Predation on artificial caterpillars following understorey fires in human-modified Amazonian forests

Liana Chesini Rossi[1,2*], Erika Berenguer[3,4], Alexander Charles Lees[2,5], Jos Barlow[4,6], Joice Ferreira[7,8], Filipe M. França[9], Paulo Tavares[8], Marco Aurélio Pizo[1]

[1] Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista (UNESP), Rio Claro, SP, Brazil

[2] Division of Biology and Conservation Ecology, Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK

[3] Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK

[4] Lancaster Environment Centre, Lancaster University, Lancaster, UK

[5] Cornell Lab of Ornithology, Cornell University, Ithaca, USA

[6] Setor de Ecologia e Conservação, Universidade Federal de Lavras, Lavras, MG, Brazil

[7] Embrapa Amazônia Oriental, Belém, PA, Brazil

[8] Programa de Pós-Graduação em Ecologia (PPGECO) e Programa de Pós-Graduação em Ciências Ambientais (PPGCA), Universidade Federal do Pará, Belém, PA, Brazil

[9] School of Biological Sciences, University of Bristol, Bristol, UK

*** Correspondence**

Liana Chesini Rossi, Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista (UNESP), CEP 13506-900, Rio Claro, SP, Brazil.

Email: lianachesinibio@gmail.com

ABSTRACT

Tropical forests are facing several impacts from anthropogenic disturbances, climate change and extreme climate events, with potentially severe consequences for ecological functions, such as predation on folivorous invertebrates. Folivory has a major influence on tropical forests by affecting plant fitness and overall seedling performance. However, we do not know whether predation of folivorous arthropods by birds, mammals, reptiles and other arthropods is affected by anthropogenic disturbances such as selective logging and forest fires. We investigated the impacts of both pre-El Niño human disturbances and the 2015-2016 El Niño understorey fires on the predation of 4,500 artificial caterpillars across 30 Amazonian forest plots. Plots were distributed in four pre-El Niño forest classes: undisturbed, logged, logged-and-burned and secondary forests, of which 14 burned in 2015-16. We found a higher predation incidence in forests that burned during the El Niño in comparison to unburned ones. Moreover, logged-and-burned forests that burned again in 2015-16 were found to have significantly higher predation incidence by vertebrates than other forest classes. However, overall predation incidence in pre-El Niño forest disturbance classes was similar to undisturbed forests. Arthropods were the dominant predators of artificial caterpillars, accounting for 91.5% of total predation attempts. Our results highlight the resilience of predation incidence in human-modified forests, although the mechanisms underpinning this resilience remain unclear.

KEYWORDS

Amazon, arthropods, dummy caterpillar, El Niño, forest fires, forest regeneration, herbivory control, forest degradation

1 INTRODUCTION

Degraded primary forests, including those affected by human-driven disturbances, such as selective logging and understorey fires, are rapidly becoming ubiquitous in the tropics (Lewis, Edwards, & Galbraith, 2015). Between 1995 and 2017, more Amazonian forests were degraded by human activities than deforested (337,427 km^2 of degradation vs 308,311 km^2 of deforestation; Matricardi et al., 2020). Amazonia is also undergoing rapid changes in regional climate – in the past 40 years, the average temperature has increased by 1.5°C (Gloor et al., 2015) and the dry season has become longer and drier (Fu et al., 2013). Degraded forests have more open canopies and combined with rising temperatures and changing rainfall regimes this leaves forests more likely to sustain understorey fires (Holdsworth & Christopher, 1997). During the 2015-16 El Niño, over one million hectares of forests burned in the lower Tapajós region in eastern Brazilian Amazon, even affecting previously undisturbed forests (Withey et al., 2018).

The impacts of human disturbance on species richness and composition in Amazonian forests have been intensively studied. Selective logging, for example, disproportionately affects terrestrial insectivorous passerine birds (Hamer et al., 2015; Moura et al., 2016), while understorey fires negatively impact the abundance of predatory ants (Paolucci et al., 2016). Understorey fires can also lead to severe structural changes to forests resulting from high tree mortality (Berenguer et al., 2021; Silva et al., 2018), leading to shifts in vertebrate (Barlow & Peres, 2004; Moura et al., 2013), invertebrate (França et al., 2020; Silveira et al., 2016) and plant communities (Berenguer, Malhi, et al., 2018). Although such drastic modifications in community composition caused by anthropogenic disturbance would likely affect several ecosystem functions, there is little information about anthropogenic impacts on ecological processes, especially on herbivory control – i.e., predation incidence on folivorous arthropods (Murray et al., 2020; Schwab et al., 2021).

