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El Niño impacts on human-modified tropical forests: Consequences for dung beetle diversity and associated ecological processes

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Abstract

Our knowledge of how tropical forest biodiversity and functioning respond to anthropogenic and climate-associated stressors is limited. Research exploring El Niño impacts are scarce or based on single post-disturbance assessments, and few studies assess forests previously affected by anthropogenic disturbance. Focusing on dung beetles and associated ecological functions, we assessed (a) the ecological effects of a strong El Niño, (b) if post-El Niño beetle responses were influenced by previous forest disturbance, and (c) how these responses compare between forests impacted only by drought and those affected by both drought and fires. We sampled 30 Amazonian forest plots distributed across a gradient of human disturbance in 2010, 2016, and 2017—approximately 5 years before, and 3–6 and 15–18 months after the 2015–16 El Niño. We found 14,451 beetles from 98 species and quantified the beetle-mediated dispersal of >8,600 seed mimics and the removal of c. 30 kg of dung. All dung beetle responses (species richness, abundance, biomass, compositional similarity to pre-El Niño condition, and rates of dung removal and seed dispersal) declined after the 2015–16 El Niño, but the greatest immediate losses (i.e., in 2016) were observed

within fire-affected forests. Previous forest disturbance also influenced post-El Niño dung beetle species richness, abundance, and species composition. We demonstrate that dung beetles and their ecological functions are negatively affected by climate-associated disturbances in human-modified Amazonian forests and suggest that the interaction between local anthropogenic and climate-related stressors merits further investigation.

Abstract in Portuguese is available with online material.

KEYWORDS

Amazonia, biodiversity, Brazil, drought, ecological functions, El Niño, fires, tropical rain forests

1 | INTRODUCTION

El Niño Southern Oscillation (ENSO) events are becoming increasingly frequent and severe (Timmermann et al., 2018), potentially due to human-induced climate change (Cai et al., 2014). Over the last 40 years, strong ENSO events have been associated with changes in precipitation patterns in tropical rain forests, leading to extreme droughts and forest fires (Juárez-Orozco, Siebe, & D. Fernández y Fernández., 2017). The frequency and extent of forest fires are further exacerbated by decadal-scale increases in dry season lengths (Fu et al., 2013), the spread of fire-dependent agriculture, and the increases in forest flammability that results from human-driven disturbances such as logging and fragmentation (Hardwick et al., 2015; Uhl & Kauffman, 1990).

Despite advances in our knowledge of El Niño consequences for the carbon cycle (Berenguer et al., 2018; Malhi et al., 2018), our understanding of the impacts for biodiversity and related ecosystem functions remains limited, especially in human-modified tropical forests. While detailed studies have been conducted following experimental fires (e.g., ≤50-ha forest plots; Balch, Massad, Brando, Nepstad, & Curran, 2013; Brando et al., 2014; Oliveras et al., 2014), these may underestimate the effects of large-scale megafires which can affect millions of hectares (e.g., Withey et al., 2018). In these fires, burned forests may be tens of kilometers away from source populations in unburned forests or isolated by a matrix of agricultural land-uses. Furthermore, large-scale fires may have higher fire intensities as severe droughts also result in a drier fuel layer (Brando et al., 2019) and increased fuel loads (Brando et al., 2008).

Where large-scale studies assessing the ecological consequences of wildfires have taken place, they often lack pre-fire information (e.g., Barlow & Peres, 2004) and rely on space-for-time approaches that may underestimate biotic changes in tropical forests (Christie et al., 2019; França, Louzada, et al., 2016). Furthermore, it is not clear how previous anthropogenic forest disturbance, such as selective logging, influences the response of biodiversity and associated functions to ENSO-mediated droughts and wildfires, or whether changes in biodiversity result in further changes in ecosystems functioning. Addressing these knowledge gaps is critically important given the increased likelihood

of severe dry seasons (Duffy, Brando, Asner, & Field, 2015) and the increased rates of human-driven forest modification that is expected for tropical regions (Lewis, Edwards, & Galbraith, 2015).

