Drought and presence of ants can influence hemiptera in tropical leaf litter

9 authors, including:

Anna E. Goldman
The University of Hong Kong
1 PUBLICATION   **6** CITATIONS

Timothy Bonebrake
The University of Hong Kong
132 PUBLICATIONS   **6,315** CITATIONS

Pak Nok Toby Tsang
The University of Hong Kong
14 PUBLICATIONS   **99** CITATIONS

Theodore Alfred Evans
University of Western Australia
179 PUBLICATIONS   **5,303** CITATIONS

ORIGINAL ARTICLE

bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION WILEY

Drought and presence of ants can influence hemiptera in tropical leaf litter

Anna E. Goldman[1] | Timothy C. Bonebrake[1] | Toby P. N. Tsang[1] | Theodore A. Evans[2] | Luke Gibson[3] | Paul Eggleton[4] | Hannah M. Griffiths[5] | Catherine L. Parr[5] | Louise A. Ashton[1,4,6]

[1]School of Biological Sciences, The University of Hong Kong, Hong Kong, China

[2]School of Biological Sciences, University of Western Australia, Perth, WA, Australia

[3]School of Environmental Science and Engineering, Southern University of Science and Technology, Shenzhen, China

[4]Department of Life Sciences, Natural History Museum, London, UK

[5]School of Environmental Sciences, University of Liverpool, Liverpool, UK

[6]Environmental Futures Research Institute, Griffith University, Brisbane, QLD, Australia

Correspondence
Louise A. Ashton, School of Biological Sciences, The University of Hong Kong, Hong Kong, China.
Email: Lashton@hku.hk

Associate Editor: Emilio Bruna
Handling Editor: Roger Kitching

Abstract

Climate change is predicted to impact tropical rain forests, with droughts becoming more frequent and more severe in some regions. We currently have a poor understanding of how increased drought will change the functioning of tropical rain forest. In particular, tropical rain forest invertebrates, which are numerous and biologically important, may respond to drought in different ways across trophic levels. Ants are a diverse group that carry out important ecosystem processes, shaping ecosystem structure and function through predation and competition, which can influence multiple trophic levels. Hemiptera are a mega-diverse order, abundant in tropical rain forests and are ecologically important. To understand the roles of ants in exerting predation and competition pressure on invertebrates in tropical rain forests during drought and a post-drought period, we established a large-scale ecosystem manipulation experiment in Maliau Basin Conservation Area in Malaysian Borneo, suppressing the activity of ants on four 0.25 ha plots over a two-year period. We sampled hemipterans found in the leaf litter during a drought (July 2015) and a post-drought period (September 2016) period. We found significant shifts in the assemblage of hemipterans sampled from the leaf litter following ant suppression. Specifically, for ant-suppression plots, the species richness and abundance of herbivorous hemipterans increased only during the post-drought period. For predatory hemipterans, abundance increased with ant-suppression regardless of drought conditions, and we found marginal evidence for a species richness increase during the post-drought period with little or no change in the drought period. These results illustrate how ants in tropical forests structure invertebrate communities and how these effects may vary with climatic variation.

Abstract in Malay is available with online material.

KEYWORDS

Borneo, drought, food web, formicidae, hemiptera, Malaysia

Paul Eggleton, Hannah M. Griffiths, Catherine L. Parr and Louise A. Ashton authors contributed equally to this work.

---

1 | INTRODUCTION

Predators can exert strong ecosystem-level effects, for example, by controlling the number of herbivores and therefore herbivory rates, with knock-on effects that occur across multiple trophic levels (Schmitz, Hambäck, & Beckerman, 2000; Terborgh, 2015). Specifically, predators can cause trophic cascades, as "changes in predator numbers [that] affect the success of a subset (one or a few) of the plant species... [or] any multilink linear food-web interaction" (Polis, Sears, Huxel, Strong, & Maron, 2000). Tropical forests are home to a high diversity of arthropods and invertebrates, although the complexity of interactions between guilds and species in such ecosystems remain poorly studied (Basset et al., 2012). The importance of food-web interactions in tropical forest floors is particularly understudied, despite the importance of organisms, such as termites and microbes on the forest floor, driving decomposition and ecosystem function (Lensing & Wise, 2006; Liu, Chen, He, Hu, & Yang, 2014).

Ants are among the most abundant animal groups and can serve many ecological roles including herbivores, scavengers, predators and/or plant defenders (Agrawal & Rutter, 1998; Ewers et al., 2015; Griffiths et al., 2018; Heil & McKey, 2003; Klimes, Janda, Ibalim, Kua, & Novotny, 2011; Parr et al., 2017). Ant species can vary from largely herbivorous to specialized predators; however, most ants are facultatively omnivorous (Denmead et al., 2017; Hölldobler & Wilson, 1990; Hyodo et al., 2016), and are thought to play key roles in structuring ecosystems and food webs (Blüthgen, Gebauer, & Fiedler, 2003). For example, in a lowland tropical rain forest in Malaysia, Griffiths et al. (2018) used a large-scale experimental manipulation to demonstrate that ants carry out over 50% of resource removal and nutrient redistribution.

The predatory nature of some tropical ant species (Dejean, Corbara, Orivel, & Leponce, 2007) presents the possibility of food-web interactions driven by changes in the abundance and species composition of these top predators. Ant predators have been shown to influence pollination, for example, by preferentially consuming non-pollinating fig wasps on fig trees (Wang, Geng, Ma, Cook, & Wang, 2014). Outside the tropics, Mestre, Piñol, Barrientos, and Espadaler (2016) found that the presence of one single predatory ant species (*Lasius grandis*) caused large declines in generalist predators and increases in aphids. Importantly, predatory ants in the tropics appear to be sensitive to land-use change and disturbance (e.g., in the tropical forests of Borneo; Luke, Fayle, Eggleton, Turner, & Davies, 2014; Matsumoto, Itioka, Yamane, & Momose, 2009). Given the key functional role ants play in the regulation and influence of ecosystem processes, understanding how ants may contribute to trophic interactions within arthropod communities could provide essential insights, particularly in tropical rain forests.

