA, version 1.49u) we calculated leaf area considering holes (Ah, cm2), then adjusted to fill damaged area to estimate leaf original area (Anh, cm2). The difference between original area (Anh) and area excluding damage (Ah) was divided by original area (Anh) to calculate proportional leaf area loss (H) (as Metcalfe *et al.* 2014). For compound leaves we considered leaflets as leaves, surveying incidence and severity for each leafy tissue blade.

We understand that measuring proportion of missing leaf area at a point in time does not represent the rate of consumption but each plant's lifetime accumulated herbivory damage, with no regard of the duration of this study. However, this approach is suitable considering heights of Amazonian canopies (Schowalter 2011) and intensive sampling effort, precluding monitoring of rates (Souza *et al*. 2013).

Environmental variables

Forest disturbance history - We used plot-level forest biomass as a continuous index of forest condition (i.e. disturbance history). Although we also used categories of forest disturbance history, these are quite crude and risk obscuring a lot of important variation in terms of disturbance intensity (i.e. timber volume removed, collateral damage, or fire intensity) and time-since disturbance (i.e. time for recovery or additional delayed mortality). We predicted plot biomass would be a more accurate - and continuous - index of forest condition.

Across all 20 plots, all stems of trees, palms and lianas ≥10cm DBH were measured and identified to species level. We then used Chave's equation for tropical moist forests to convert DBH and species specific wood density to estimate the above-ground dry biomass of each individual (for details on biomass estimation see Berenguer *et al*. 2015). The sum of all individuals' biomass is the plot-level biomass.

Soil fertility - One of the most used parameters to infer soil fertility is pH, with the potential to change nutrients availability for plants even in tropical soils where, due to deepness, leached and age; are naturally acidic (Furtini-Neto et al. 2001). Soil samples were collected within each of the 250m transects at five points equally spaced (50 m). Soil pH characterization was performed for each study site collecting at three depths: 0–10, 10–20, and 20–30 cm (for details, see Durigan *et al*. 2017).

Landscape configuration – We assessed forest configuration of the region using the 2014 Terraclass maps which provide a close temporal match to the year of our field collection (2015). To assess proportion of surrounding primary forest on Terraclass maps we delimited a 1km buffer from each transect using its geographic coordinates to then measure our amount of 'forest' TerraClass category. Details on that project, description of class and methodology can be found in INPE website (Almeida *et al*. 2016) .

Statistical analysis

To compare incidence levels of herbivory between forms (chewing, mining and galling), we ran a Kruskal-Wallis (non-parametric ANOVA) followed by multiple comparison test after Kruskal-Wallis (kruskalmc function, package "pgirmess") to compare difference between forms pairwise.

To access the relationships between the incidence and severity of each herbivory type along the disturbance gradient, we used two different general linear mixed-effect models (GLMM) with site as a random factor: the null model and the model in which herbivory varied along forest classes. To test the difference of incidence and severity of herbivory of each form we ran analysis of variance (ANOVA). After we used pairwise interactions through 'Test Interactions' function (package *phia*) to check if variance of herbivory was significant between each forest disturbance classes.

To examine how the three different forms of herbivory (i.e. chewers, miners, and gall-formers) responded to environmental factors, we analysed the response of mean herbivory severity of each form to: plot aboveground biomass (a proxy of disturbance intensity and time-since disturbance), soil pH (a proxy of soil fertility) and primary forest cover in a 1Km buffer (a measure of landscape configuration). All models used Generalized Additive Models (GAMs) as these allowed non-linear trends that were better suited to understand the variance of responses to our predictor variables. We tested several adjusts changing kurtosis 'k' argument; choosing the smallest AIC, followed by higher deviance explained when suited. Full model passed through best models testing using the 'dredge' function from the 'MuMIn' package to test models defined by all possible variable combinations and rank them by their AICc-based model weight (Burnham & Anderson 2002).

Naive and weighted herbivory

As a third approach of measuring herbivory level, to understand if species dominance in site influenced herbivory levels, we used mean herbivory severity per species and basal area of all stems sampled to result in a plant species dominance adjusted herbivory variable. Weighting process consisted on multiplying contribution of each species to total basal area in site by that species' mean herbivory severity. When comparing pervious to weighted analyses, we will refer to unadjusted herbivory as 'naive'.

To assess if species dominance per plot influenced severity for each form of herbivory, we analysed weighted severity per plot along each environmental co-variable above cited. For that, we again chose generalized models. All analyses were carried out in Rstudio (linked to R version 3.3.1 GUI 1.68 Mavericks build).

Results

We sampled herbivory levels in 1102 trees of 268 species across 20 sites. All sampled individuals had signs of herbivory from at least one of the three forms, varying in severity and incidence. In total we measured herbivory incidence for all 199,869 leaves, analysing severity when damage was present. Overall levels of herbivory were low, about one third of leaves examined had no damage at all and 100% area loss was rare.

Herbivory Incidence between invertebrate-mediated forms

Incidence levels differed between invertebrate-mediated forms of herbivory (Kruskal-Wallis p-value< 0.0001 ***, Chisq= 1469.8, df=2) even between mining and galling (multiple comparison results are shown of Figure 2 legend). Chewing presented the highest incidence (mean of 76.7%), followed by mining incidence (34%) that was greater than galling levels (21.6%) (Figure 2).