Due to their hyper abundance (average of 18,439 species/ hectare in tropical forests; Basset et al., 2012) and diversity in the use of resources, arthropods can influence several ecosystem processes. For example, folivorous arthropods can create intense pressure on plant communities (Barreto et al., 2021), causing reductions in leaf area (Morrison & Lindell, 2012) and negative impacts on plant fitness and biomass (Dirzo, 1984; Van Bael, Brawn, & Robinson, 2003). Top-down control by predatory species such as vertebrates, other arthropods and parasitoids may help regulate the abundance of folivorous arthropods (Hairston, Smith, & Slobodkin, 1960; Mäntylä, Klemola, & Laaksonen, 2011). In tropical forests, other arthropods (Lemessa, Hambäck, & Hylander, 2015; Zvereva, Paolucci, & Kozlov, 2020) and birds (Mäntylä et al., 2011; Van Bael, Brawn, & Robinson, 2003) are the most important predators of folivorous arthropods, exerting significant herbivory control (Vidal & Murphy, 2018). However, the relative importance of predator groups, such as arthropods and birds, is not static – i.e., it can be altered by changes in forest condition (Dodonov et al., 2016). Previous studies investigating the impact of forest quality on predation incidence on folivorous arthropods found a decrease in predation incidence with increasing forest disturbance (Boesing, Nichols, & Metzger, 2017; Schwab et al., 2021). However, most studies have focused on disturbances that occurred several years prior to sampling (Boesing, Nichols, & Metzger, 2017; Edwards et al., 2012) and, to the best of our knowledge, no studies have investigated the impact of recent understorey fires on the predation of folivorous arthropods.

Artificial caterpillars are a frequently-used tool to evaluate the impact of forest disturbance on predation incidence (Meyer, Koch, & Weisser, 2015; Murray et al., 2020; Roels, Porter, & Lindell, 2018; Roslin et al., 2017; Schwab et al., 2021; Seifert, Lehner, Adams, & Fiedler, 2015). Even though predation on artificial caterpillars is often lower in comparison to natural prey (Lövei & Ferrante, 2017; Nagy, Schellhorn, & Zalucki, 2020), the technique is still a robust way of comparing predation incidence between habitat types (Roels et al., 2018; Schwab et al., 2021; Tvardikova & Novotny, 2012). Furthermore, this methodology allows the identification of predators by assessing the types of marks left on the 'predated' artificial caterpillars (Low, Sam, McArthur, Posa, & Hochuli, 2014), which is key to comparing the role of different predator groups on the control of folivorous arthropods (Ferrante et al., 2021; Lemessa et al., 2015; Roslin et al., 2017; Sam, Koane, & Novotny, 2015). For example, in primary rainforests in Costa Rica, arthropods accounted for 86% of all predation incidences on artificial caterpillars, whilst birds accounted for just 11% (Seifert et al., 2015).

Here, we aim to explore how predation incidence on folivorous arthropods varies in human-modified Amazonian rainforests. Using 4,500 artificial caterpillars, as a proxy of folivorous arthropods, we assessed the predation incidence within four pre-El Niño human-modified forest classes: undisturbed, logged, logged-and-burned and secondary forests. During the 2015–2016 El Niño, almost half of these forests were affected by understorey fires. We examined whether there were differences in the total predation incidence and in predation incidence by different predator groups (a) among pre-El Niño forest disturbance classes without recent fires, and (b) between forests affected by understorey fires during the recent El Niño (EN) and those that remained unaffected. Based on the negative impacts of human-driven disturbances on predator communities – which has been suggested to reduce the top-down control of folivorous arthropods (Murray et al., 2020) – we expect predation incidence to be lower in pre-

EN disturbed forests when compared to undisturbed ones, and for it to be even lower in EN-fire-affected forests.