Climatic variation and weather can also influence trophic interactions by altering the resources available to plants and animals and by affecting the activity of partners in those interactions. Climate change modeling has shown that drought in tropical rain forests may become more severe and frequent in the future,

although there is still large uncertainty around these estimates (Dai, 2013).

In tropical forests, there is evidence that droughts can trigger increased herbivory and insect outbreaks (Coley, 1998). Furthermore, there is some suggestion that these outbreaks are caused by predation release as animals at higher trophic levels can be more negatively affected by droughts than lower trophic levels (Preisser & Strong, 2004). Rodríguez-Castañeda (2013) also found that predation effects of tropical ants specifically tended to be higher in high temperature and high-precipitation environments that favor ant activity.

Here, we assess how ants shape part of the hemipteran community through a large-scale experimental manipulation of ant abundance in Malaysian Borneo. Hemipterans are a diverse and important insect group and changes in their communities could have important consequences for ecosystem function (Andrew & Hughes, 2005), including changes to productivity and nutrient cycling. We measured the response of both predatory and herbivorous hemipteran species sampled from the leaf litter, to ant suppression. We carried out this experiment during the 2015–16 El Nino drought in Malaysian Borneo and were therefore able to assess if differing climatic conditions affected ant-mediated influence of hemipteran assemblages. We hypothesized that (a) ant suppression would increase herbivorous hemipteran abundance, species richness and alter community composition observed in the leaf litter, through reduced predation pressure, (b) ant suppression would also have a positive effect on predatory hemipterans richness and abundance, through competitive release and (c) during drought conditions, trophic interactions would decline, resulting in a dampening of the top-down control on the herbivorous hemipteran assemblages.

2 | METHODS

We used a set of experimental ant-suppression plots in Maliau Basin Conservation Area in Malaysian Borneo (4.8531°N, 116.8439°E) established by Griffiths et al. (2018) as part of the Biodiversity and Land-Use Impacts (BALI) project. The conservation area is 588 km^2 of primary rain forest, ranging from 300 m above sea level (asl) to 1675 m asl. The mean annual rainfall for the Basin is 2,838 ± 93 mm (from climate-data.org).

The experimental design consisted of eight plots located within a 42-ha area. Each plot was 50 m × 50 m with treatment plots having an additional a 15 m buffer zone around each treatment plot. Four plots were treated to suppress ants and four plots served as controls with no treatment (Figure 1). Epigaeic ants were suppressed, starting in October 2014, primarily with Synergy Pro™ (active ingredients: hydramethylon and pyriproxyfen). These baits are specific: The oily nature of the baits attracts ants, while previous baiting trials have shown no discernible environmental effects (reviewed by Vander Meer, Pereira, Porter, Valles, & Oi, 2007). The ants take the bait granule back to their nests, which limits exposure to non-target organisms. Initial poisoning of the ant-suppression plots also included cat food baits soaked in imidacloprid; however, the most effective treatment

was Synergy Pro, which was used subsequently throughout the experiment. Our suppression method specifically targets ground ants, as baits are scavenged and the active ingredient is consumed within ant nests. We tested for pesticide residue and found no evidence of contamination in seedlings or the soil. Other invertebrate groups were not adversely affected by the application of ant baits (Griffiths et al., 2018). Our suppression treatments reduced ant populations by as much as 93% in treated plots (Griffiths et al., 2018).

In 2015, Borneo experienced a strong *El Nino*-driven drought event. Rainfall at Danum Valley (the nearest available weather station to our plots) during our study period showed distinct drought and post-drought periods (Figure S1), creating a natural abiotic/environmental contrast for examining the effects of ant suppression in a drought (2015) versus a post-drought (2016) year.

We sampled hemipterans in the leaf litter using Winkler extractions in July 2015, during a drought and again in September 2016 during a post-drought period. Two, 50 m transects were placed perpendicularly crossing across the middle of each ant suppression and control plot. Every 7 m along each transect, we collected and sieved 1 m^2 of leaf litter, which was hung in Winkler bags for three days, collecting a total of 15 leaf litter samples per plot. There are several groups of tropical hemipterans that are found in the leaf litter (e.g., Schizopteridae); here, we sampled the subset of the total hemipteran community that are readily sampled using Winkler extractions. Although this sampling method may include species that also occur in other layers of the rain forest, we expected that the invertebrates sampled in leaf litter would be the most sensitive to the suppression of ground-layer ants.

We sorted adult hemipterans from samples to morphospecies and classified most morphospecies to either genera, family or suborder, following Capinera (2008). All specimens were identified as either predators or herbivores based on front leg modifications (for grasping and snatching), stylet shape and size (Capinera, 2008).

FIGURE 1 Map of the control (C) and ant (A) plots at Maliau Basin Conservation Area, Sabah, Malaysia

To determine whether or not sampling efforts were sufficient in capturing the assemblage of hemipterans, we used the R-package iNEXT to calculate the total sampling coverage for each treatment and year combination (Hsieh, Ma, & Chao, 2016). The results ranged from 89.6% to 95.4%, indicating that we were close to sampling complete assemblages.