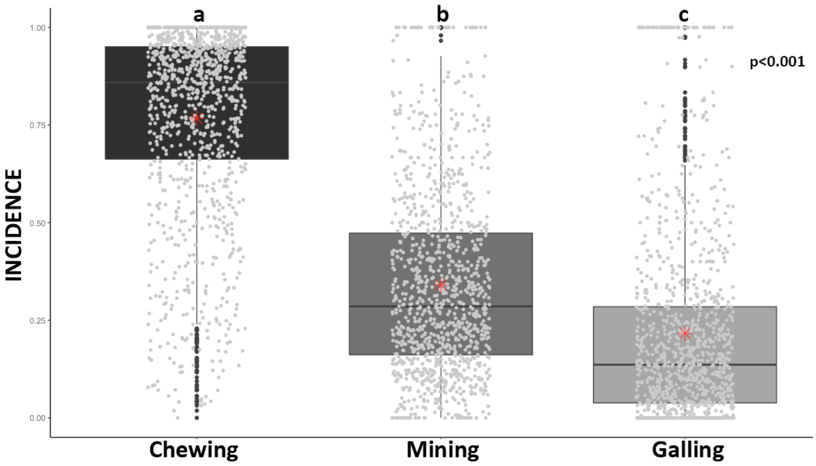

Figure 2 Boxplots compare proportion of damage inflicted leaves (aka incidence) between forms of herbivory. Multiple comparisons test after Kruskal-Wallis demonstrated that all groups differed statistically between each: chewing-mining (TRUE difference; obs. dif.= 1059.9; critical dif.= 97.35), chewing-galling (TRUE difference; obs. dif.= 1519.4; critical dif.= 97.35) and mining-galling (TRUE difference; obs. dif.= 459.6; critical dif.= 97.35). Black dots stand for outliers while light grey for actual data distribution, red asterisks represent mean values.

Herbivory across forest disturbance classes

Herbivory incidence did not show significant differences between disturbance classes (Figure 3a-c). Chewing severity varied along the forest disturbance gradient (p-value= 0.002, Chisq Chi= 14.7, df= 3) peaking at 7.82% of leaf area affected in logged and 7.07% in logged and burnt sites, followed by undisturbed primary forests (5.91%) and secondary classes (5.28%; Figure 3d). Neither severity of miners (p-value= 0.8164, df= 3; ChisqChi= 0.9373) and gall-formers (p-value= 0.6854, Df= 3, ChisqChi= 1.4866) responded to the disturbance gradient (Figure 3e and 3f).

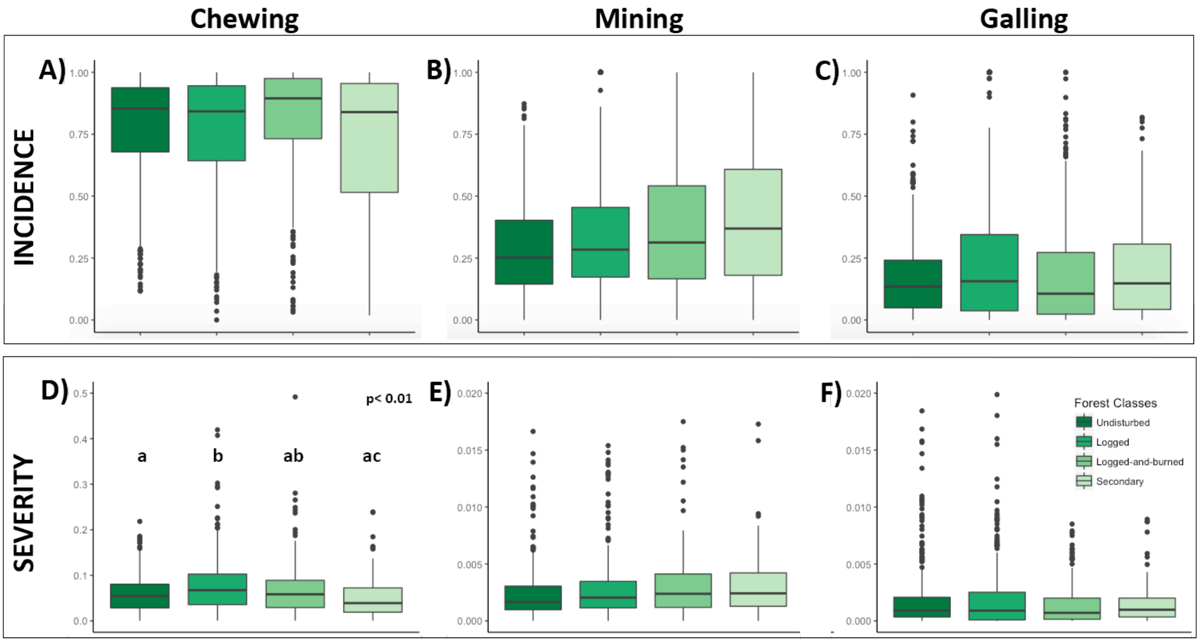

Figure 3 Herbivory levels along the disturbance gradient, forest classes shown in legend box scaling through green tones. Darker green stand for less intensively disturbed forest classes. Invertebrate-mediated herbivory forms are represented per columns: chewing (A and D), mining (B and E) and galling (C and D). For each form, above we show incidence results - displaying proportion of leaves damaged by each form of herbivory. Plots below indicate mean leaf area damaged – severity level- by each form per stem. Notice that severity plots' y-axes are not on the same scale.