We address these knowledge gaps by evaluating changes in biodiversity and some ecological processes in a region of the Amazon affected by a mega fire and intense drought in the 2015–16 El Niño event (Figure 1). We focus on dung beetles (Coleoptera: Scarabaeinae), because they (a) had been sampled in >200 forest plots in 2010, 5 years before the 2015–16 El Niño, encompassing a gradient of pre-El Niño forest disturbance, from undisturbed primary forests to logged primary forests and logged-and-burned primary forests (Barlow et al., 2016; Gardner et al., 2013); (b) are a cost-effective indicator group (Gardner, Barlow, et al., 2008); and (c) perform a number of important ecological functions that can be readily assessed in the field (e.g., França, Louzada, & Barlow, 2018; Nichols et al., 2008; Raine et al., 2019). We returned to 30 of these forest plots between 3–6 and 15–18 months after the ENSO drought and related wildfires, repeating the sampling techniques used in 2010. This design allowed us to have a full-factorial design (Table S1) to assess the following questions: (a) Are there post-El Niño declines in dung beetle communities and ecological functions?; (b) Are post-El Niño beetle responses influenced by previous forest disturbance?; and (c) Are beetle communities and ecological functions in forests only affected by the El Niño drought different from those affected by both drought and fires?

2 | METHODS

2.1 | Study region

We conducted our study in three municipalities in the Brazilian Amazon: Belterra, Santarém, and Mojuí dos Campos in the state of Pará (Figure 1). The climate in this region is characterized as hot-humid (Köppen's classification), and the annual average temperature and precipitation are 25°C and 1,920 mm, respectively, with short dry seasons between August and October (Figure S1), which are longer and drier during El Niño years (Jolly et al., 2015).

2.2 | Sampling design

We sampled dung beetles and beetle-associated ecological functions within 30 forest plots (Figure 1) distributed along a pre-El Niño disturbance gradient, including undisturbed primary forests (n = 10), logged primary forests (n = 10), and logged-and-burned primary forests (n = 10). Between October and December 2015, half of these forests plots were impacted by understory fires that occurred during the exceptionally dry weather caused by the extreme 2015–16 El Niño event, while unburned controls were preserved in all of our previous forest disturbance classes (hereafter fire-affected and drought-only forests, respectively; Table S1).

2.3 | Data collection

Dung beetles and ecological functions were surveyed in exactly the same locations (Figure 1) and following the same sampling techniques in all three surveys (Figure S2). The first data collection occurred in June–July 2010, around 5 years before the 2015–16 El Niño. The second and third surveys took place in June–July 2016 (as in 2010, end of the rainy season; Figure S1) and March–April 2017 (in the rainiest months in the study region; Figure S1), approximately 3–6 and 15–18 months after the El Niño-associated uncontrolled fires that affected our study region. At each of the 30 forest sites, beetles and their ecological functions were sampled at three sampling points (0, 150 and 300 m) along a 300-m transect. We used nine dung-baited pitfall traps (three traps per sampling point; Figure S2c) to sample dung beetles, resulting in a total of 810 dung-baited pitfall traps (270 pitfalls/year). All trapped dung

beetles were identified to species or morphospecies. Dung beetle species-level average body mass was calculated from the dry body weight of 15 individuals using a *Shimadzu* balance with precision of 0.0001 g. Rates of dung removal and secondary seed dispersal were assessed between 3 and 4 weeks after the dung beetle surveys. At each sampling point, we placed a mesocosm arena with ~0.79-m^2 area (Figure S2a,b) and containing, in the centre, a 200-g dung pile (4:1 pig to human ratio, following França et al., 2018) mixed with 50 seed mimics (3.5-mm diameter, as in Braga et al., 2017; Braga, Korasaki, Andresen, & Louzada, 2013). Further methodological details are described in Supporting Information.