We ran three analyses with respect to diversity and community responses to ant suppression. First, we used a generalized linear mixed-effect model (GLMM) to test the effect of ant-suppression treatment on species richness and abundance of all hemipterans, herbivorous hemipterans and predatory hemipterans. Only adult hemipterans were considered. We added a two-way interaction between year and treatment, as we hypothesized that ant exclusions would have weaker effects on hemipteran assemblages during drought due to reduced ant activity. We also evaluated whether ant suppression increased relative species richness and relative abundance of herbivorous hemipterans. Relative herbivorous hemipteran species richness and abundance were calculated as the proportion of herbivore hemipteran species and individuals in the hemipteran assemblage. For the GLMM we used a Conway–Maxwell–Poisson distribution, using function glmmTMB in package *glmmTMB* (Magnusson et al., 2017) which can model this distribution, for all metrics except relative species richness and abundance, for which we used a beta distribution as they are proportion data. Compared with other distributions used for analyzing count data, Conway–Maxwell–Poisson distribution has increased model performance because it addresses violations of equi-dispersion flexibly (Lynch, Thorson, & Shelton, 2014). In all models, we treated year and treatment as fixed effects, and included their interaction. Plot was treated as a random effect.

If we detected a significant interaction term, we conducted pairwise comparisons (using GLMM) between ant suppressed and control plots in each year separately. We did not conduct other pairwise comparisons (e.g., comparing plots from different treatments and years) as we are specifically interested in how drought conditions affect the impacts of ant suppression on hemipteran communities. Only treatment was included as a fixed factor, while plot was retained as a random effect in all pairwise comparisons. We applied Bonferroni correction to *p*-values from all pairwise comparisons. If no significant interaction was detected, we dropped the interaction term and ran GLMM again to test if the main effects of treatment and years were significant, as recommended in Crawley (2007).

Second, we carried out non-metric multidimensional scaling of the full hemipteran communities in both years with treatment as the grouping variable in package *vegan* (Oksanen et al., 2007). We used PERMANOVA with 9,999 permutations to test the differences across treatments using the *vegan* function adonis2.

We used indicator analysis (IndVal) to identify whether there are species characteristic of the control or suppression plots. For each species, we calculated indicator values for all year and treatment combinations, based on their relative frequency and abundance (Dufrene & Legendre, 1997). IndVal values are high if individuals of a species are found across all sites within a group (specificity) and they are only present within a particular group of sites (fidelity) (Dufrene
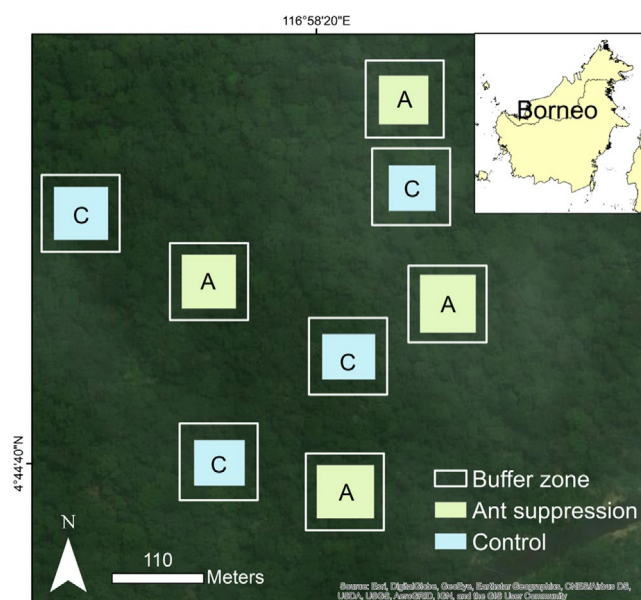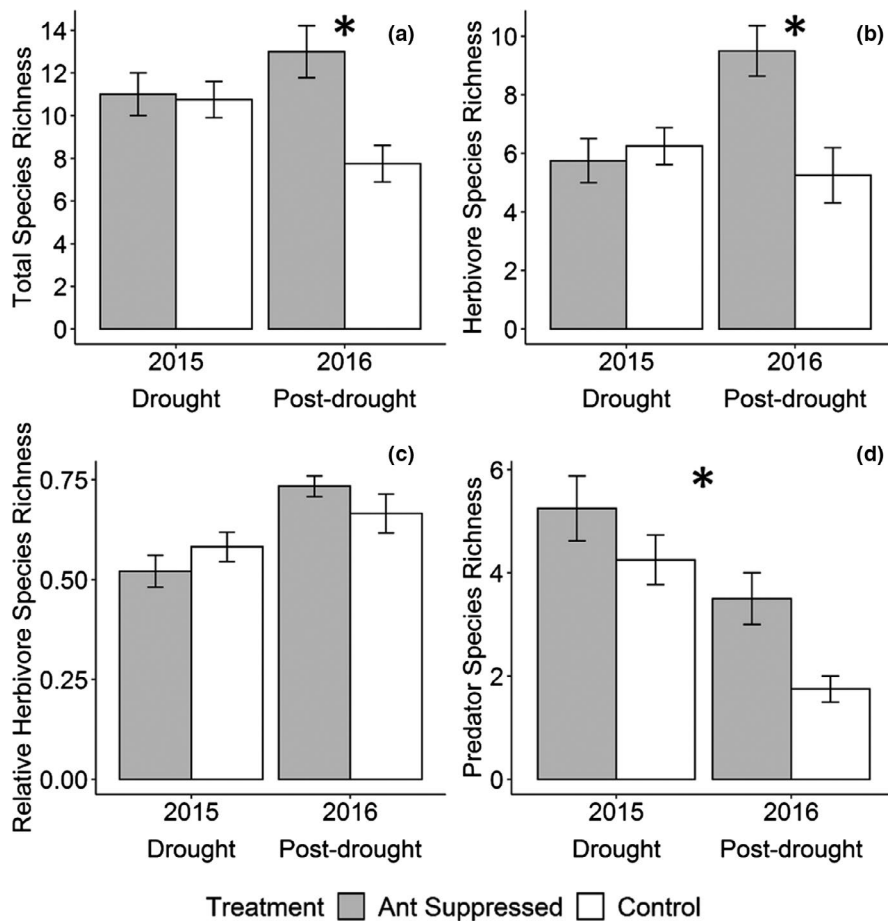
FIGURE 2 Total (a) and relative (b) species richness of herbivorous hemipterans, (c) relative herbivore species richness and (d) species richness of predators across treatments (ant suppressed and control) and across years. Error bars represent standard error. Asterisk (*) indicates significant effects ($p < .05$). When there is a significant interaction effect between year and treatment, we place an asterisk on year that ant suppression had a significant impact. When only the main effect of treatment is significant, the asterisk is placed in the top middle of the panel. When all predictors involving ant suppression or all pairwise comparisons are insignificant, no asterisk is placed in the panel

