

## LETTER

## Spatial covariance of herbivorous and predatory guilds of forest canopy arthropods along a latitudinal gradient

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**Abstract**

In arthropod community ecology, species richness studies tend to be prioritised over those investigating patterns of abundance. Consequently, the biotic and abiotic drivers of arboreal arthropod abundance are still relatively poorly known. In this cross-continental study, we employ a theoretical framework in order to examine patterns of covariance among herbivorous and predatory arthropod guilds. Leaf-chewing and leaf-mining herbivores, and predatory ants and spiders, were censused on > 1000 trees in nine 0.1 ha forest plots. After controlling for tree size and season, we found no negative pairwise correlations between guild abundances per plot, suggestive of weak signals of both inter-guild competition and top-down regulation of herbivores by predators. Inter-guild interaction strengths did not vary with mean annual temperature, thus opposing the hypothesis that biotic interactions intensify towards the equator. We find evidence for the bottom-up limitation of arthropod abundances via resources and abiotic factors, rather than for competition and predation.

**Keywords**

Araneae, community ecology, competition, Formicidae, guilds, Lepidoptera, predation, spatial interactions.

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**INTRODUCTION**

Generations of ecologists have sought to identify and disentangle the factors that generate and maintain the large numbers of species living in forest canopies (Basset *et al.*, 2015). The fondness for species richness (Hammond, 1992; Ozanne *et al.*, 2003; Hamilton *et al.*, 2010), however, often means that equally important patterns of arthropod abundance are overlooked in forest ecosystems. The species-energy theory predicts that large-scale patterns of diversity follow patterns in the density of individual organisms, which in turn track the available energy over space and time (Wright, 1983; Clarke and Gaston, 2006). Indeed, there seems to be a general increase in arthropod species richness and abundance, as well as in herbivory and predation rates, with temperature towards lower latitudes and elevations (Dyer and Coley, 2002; Lim *et al.*, 2015; Roslin *et al.*, 2017; Lister and Garcia, 2018; Libra *et al.*, 2019), albeit with exceptions (Basset *et al.*, 1992; Supriya *et al.*, 2019). These trends should be reconsidered in

the context of tree species richness and biomass, both of which typically decrease with increasing latitude and altitude (Del Grosso *et al.*, 2008). In addition, the standardisation of arthropod abundances per unit of forest biomass is advisable for consistency in analyses but has previously been omitted. Such a crucial knowledge gap is perhaps not surprising, considering that arthropods are predominantly studied at the level of individual plant stems and/or limited sets of species, rather than in plot-based surveys (but see Volf *et al.*, 2019). Thus, the extent to which arboreal arthropod abundance patterns are driven by plant biomass along fundamental ecological gradients remains relatively unknown.

Patterns of abundance and their drivers often differ or contrast among arthropod guilds. For example in contrast to the general trend, the abundances of predatory and herbivorous arthropods responded negatively to mean annual temperature in a grassland ecosystem (Welti *et al.* 2020). Additionally, no significant increase in herbivory rate was observed for leaf miners and external chewers along a latitudinal gradient

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(Andrew and Hughes, 2005b). Furthermore, caterpillar specialists and generalists responded differently to latitude in terms of abundance (Salazar and Marquis, 2012). Such examples highlight the need for detailed multi-guild studies as well as the importance of clearly defining guild concepts (Simberloff and Dayan, 1991).

Arthropod abundances in canopy ecosystems may be limited by the agency of several theoretical mechanisms: bottom-up effects of quantity and/or quality of resources (hypothesis 1; H1) and competition (H2), or top-down impacts of natural enemies (H3) and abiotic factors (H4). The relative importance of these factors may determine covariance in guild abundances across individual host trees or forest plots (Table 1). The abundance of primary consumers (herbivorous guilds) could be positively correlated across their host trees if driven by the local abundances of primary producers (plant resources) (H1; Whitfeld *et al.*, 2012). A negative correlation among herbivorous guilds could indicate inter-guild competition (H2), whereas uncorrelated inter-guild abundances would be an indication of top-down control by natural enemies (H3), assuming that the natural enemies act in density-dependent fashion, thus suppressing the densities of various host guilds similarly (Walker and Jones, 2001; Floren *et al.*, 2002). Net Primary Production (NPP) is one of the most important variables in terrestrial ecosystems (Roy *et al.*, 2001; Pontarp *et al.*, 2019), and the seemingly simple temperature gradient (as a proxy for NPP across latitude or altitude) could be a limiting factor in arthropod abundance for individual trophic levels and their taxa (Oksanen *et al.*, 1981). Therefore, positive correlations among herbivorous guilds could indicate abiotic factors as drivers (e.g. climate), since the abundances of most guilds will tend to respond similarly to key climatic variables (e.g. temperature) at a local scale (H4). Analogous expectations would also apply to abundance covariance in predatory guilds.

Correlation among the abundances of guilds from different trophic levels, such as herbivores and predators, is more difficult to predict. When the abundances of both are determined by resources, we may expect a cascading effect of biomass availability, from plants via herbivores to predators, and thus a positive correlation between herbivore and predator abundances (H1; Holt, 1984). If driven by competition, abundances between herbivore and predator guilds are likely to be uncorrelated (H2), because competitive intensity is unlikely to correlate across trophic levels (Room and Smith, 1975; Hooks *et al.*, 2003; Tobin and Bjørnstad, 2003; Liere *et al.*, 2012). When both herbivore and predatory guilds are controlled by a predator from a higher trophic level (so called natural

enemies), their abundances are likely to be negatively correlated (H3) via a negative trophic cascade, where the negative impact of natural enemies on predators benefits their herbivores (Mooney, 2007). If driven by abiotic factors, we would see a positive correlation between abundances of both herbivores and predators, as they would be affected by local abiotic fluctuations in a similar way (H4).