Which factors influence herbivory

Model selection revealed support for the positive association between aboveground biomass on chewing severity (Table 1a: Figure 4). When chewing was weighted by plant species dominance, model containing forest amount in 1km buffer had the lowest AICc, providing the best explanation for the variation in plot-level herbivory with negative influence (Table 1b; Figure 4).

Table 1 AICc-based model selection of each invertebrate-mediated herbivory form per plot: (i) mean chewing damage, (ii) dominance weighted chewing damage, (iii) mean mining damage, (iv) dominance weighted mining, (v) mean galling and, (vi) dominance weighted galling. Generalized Linear Models include Above Ground Biomass (AGB), Soil pH (pH) and Forest Amount in 1km buffer (FR) as fixed factors. We also show the number of predictor variables (K), AICc differences (Δ) and Akaike weights (ω).

Model Ranks		Model	df	AICc	Δ	ω	Cumulative ω
a) Mean Chewing Damage							
	1	**AGB**	**4**	**-115.1**	**0**	**0.78**	**0.78**
	2	AGB + pH	5	-111.0	4.11	0.10	0.87
	3	FR	5	-110.4	4.76	0.07	0.95
b) Weighted Chewing							
	1	**FR**	**3**	**-43.4**	**0**	**0.47**	**0.47**
	2	AGB + FR	4	-41.2	2.22	0.15	0.62
	3	AGB + FR + pH	5	-40.5	2.89	0.11	0.73
	4	FR + pH	4	-40.4	3	0.10	0.84
	5	null	2	-39.4	4.06	0.06	0.90
c) Mean Mining Damage							
	1	**null**	**2**	**-151.0**	**0**	**0.55**	**0.55**
	2	pH	3	-148.7	2.35	0.17	0.72
	3	AGB	3	-148.6	2.46	0.16	0.88
	4	AGB + FR	4	-146.2	4.82	0.05	0.93
d) Weighted Mining							
	1	**null**	**2**	**-151.3**	**0**	**0.49**	**0.49**
	2	FR	3	-148.9	2.35	0.15	0.65
	3	AGB	3	-148.5	2.76	0.12	0.77
	4	pH	3	-148.4	2.89	0.12	0.89
	5	AGB + FR	4	-146.8	4.48	0.05	0.94
e) Mean Galling Damage							
	1	**AGB + pH**	**5**	**-195.4**	**0**	**0.36**	**0.36**
	2	**null**	**2**	**-195.0**	**0.36**	**0.30**	**0.66**
	3	**AGB**	**3**	**-194.5**	**0.86**	**0.24**	**0.90**
f) Weighted Galling							
	1	**null**	**2**	**-198.2**	**0**	**0.44**	**0.44**
	2	AGB	3	-195.9	2.3	0.14	0.59
	3	pH	3	-195.5	2.65	0.12	0.70
	4	FR	3	-195.5	2.73	0.11	0.82
	5	AGB + pH	4	-195.2	2.99	0.10	0.92
	6	AGB + FR	4	-193.1	5.12	0.03	0.95

Models are shown up top 95% of cumulative Akaike weights, cumulative ω.

There was no convincing evidence to suggest that mining severity, either naive or weighted, were influenced by the explanatory variables tested, as null models ranked higher than any other combination (Table 2iii and 2iv). Aboveground biomass was present in two of the top ranked naïve models for galling severity with positive influence (Table 2e; Figure 4) but when adjusted by stem species dominance, models containing this variable ranked lower than null model (Table 2 vi).