& Legendre, 1997). We then assessed their statistical significance based on 10,000 permutations. To assess whether some species always respond similarly to ant suppression irrespective of drought conditions, we also calculated indicator values based on treatment only using the IndVal function in package *labdsv* (Roberts, 2016).

3 | RESULTS

We collected 465 individuals and 42 species in total across all 8 control and ant-suppression plots (Table S1). Eleven out of 42 hemipteran species were singletons (i.e., only one individual was found). Twenty-four non-singleton species were sampled in control and ant-suppressed plots, while seven non-singleton species were restricted to ant-suppressed plots only. No species were exclusive to control plots. In 2015, we recorded similar numbers of species in ant suppressed (total species = 22) and control plots (total species = 23), while in 2016 ant-suppressed plots were higher than control plots (total species = 28 and 15 respectively). We also recorded more individuals in ant suppressed (total abundance in 2015 = 153, 2016 = 114) than control plots (total abundance in 2015 = 141, 2016 = 57) in all years.

For species richness of all (Figure 2a) and herbivorous hemipterans (Figure 2b), we recorded a significant interaction between the ant-suppression treatment and drought conditions ($p = .003$ and < 0.001, respectively, see Table S1 for full results). Pairwise

comparisons showed total and herbivore richness was higher on ant-suppression plots in 2016 (Bonferroni corrected $p < .001$ for both metrics) but not 2015 (Bonferroni corrected $p = 1$ for both metrics).

Simplified models showed that predatory hemipteran species richness was significantly higher in ant-suppressed plots across years ($p = .003$), but not relative herbivore species richness ($p = .98$) (Table S2). For predatory hemipteran species richness and relative herbivore species richness, the interaction term was marginally insignificant ($p = .05$–$.07$) (Figure 2c,d). Due to the marginal effect, we conducted both pairwise comparisons and model simplification. For pairwise comparisons, predator species richness was significantly higher on ant-suppression plots in 2016 (Bonferroni corrected $p < .001$) but not 2015 (Bonferroni corrected $p = .28$). In contrast, no pairs exhibited significant differences for relative herbivore richness (Bonferroni corrected $p = .38$–0.40).

We detected a significant interaction term between year and treatment in explaining abundance variation for all (Figure 3a) and herbivorous hemipterans (Figure 3b, see Table S1 for full results), with pairwise comparisons showing that ant suppression significantly increased both metrics in 2016 (Bonferroni corrected $p < .001$ for both metrics) but not 2015 (Bonferroni corrected $p \geq .38$). The interaction term was not significant for predatory hemipterans ($p = .30$) (Figure 3c), but their abundance was significantly higher in ant-suppressed plots regardless of year ($p = .006$). There was a

FIGURE 3 Total abundance (a), herbivore abundance (b), relative herbivore abundance (c) and predator abundance (d) of hemipterans in plots. Error bar represents standard error. Asterisk (*) indicates significant effects ($p < .05$). When there is a significant interaction effect between year and treatment, we place an asterisk on year that ant suppression had a significant impact. When only the main effect of treatment was significant, the asterisk is placed in the top middle of the panel. When all predictors involving ant suppression or all pairwise comparisons are insignificant, no asterisk is placed in the panel
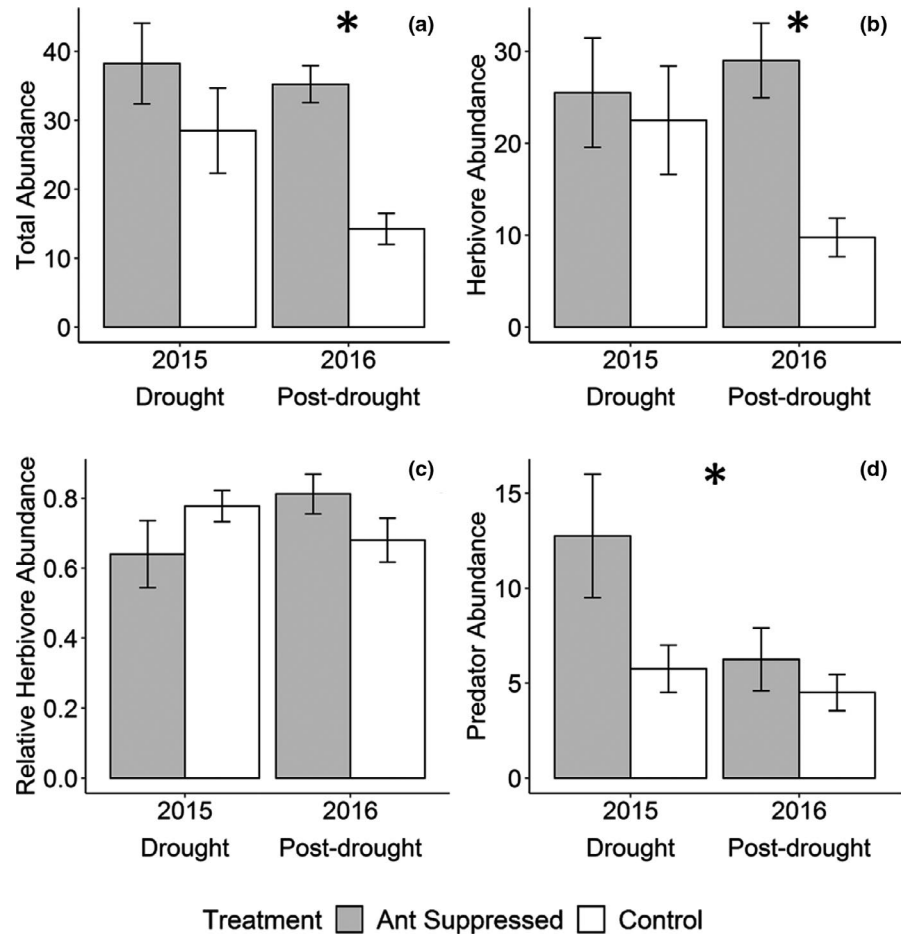
significant interaction effect on relative abundance of herbivorous hemipterans ($p = .02$) (Figure 3d), but pairwise comparisons showed that the effect of ant suppression had no significant effects in 2015 (Bonferroni corrected $p = .34$) and 2016 (Bonferroni corrected $p = .12$).