Guild covariance can indirectly indicate the processes that drive their abundances, although numerous scenarios become possible when individual guilds are each controlled by a different driver. Unfortunately, multi-guild analyses are rare. Bird *et al.* (2019) showed in their meta-analysis that competition tends to be stronger among herbivorous guilds (inter-guild competition) rather than within them (intra-guild competition), suggesting a greater importance of studying inter-guild competition in herbivorous arthropods. In contrast, species diversity was not correlated among five herbivorous guilds across 38 plant species in a study from Papua New Guinea, pointing to the weak effect of competition (Novotny *et al.*, 2012). This could be explained via the *Green World Theory*, which posits that herbivorous arthropods should be under such intense pressure from natural enemies that strong competition among them is scarce (Hairston *et al.*, 1960).

Similarly, inter-guild competition can be observed in predators. For example spiders partly compete with ants for prey (Halaj *et al.*, 1997; Mestre *et al.*, 2012), and negative co-occurrence of ants and spiders was observed in the canopies of a lowland rainforest (Katayama *et al.*, 2015). However, arboreal ants are well known to consume the sugar-rich secretions of Hemiptera and plant extrafloral nectaries (Davidson, 1997; Davidson *et al.*, 2003), and can therefore be considered similar to primary consumers (herbivores). This would result in different than expected patterns between spider and ant abundances if competition between them or shared enemies were the main driver, but in no effect if driven by resource limitation or abiotic factors (Table 1).

The relative importance of biotic as opposed to abiotic factors tends to increase towards tropical latitudes (Schemske *et al.*, 2009). Predation by arthropods increases along both altitudinal and latitudinal gradients (Novotny *et al.*, 2006; Sam *et al.*, 2015a; Roslin *et al.*, 2017; Libra *et al.*, 2019), whereas predation by birds remains constant along latitude and from low to mid altitudes in the tropics, and decreases towards high altitudes (Sam *et al.*, 2015a; Roslin *et al.*, 2017). The response to harsh environmental conditions presumably leads to a universal decline in abundance and species diversity of arthropod guilds at high elevations close to the forest timberline.

**Table 1** Hypothesised correlations among herbivore and predatory guilds across host trees in scenarios where both guilds' abundances are driven by either resource abundance, inter-guild competition, their natural enemies, or abiotic factors (Hairston *et al.*, 1960). See the text for explanation

Relationship between		Driver			
		Resources (H1) Covariance	Competition (H2)	Enemies (H3)	Abiotic (H4)
Guild A Herbivores	Guild B Herbivores	Positive	Negative	Zero	Positive
Predators	Predators	Positive	Negative	Zero	Positive
Herbivores	Predators	Positive	Zero	Negative	Positive

In this study, we aim to test the effects of resource limitation, competition, enemy pressure and abiotic factors using inter-guild correlations in the abundances of two herbivorous guilds (externally feeding caterpillars and leaf miners) and two predatory guilds (ants and spiders) from forest plots with various abiotic characteristics. We compare arthropod assemblages among individual trees, but also take a 'whole forest' perspective, examining complete assemblages from 0.1 ha forest plots. This approach is well suited to disentangle the effects of environmental factors, such as temperature, from the effects of heterogeneous vegetation. We focus on identifying the relationship between arboreal arthropod abundances and a mean annual temperature gradient. We hypothesise that overall arthropod abundances will increase positively with mean annual temperature. Furthermore, we predict that bottom-up and abiotic factors will be stronger predictors of arthropod community abundance than top-down mechanisms and that correlations in inter-guild abundances will vary with increasing mean annual temperature (see all the theoretical outcomes in Table 1).

## MATERIALS AND METHODS

### Field sites and experimental design

We studied lowland temperate forests in Mikulčice (Czech Republic (CZE); 1 plot) and Toms Brook (Virginia, USA; 2 plots), and tropical forests in Papua New Guinea (PNG): lowland forest in Wanang (2 plots), mid-elevation forest in Numba (2 plots), and montane forest in Yawan (2 plots). All plots were located in old-growth forests (secondary forests, forest edges, plantations, stands with non-native vegetation and large gaps were all avoided). For detailed information about location, climate, elevation, etc. at each site and individual plots see Fig. 1, Table S1 and Supporting Information: Supplementary Materials and methods.

### Sampling methods

Each plot was 0.1 ha in size, rectangular and chosen to represent the typical vegetation structure and species composition of local broadleaf forests. The vegetation of each plot was surveyed, and all stems with a diameter at breast height (DBH)  $\geq 5$  cm were tagged, mapped and identified to species. The plots were then gradually felled and sampled for arthropods (see detailed protocols in Volf *et al.*, 2019). We took advantage of ongoing logging operations (CZE, USA) or subsistence shifting agriculture (PNG) at our sites to avoid contributing to net deforestation. The felled trees were stripped of leaves and the total leaf biomass of the foliage was weighed. We estimated the total leaf area of the foliage using a ratio of leaf area to weight measured from randomly selected leaf samples for each tree (see details in Volf *et al.*, 2019).

The felled trees were exhaustively surveyed for focal taxa (non-flying arthropods) by manually searching the foliage. Our focal taxa included all leaf-chewing lepidopteran larvae (free feeding and shelter-builders), leaf miners, spiders and ants. We only used data on the number of live leaf miners since abandoned mines do not reflect the population size at

the time of sampling. All live mines, caterpillars and spiders were collected. For ants, we hand-collected foraging individuals during a standardised search immediately upon felling, beginning with the base of the trunk and working up to the top of the canopy (Klimes *et al.*, 2015). In addition, we sampled all ant nests found during the destructive sampling (including cryptic nests inside tree tissues and the attached epiphytes and lianas, see details in Klimes *et al.*, 2015; Mottl *et al.*, 2019; Plowman *et al.*, 2019). The size of nests was visually estimated on a three-level categorical scale: (1)  $<100$ , (2) 100–1000 and (3)  $>1000$  individuals. We used the values 50, 500 and 1500 individuals, respectively, to represent these categories in our analyses. We calculated the total number of ant individuals sampled outside the nest for each tree (freely foraging on a tree; *Foraging ants* hereafter) and estimated the total ant abundance for each tree (foraging and nest ants summed; *All ants* hereafter). Unlike abundances of other arthropods, the overall abundances for ants are more likely to be underestimated, as our nest size estimates are probably conservative. However, this sampling allows the examination of each nest, including cryptic nests (in tree cavities, under epiphytes, etc.), which could easily be overlooked (Yanoviak *et al.*, 2003). Therefore, it is more precise than other methods used for ant sampling (e.g. beating, fogging). Note that spiders were not sampled in Wanang (both plots) and the plot A in Yawan.