2 METHODS

2.1 Study area

Our study area is located in the municipalities of Belterra, Mojuí dos Campos and Santarém in eastern Amazonia (Figure 1). The landscape encompasses around 1 million hectares of undisturbed and disturbed primary and secondary forests immersed in an agriculture matrix comprising both large and small private landholdings (Gardner et al., 2013). In 2015 and 2016, the region experienced an abnormally long dry season associated with a strong El Niño event, which resulted in multiple understorey fires (see Aragão et al., 2018). Prior to the El Niño, we installed 30 study plots (250 x 10 m, 0.25 ha), distributed into undisturbed, selective logged forests (hereafter called 'logged'), logged-and-burned, and secondary forests (hereafter called 'pre-EN forest disturbance classes', Table S1). Logging took place ≥ 18 years prior to sampling, an estimate derived from a combination of field assessments and a visual inspection of satellite images between 1988-2010 (Gardner et al., 2013). Plots were located in *terra firme* forests separated by at least 1.5 km from each other. Between November 2015 and January 2016, i.e., during the El Niño, 14 plots burned (hereafter 'EN-fire-affected plots'), while 16 remained unburned (Figure 1; Table S1).

2.2 Data collection

Predation experiments were conducted between April 10 and June 15 2019, corresponding to the middle-end of the wet season. All artificial caterpillars were green, made from odourless non-toxic coloured plasticine (Lewis NewplastTM) mixing an equal portion of dark and light green to create medium green coloured caterpillars (Low et al., 2014; Roslin et al., 2017). Artificial caterpillars (hereafter 'caterpillars') were crafted to mimic cryptic Lepidoptera larvae in colour, shape (i.e., looping position), and size (i.e., 2.5 × 30 mm), thus resembling one of the most globally abundant folivorous groups (Zvereva et al., 2019). Caterpillars were sufficiently malleable to record predation marks. We fixed the caterpillars to the vegetation by passing a wire longitudinally through them (Figure 2a). When placing caterpillars in the field, we removed all handling marks to avoid misidentifying them with predator's marks.

We established five 20 × 5 m sub-plots within each of the 30 forest plots. We placed 30 caterpillars in each sub-plot, totalling 150 caterpillars per forest and 4,500 caterpillars across the experiment. All caterpillars were installed on understorey vegetation branches, between 1.0 – 4.5 m from the ground, separated by at least 1 m from each other. Although predation incidence is often reported as being higher in the canopy (Loiselle & Farji-Brener, 2002), we only evaluated predation in the understorey due to the difficulties of placing caterpillars in the tall canopy (i.e., 30-50 m). All branches were chosen to prevent the caterpillars from being obscured by vegetation. The position of the caterpillars was marked with a tag on another branch of the same plant. This approach facilitated recovery while limiting the risk to obstruct or influence predator behaviour. After 14 days of field exposure, a single observer (LCR) recovered all caterpillars and assessed whether they had been predated, attributing predation marks to different predator groups.

The identification of predation marks on recovered caterpillars was based on the beak, mandibular tooth or radula marks guided by images available in the literature (Low et al., 2014; Tvardikova & Novotny, 2012) and an online identification guide (available at https://tvardikova.weebly.com/downloads.html). We also complemented our arthropod bite mark assessment through direct observations – i.e., when we saw real attacks on caterpillars (Figure S2). All predation marks were attributed to one of four predator groups: arthropods, birds, reptiles and mammals (Roels et al., 2018). Arthropod predators include ants, wasps, beetles and isopods (Howe, Lövei, & Nachman, 2009), while mammalian predators include marsupials and rodents (Low et al., 2014). Multiple marks made by the same type of predator on a single caterpillar were categorized as a single predation event. Of the 4,500 installed caterpillars, 28 were unrecovered because they were either crushed by a falling tree or lost due to the disappearance of the flag.

2.3 Data analysis

We analysed two response variables: (a) total predation incidence, measured as presence/absence of predation marks on caterpillars, and (b) predation incidence by different predator groups, separated into two categories: arthropods and vertebrates (i.e., birds, mammals and reptiles).

2.3.1 Predation incidence across pre-EN forest disturbance classes and EN-fire-affected plots

In our first model (Model 1), we assessed the effects of pre-EN forest disturbance on total predation incidence, removing plots that burned during the 2015-16 El Niño (n = 16). Our second model (Model 2) explored the impact of the El Niño understorey fires on total predation incidence including all forest plots (n = 30).

2.3.2 Effects of different predator groups across pre-EN forest disturbance classes and EN-fire-affected plots

In this set of analyses, we evaluated the differences in predation incidence caused by arthropod (Model 3) and vertebrate predators (Model 4). These two response variables were analysed across the pre-EN forest disturbance classes but did not include plots that burned in 2015-16 (n = 16). Our last two models assessed the impact of the 2015-16 El Niño understorey fires on the same response variables, thus leading to a model including arthropods (Model 5) and another including only the vertebrate predators (Model 6). Models 5 and 6 included all sampled plots (n = 30). Given that we were testing the difference in predation incidence between arthropods and vertebrates, Models 3-6 only included caterpillars with predation marks.