Assemblage composition differed between control versus. ant-suppressed plots in both 2015 and 2016, but the interaction between the two factors was not significant (Figure 4. PERMANOVA treatment; pseudo-$F = 2.84$ $p = .006$, year; pseudo-$F = 2.40$ $p = .02$, treat*year; pseudo-$F = 1.68$ $p = .10$). Indicator analysis identified four morphospecies characteristic of the ant-suppression plots in 2015 ($p < .05$): Homoptera sp. 1 IndVal = 0.60, Berytidae sp. 1 IndVal I = 0.63, Enicocephilidae sp. 2 IndVal = 75 and *Neuroctenus* sp. 1 IndVal = 0.75) (Figure 4). Three of those morphospecies are predators: Berytidae sp. 1, Enicocephilidae sp. 2 and *Neuroctenus* sp. 1. When grouped according to treatment only, *Neuroctenus* sp. 1 is the only significant indicator of ant-suppressed plots (IndVal = 0.69), while for control plots no species were significant. Homoptera sp. 1 and *Neuroctenus* sp. 1 were numerically dominant in the ant-suppressed plots in 2015, ranking 1 and 3, respectively (see Figure S2 for rank-abundance distributions). Berytidae sp. 1 and Enicocephilidae sp. 2 were relatively uncommon and ranked 8 (tied ranks). Three of those morphospecies are predators (Berytidae sp. 1, Enicocephilidae sp. 2 and *Neuroctenus* sp. 1). When grouped

according to treatment only, *Neuroctenus* sp. 1 (ranked 3 and 9.5 in ant-suppressed plots in 2015 and 2016) was the only significant indicator of ant-suppressed plots (IndVal = 0.69), while for control plots no species were significant. No indicators ($p > .05$) were found in 2016 or in 2015 control plots.

4 | DISCUSSION

Ant suppression affected richness, abundance and community composition of hemipterans encountered in the leaf litter, but this effect varied with drought conditions. We found that (a) the presence of ants suppresses the abundance and species richness of herbivore hemipterans but only in the post-drought period and (b) the presence of ants has a negative effect on predatory hemipteran species richness and abundance, but with only a marginal interaction effect for richness. This positive effect was only significant for species richness under post-drought conditions. Finally, (c) the finding that herbivorous hemipterans only increased in abundance (and species richness) in the absence of ants in the post-drought year suggests climatic factors influence trophic relationships in key ways for tropical forest invertebrates. These results contribute to the growing literature highlighting the importance of ants in structuring invertebrate communities and ecosystem function (Griffiths et al., 2018;
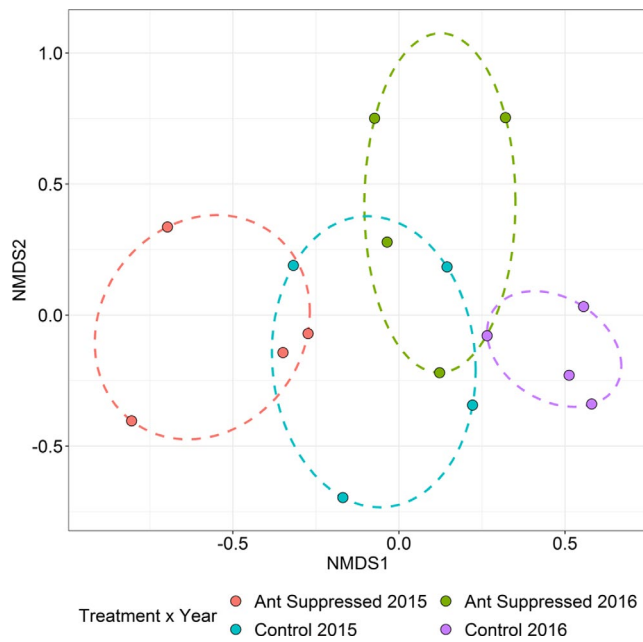
FIGURE 4 Non-metric multidimensional scaling of hemipteran communities in ant suppressed and control plots for both 2015 (drought year) and 2016 (post-drought year)

Hunt, 2003; Parr et al., 2017; Philpott & Armbrecht, 2006; Poulsen & Sapountzis, 2012; Rodríguez-Castañeda, Brehm, Fiedler, & Dyer, 2016; Russell et al., 2009). Finally, we show how understanding the important but complex trophic interactions between ants and hemipterans is further complicated by climatic variation (Figure 5).