### Data analyses

All analyses were conducted using R 3.5.2 (R Core Team 2016) and the *nlme* package (Pinheiro *et al.*, 2014).

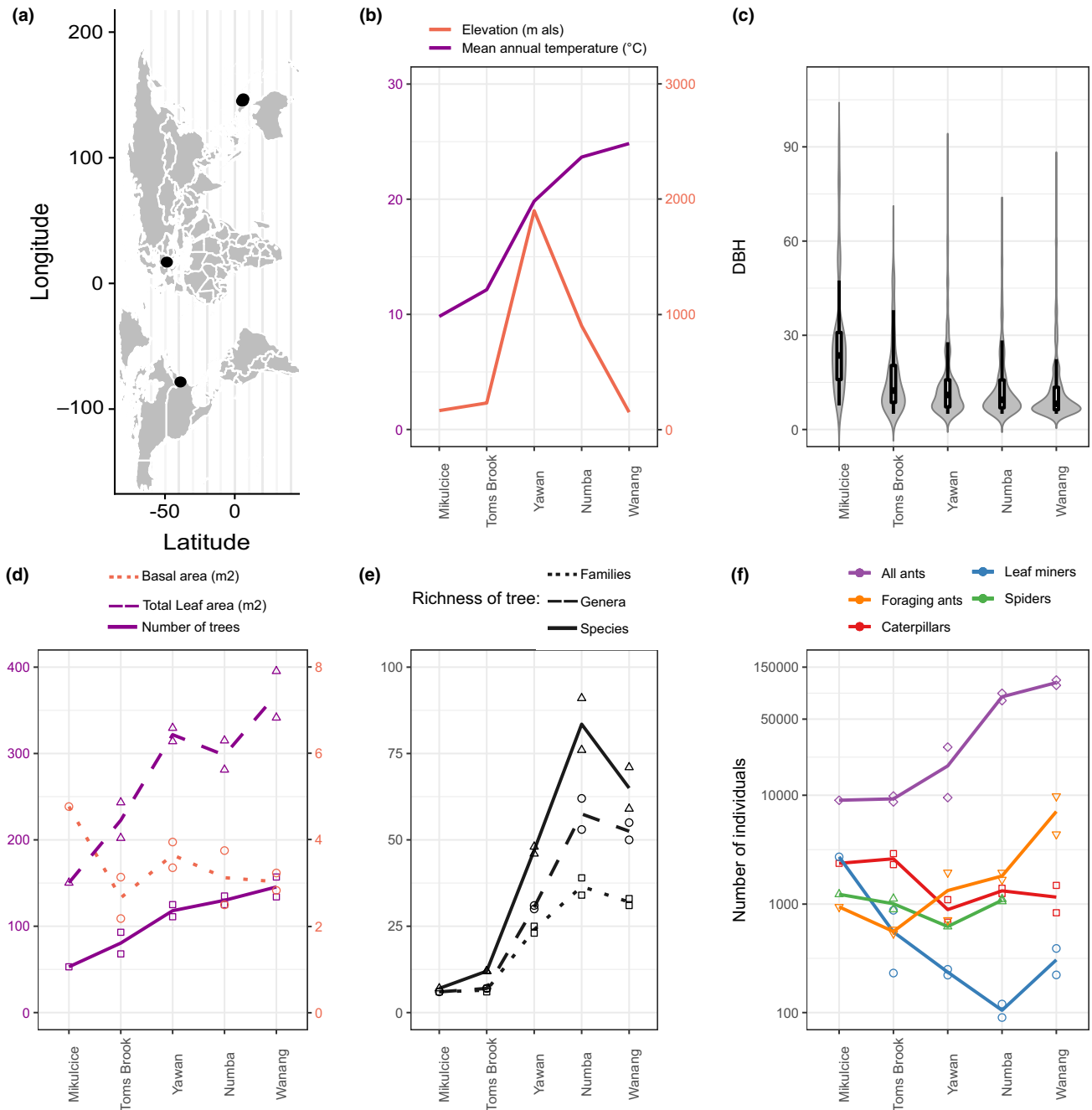
### Preparation of datasets

We generated both tree-based and plot-based datasets. In the *Tree dataset*, each of the 1001 sampled trees was characterised by DBH, cut-down date, species identity, total leaf biomass, total leaf area, spatial coordinates in the plot and the number of arthropod individuals from the focal taxa; for ants, we used both *All ants* and *Foraging ants*. All arthropods found on epiphytes or lianas were included in the host tree data for the analyses. Note that in two plots (USA A and Numba B) the spatial coordinates for trees were not available (Supporting Information: Supplementary Materials and methods). The season of sampling was determined as the date of sampling for each tree, disregarding the year.

The *Plot dataset* comprised nine plots characterised by the number of tree individuals and tree species, mean DBH, total basal area (BA), total leaf area and total abundance of the focal taxa of arthropods.

### Arthropod abundances along the temperature gradient

Our sampling design included lowland temperate forests (USA, CZE), and tropical forests along an altitudinal gradient (PNG). We used the mean annual temperature to unify both latitudinal and altitudinal gradients in a joint analysis. Mean annual temperature was chosen over other climatic indices because it is correlated with other abiotic variables (Fig. S1)



**Figure 1** Characteristics of study sites and individual plots: (a) position of individual sampling sites; (b) elevation (in meters above sea level) and mean annual temperature (MAT) for each site; (c) the distribution of DBH values per site (boxes indicate the 1st and 3rd quartile, central line the median and whiskers 1.5 times the interquartile range); (d) the total number of trees, basal area (in m<sup>2</sup>) and leaf area (in m<sup>2</sup>) per plot; (e) the number of tree families, genera and species per plot and (f) and the number of arthropods per plot for each focal taxon. The data for mean annual temperature (MAT) were obtained from WorldClim 2.0 database (30' resolution, <http://worldclim.org>), representing average climate data from 1970 to 2000. The total number of arthropod individuals shows recorded (herbivores and spiders) or quantitatively estimated (ants) values. Note that spiders were not sampled in three plots (see Materials and methods for details). Individual sites are ordered by the MAT from left to right.