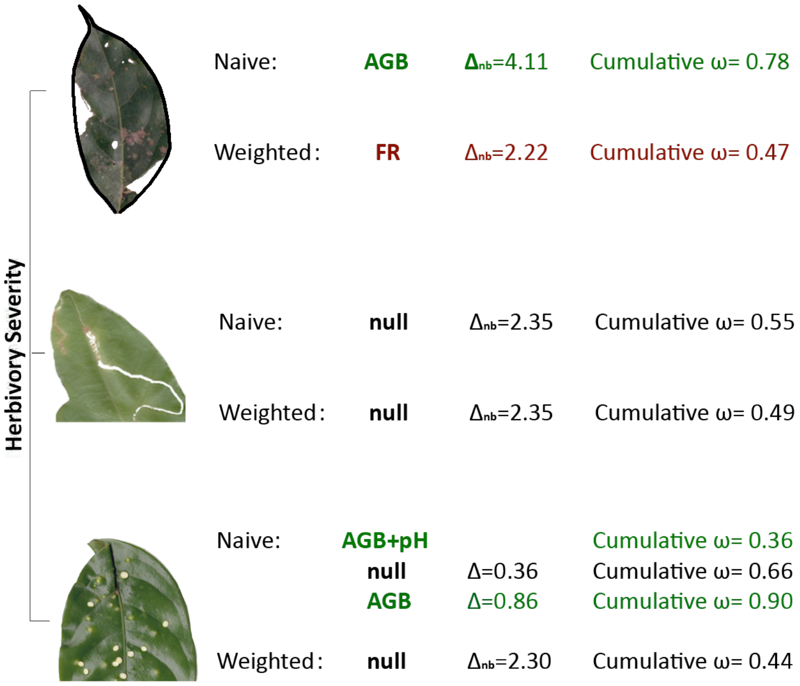

Figure 4 Scheme shows best-selected models testing environmental variable reflecting forest disturbance history (aboveground biomass, AGB), landscape configuration (forest amount in 1 km buffer, FR) and soil fertility (pH). We present cumulative weights (ω) and delta AICc of the next best model (Δnb) when only one scored Δ<2 or the actual delta. Variable abbreviation was coloured to display direction of support, green stand for positive influence while red for negative.

Discussion

We demonstrated in a large-scale research on herbivory levels along tropical forest disturbance, only slight support for several other studies that found effects on this complex ecological process (Arnold and Asquith, 2002; Fáveri et al., 2008; Ruiz- Guerra et al., 2010; De la Vega et al., 2012). Chewing was found to be the most dominant form of invertebrate–mediated herbivory, followed by miners and gall-formers. This seems to be a rule

(Vasconcelos 1999; García-Guzmán and Dirzo 2004; Pontes Ribeiro and Basset 2007) specially if we can consider that external feeders of more generalists than endophagous guilds (Jactel & Brockerhoff 2007). Herbivory have not overall changed along disturbance classes in Amazonian forests, with the exception of chewing severity. This finding can be attributed to compensatory effects of disturbance, bottom-up and top-down controls over herbivores pressure. We found, for most of the herbivory levels we assessed, no convincing evidence to suggest influence by the explanatory variables we tested. Beyond environmental factors, literature had reported a range of effects on herbivory in human-altered landscapes, finding weak links as we found (Souza et al., 2013; Peter et al., 2014; Morante-Filho *et al.* 2016), positive (Arnold and Asquith, 2002; Elzinga *et al.* 2005) or negative (in tropical region; Fáveri *et al.* 2008; Ruiz-Guerra *et al.* 2010; De la Vega *et al.* 2012).

Herbivory Incidence between invertebrate-mediated forms

We found a noticeable contrast in incidence between invertebrate-mediated forms of herbivory: most common type of damage was by chewers, followed by mining and galling. We can expect different levels between external feeders and endophagous insects in anthropogenic landscapes (Cornell and Hawkins 1995; Murakami *et al.* 2008). Tropical forests were found to have greater herbivory attributed to leaf chewing herbivores before (García-Guzmán and Dirzo 2004; Pontes Ribeiro and Basset 2007). The dominance pattern we observed – chewers, followed by miners and lastly gall-formers-, was also found in a study that surveyed these same three invertebrate-mediated forms of herbivory in canopy of primary forests in the Neotropics (Vasconcelos 1999). As miners and gall-formers, compared to external feeders, present a closer relationship with host by feeding under plants tissues, we believe these species could be considered of higher specialization while chewers' habits provide less dependence on host displaying generalist behaviour. If this reasonability is right, our findings agree with previous studies in that specialized guilds occur at lower densities (With and Pavuk 2011) and that, on species-rich tropical forests, herbivory is known to be dominated by generalists that are supposed to be favoured by the range of resources in these plant communities (Pfisterer, Diemer & Schmid 2003; Jactel & Brockerhoff 2007).

Herbivory across forest disturbance classes

Despite slight evidence, overall herbivory did not respond to forest disturbance classes. With the exception of chewing severity, most of the levels (incidence or severity) we surveyed from the three forms of invertebrate-mediated herbivory did not vary along the gradient. This apparent absence of correlation between forest disturbance and herbivores' damage is unexpected considering other studies that found variance across environmental gradients (in review by Andrew *et al.* 2012) and even for mining and galling, as potential increased sensitivity to habitat change is attributed to them (With and Pavuk, 2011) due to endophagous insects' narrower feeding range of (Schoonhoven et al. 2008). Human-driven disturbances beyond direct effects on herbivorous species can result in changes in plant resources and natural enemies (i.e. potential predators of herbivorous insects) (Foley *et al.* 2005), possibly modifying the control of herbivores through top-down and/or bottom-up paths. We believe these two paths of control combined can help understand our results. It is well demonstrated that plant diversity is an important predictor of arthropod diversity and abundance (Parker, Salminen and Agrawal, 2010; Araújo *et al.* 2013; 2014), with the potential to affect their interactions (Haddad *et al.* 2011; Moreira *et al.* 2012; Abdala-Roberts and Mooney, 2014). Bottom-up effects can operate in disturbed landscapes through enhanced mortality of large shade-tolerant trees and other undisturbed forest plant species substituted by pioneers and generalists (Laurance et al., 2006; Arroyo- Rodríguez et al., 2016), this can specially impair herbivores of higher host specificity (Guimarães *et al.* 2014). Control of herbivores in a top-down manner occurs when triggering cascading effects. Changes conditions cause a relaxation of top-down effects (e.g. Thies et al. 2003), as vulnerability is one of the perks of higher trophic-level position (Holt et al. 1999). Insectivorous birds were shown to be sensitive to declines in plant biodiversity (Barlow *et al.* 2007; Gibson *et al.* 2011; Moura *et al.* 2016). For instance, forest cover loss has been shown to decrease diversity and abundance of insectivorous birds (Moura *et al.* 2013; 2016; Morante-Filho *et al.* 2015; 2016 Dodonov *et al.* 2016), causing a release of consumers and consequently increasing levels of herbivory (Sanz *et al.* 2011; Van Bael *et al.* 2003; Peter *et al.* 2015). Thus, absence of alteration in herbivory levels were likely offset by disturbance, either lowering resource availability or directly harming abundance and richness of herbivore species; and positive effect of top-down control relaxation of top-down control.