In the post-drought year, the effect of herbivorous hemipterans responding positively to ant suppression was most pronounced with higher abundance on ant suppression than control plots. With ant

activity suppressed, hemipterans generally, and herbivore hemipterans specifically, would likely be released from some predation pressure (Matsumoto et al., 2009); however, during the drought year, this effect may be suppressed. Predator presence or absence can have unexpected effects on herbivores; for example, the presence of predatory mantids can increase the number of herbivorous hemipterans if those predators more negatively affect other herbivores (Fagan & Hurd, 1994) potentially initiating trophic cascades (Moran & Hurd, 1997). Our results may be due to ants exerting predation pressure on some groups of herbivorous hemipterans, potentially benefiting other herbivorous groups. The tripling of abundance of herbivore hemipterans in the ant-suppressed plots in the post-drought period suggests that ants exert considerable top-down control on herbivorous hemipterans. Our results are consistent with previous research (Rodríguez-Castañeda, 2013) that suggests that the predatory effect of ants is highest in non-drought conditions, when ant activity is favoured.

Ant suppression enhanced predatory hemipteran species richness and abundance significantly, but we also detected marginal significance ($p = .05$) that such treatment only has positive impacts on predator species richness in post-drought conditions. These results could be indicative of complex and as yet unclear interactions between resource availability (plants) and/or the abundance of other species involved in trophic interactions within the community (Jamieson, Trowbridge, Raffa, & Lindroth, 2012). Intra-guild hemipteran (i.e., predators feeding on predators) predation is especially common, leading to non-linear trophic links; such non-linearity could further result in complicated trophic responses to ant suppression (Rosenheim, Wilhoit, & Armer, 1993). Langellotto and Denno (2004) found that hemipteran predators increased in abundance with increasing habitat complexity, perhaps as a consequence of more
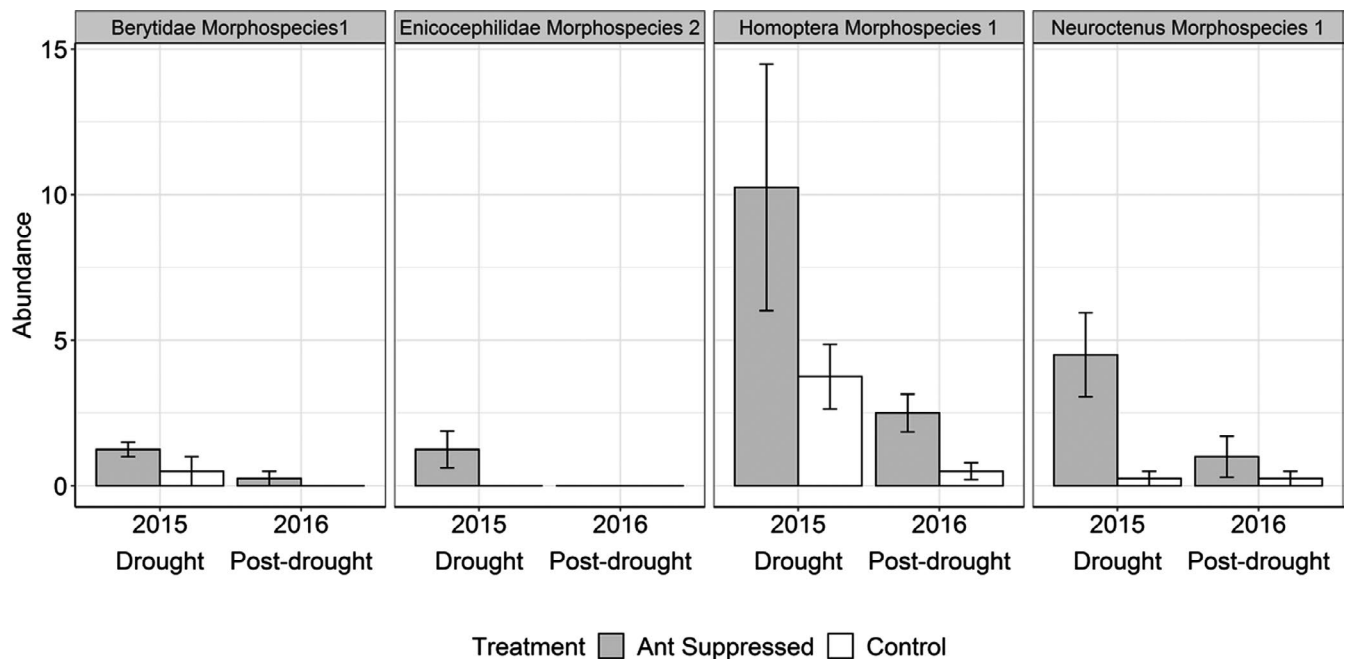

FIGURE 5 Abundance of indicator morphospecies averaged across treatment and year. Error bars represent standard error

available niche space. Drought conditions could have led to habitat structure changes that affected hemipteran predators through reduced habitat complexity. Indeed, a large increase in termite abundance during the drought, with subsequent knock-on effects, including increased leaf litter decomposition (Ashton et al., 2019), may also have reduced the habitat available for hemipterans living in leaf litter and therefore the observed effects of ant suppression.

Our understanding of the full extent of role of ants in shaping ecosystem structure, such as the communities of predatory and herbivorous hemipterans, is limited by a number of constraints and knowledge gaps. There are relatively few natural history studies of hemipteran species for this region and in some cases basic taxonomic information is also missing, which places limitations on our findings and explanation of some of the results. Though we can identify predators and herbivores, the species-level ecological roles of hemipterans in this study remain unknown.

Given the strong context-dependence of trophic interactions on climate shown here, climate change could shift the balance of ant-mediated control on insect communities. Such indirect consequences of climate change on species interactions are known to have greater impacts on species than the direct effects themselves (Ockendon et al., 2014). Efforts to combat the effects of both climate change and habitat loss/disturbance on diverse tropical forests will therefore benefit from further long-term research on interactions between ants, hemipterans and other invertebrate species.