and it is commonly used in macro-ecological studies focusing on arthropods as a proxy of climate (e.g. Kaspari *et al.*, 2000; Trøjelsgaard and Olesen, 2013; Kambach *et al.*, 2016; Welti *et al.* 2020). Selecting a single variable to represent a combination of biotic and abiotic properties is complicated, since such variables are often intercorrelated. In our system, a graphical model using the concept of conditional independence suggests

that mean annual temperature is affected by both elevation and latitude while it affects biotic variables (e.g. number of trees, trees diversity) (Fig. S2). The temperature data were obtained from WorldClim 2.0 database (30' resolution, <http://worldclim.org>), representing average climate data for 1970–2000. The relationship between arthropod abundance and mean annual temperature was analysed using forest plots



as data points. We selected four different measures of abundance to examine the values in the context of tree biomass, and to increase the reproducibility of the results: (1) total number of individuals in each plot, that is per 1000 m<sup>2</sup> of land area ( $N_{\text{tot}}$ ), (2) average number of individuals per tree ( $N_{\text{tree}}$ ), (3) average number of individuals per 1 m<sup>2</sup> of foliage ( $N_{\text{leaf}}$ ); and (4) average number of individuals per 1 m<sup>2</sup> of tree basal area ( $N_{\text{BA}}$ ).

### Model building

For each arthropod group and each abundance measurement we created three GLM models as  $\text{GLM}(\text{arthropodabundance} \sim \text{MAT})$  with different error distributions (Poisson, negative binomial and Gamma; all suited to dealing with heteroscedasticity in non-negative data). We did not include the site as a random factor in our models as it is cross-correlated with our sampling localities, and adding a three-level random effect to a model with nine plots would result in variance-covariance matrices being estimated as zero (singular fit), and therefore drastically reduce the power of the model. We then selected the best model based on the parsimony (AIC). We test the significance of a relationship based on the difference in deviance between the null model ( $y \sim 1$ ) and final.

### Standardisation by tree size and sampling season

The abundance of arthropods can depend on the amount of resources (e.g. foliage biomass) available, as well as heterogeneity of available microhabitats and microclimate in each tree, and as such can vary non-linearly with tree size, expressed by either DBH or foliage biomass (see Figs S3–S4). Furthermore,

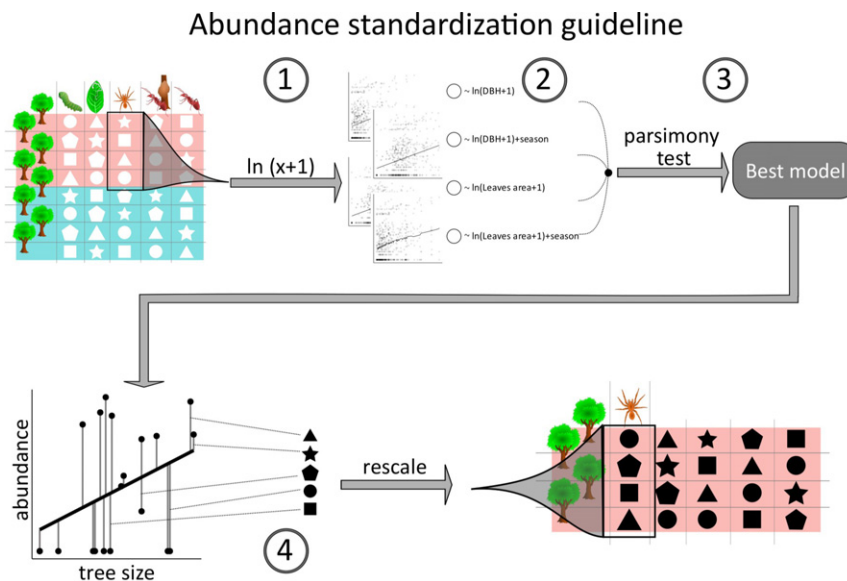
arthropod abundance can also vary seasonally (see Fig. S5). We have therefore developed a protocol to standardise arthropod abundances across trees of different sizes sampled at different seasons (Fig. 2) and used it to calculate *Standardised Abundances*, which are independent of tree size and season.

### Arthropod abundance correlations

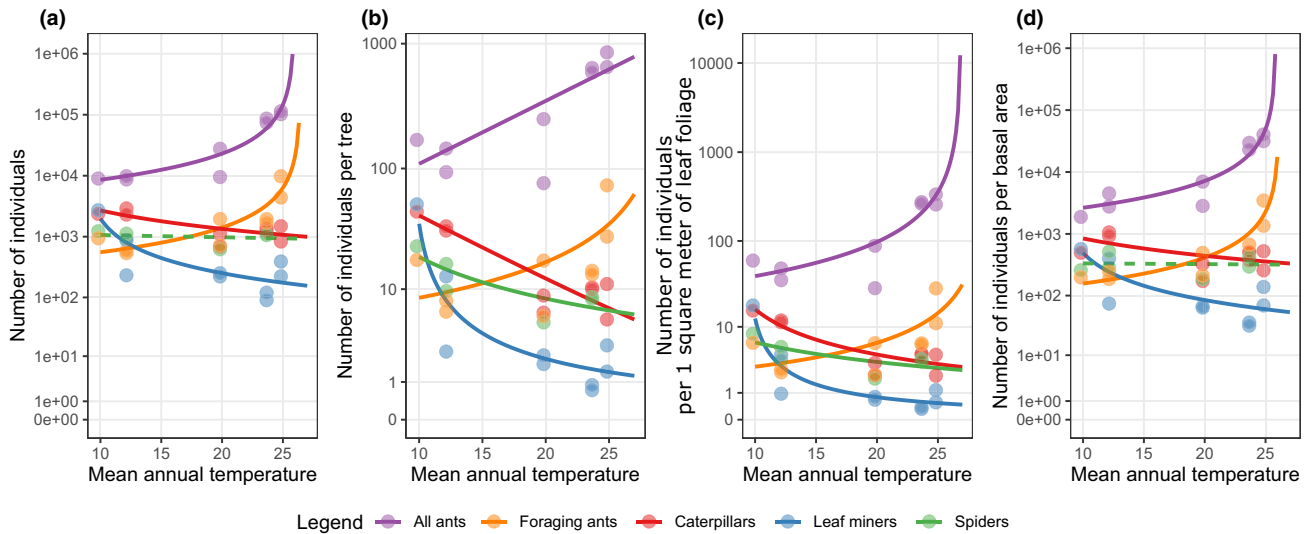
The relationships among the focal taxa abundances were tested within each plot, using individual trees as the unit of analysis. We tested all pairwise combinations of the focal taxa, except the *All ants* vs. *Foraging ants* comparison where the latter group is a subset of the former. We used linear regression with LM ( $N_{\text{taxon1}} \sim N_{\text{taxon2}}$ ) and estimated beta regression coefficients (RC) if there was a significant relationship between taxa (significances were corrected using Sidak correction of significance; Sidak, 1967). We expressed arthropod abundance as a) a log-transformed number of individuals per tree, and b) as the *Standardised Abundance* (see Fig. 2).