2.4 | Statistical analyses

To address our research questions, we examined changes in six response variables: species richness, abundance, species composition, biomass, and rates of dung removal and seed dispersal. All analyses were performed within the R Studio version 3.3.1 (R Core Team, 2019) and conducted at the plot-level: community attributes (richness, abundance, and biomass) were the sum of values from each of the nine pitfall traps, and rates of ecological functions were the average of the values recorded in the three arenas. Dung beetle biomass at the plot-level was calculated by multiplying the average body mass of each species by their abundance. Species composition was measured as pairwise beta-diversity (Socolar, Gilroy, Kunin, & Edwards, 2016), based on the Bray–Curtis similarity index (1-dissimilarity) calculated for each forest plot and year through the *vegdist* function ("vegan"; Oksanen et al., 2015). Post-El Niño species composition therefore represents the
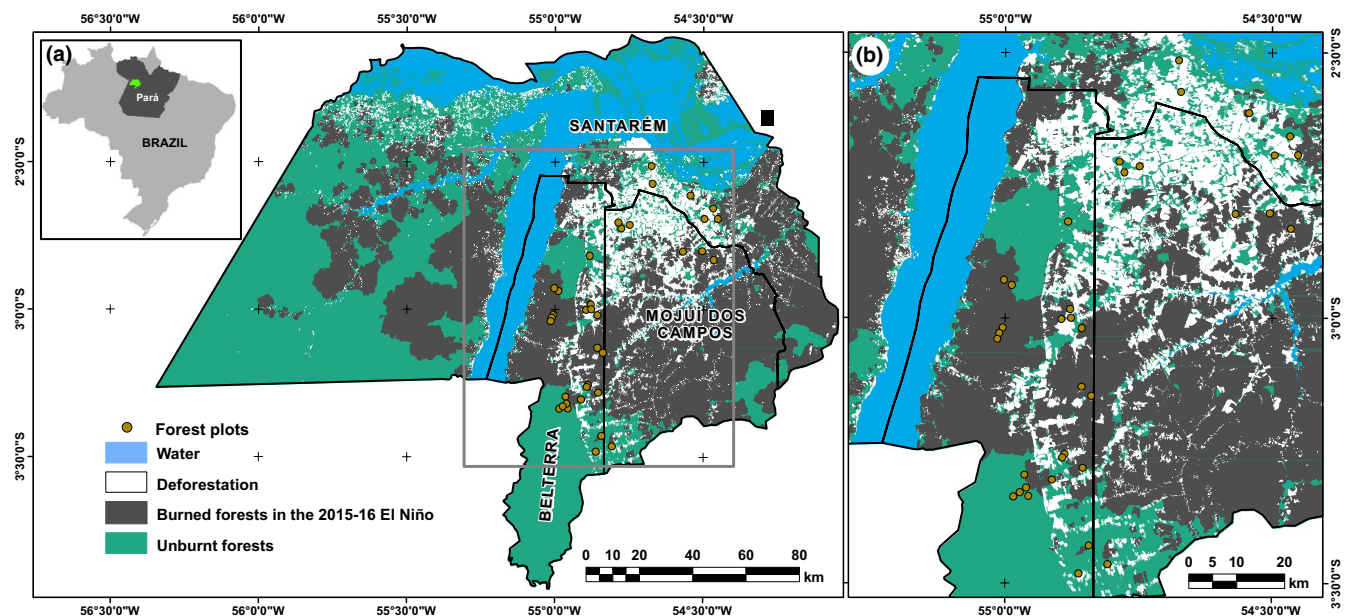
FIGURE 1 Map showing the location of our study region in the eastern Brazilian Amazonia. (a) Around 8,072 km^2 of primary forests from the total area in the map (*ca* 27,418 km^2) were burned during the 2015–16 El Niño event. The inset shows the study region (light green) within Brazil (light gray) and state of Pará (dark gray). (b) The map within the study region—shown by the gray border in (a). Also shown in these panels are the locations of the 30 sampled forest plots (beige-filled circles)

compositional similarity of each post-El Niño survey (i.e., 2016 and 2017) to the pre-El Niño condition in the same forest plot. Pre-El Niño species composition was based on the average compositional similarity of each surveyed forest to the ten undisturbed forests surveyed before the El Niño. For undisturbed forests, we considered the average compositional similarity of each plot to the other nine undisturbed forests surveyed in 2010.

We conducted a three-way full-factorial (Table S1) repeated-measures analysis of variance (RM-ANOVA) using the *ezANOVA* function ("ez" package; Lawrance, 2016), with "Forest type" (3 levels: undisturbed, logged, or logged-and-burned) and "El Niño classes" (2 levels: drought-only vs. fire-affected) as between subject factors, "Year" (3 levels: 2010, 2016 or 2017) as within-subject factor and their interactions. The assumption of sphericity was not violated for any of our dependent variables (Mauchly's test, Table S2; all *p*-values ≤.2). When two factors or interaction terms were statistically significant, we therefore used Tukey's Wholly Significant Difference through the "lsmeans" package to assess post hoc differences (Lenth, 2016). Plots were generated by using the *ezPlot* function ("ez"; Lawrance, 2016) and subsequently modified using "ggplot2" (Wickham, 2009).

Gaussian distributions for all response variables and model residuals were tested using the Shapiro-Wilk normality test through the *Shapiro.test* function ("stats"; Crawley, 2002). Data normality and homoscedasticity were achieved for biomass, abundance, and dung removal rates after rank-transformation. We used the package "dplyr" for data cleaning and the function *pearson.test* in "stats" to assess the residual independence from all RM-ANOVAs (Table S2). As sites that are closer together are expected to hold more similar communities (Kühn & Dormann, 2012), we also assessed spatial autocorrelation within our datasets by performing Pearson-based Mantel tests using the *mantel* function with 1,000 permutations ("vegan"; Oksanen et al., 2015). Mantel tests were made separately for dung beetle richness from each survey.