ORCID

Timothy C. Bonebrake https://orcid.org/0000-0001-9999-2254
Toby P. N. Tsang https://orcid.org/0000-0002-8176-7777
Theodore A. Evans https://orcid.org/0000-0002-0558-3036
Paul Eggleton https://orcid.org/0000-0002-1420-7518
Hannah M. Griffiths https://orcid.org/0000-0002-4800-8031
Catherine L. Parr https://orcid.org/0000-0003-1627-763X
Louise A. Ashton https://orcid.org/0000-0001-6471-0827

REFERENCES

Agrawal, A. A., & Rutter, M. T. (1998). Dynamic anti-herbivore defense in ant-plants: The role of induced responses. *Oikos*, 227–236. https://doi.org/10.2307/3546834

Andrew, N. R., & Hughes, L. (2005). Diversity and assemblage structure of phytophagous Hemiptera along a latitudinal gradient: Predicting the potential impacts of climate change. *Global Ecology and Biogeography*, *14*, 249–262. https://doi.org/10.1111/j.1466-822x.2005.00149.x

Ashton, L. A., Griffiths, H. M., Parr, C. L., Evans, T. A., Didham, R. K., Hasan, F., … Eggleton, P. (2019). Termites mitigate the effects of drought in tropical rainforest. *Science*, *363*, 174–177. https://doi.org/10.1126/science.aau9565

Basset, Y., Cizek, L., Cuenoud, P., Didham, R. K., Guilhaumon, F., Missa, O., … Leponce, M. (2012). Arthropod diversity in a tropical forest. *Science*, *338*, 1481–1484. https://doi.org/10.1126/science.1226727

Blüthgen, N., Gebauer, G., & Fiedler, K. (2003). Disentangling a rainforest food web using stable isotopes: Dietary diversity in a species-rich ant community. *Oecologia*, *137*, 426–435. https://doi.org/10.1007/s00442-003-1347-8

Capinera, J. L. (2008). *Encyclopedia of entomology*. Berlin, Germany: Springer Science & Business Media.

Coley, P. D. (1998). Possible effects of climate change on plant/herbivore interactions in moist tropical forests. *Climate Change*, *39*, 455–472.

Crawley, M. J. (2007). *The R book*. Chichester, UK: John Wiley & Sons Ltd.

Dai, J. (2013). Increasing drought under global warming observations and models. *Nature Climate Change*, *3*, 52–58.

Dejean, A., Corbara, B., Orivel, J., & Leponce, M. (2007). Rainforest canopy ants: The implications of territoriality and predatory behavior. *Functional Ecosystems and Communities*, *1*, 105–120.

Denmead, L. H., Darras, K., Clough, Y., Diaz, P., Grass, I., Hoffmann, M. P., … Tscharntke, T. (2017). The role of ants, birds and bats for ecosystem functions and yield in oil palm plantations. *Ecology*, *98*, 1945–1956. https://doi.org/10.1002/ecy.1882

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a asymmetrical approach. *Ecological Monographs*, *67*, 345–366.

Ewers, R. M., Boyle, M. J. W., Gleave, R. A., Plowman, N. S., Benedick, S., Bernard, H., … Turner, E. C. (2015). Logging cuts the functional importance of invertebrates in tropical rainforest. *Nature Communications*, *6*, 6836. https://doi.org/10.1038/ncomms7836

Fagan, W. F., & Hurd, L. E. (1994). Hatch density variation of a generalist arthropod predator: Population consequences and community impact. *Ecology*, *75*, 2022–2032.

Goldman, A. E., Bonebrake, T. C., Tsang, T. P. N., Evans, T. A., Gibson, L., Eggleton, P., …Ashton, L. A. (2019). Data from: Drought and presence of ants can influence hemipitera in tropical leaf litter. Dryad Digital Repository. https://doi.org/10.5061/dryad.r2280gb95

Griffiths, H. M., Ashton, L. A., Walker, A. E., Hasan, F., Evans, T. A., Eggleton, P., & Parr, C. L. (2018). Ants are the major agents of resource removal from tropical rainforests. *Journal of Animal Ecology*, *87*, 293–300. https://doi.org/10.1111/1365-2656.12728

Heil, M., & McKey, D. (2003). Protective ant-plant interactions as model systems in ecological and evolutionary research. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 425–553. https://doi.org/10.1146/annurev.ecolsys.34.011802.132410

Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Cambridge, MA: Harvard University Press.

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecology Evolution*, *7*, 1451–1456. https://doi.org/10.1111/2041-210X.12613

Hunt, J. H. (2003). Cryptic herbivores of the rainforest canopy. *Science*, *300*, 916–917.

Hyodo, F., Kishimoto-Yamada, K., Matsuoka, M., Tanaka, H. O., Hashimoto, Y., Ishii, R., & Itioka, T. (2016). Effects of remnant primary

forests on feeding habits of ants in a secondary forest in Sarawak, Malaysia: An isotopic study. *Food Webs*, 6, 48–54. https://doi.org/10.1016/j.fooweb.2016.02.002

Jamieson, M. A., Trowbridge, A. M., Raffa, K. F., & Lindroth, R. L. (2012). Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. *Plant Physiology*, 160, 1719–1727. https://doi.org/10.1104/pp.112.206524

Klimes, P., Janda, M., Ibalim, S., Kua, J., & Novotny, V. (2011). Experimental suppression of ants foraging on rainforest vegetation in New Guinea: Testing methods for a whole-forest manipulation of insect communities. *Ecological Entomology*, 36, 94–103. https://doi.org/10.1111/j.1365-2311.2010.01250.x

Langellotto, G. A., & Denno, R. F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. *Oecologia*, 139, 1–10. https://doi.org/10.1007/s00442-004-1497-3