Next, the analyses were also repeated using the least-squares model, as GLS ( $N_{\text{taxon1}} \sim N_{\text{taxon2}}$ ) with the spatial coordinates of trees as a rational quadratic spatial correlation structure, taking into account that individual trees within the plot may not be independent data points. We could calculate this correction for just seven plots where the tree coordinates were available (Supporting Information: Supplementary Materials and methods).

Finally, to mitigate potential noise arising from non-predacious ant individuals, we assigned all ant individuals from four genera (*Polyrhachis*, *Camponotus*, *Calomyrmex* and *Echinopla*) as herbivorous (based on the literature and available stable isotope analyses; Bluthgen *et al.*, 2003; Davidson



**Figure 2** Abundance standardization procedure filtering out the effect of tree size (measured as DBH and leaf foliage area) and sampling season applied to the matrix of individual trees  $\times$  focal arthropod taxa abundance. Note that different symbols in the matrix represent examples of abundance values and colour represents different plots. 1) transform abundances as  $\ln(x + 1)$ ; 2) create 4 cubic smoothing splines with transformed abundances as a dependent variable, DF arbitrarily set as 5 and independent variables as: a)  $\sim \ln(\text{DBH} + 1)$ , b)  $\sim \ln(\text{DBH} + 1) + \text{season}$ , c)  $\sim \ln(\text{LeafArea} + 1)$ , d)  $\sim \ln(\text{LeafArea} + 1) + \text{season}$ . 3) transform all 4 smoothing splines into GLMs and select the best one based on AIC parsimony. 4) standardise residuals from the best fitting GLM model so that they have the same range as  $\ln(\text{DBH} + 1)$  and use those values as the *Standardised Abundance*.



**Figure 3** Relationship between mean annual temperature (MAT) and the number of arthropod individuals per plot (a), per tree (b), per 1 m<sup>2</sup> of foliage (c) and per 1m<sup>2</sup> of basal area (d). Each focal arthropod group is represented by the best GLM model (see Materials and methods). Dashed lines represent non-significant relationships (see Table S1 for the models and their significances).

*et al.*, 2003). We excluded herbivorous individuals (21.7% of all ant abundances) from *All ant* and *Foraging ant* datasets and repeated the linear regression between arthropod taxa.

#### Number of interactions along the temperature gradient

To explore how many inter-guild interactions (i.e. significant correlations of their abundances) were observed in each plot, we created an *Interaction index* calculated as: the number of significant pairwise combinations of the focal guilds in each plot divided by the number of all tested combinations. The *Interaction index*, range between 0 (there were no significant correlations between guilds) to 1 (all possible interactions were significant). We calculated the *Interaction index* using both the original abundances and the *Standardised Abundances*. We tested the relationship between the *Interaction index* and mean annual temperature of each plot, using a GLM (*Interaction index* ~ MAT) with binomial error distribution and differences in deviance between the GLM model and null model ( $y \sim 1$ ).

## RESULTS

In total, we sampled 1001 trees in nine 0.1 ha plots at the five study sites across three continents. These plots comprised 293 sampled tree species in 70 families, with a total basal area of 29.7 m<sup>2</sup> and 2.6 ha of leaf foliage (Fig. 1d and e). The forest structure changed dramatically among the plots: the number of trees per plot varied from 53 in Mikulcice to 157 in Wanang A; the total leaf area from 150.3 m<sup>2</sup> in Mikulcice to 395.4 m<sup>2</sup> in Wanang A; the mean DBH from 11.7 cm in Wanang A to 28.2 in Mikulcice; and the total number of tree species from 7 in Mikulcice to 91 in Numba A (Fig. 1d and e). This variation reflected a high number of relatively big trees in Mikulcice and an increasing number of smaller stems with increasing mean annual temperature (Fig. 1c). In total,

we sampled 14 333 caterpillars, 5123 leaf miners, 6037 spiders, 1849 ant nests (with estimated 418 700 ants) and 22 525 foraging ants (Fig. 1F, Table S1).