We did not find higher herbivory levels of any form on secondary sites. This pattern was found for neotropical trees when standing levels of herbivory between pioneer and late successional trees did not differ (Vasconcelos 1999). Compared to primary forests, secondary site are expected to be richer in fast growing plant species that are more attractive to herbivores (Coley et al. 1985; Schadler et al. 2003). However, such plant species may be highly tolerant of damage leading to a successful defense strategy (Agrawal 2000). Successional status was also found to present greater damage by herbivory (Coley, 1983; Dirzo, 1984; de la Cruz & Dirzo, 1987). Studies with herbivory along successional gradients do not provide conclusive patterns as dealing with herbivory is complex due to being a process depending on a range of community features. We found difficult to propose an explanation to why herbivory levels of secondary forests were same as undisturbed forests but it is possible these secondary forests we surveyed are composed by communities that are already re-established and prepared for herbivores pressures, either by enhanced bottom-up control or compensating damage with higher production of leaves.

We found no overall change in levels of herbivory responding to disturbance, except for enhanced chewing severity in lightly disturbed forests: our logged sites. Although herbivores of higher host specificity can struggle with lower availability of shade tolerant species (Guimarães *et al*. 2014), higher availability of pioneers can offer release of resource limitation (Urbas et al. 2007; Falcão et al. 2011). Generalist herbivores can particularly benefit with these groups of fast growing, light-demanding plant species known to have high tissue nitrogen content, soft and juicy foliage and of low investment in chemical defence (Coley, Barone & Barone 1996; Vasconcelos 1999; Schuldt *et al*. 2012). Martinson and Fagan (2014) demonstrated a widespread disruption in arthropods interactions lead by habitat loss itself and fragmentation as a consequence. Dodonov *et al*. (2016) found significantly increase in local herbivory explained by forest cover loss in the Atlantic forest. Similarly, Morante-Filho *et al*. (2016) also found increased leaf damage by chewing following forest cover loss in tropical forest. If a more generalist behaviour can be attributed to chewers due to external feeding habits, instead of top-down control offsetting disturbance and/or bottom-up control, thus, increased chewing severity at intermediate disturbance (logged sites) may be due to smaller influence of direct effects of disturbance but combined relaxation of the two types of control: higher resource availability and decreased predation. We found support in the literature for positive effects in herbivory promoted by similar mechanisms that we believe offset effects of overall herbivory: increased herbivory due to changes in microclimate (Laurance et al. 1998; 2006; Rocha-Santos *et al*. 2016); relaxation of top-down control leading to the proliferation of herbivorous insects (Wirth et al. 2008; Guimarães *et al*. 2014; Leal et al. 2014); and higher abundance of pioneer species (Tabarelli et al. 2012; Guimarães *et al*. 2014; Leal et al. 2014) that are acquisitive and of palatable poorly defended broad leaves (Coley et al. 1985).

The above tendency was not carried out to more intensively disturbed sites as lower levels of herbivory were found at logged and burnt class. This may be explained due to enhanced influence of disturbance as an alternative control, suggesting fire as reaching a threshold to reducing these herbivores' activity, abundance and/or diversity more directly. We found chewing herbivory levels to be more responsive to disturbance than mining and galling levels, what does not mean general susceptibility as these levels are the outcome of a complex interaction net being hard to assume which form of herbivory is more sensitive than other. As changes in herbivore species may involve significant long-term impacts on plant community structure and composition, affecting primary productivity (Gera et al. 2013) and soil nutrient cycling dynamics (Metcalfe et al. 2013). We found different results for chewing incidence and severity along disturbance classes: although incidence of chewing herbivory remained the same, severity displayed a slight increase. That means that whatever was the proximal mechanism that favoured chewers also resulted in higher intensity of leaf damage (severity) but not in higher proportion of leaves affected. A simple explanation resides in pioneers' leaves better palatability and/or broader leaves (Coley *et al*. 1985) allowing enhanced consumption but not necessarily more leaves affected. What could explain would be enhanced recruitment rates of these insect herbivores in a way that most individuals were in early stages of development when consumption rate are higher, what works for caterpillars for instance.