3 | RESULTS

Across our three surveys, we sampled 14,451 dung beetles (8,070, 3,733, and 2,648 individuals, in 2010, 2016, and 2017, respectively) from 98 species (*2010*:75; *2016*:65, and *2017*:68). Dung beetles removed >30 kg of dung (*2010*:13.3; *2016*:11.1; and *2017*:5.7 kg; representing 74.1%, 62.2%, and 32.1% of the total dung placed, respectively) and dispersed >8,600 seed mimics (*2010*:3,393 [or 75.1% of total seeds placed]; *2016*:2,632 [58.4%]; and *2017*:2,664 [59.2%]). Mantel tests of distance between forests showed a weak but significant effect of spatial autocorrelation on pre-El Niño beetle richness (R^2 = .19, *p* = .009), but this was not significant in either of the post-El Niño surveys (*2016*: R^2 = .003, *p* = .33; and *2017*: R^2 = .11, *p* = .06).

All dung beetle responses declined in the post-El Niño surveys (Figure 2a–r). Reductions in species richness and abundance varied significantly among surveyed years, forest types, and El Niño classes (RM-ANOVA *Year × Forest type × El Niño* species richness $F_{4,48}$ = 2.9, *p* = .02;

abundance $F_{4,48}$ = 3.6, *p* = .01; Table S2 and Figure 2a–f). Post hoc pairwise comparisons showed that undisturbed forests that burned during the El Niño had significantly lower species richness and abundance in 2016 and in 2017 when compared with (a) all forests in the pre-El Niño survey and (b) undisturbed forests and logged forests that were impacted only by the El Niño drought (Figure S3). Dung beetle species richness and abundance were significantly higher in undisturbed forests and logged forests sampled before the El Niño than in either of the post-El Niño assessments, in logged forests and logged-and-burned forests sampled after the El Niño fires (Figure S3), or in logged-and-burned forests affected by drought only (Figure S3).

Species composition varied significantly among years and forest types (RM-ANOVA *Year × Forest type* $F_{4,48}$ = 2.9; *p* = .02; Table S2 and Figure 2g–i). The reductions of the pre-El Niño compositional similarity were greater in fire-affected forests than in those affected only by drought during the El Niño (RM-ANOVA *Year × El Niño* $F_{2,48}$ = 12.6, *p* < .0001; significant post hoc comparisons are shown in Figure S3). Dung beetle biomass varied significantly among years (RM-ANOVA $F_{2,48}$ = 35.1, *p* < .0001) and El Niño classes (RM-ANOVA $F_{1,24}$ = 24.0, *p* < .0001; Figure 2j-l). Post hoc analyses supported these findings, demonstrating that beetle biomass in 2017 within fire-affected undisturbed forests was lower than (a) in all forests surveyed before the El Niño and (b) in those logged forests and logged-and-burned forests that were affected by drought only and surveyed in 2016 (Figure S3).

When assessing post-El Niño changes in dung beetle ecological functions, rates of dung removal and seed dispersal varied among years and El Niño classes (RM-ANOVA: *El Niño × Year* dung removal $F_{2,48}$ = 7.0, *p* = .002; seed dispersal $F_{2,48}$ = 4.2, *p* = .02; Figure 2m-r). Post-El Niño dung removal rates were significantly higher in drought-only impacted forests surveyed in 2016 when compared to fire-affected forests surveyed in 2017 (Figure S3). Dung removal rates also declined significantly between 2016 and 2017 within undisturbed forests that were affected by drought only (Figure S3). Finally, post hoc comparisons suggested that seed dispersal rates in 2016 within logged-and-burned forests that burned again during the El Niño were significantly lower than those found in (a) pre-El Niño logged forests and logged-and-burned forests (Figure S3), and (b) undisturbed forests and logged-and-burned forests affected by drought only (Figure S3). Rates of seed dispersal in 2017 within logged-and-burned forests affected by El Niño fires were still lower than the pre-El Niño condition (*t*-test, *t*-ratio = 3.6, *p* = .04; Figure S3).