To test the effect of pre-EN forest disturbance classes and El Niño understorey fires on predation incidence, we used generalized linear mixed-effects models with a binomial response with logit link function and response variable as presence/absence data. All models had forest class as a fixed effect and plot as a random effect, and were built with the ‘glmer’ function of the ‘lme4’ package (Bates et al., 2018). We tested the significance and selected the optimum models running likelihood ratio tests in the ‘ordinal’ package with the ‘drop1’ function using the Chi-square distribution. Models 2 and 6 had differences in the least-square means of predation in each forest class (including pre-EN forest disturbed classes and EN-fire-affected plots) tested with ‘emmeans’ with ± 95% confidence interval (Lenth, Singmann, Love, Buerkner, & Herve, 2020). The predation incidence in undisturbed forests served as a baseline for comparison to all other models. All analyses were performed in R 3.5.1 (R Core Team, 2018).

3 RESULTS

We recovered 99.4% of the caterpillars (n = 4,472) of which 2,858 (64.9%) exhibited predation marks after 14 days exposed. We were unable to identify the predator group for only one caterpillar – although we suspect it was a bird (Figure S1), which was subsequently removed from all analyses. Predation marks were mainly made by arthropods (n = 2,615, 91.5%; Figure 2 h-j), followed by birds (n = 247, 8.6%; Figure 2 b-d), mammals (n = 158, 5.5%; Figure 2 e-g) and reptiles (n = 2, 0.06%). Only 7% (n = 200) of the attacked caterpillars had marks belonging to more than one predator group. The percentages were measured based on the total number of caterpillars that exhibited predation marks (n = 2,858), not on the total number of marks, therefore, the total number of marks does not represent 100%.

3.1 Effects of pre-EN forest disturbance classes and El Niño understorey fires on total predation incidence

Among the plots that did not burn in 2015-16, there were no significant differences in predation incidence between pre-EN forest disturbance classes (Figure 3; Table S2). When including EN-fire-affected plots, we found that predation incidence was significantly higher in pre-EN undisturbed forests that experienced fires in 2015-16 (Figure 3; Table S2; Table S3).

3.2 Effects of pre-EN forest disturbance classes and El Niño understorey fires on the predation by different groups

Predation incidence by arthropods was higher than by vertebrates in all forest classes, irrespective of fire occurrence in 2015-16 (Figure 4). Predation incidence by arthropods was not affected by either the pre-EN forest disturbance classes or El Niño-associated fires (Figure 4a; Table S2). We also found no difference in predation incidence by vertebrates across the different pre-EN forest disturbance classes (Figure 4b; Table S2). When analysing the effects of the recent El Niño fires, we found that logged-and-burned forests that burned again in 2015-16 presented significantly higher predation incidence by vertebrates than both undisturbed and logged-and-burned forests that were not affected by fires in 2015-16 (Figure 4b; Table S4).

4 DISCUSSION

We found no differences in predation incidence among pre-EN forest disturbance classes. Although we demonstrate that predation incidence on artificial caterpillars may increase in the aftermath of Amazonian understorey fires, this evidence is not strong – e.g., most EN-fire-affected forests exhibited similar predation incidence to those of unburned forests. The range of predation incidence was more variable within pre-EN disturbed forests in comparison with pre-EN undisturbed ones, and in EN-fire-affected forests when compared to unburned ones. Our results also suggest that predation incidence on artificial caterpillars in undisturbed and human-modified Amazonian forests is predominantly driven by arthropods.

4.1 Predation incidence across pre-EN forest disturbance classes

We expected predation incidence to be strongly impacted by pre-EN forest disturbance, being lower in disturbed forests when compared to undisturbed ones, given that human-driven disturbances can negatively impact predator communities (Moura et al., 2013; Symes, Edwards, Miettinen, Rheindt, & Carrasco, 2018). Surprisingly, our results showed no effect of pre-EN forest disturbance on predation. However, it is important to recognise that our study plots are distributed within a large forested matrix, which can act as a source for species colonisation (Tscharntke et al., 2012). As such, in more fragmented landscapes, with small and isolated fragments, where forest faunas are more impoverished, predation incidence on folivorous arthropods may be less resistant to anthropogenic impacts (Fáveri, Vasconcelos, & Dirzo, 2008; Lees & Peres, 2006).