Which factors influence herbivory

In a recent global meta-analysis herbivory in the tropical zone was noticed to be independent of climate (Kozlov et al. 2015) despite that, there is growing evidence in the literature that generalizations are not consistent (Andrew *et al*. 2012). In an extensive literature review, Andrew and colleagues (2012) found herbivory of different forms responding to different environmental gradients. When testing plot-level environmental variables reflecting forest disturbance history, soil fertility and landscape configuration we found weak link between herbivory and these environmental disturbance variables what evokes a clue that herbivory may be more responsive to biotic components (intra- and inter-specific interactions) than to environmental cues. Adding more complexity to the resulting levels, compared to chewers, endophagous species (miners and gallers) may differ in their responses to biotic and abiotic factors (Castagneyrol et al., 2012; de Araújo et al., 2015). Both mining and galling naive and weighted severity levels had the null model as of greater explanation. We argue that herbivory in disturbed tropical forests are regulated by rather broader spectra of factors (Maguire *et al*. 2015) since we deal with a wide range of characteristics, such as feeding forms, mobility potential, plant organ preference, host specialization, etc; factors that can define species' perception of their habitat (Van Nouhuys 2005). We dealt with three invertebrate-mediated forms of herbivory testing the same variables but they all displayed differences in results; we argue that these differences may be driven by group-specific habits responding to different cues. Previous study found that, compared to external feeders, endophagous insects could be less affected by habitat loss as they feeding habit consisted on sheltering inside plant tissue (Connor and Taverner 1997), this may outcome as a successful defence strategy buffering effects of changing conditions for these species. Chewing levels again were more responsive to disturbance, with positive influence of forest disturbance history (aboveground biomass). Aboveground biomass (AGB) had positive effect on chewing: higher biomass lead to higher chewing damage; probably reflecting higher leaf biomass due to enhanced abundance of pioneer species that are of broad, palatable and poorly defended leaves (Coley et al. 1985; Tabarelli et al. 2012; Guimarães *et al*. 2014). When we examined chewing weighted form, which means we removed the effect of species dominance, biomass lost strength and negative influence of landscape configuration (forest amount in 1km buffer) took part instead. It seems odd but lower herbivory along gradient of forest cover is justifiable if we think through a disturbance gradient rationality:

more primary forest cover can represent lower rates of disturbance of basal levels of herbivory. Lower herbivory may not only be due to lower disturbance but also possibly because herbivore damage can be less aggregated (i.e. more evenly distributed) along the continuous coverture of primary forest.

Although most of the world's biota is retained in tropical forests regions that are suffering particularly severe impacts (Fahrig, 1997) and associated landscape configuration has also been in constant change (Haddad *et al.* 2015), we found weak evidence that amount of primary forest in 1km buffer influenced herbivory. Landscape configuration could give a clue on a net source-sink system of herbivores. For instance, Metcalfe and colleagues (2014) found that plots surrounded by a matrix of similar forests were unlikely to be permissive for migratory herbivores. That study, when taking landscape configuration for account, showed that rather than resource availability, herbivory levels were driven by community properties (i.e. physical-chemical properties of the resource), reinforcing our suspicions that herbivory may be more responsive to biotic components. We did not find evidence of herbivory severity levels responding to soil fertility. Herbivory mediates organic material transference to the soil, potentially affecting soil processes (Bardgett and Wardle 2003; Hartley and Jones 2004), despite relevancy of this role, how herbivory-mediated nutrient cycling vary with environmental changes is highly overlooked (Metcalfe *et al.* 2014). Studies that examine how aboveground processes' such as herbivory influence in belowground are common (Nadelhoffer 2000; Bardgett *et al.* 2005), however evidence of herbivory effects on soil fertility and nutrient availability are scarce (Blue *et al.* 2011). Vasconcellos (1999) compared herbivory levels between forests of unfertile soils from the Amazon basin and those of fertile (volcanic) soils in Central America finding no clear differences. These soils were observed to have high heterogeneity in more intensive land uses (de Carvalho *et al.* 2016) thus, it is possible that our study scale was not the best suited to compare such indirect link such as pH and herbivory as more disturbed sites were still as acidic as undisturbed ones. Testing this other parameters such as sum of basis (SB), cation exchange capacity (CEC) and aluminium saturation (%m), could complement our findings to judge if soil fertility influences herbivory. As expected for a tropical region (Furtini-Neto et al. 2001) all soils were generally low on pH which means very acidic and that was maybe why we did not find any clear response; so the possibility that soil fertility may in part cause differences in herbivory levels cannot be ruled out. Understanding different results between naive and weighted forms of the same variable is a little trickier. Possibly, we demonstrated that higher herbivory noticed in logged forests could be driven by higher levels among certain species that are less dominant. This would be consistent, for example, with higher rates among pioneer species as they have a small diameter at breast heigh (DBH) and contribute little to plot basal area.