4 | DISCUSSION

We evaluated dung beetle communities and the ecological processes of dung removal and secondary seed dispersal along a gradient of human-modified Amazonian forests, before and after an extreme drought and forest fires that occurred during the 2015–16 El Niño—considered one of the strongest events to date (Timmermann et al., 2018). Our investigation provides important insights into how the interactions between human-driven disturbances and El Niño-related
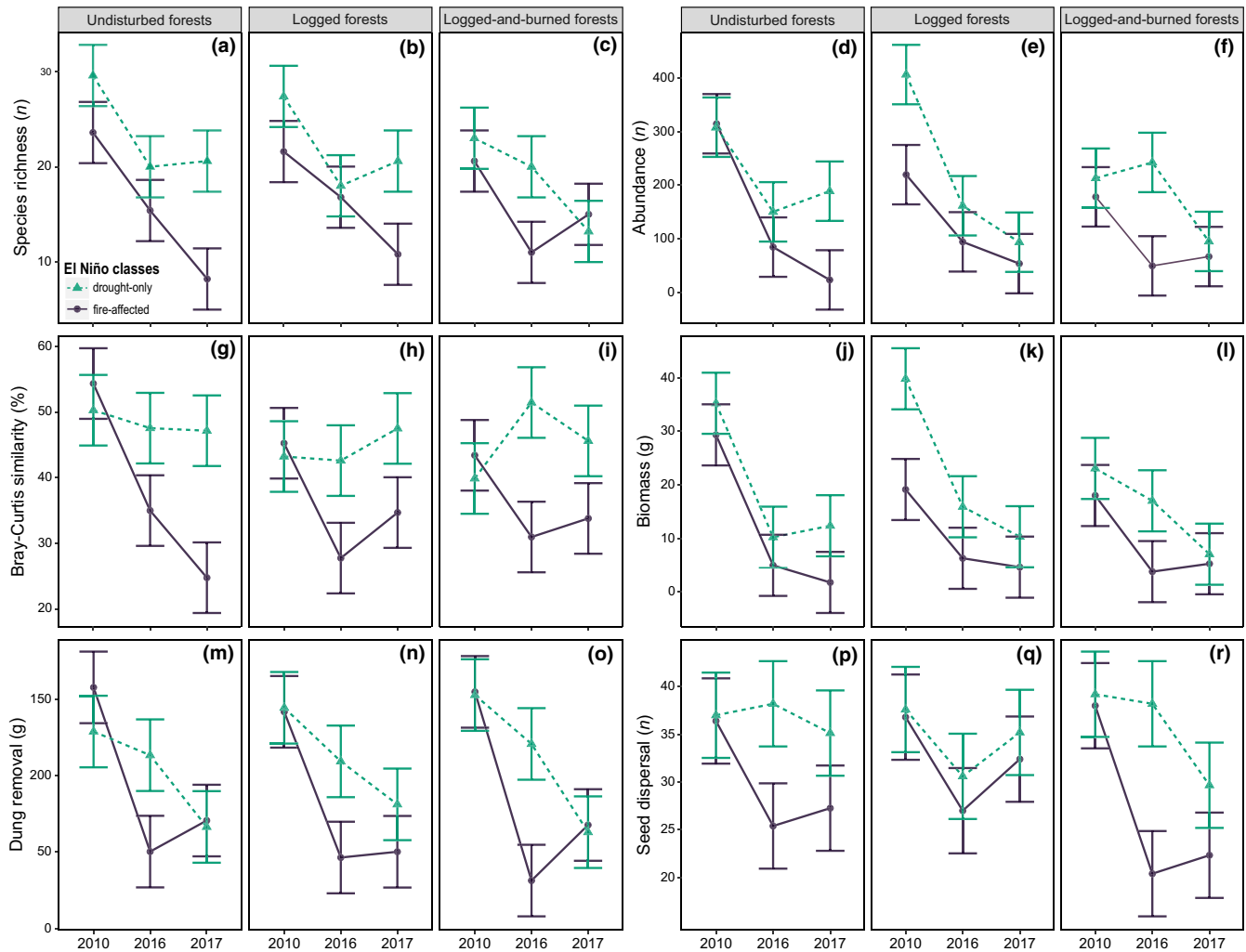
FIGURE 2 Dung beetle responses to El Niño-induced drought and fires in previously undisturbed and human-modified Amazonian forests. (a–c) Dung beetle species richness, (d–f) abundance, (g–i) compositional similarity, (j–l) biomass and rates of (m–o) dung removal, and (p–r) secondary seed dispersal were sampled within 30 forest plots (*n* = 5 plots per forest type and El Niño class) in the eastern Brazilian Amazon region, near Santarém in the State of Pará. Surveys were carried out in 2010 (i.e., pre-El Niño survey) and in 2016 and 2017— around 3–6 months and 15–18 months after the 2015–16 El Niño fires affected half of these forest plots. Models were repeated-measures ANOVA treating "Year" as the repeated measure, and "forest classes" and "El Niño classes" as grouping factors for each response variable. To facilitate post hoc visual comparisons within the analyzed data, error bars depict Fisher's least significant difference on the three-way interaction (*ezPlot*, by default; Lawrance, 2016); thus non-overlapping bars can be interpreted as being significantly different