4.2 Predation incidence in EN-fire-affected forests

Given that forest fires drive shifts in the community composition of predatory arthropods and vertebrates by altering habitat availability (Barlow, Peres, Henriques, Stouffer, & Wunderle, 2006; Kelly et al., 2020; Paolucci et al., 2016; Silveira et al., 2016), we expected a lower predation incidence in EN-fire-affected forests. However, predation incidence remained similar between most EN-fire-affected and unaffected sites, only becoming significantly higher in previously undisturbed forests that burned in 2015-16. We cannot pinpoint the exact mechanism behind these findings – one possibility is that the increased density of vegetation in the understorey of recently burned forests - as a result of light gaps created by tree mortality, enhances environmental complexity, thus facilitating some arboreal arthropod and vertebrate predators to find their prey (Jimenez-Soto, Morris, Letourneau, & Philpott, 2019; Yang et al., 2018). This would be particularly important in pre-EN undisturbed forests, as these forests retain a more open understorey than forests that have been affected by logging or fire in the recent past (Berenguer et al., 2014). Another possibility for the higher predation incidence in previously undisturbed forests that burned in 2015-16 is the dominance of pioneer plant species with lower amounts of secondary compounds (Barton & Koricheva, 2010; Boege & Marquis, 2006; Silva et al., 2018) in the understorey of recently burned forests may provide a local and ephemeral increase in resources for folivorous arthropods. Pioneer species would have been common in pre-EN disturbed forests, but not in undisturbed ones (Berenguer, Gardner, et al., 2018), thus providing new resources in these forests.

4.3 The role of different predator groups

Studies across the globe, including tropical forests, have found a high incidence of arthropod predation on artificial caterpillars (Fáveri et al., 2008; Loiselle & Farji-Brener, 2002; Roslin et al., 2017; Witwicka, Frydryszak, Anto, & Czarnoleski, 2019; Zvereva et al., 2020). Arthropod predation can account for up to 98% of the total predation attempts on artificial caterpillars in undisturbed rainforests after 48 hours of exposure (Seifert, Schulze, Dreschke, Frötscher, & Fiedler, 2016), a figure similar to ours (91% on average, after 14 days). This high predation incidence by arthropods is expected due to their high diversity and abundance in tropical regions (Novotny et al., 2006; Sam, Koane, & Novotny, 2015). Our results show that the predation incidence exerted by arthropods can be maintained at high levels even after forest disturbance. However, we do not know whether this finding is due to resilience to disturbance of the arthropod predator community or due to high functional redundancy in the system (e.g., Nunes et al., 2021). In other words, even if some species of arthropod predators disappear after fires, others that perform the same function (i.e., predation of folivorous arthropods) may maintain predation incidence comparable to unburned forests (Perez-Alvarez, Grab, Polyakov, & Poveda, 2021).

Among vertebrates, predation incidence upon artificial caterpillars varies widely. In the case of birds, from 1% to 52% in tropical forests (Molleman, Remmel, & Sam, 2016; Sam et al., 2015). After 14 days of exposure, our results of 8.6% are within the lower end of this range. Mammals predated 5.5% of the caterpillars, a figure slightly higher than that previously reported– i.e., <1% to 4% (Schwab et al., 2021; Seifert et al., 2015). Predation of caterpillars by reptiles is generally rare (Murray et al., 2020; Schwab et al., 2021), with some studies not registering any (Roels et al., 2018; Roslin et al., 2017; Zvereva et al., 2020). We found only two caterpillars predated by reptiles, out of the 2,858 which presented predation marks.

4.4 Caveats

Artificial caterpillars are an effective method to infer predation incidence across habitats and among predator groups (Howe et al., 2009; Lövei & Ferrante, 2017; Roslin et al., 2017; Schwab et al., 2021). Through the standardization of this methodology, it is possible to compare predation incidence and predator composition among areas (Lövei & Ferrante, 2017). However, we highlight that our results should be carefully interpreted as these caterpillars are a simple visual approximation of real prey (Howe et al., 2009; Murray et al., 2020). Important factors such as posture and mobility (Lövei & Ferrante, 2017; Suzuki & Sakurai, 2015), olfaction (Hughes, Price, & Banks, 2010; Mäntylä et al., 2011; Sam et al., 2015), colour (Ghim & Hodos, 2006), leaf damage (Sam, Koane & Novotny, 2015) and plant chemical responses are not manifested in artificial models (Amo, Jansen, van Dam, Dicke, & Visser, 2013; Heil & Kost, 2006; Pearse et al., 2020). Furthermore, the colour and shape of our caterpillars are likely biased towards soliciting interactions from generalist predators (Boesing et al., 2017). Therefore, the study design may fail to record specialized interactions (Zvereva et al., 2019, 2020). Moreover, natural pray abundance can also be an important driver of predation incidence – e.g., higher prey abundances lead to predator satiation, which may affect the attack incidence on artificial caterpillars. Finally, given that we sampled EN-fire-affected forests three years after they burnt, we may have failed to detect any immediate post-fire changes in predation incidence – e.g., perhaps three years was enough time for predation to be re-established in pre-EN-forest classes.