#### Arthropod abundance along the temperature gradient

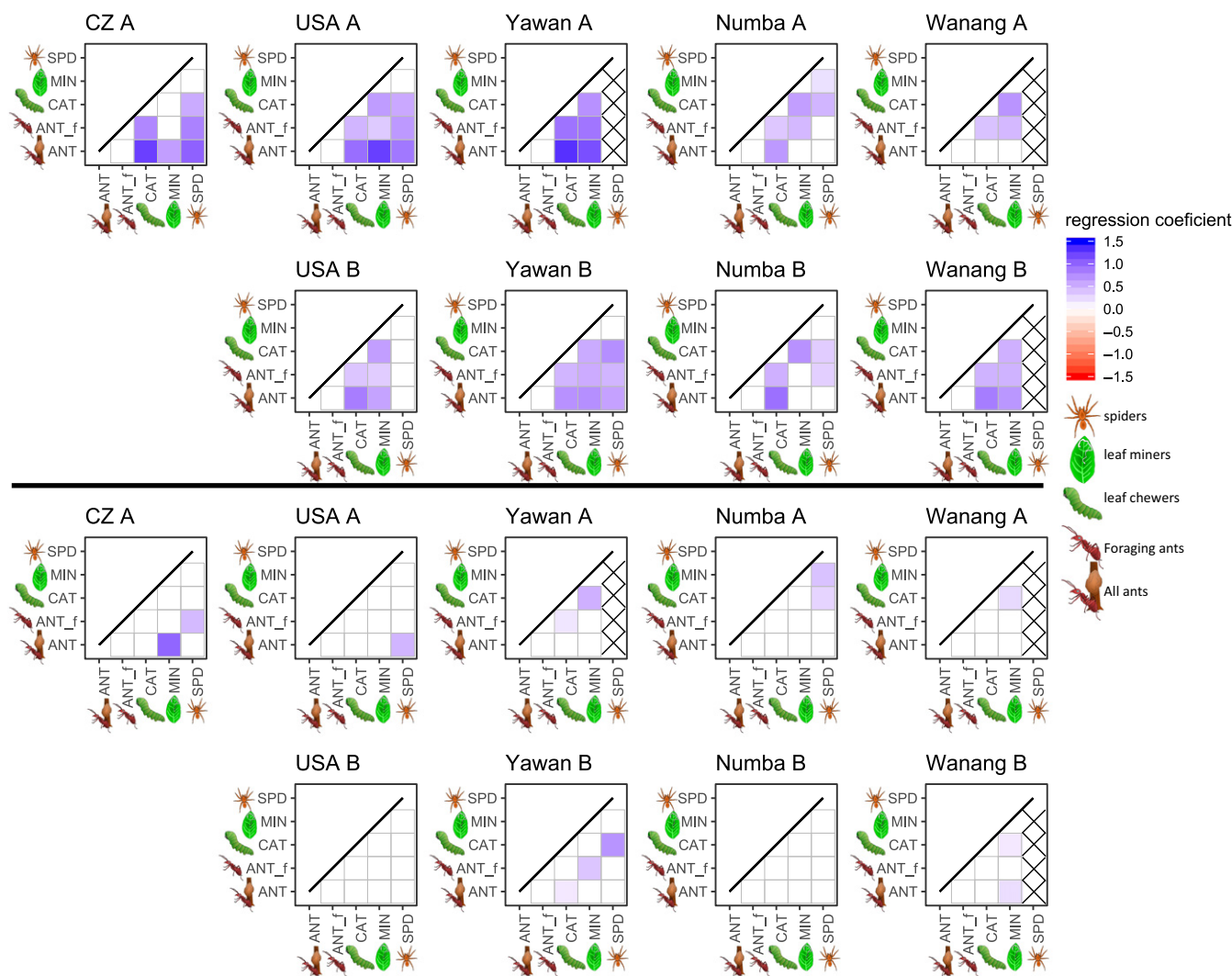
The total number per plot,  $N_{\text{tot}}$ , of ants significantly increased, and significantly decreased for leaf miners and caterpillars with increasing mean annual temperature (Fig. 3a, Table S2). Per tree numbers,  $N_{\text{tree}}$ , significantly decreased with temperature in caterpillars, leaf miners and spiders, and significantly increased in ants (Fig. 3b, Table S2). Similar trends were found for  $N_{\text{leaf}}$  (Fig. 3c, Table S2) with every guild group affected significantly.  $N_{\text{BA}}$  significantly increased for *All ants* and *Foraging ants* and significantly decreased for leaf miners and caterpillars with increasing temperature (Fig. 3d, Table S2).

#### Arthropod abundance correlations

We found 51 out of 69 (74%) possible pairwise relationships between the focal arthropod taxa to be significant when using the number of individuals on each tree as a measure of observed abundance, but only 13 out of 69 (19%) were significant when using *Standardised Abundances* (Fig. 4). However, all relationships, regardless of the data type used, were positive ( $RC > 0$ ).

Similar trends were observed when taking the spatial position of the trees into account: 69% pairwise comparisons of abundance were significantly correlated and 21% were significant using *Standardised Abundance*, with all significant relationships having  $RC > 0$  (Fig. S6).

The exclusion of herbivorous ant genera generated only minor changes, as 70% of relationships were significant in the abundance-based calculation and 17% when using *Standardised Abundances*, all with  $RC > 0$  (Fig. S7).



**Figure 4** Results from pairwise linear regressions between individual pairs of the focal arthropod groups. Each matrix represents one plot. In each plot, each pairwise combination of taxa was tested, except *All ants* vs. *Foraging ants*, using LM ( $N_{\text{taxon1}} \sim N_{\text{taxon2}}$ ). Beta regression coefficient (RC) is shown in significant relationships as a colour gradient from red (negative) to blue (positive). The arthropod abundances were quantified as a transformed number of individuals per tree  $\ln(N + 1)$  (a) and the *Standardised abundance* (b). Note that individual plots are ordered by annual mean temperature (MAT) from left to right. No negative co-occurrence of guild abundances was found.