weather and fires can affect tropical forest biodiversity and functioning. All dung beetle responses declined after the El Niño event (Figure 2a–r), demonstrating the low resistance that tropical forest dung beetles and relevant ecological processes have to extreme dry seasons and associated fire events. Previous forest disturbance significantly affected the post-El Niño dung beetle species richness, abundance, and compositional similarity to pre-El Niño condition (Figure 2a-i), while all beetle responses varied significantly between drought-only and fire-affected forests in at least one of the post-El Niño surveys (Figure 2a-r). Importantly, some dung beetle responses continued to decline up to two years after the El Niño event. Such longer-term declines were observed in both drought-only and fire-affected forests (Figure 2e, k), suggesting there is either a lag between El Niño and the effects on tropical invertebrates and their ecological processes, or that ecological condition deteriorates over

time (due to ongoing tree morality, for example—Silva et al., 2018). We discuss these results in light of the ecological consequences that interactions between climatic and local stressors can bring to tropical forest biodiversity and ecological functions.

4.1 | Direct drivers of change in dung beetle communities

We provide evidence that El Niño-induced droughts and fires can be strong direct drivers of change in dung beetle communities. Although spatial patterns of movement can vary among species (Silva & Hernández, 2015), most dung beetles are poor fliers—for example, having an estimated movement of 90 m in 48 hr (Silva & Hernández, 2015) and may not be able to escape understory fires;

even if the flame heights are low, the area scorched extends many meters in height and dense smoke reaches beyond the canopy. Droughts and warming can also affect the survival and brood production in adult dung beetles. Previous research has found a large number of beetles reabsorbing their oocytes—suggested as physiological response to heat and water stress (Tyndale-Biscoe, Wallace, & Walker, 1981), while artificial warming experiments have shown that hotter and drier conditions affected the relative survival and emigration of two dung beetle species (Holley & Andrew, 2019a), as well as disrupted dung beetle reproduction via a decline in ball burial (Holley & Andrew, 2019b).

There is, however, a lack of understanding to what extent belowground nests are affected by droughts or fires. Although temperatures at the soil surface can be extremely high even during low-intensity fires (Kennard & Gholz, 2001), these decrease abruptly with increasing depth—for example, reaching only 22–25°C between 22 and 30 cm in depth after burning for 2 hr (Beadle, 1940). But most Amazonian dung beetles nest in shallower soil layers (Griffiths et al., 2015), raising the possibility that mortality within nests contributes to the immediate post-El Niño declines in dung beetle communities. Alternatively, the belowground environment may represent a refuge for dung beetles (both larvae and adults) nesting in deeper soil layers (Gregory, Gómez, Oliveira, & Nichols, 2015; Griffiths et al., 2015), and post-drought and fire emerged beetles could help explain the time lag between the El Niño and dung beetle responses two years later.

4.2 | Indirect mechanisms underpinning post-El Niño changes in dung beetle communities

With some exceptions (e.g., Barlow et al., 2016; Cleary & Mooers, 2006), the current literature on drought- and fire-induced impacts on tropical forests is dominated by plant studies (e.g., Berenguer et al., 2018; Brando et al., 2008; Silva et al., 2018), which show increased tree mortality (Nakagawa et al., 2000), reduced carbon storage (Brando et al., 2019), and large physiological changes such as in flower and fruit production (Sakai et al., 2006). Given the scale of effects observed among the primary producers, it seems likely that invertebrate taxa would also be affected. Two obvious mechanisms could underpin these changes. First, lower post-El Niño fruit production can result in large-vertebrate famine (Barlow & Peres, 2006; Wright, Carrasco, Calderon, & Paton, 1999). These drought and fire-induced changes in vertebrate communities (Barlow, Peres, Henriques, Stouffer, & Wunderle, 2006; Peres, Barlow, & Haugaasen, 2003) are likely to result in cascading effects on dung beetles (Nichols, Gardner, Peres, & Spector, 2009), as co-declines in these two groups have been reported in other human-modified tropical forest landscapes (e.g., Bogoni, Silva, & Peres, 2019; Raine & Slade, 2019). Second, high rates of tree mortality following droughts and forest fires result in more open canopies, which may affect communities through the hotter and drier forest microclimates (Brando, Oliveria-Santos, Rocha, Cury, & Coe, 2016; Hardwick et al., 2015). Tropical dung beetles have been shown to respond to such forest

modification, both indirectly through sublethal changes on their body conditions (França, Barlow et al., 2016; Salomão, González-Tokman, Dáttilo, López-Acosta, & Favila, 2018) and directly, by reducing species-specific relative abundances and the community diversity and biomass (Barlow et al., 2016; França et al., 2016).