4.5 Conclusion

Our experimental study highlights that artificial caterpillar predation is (a) of a comparable magnitude in undisturbed, logged, logged-and-burned, and secondary Amazonian forests; (b) not largely impacted by recent understorey fires; and (c) mainly performed by arthropods. Understanding the control of folivorous arthropods in human-disturbed forests represents an important step for predicting the future of tropical forests, as herbivory control directly affects forest regeneration.

FIGURE LEGENDS

FIGURE 1 (a) Our study region in relation to the Brazilian Amazon. (b) The location of our study plots.

FIGURE 2 Examples of artificial caterpillars used in our experiment. (a) Caterpillar placed on a twig. Caterpillars with (b – d) bird, (e - f) mammal, and (h - j) arthropod predation marks.

FIGURE 3 Predation incidence on artificial caterpillars over 14 days exposure across different pre-EN forest disturbance classes. Forests include those affected by fires during the 2015-16 El Niño (red) and those that remained unaffected (blue). Different letters indicate significant differences among forest classes following pairwise comparisons (Table S3). Pre-EN forest disturbance classes: UF - undisturbed forests, LF - logged forests, LBF - logged-and-burned forests, and SF - secondary forests. Horizontal bars indicate medians, boxes comprise the upper and lower quartile of data distribution, whiskers indicate the minimum and maximum values and circles indicate outliers (i.e., values 1.5 times distant from the first and third quartiles).

FIGURE 4 Predation incidence on artificial caterpillars over 14 days exposure across different pre-EN forest disturbance classes. Forests include those affected by fires during the 2015-16 El Niño (red) and those that remained unaffected (blue). Predation incidence was divided into two groups: (a) caused by arthropods, (b) caused by vertebrates (birds, mammals, and reptiles). Different letters indicate significant differences among forest classes following pairwise comparisons (Table S4). Pre-EN forest disturbance classes: UF - undisturbed forests, LF - logged forests, LBF - logged-and-burned forests, and SF - secondary forests. Horizontal bars indicate medians, boxes comprise the upper and lower quartile of data distribution, whiskers indicate the minimum and maximum values and circles indicate outliers (i.e., values 1.5 times distant from the first and third quartiles).