### Number of interactions in the temperature gradient

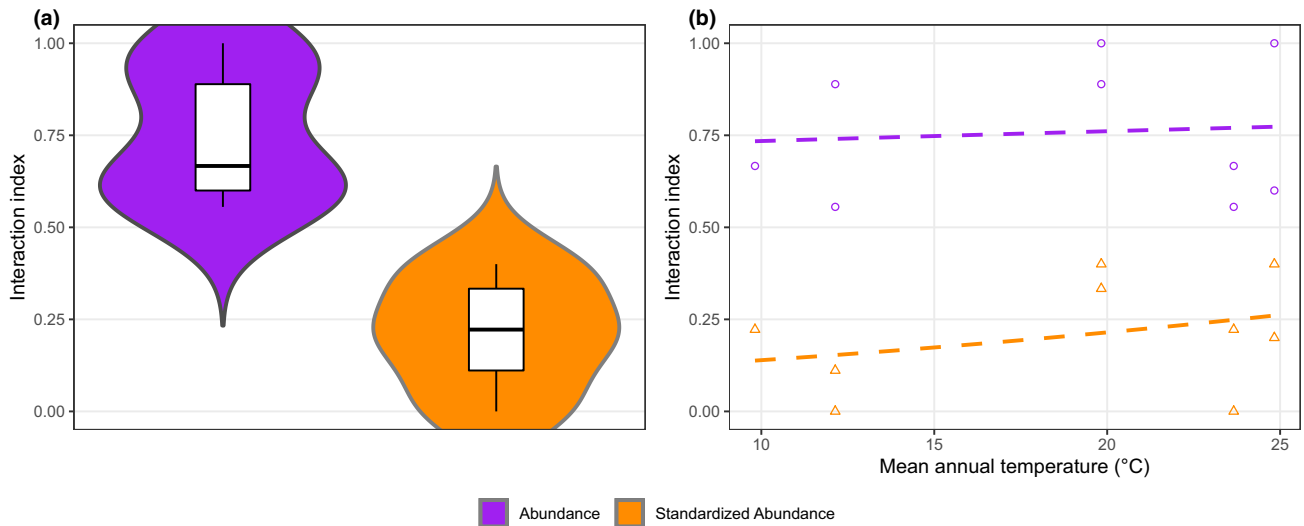
There was no significant relationship between *Interaction index* and mean annual temperature (Fig. 5), both for *Interaction index* calculated from the total arthropod abundances (deviance test; DF = 1,7;  $P = 0.83$ ; Table S3) and *Standardised Abundances* (deviance test; DF = 1,7;  $P = 0.39$ ; Table S3).

## DISCUSSION

To the best of our knowledge, this is the first study to attempt a multi-guild analysis of arboreal arthropod abundances at the whole-forest level on several continents. Furthermore, the incorporation of both plot-based and individual-based analyses applied to forest communities allowed us to quantify the effects of vegetation diversity and structure on arthropod abundance at both macro and local scales.

In contrast to our prediction, we observed negative correlations between herbivore abundance and mean annual temperature in all models. Despite a considerable change in forest structure along the temperature gradient, the trend for herbivores was consistent regardless of whether the context was per plot or plant biomass. Gaston *et al.* (2004) documented a similar increase in leaf miner abundance towards higher latitudes, whereas other studies found no latitudinal trends in the abundance of arboreal leaf chewers (Andrew and Hughes, 2005a) or leaf miners (Sinclair and Hughes, 2008). A decrease in abundance of herbivorous arthropods with increasing mean annual temperature was also observed in temperate grassland communities (Welti *et al.* 2020).

There are several complementary explanations for the observed trend. First, it is possible that tree species at lower latitudes were under selective pressure to evolve more effective chemical defences (Rasmann and Agrawal, 2011; Segar



**Figure 5** *Interaction index* calculated as the ratio of the number of significant pairwise relationships detected between pairs of the focal arthropod taxa and all possible relationships in each plot. Relationships were calculated from observed abundances (Table 2) or *Standardised Abundances* (Fig. 2). For more details about the calculation of pairwise relationships among the focal taxa see Materials and methods. The *Interaction index* variation based on the total number of relationships in each plot (boxes indicate the 1st and 3rd quartile, central line the median and whiskers 1.5 times the interquartile range) (a). Relationship between mean annual temperature (MAT) and the *Interaction index* (b). The relationship is not significant whether the *Interaction index* was calculated from normal arthropod abundance (deviance test; DF = 1,7;  $P = 0.83$ ) or from *Standardised Abundance* (deviance test; DF = 1,7;  $P = 0.39$ )

*et al.*, 2017; Volf *et al.*, 2018) because they generally experience more intense biotic interactions than do species at higher latitudes (but see Moles *et al.*, 2011; Moles & Ollerton 2016). For example *Ficus*, the most dominant tropical tree genus in terms of basal area in the PNG datasets, has diverse and potent chemical defences, including highly specific alkaloids or proteases, that strongly shape the associated herbivore communities and probably efficiently restrict feeding by many herbivores (Volf *et al.*, 2018). Second, in the tropics, the lower density of host tree species, higher herbivore specialisation and less predictable flushing of (fewer) young leaves, result in relatively scarce resources on which it is difficult to maintain large populations of specialised herbivores (Dixon *et al.*, 1987). Indeed, the caterpillar densities at our North American site during the Spring leaf flush in April were more than four times higher than the highest monthly average at any tropical site (Volf *et al.*, 2019). Finally, the contrasting trends of predators and herbivores in our results may be functionally linked, with herbivores under the control of their predators to a greater degree at high mean annual temperatures. This explanation is supported by increasing predation pressure towards lower latitudes and altitudes reported in other studies (Jeanne, 1979; Lach *et al.*, 2010; Roslin *et al.*, 2017). However, as we did not observe negative correlations among predator and herbivore abundances within individual plots, the increased abundance of canopy ants with mean annual temperature might also correspond to their eusocial mode of life in nests, which seems to be the more likely explanation. Plowman *et al.* (2019) reported a greater importance of nesting sites (microhabitat diversity and composition) as opposed to elevation (temperature) in a whole-forest study of arboreal ants from PNG, which suggests that nest space, the availability of sugar-rich resources (Davidson *et al.*, 2003), and the lack of an unfavourable

season could support a greater abundance of ants in tropical canopies.

We have shown that the increasing abundance of predators with temperature was a composite effect of two contradictory trends, as different abundance measures of ants increased with mean annual temperature, whereas spiders either decreased or did not respond significantly. This result implies that there may be competition at a larger geographical scale between ants and spiders, the two major groups of predatory arthropods in arboreal communities. This has been already suggested in smaller-scale studies (Halaj *et al.*, 1997; Mestre *et al.*, 2012). The observed pattern of increasing ant abundance along the mean annual temperature gradient is consistent with other studies from temperate and tropical forests (Jaffe *et al.*, 2007; Floren *et al.*, 2014), and studies on altitudinal gradients (Samson *et al.*, 1997; Sam *et al.*, 2015a). Michalko *et al.* (2019) showed an increasing effect of spider density on pest suppression with increasing mean annual temperature, in a meta-analysis of agro-ecosystems, but explained the observed patterns as caused by higher prey abundances and the increased strength of top-down trophic cascades in the tropics. In contrast, Rypstra *et al.* (1986) found an increasing number of spider individuals at lower latitudes and identified the variation in vegetation abundance as the main driver of abundance.