4.3 | Could pre-El Niño forest disturbance influence post-El Niño ecological communities?

Previous forest disturbance influenced the post-El Niño declines in dung beetle richness, abundance, and compositional similarity to pre-El Niño condition, while previously logged-and-burned forests had slightly faster recovery times for some dung beetle responses between 2016 and 2017. Both these findings suggest that previous forest disturbance could have acted as an environmental filter or selective force (Balmford, 1996; Nunes et al., 2016): Microclimatic changes relating to previous logging or fires (e.g., Hardwick et al., 2015; Lindenmayer, Hunter, Burton, & Gibbons, 2009) may have extirpated the most disturbance-sensitive species—as previously observed for dung beetle communities in primary forests converted to oil palm plantations in Southeast Asia (Edwards et al., 2014)—and favored the species that are more tolerant to drought and fires. This conjecture is supported by evidence showing that dung beetle species are highly susceptible to environmental modification (Beiroz et al., 2018), including changes in forest structure (Salomão et al., 2018) and microclimatic conditions (Birkett, Blackburn, & Menéndez, 2018). Perhaps more importantly, our results support that local human-driven disturbance and climate-associated stressors can act together and influence tropical forest biodiversity and functioning. Thus, focusing on a single stressor may fail to capture the magnitude of the threat faced by tropical forests and their fauna (Barlow et al., 2018; Newbold et al., 2019), which are increasingly threatened by local human-driven disturbances (Lewis et al., 2015) and are expected to have more frequent and extreme droughts in the next decades (Duffy et al., 2015).

4.4 | Exploring the resilience of dung beetle-mediated processes

The lack of influence of pre-El Niño forest disturbance on beetle-mediated processes is consistent with previous studies showing the disturbance resilience of invertebrate-mediated processes in tropical forests (Ewers et al., 2015; França et al., 2018) and confirms that community and functional attributes may be asymmetrically affected by human activities in tropical forests (Braga et al., 2013; Carvalho et al., 2020; França et al., 2018). However, forest structure is known to be a key determinant of insect communities (Basset, Charles, Hammond, & Brown, 2001), and there is presumably a threshold at which point changes in forest structure are so great that invertebrate communities and mediated processes are also affected (e.g., França, Frazão, Korasaki, Louzada, & Barlow, 2017). The lower rates of dung removal and seed dispersal in post-El

Niño surveys (Figure 2m–r) suggest this threshold was surpassed by the severe impacts of the 2015–16 El Niño drought and wildfires on vegetation and forest structure in this region (Berenguer et al., 2018; Silva et al., 2018; Withey et al., 2018). These lower rates of ecological functions—which occurred within both drought-only and fire-affected forests—could be attributed to the higher vulnerability of large-bodied dung beetles to forest disturbance (Larsen, Williams, & Kremen, 2005). For example, we found 61 individuals of *Coprophanaeus lancifer* (Linné, 1767) during the pre-El Niño survey in 2010, while only 11 and 5 specimens were sampled in 2016 and 2017, respectively. This is the largest dung beetle species found in the study region and belongs to one of the most important functional groups (large tunnelers) performing ecosystem functions of soil bioturbation (Gregory et al., 2015) and dung and seed removal (Slade, Mann, Villanueva, & Lewis, 2007).

4.5 | Dung beetle responses between El Niño drought-only impacted and fire-affected forests

We found dung beetle responses declining within both drought-only and fire-affected forests. However, as expected by the relative severity of the impacts on vegetation, El Niño fire-affected forests showed greater immediate declines (i.e., in 2016; Figure 2f–h, m–o) and longer-term losses in beetle responses (i.e., in 2017; Figure 2a,b,d, g–i) when compared to those forests that only experienced the drought. These findings provide evidence that both El Niño-related extreme droughts and fire events can bring drastic consequences not only for plant communities and carbon cycling (Silva et al., 2018; Withey et al., 2018) but also for fauna diversity and associated ecological functions.

However, drought effects on dung beetles were surprisingly strong considering that tree mortality in drought-affected forests is only 1%–3% (Phillips et al., 2010) compared with 50% or more in drought and fire-affected forests (e.g., Barlow et al., 2012). Furthermore, while there was a slight recovery in some fire-affected forests between 2016 and 2017 (e.g., Figure 2c,f,l–o,r), most dung beetle responses in drought-only forests declined even more from 2016 to 2017. It is not yet clear why droughts should have such a strong and long-lasting impact, or why the relative magnitude of effects from fire and drought-and-fire for dung beetles should be so different from vegetation. Furthermore, as human activities such as logging and fires can affect forest structure and composition for decades (Osazuwa-Peters, Chapman, & Zanne, 2015; Silva et al., 2018), it is unclear at what point and if the dung beetle-mediated ecosystem functioning will return to pre-disturbance levels.