Implications and Conclusions

Despite invertebrate herbivores' great importance for tropical forest ecosystems, we found a weak link between disturbance and herbivory levels in these Amazon forests. We found slight evidence of altered herbivory indicating that human-driven forest disturbance can influence invertebrate-mediated herbivory levels and apparent lack of effect in mining and galling levels may be occulted by offsets. It is possible that abiotic factors may not be the main drivers of herbivory levels in these disturbed areas, but a more direct effect on herbivory could be displayed analysing biotic features such as those related to community structure, associated species composition, interspecific variation, etc. Food web structure play a role as great as plant diversity on communities, with the potential to alter or even nullify effects on biodiversity (Bruno *et al.* 2008; Duffy *et al.* 2005, Gruner *et al.* 2008) and perhaps the patterns we found for the effect of disturbance was buffered by this feature. Regardless of ultimately identifying the exact mechanisms involved, here we have shown effects of forest disturbance on levels of damage by three invertebrate-mediated forms of herbivory in Amazonian forests. We argue some early clues about the effects of human influence in tropical forests, finding that the ecosystem process of herbivory is maintained. An important issue regarding herbivory process maintenance is whether, once these levels vary, if trends are reversible. We are aware that local herbivory pressure is ultimately the outcome of a complex of interacting features that could ultimately be more informative of the proximal mechanisms and other studies can help achieve the indirect impact of these pathways triggered by forest disturbance. However, the main goal of the study was to access if herbivory levels themselves were altered due to disturbance. Looking at the process of herbivory as important ecological and functional role it plays, a relevant outcome can be evoked regarding maintained functionality of these tropical ecosystems. We believe this scenario of 'disturbance resistance' could be due to resistance of few common dominant species that maintain herbivory levels or species of redundant functional role replacing those that are lost. Either way is very interesting to look at our findings as a demonstration that levels of disturbance we analysed were not sufficient to impair this ecosystem-level functional process. Our study suggests that despite forest disturbance, some links are somehow being maintained on this complex tropical network for now. We provide implications for conservation policies to focus on maintenance of functionality of ecological processes outcomes such as herbivory and encouraging monitoring of these.

Disturbance is a generalized threat to biodiversity, indirectly impacting ecological interactions with possible far-reaching consequences for tropical forests(Ayres & Lombardero 2000). Herbivory is a key ecological interaction being an interesting field to explore specially in human-altered tropical rainforests, with the potential to unravel critical consequences for both herbivores (Coley 1998; Bale et al. 2002; Deutsch et al. 2008) and forest ecosystems (Clark et al. 2003; Feeley et al. 2007). Despite growing concerns and current rates of disturbance, negative impacts on diversity not necessarily extends to ecological interactions. We found no overall changes in herbivory levels along disturbance in Amazonian forests surveyed; these results are explained by interacting regulatory factors. Chewers dominated herbivory levels, followed by miners and gall-formers. This hierarchical order probably is determined by success in exploitation of the great range of resources in these plant rich communities. Herbivory levels along disturbance appeared to be caused by both bottom-up effects (Coley and Barone 1996; Souza *et al.* 2013; Guimarães *et al.* 2014; Leal *et al.* 2014) and smoothed of top-down control of herbivores by birds or predatory arthropods (Dodonov *et al.* 2016; Pardini *et al.* 2010; Banks-Leite *et al.* 2014; Morante-Filho et al., 2016). No variance in herbivory seem to be the case where disturbance and/or bottom-up control are offset by top-down mechanisms while increased chewing levels may be justified by joint relaxations. Weak link between herbivory and environmental disturbance variables evokes a clue that herbivory may be more responsive to biotic components (intra- and inter-specific interactions) than to environmental cues. Marked different responses between forms of herbivory seem to relate to feeding habits, endophagous forms had no apparent response to disturbance probably due to sheltering under plant tissues. Non-linear trends of herbivory evidence the complex and indirect effect of disturbance on this ecological process. Our results bring insights for tropical forest functioning since drivers of environmental change that affect biodiversity are likely to result on long-term ecosystem impacts (Smith, Knapp and Collin 2009). Tropical forest landscapes are suffering unprecedented rates of disturbance and we found evidences slight effect of light pressures of disturbance. Herbivory not only can be functionally resistant to disturbance, but also play critical role on forest regeneration, contributing in several ways to forest resilience as a whole (Ayres & Lombardero 2000). We encourage studies that can incorporate effects on herbivory considering its functional resistance and role on community resilience in response to human-driven disturbances to help understand it and investigating potential consequences of supressing this ecosystem-level functional process.

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Appendix 1 – Herbivory sampling methods complementary material