The correlations we observed among guild abundances in tree canopies were either lacking or were positive, with no particular pair of guilds consistently correlated across multiple sites. This pattern has a rather trivial explanation: it is driven by tree size, that is resource availability. Larger trees have greater biomass than smaller trees and can support more members of each guild. The number of arthropod individuals increased with tree size linearly in some cases, whereas in others larger trees harboured either higher or lower number of arthropods than expected based on their size (Fig. S1-2).



This non-linearity can probably be attributed to the distribution of microhabitats, some of which were found only on large-canopy trees, or trees with numerous lianas or epiphytes (Klimes, 2017). Indeed, microhabitat richness was found to be the main driver for the pattern in arboreal ant communities in other extensive whole-forest studies (Klimes *et al.*, 2015; Mottl *et al.*, 2019; Plowman *et al.*, 2019). A similar pattern of tree biomass affecting the abundances of arboreal arthropods has also been observed in specialist herbivores feeding only on a single tree genus or species (Novotny *et al.*, 2006, 2010). The pattern mostly disappeared, however, after standardising the abundances by tree biomass (tree size or foliage leaf area). Despite some relationships remaining significant after standardisation, all remained positive, thus ruling out competition between taxa or a common enemy as an explanation. Accounting for the spatial distribution of trees did not alter the results, probably because trees in old-growth forests have developed size hierarchies throughout the course of succession. As a result, they tend to have weaker spatial autocorrelation (Fibich *et al.*, 2016) or their spatial distribution tends to be indistinguishable from random at our spatial scale (Legendre and Fortin, 1989).

The pattern of individual aggregation could be interpreted in a number of ways, from the particular behaviour of each guild (not sharing resources and natural enemies with other guilds), to some combination of abundances driven by resources and/or top-down regulation by natural enemies (Table 1). However, the only robust conclusion we can draw from this pattern is that the absence of competition within both herbivore and predatory guilds would manifest itself in negative correlations. No significant correlation, negative or positive, was observed among insect abundances in a previous study of herbivorous guilds from several selected plant families in PNG (Novotny *et al.*, 2012). Our results suggest that this pattern could scale up to the whole canopy ecosystem for both herbivorous and predator arthropods, irrespective of the mean annual temperature of the plot.

Predation pressure on herbivores, based on the rates of attack on exposed dummy caterpillars or insect baits, has been shown to be particularly high in the lowland tropics (Novotny *et al.*, 2006; Roslin *et al.*, 2017), which could plausibly suggest the existence of a negative abundance relationship between herbivorous and predatory guilds in these ecosystems. However, we did not observe such a trend, possibly due to the methodological differences between our study, in which real herbivores and predators were sampled, and studies that estimated predation rates using proxies, such as baits. First, attack rates on dummy caterpillars may overestimate actual predation, since dummy caterpillars do not harbour traits such as odour, colorisation and movement (Sam *et al.*, 2015b), or defence mechanisms against predation. Note also that dummy caterpillars rarely reveal any predation by spiders. Secondly, arboreal ants may function more like omnivores, harvesting a good portion of their nutrients from hemipteran symbionts and extrafloral nectaries (Davidson, 1997; Bluthgen *et al.*, 2003) or by scavenging, rather than being full-time predators of herbivores. Finally, we cannot exclude the possibility that spiders may be more efficient predators of arthropod groups other than those selected for

our study (Birkhofer and Wolters, 2012). Interestingly, the frequency of significant inter-guild correlations did not change with mean annual temperature. This is in contrast with the expectation of increasing intensity of biotic interactions, including herbivory and predation, towards the lowland tropics (Dyer and Coley, 2002).

Plot-based studies that survey entire forest communities, while also recording the fine-scale distribution of plants, are a prerequisite for the understanding of complex food webs in forest ecosystems. In botany, plot surveys have become the norm (Anderson-Teixeira *et al.*, 2015). It is now feasible, using the methodological framework described in Volf *et al.* (2019), to expand them to arthropod communities. While the species richness of insects and its drivers are now better understood (e.g. Basset *et al.*, 2012), plot-based censuses can become a useful tool to assess the abundances of arthropods and improve our understanding of habitat- and temporal-driven changes. For example studies of whole-forest arthropod communities have already revealed the contrasting effect of forest age on leaf-chewing communities (Redmond *et al.*, 2018) and tree-dwelling ants (Mottl *et al.*, 2019), suggesting the importance of microhabitats for ants. In the light of recent reports of a worldwide decline in insects (Basset and Lamarre, 2019), the need to understand the processes underpinning arthropod ecology becomes increasingly important.

Large-scale surveys, such as this study and those previously mentioned, have allowed us to explore broad ecological patterns among multiple arthropod guilds. We provide evidence for the bottom-up limitation of arthropods by resources and abiotic factors, rather than by competition and predation, in old-growth forests. Furthermore, we suggest that the design of manipulative experiments would enable ecologists to delve into the drivers and mechanisms behind our results. For example Klimes *et al.* (2011) showed that manipulative experiments of arthropods are feasible at the whole-forest plot level, and Mottl *et al.* (2020) found that tropical ants were limited by nest site availability (i.e. resource availability) by manipulating artificial nests. We hope that our findings will stimulate interesting questions for future research, whether to highlight potentially interesting relationships or to experimentally tease apart the underlying mechanisms of arthropod ecology.

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## AUTHORS' CONTRIBUTIONS

OM led the manuscript writing, analysed and interpreted the data. OM, VN, GW, PF, PK and MV conceived the ideas and designed the study. OM, PK, MV, RT, JA, TB, GC, EG, AG, GL, ML, MM, KM, GN, NSP, CR, CLS and JV led the data collection for the arthropod guilds in different sites. OM, PK, MV, KAT, PB, PD, OK, GL, SEM, NSP, CR and CLS contributed to data management. PF contributed to data analysis. VN, PF, PK, MV and RT contributed to text and interpretation of the results. All authors gave final approval for publication.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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