FIGURES

FIGURE 1

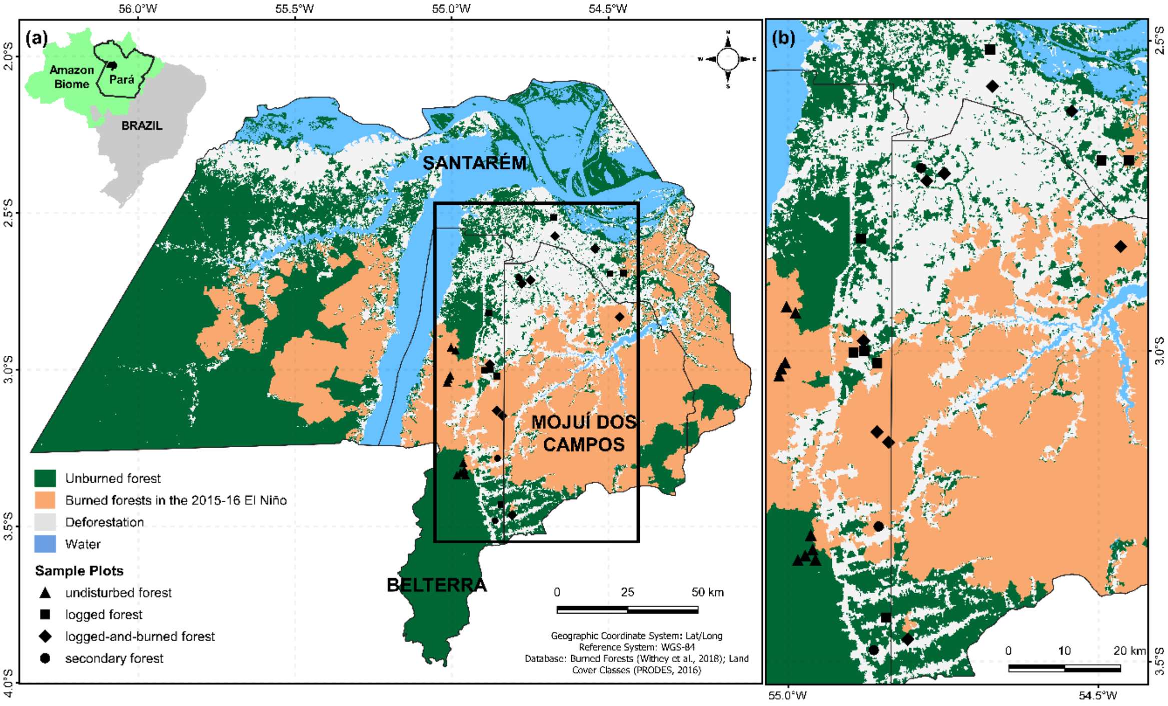


FIGURE 2

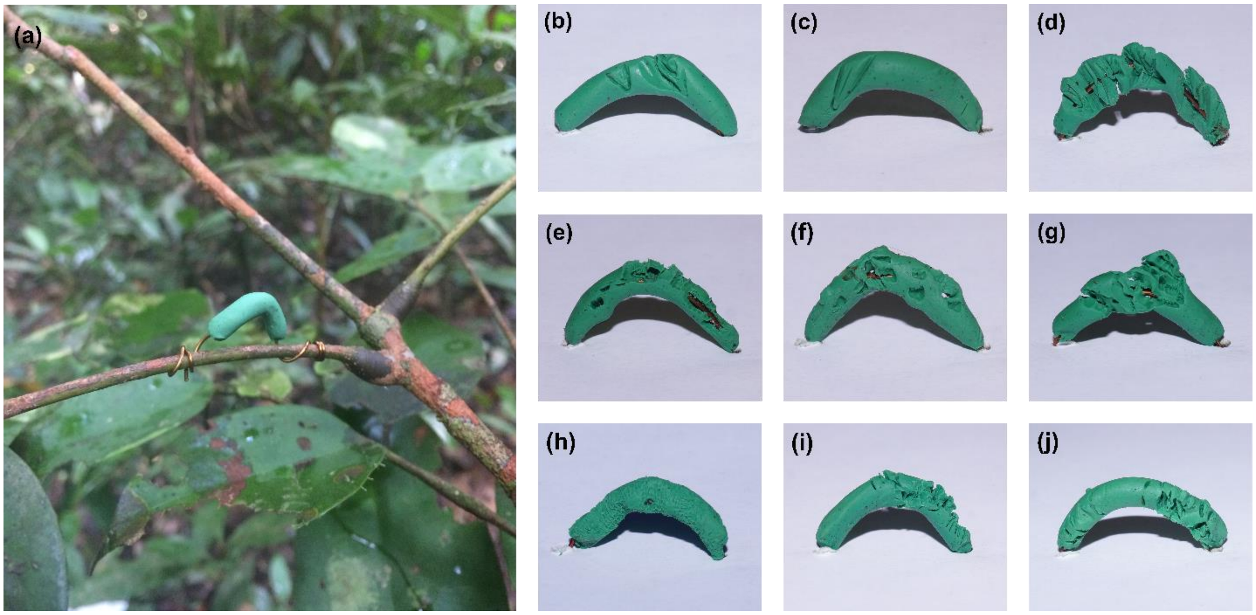


FIGURE 3

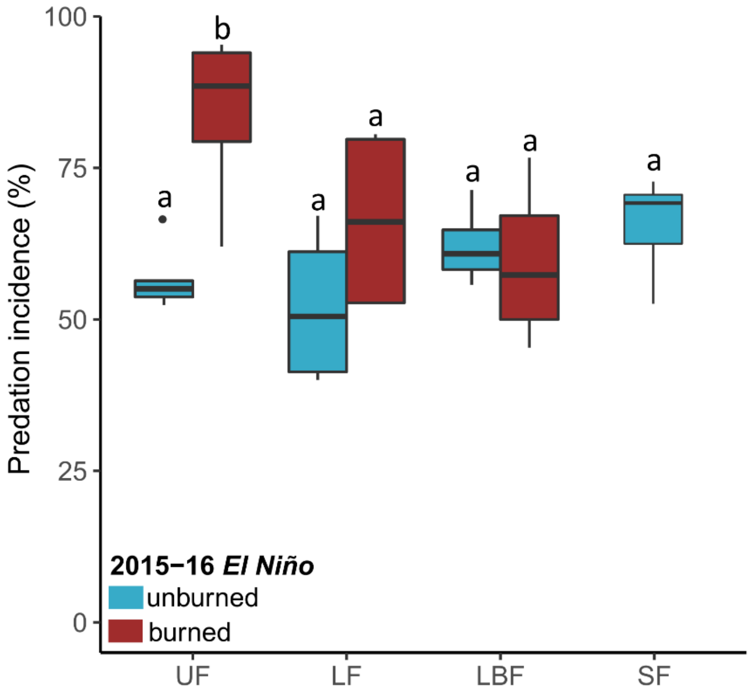
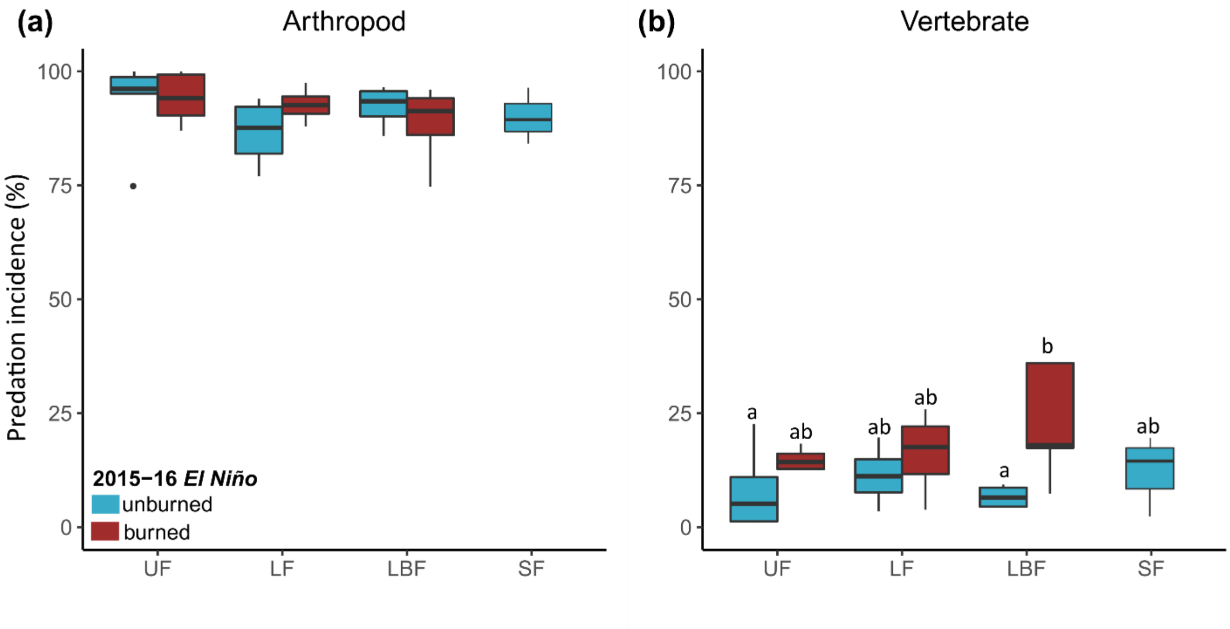

Predation incidence (%)
100
75
50
25
0
b
a
a
a
a
a
a
2015−16 *El Niño*
unburned
burned
UF
LF
LBF
SF

FIGURE 4


(a)
Arthropod
(b)
Vertebrate
Predation incidence (%)
100
75
50
25
0
UF
LF
LBF
SF
a
ab
ab
ab
a
b
ab
2015–16 El Niño
unburned
burned

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHOR CONTRIBUTION

LCR, EB and ACL conceived the original idea of this study. LCR and EB conceived the study design, conducted the experiment and organized the database. LCR and EB conducted the data analyses with input from JB and FF. LCR wrote the manuscript, with significant contributions of all co-authors. All authors discussed the results and revised the manuscript before submission.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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