4.6 | Research limitations

While our findings are likely to reflect the short-term sensitivity of tropical invertebrates and associated processes in human-modified forests to El Niño drought and fires, they are not without limitations.

One key issue is that our pre-El Niño plots were sampled nearly 5 years before the event. Although assessments of the vegetation suggest minimal differences between 2010 and pre-El Niño samples in 2016, at least some of the influence of El Niño on invertebrate communities may be obscured by pre-El-Niño changes in biodiversity through processes such as succession (e.g., Lennox et al., 2018), longer-term disturbance responses (e.g., Silva et al., 2018), or ecological drift and competition (e.g., Levi et al., 2019; Ulrich, Puchałka, Koprowski, Strona, & Gotelli, 2019). As such, while before–after studies hold many advantages when the before assessment is immediately before the disturbance (e.g., Christie et al., 2019; França, Louzada, et al., 2016), there is a risk that the ecological signal will become degraded with greater temporal disconnection.

Another potential limitation relates to seasonality. We sampled dung beetles at the end of the rainy seasons in 2010 and 2016, and in the rainiest months in 2017 (March–April; Figure S1). Thus, our research does not take seasonality into account, which can play a significant role in dung beetle responses to forest disturbance (Andrade et al., 2011; but see Gardner, Hernández, Hernández, Barlow, & Peres, 2008). Furthermore, the post-El Niño samples only extended to 15–18 months after the fires occurred in our forest plots, and patterns may be dominated by non-equilibrium processes, including high levels of instability and stochasticity, which often dominate the short-term responses of ecological communities to disturbance (Mori, 2011) and can result in black-swan events in animal populations (Anderson, Branch, Cooper, & Dulvy, 2017). As our assessments are restricted to a single taxon and their associated functions, more long-term research is therefore needed to understand how reproducible our results are in other taxa performing key ecosystem processes in tropical forests, such as ants (Griffiths et al., 2018), termites (Ashton et al., 2019), and seed-disperser vertebrates (Paolucci et al., 2019). This would foster a better knowledge of how resilient tropical forest fauna and ecosystem functioning are to the interactions between human- and climate-associated stressors.

5 | CONCLUSIONS

By exploring the impacts of the 2015–16 El Niño on dung beetle communities and associated ecological processes across a gradient of previous forest disturbance in the Amazon, we confirm the threat posed by extreme drought and fire events for biodiversity and functioning of human-modified tropical forests. We found that undisturbed forests were more sensitive than logged-and-burned forests for most dung beetle responses, and that El Niño drought alone and/or combined with fires can result in drastic losses in beetle diversity, abundance, biomass, and rates of dung removal and seed dispersal that can last for at least 18 months. Our results, therefore, suggest that local human-driven disturbances and climate-associated stressors can interact in different ways and that these interplays may asymmetrically affect the community and functional attributes of tropical forest invertebrates. However, future investigations, with more tightly controlled pre-disturbance conditions and longer-term

tracking of recovery, are needed to better understand the interactions between multiple forest stressors.

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

F.M.F. conceptualized the study goals and analyzed all data. J.F. and J.B. designed the pre-El Niño experimental design with input from E.B., J.N.C.L., V.H.F.O. and R.F.B. Plot selection and subsequent authorizations from landowners and Brazilian environmental agencies were performed by J.F., E.B., and F.F. Fieldwork and beetle identification were conducted by R.B. and V.H.O. (2010) and F.F. and L.F.M. (2016–2017). F.Z.V.M. validated all beetle identifications. L.F.M. and V.H.O. measured beetle body mass. J.B., J.F., E.B. and F.F. contributed for funding acquisition. F.Z.V.M., R.F., and J.N.C.L. provided study equipment and materials for laboratory and field work. A.F.P. supported in data visualization. Manuscript writing was led by F.F. with inputs from J.B., J.F. and R.F. The manuscript was reviewed by J.F., J.B., L.F.M., E.B., R.F. and R.B. All authors gave final approval for publication.

ETHICAL APPROVAL

Surveys in Brazilian protected areas occurred with appropriate state and federal permits (Brazil: SISBIO n. 24164 in 2009, and 53271 in 2016–17).

DATA AVAILABILITY STATEMENT

The data used in this study are archived at the Environmental Information Data Centre (NERC-EIDC; https://doi.org/10.5285/799db965-3ce7-4e9b-8590-de6a8624d652).

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SUPPORTING INFORMATION

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