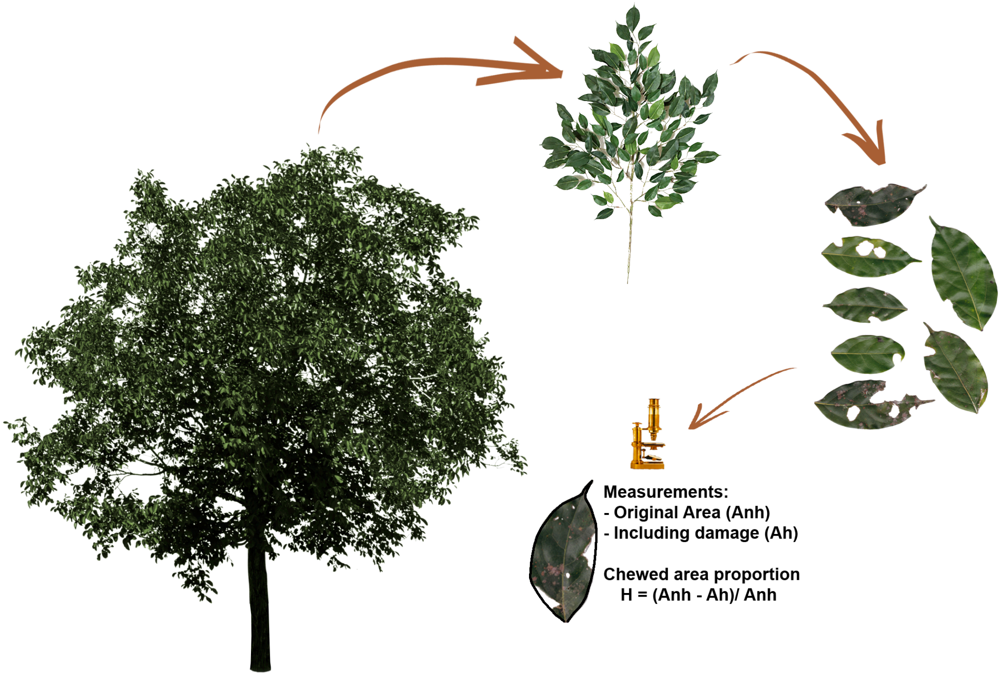

Figure 1 Example of our methods and how we measured herbivory. From each stem >10cm DBH that were part of 80% of plot basal area, we collected a fully sunlight branch. From this branch we assessed total number of leaves and number affected by each form of invertebrate mediated herbivory. Then randomly selected 30 chewed leaves to scan which we drew the outline (when damaged on the edges) recreating initial leaf area. On ImageJ we calculated leaf original area (Anh) and leaf area including damage (Ah), the difference between Anh and Ah was divided by Anh to calculate proportional leaf area loss (H).

Figure 2 Example of scanned chewed leaves with outlines drawn from *Micropholis egensis* (Sapotaceae; DBH= 20.1) of one of our logged sites.

Appendix 2 – Plots of naive and weighted herbivory severity along environmental variables

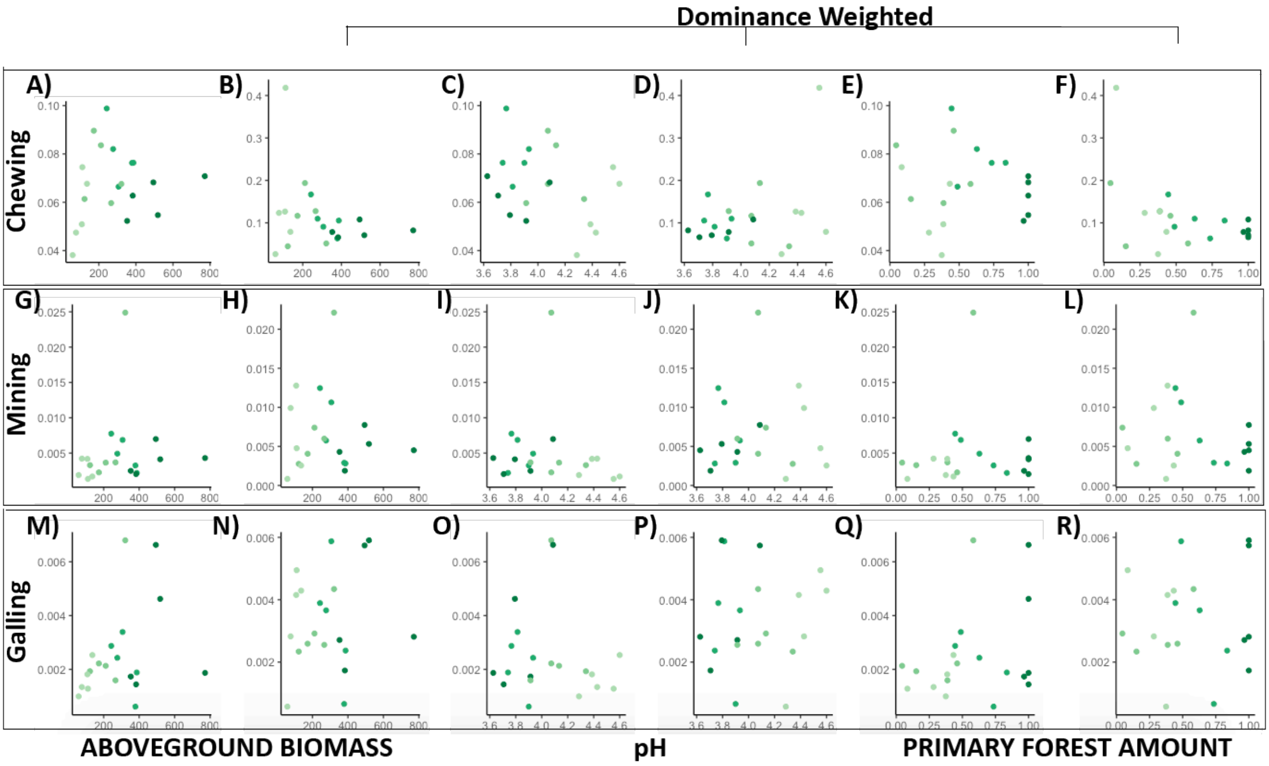

Figure 1 Mean herbivory severity of each form along disturbance variables representing forest disturbance history – biomass; soil fertility – pH; and landscape disturbance – primary forest amount in 1km buffer. Forms of herbivory are organized per rows intercalated with weighted form. All environmental variables are separated per figure columns. Plots with grey background represent models that ranked Δ<2.