Lensing, J. R., & Wise, D. H. (2006). Predicted climate change alters the indirect effect of predators on an ecosystem process. *Proceedings of the National Academy of Sciences USA*, 103, 15502–15505. https://doi.org/10.1073/pnas.0607064103

Liu, S., Chen, J., He, X., Hu, J., & Yang, X. (2014). Trophic cascade of a web-building spider decreases litter decomposition in a tropical forest floor. *European Journal of Soil Biology*, 65, 79–86. https://doi.org/10.1016/j.ejsobi.2014.10.004

Luke, S. H., Fayle, T. M., Eggleton, P., Turner, E. C., & Davies, R. G. (2014). Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. *Biodiversity and Conservation*, 23, 2817–2832. https://doi.org/10.1007/s10531-014-0750-2

Lynch, H. J., Thorson, J. T., & Shelton, A. O. (2014). Dealing with under-and over-dispersed count data in life history, spatial, and community ecology. *Ecology*, 95, 3173–3180. https://doi.org/10.1890/13-1912.1

Magnusson, A., Skaug, H. J., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., …Brooks, M. E. (2017). glmmTMB: generalized linear mixed models using template model builder. R package version 0.1, 3.

Matsumoto, T., Itioka, T., Yamane, S., & Momose, K. (2009). Traditional land use associated with swidden agriculture changes encounter rates of the top predator, the army ant, in Southeast Asian tropical rain forests. *Biodiversity and Conservation*, 18, 3139–3151. https://doi.org/10.1007/s10531-009-9632-4

Mestre, L., Piñol, J., Barrientos, J. A., & Espadaler, X. (2016). Differential ant exclusion from canopies shows contrasting top-down effects on community structure. *Oecologia*, 180, 193–203. https://doi.org/10.1007/s00442-015-3442-z

Moran, M. D., & Hurd, L. E. (1997). A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. *Oecologia*, 113, 126–132. https://doi.org/10.1007/s004420050360

Ockendon, N., Baker, D. J., Carr, J. A., White, E. C., Almond, R. E. A., Amano, T., … Pearce-Higgins, J. W. (2014). Mechanisms underpinning climatic impacts on natural populations: Altered species interactions are more important than direct effects. *Global Change Biology*, 20, 2221–2229. https://doi.org/10.1111/gcb.12559

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G., Solymos, P., … Wagner, H. (2007). The vegan package. *Community Ecology Package*, 10, 631–637.

Parr, C. L., Dunn, R. R., Sanders, N. J., Weiser, M. D., Photakis, M., Bishop, T. R., … Chick, L. (2017). GlobalAnts: A new database on the geography of ant traits (Hymenoptera: Formicidae). *Insect Conservation and Diversity*, 10, 5–20.

Philpott, S. M., & Armbrecht, I. (2006). Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecological Entomology*, 31, 369–377. https://doi.org/10.1111/j.1365-2311.2006.00793.x

Polis, G. A., Sears, A. L., Huxel, G. R., Strong, D. R., & Maron, J. (2000). When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution*, 15, 473–475. https://doi.org/10.1016/S0169-5347(00)01971-6

Poulsen, M., & Sapountzis, P. (2012). Behind every great ant, there is a great gut. *Molecular Ecology*, 21, 2054–2057. https://doi.org/10.1111/j.1365-294X.2012.05510.x

Preisser, E. L., & Strong, D. R. (2004). Climate affects predator control of an herbivore outbreak. *American Naturalist*, 163, 754–762. https://doi.org/10.1086/383620

Roberts, D. W., (2016).Package 'labdsv' Ordination and Multivariate Analysis for Ecology.

Rodríguez-Castañeda, G. (2013). The world and its shades of green: A meta-analysis on trophic cascades across temperature and precipitation gradients. *Global Ecology and Biogeography*, 22, 118–130. https://doi.org/10.1111/j.1466-8238.2012.00795.x

Rodríguez-Castañeda, G., Brehm, G., Fiedler, K., & Dyer, L. A. (2016). Ant predation on herbivores through a multitrophic lens: How effects of ants on plant herbivore defense and natural enemies vary along temperature gradients. *Current Opinion in Insect Science*, 14, 73–80. https://doi.org/10.1016/j.cois.2016.02.001

Rosenheim, J. A., Wilhoit, L. R., & Armer, C. A. (1993). Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia*, 96, 439–449. https://doi.org/10.1007/BF00317517

Russell, J. A., Moreau, C. S., Goldman-Huertas, B., Fujiwara, M., Lohman, D. J., & Pierce, N. E. (2009). Bacterial gut symbionts are tightly linked with the evolution of herbivory in ants. *Proceedings of the National Academy of Sciences USA*, 106, 21236–21241. https://doi.org/10.1073/pnas.0907926106

Schmitz, O. J., Hambäck, P. A., & Beckerman, A. P. (2000). Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. *American Naturalist*, 155, 141–153. https://doi.org/10.1086/303311

Terborgh, J. W. (2015). Toward a trophic theory of species diversity. *Proceedings of the National Academy of Sciences*, 112, 11415–11422. https://doi.org/10.1073/pnas.1501070112

Vander Meer, R. K., Pereira, R. M., Porter, S. D., Valles, S. M., & Oi, D. H. (2007). Area-wide suppression of invasive fire ant Solenopsis spp. populations. In M.J.B. Vreysen, A.S. Robinson & J. Hendrichs (Eds.), *Area-wide control of insect pests* (pp. 487–496). Dordrecht, The Netherlands: Springer.

Wang, B., Geng, X. Z., Ma, L. B., Cook, J. M., & Wang, R. W. (2014). A trophic cascade induced by predatory ants in a fig–fig wasp mutualism. *Journal of Animal Ecology*, 83, 1149–1157. https://doi.org/10.1111/1365-2656.12219

SUPPORTING INFORMATION

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