HIGHLIGHTED STUDENT RESEARCH

Bromeliads affect the interactions and composition of invertebrates on their support tree

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Abstract

Individual species can have profound effects on ecological communities, but, in hyperdiverse systems, it can be challenging to determine the underlying ecological mechanisms. Simplifying species' responses by trophic level or functional group may be useful, but characterizing the trait structure of communities may be better related to niche processes. A largely over-looked trait in such community-level analyses is behaviour. In the Neotropics, epiphytic tank bromeliads (Bromeliaceae) harbour a distinct fauna of terrestrial invertebrates that is mainly composed of predators, such as ants and spiders. As these bromeliad-associated predators tend to forage on the bromeliads' support tree, they may influence the arboreal invertebrate fauna. We examined how, by increasing associated predator habitat, bromeliads may affect arboreal invertebrates. Specifically, we observed the trophic and functional group composition, and the behaviour and interspecific interactions of arboreal invertebrates in trees with and without bromeliads. Bromeliads modified the functional composition of arboreal invertebrates, but not the overall abundance of predators and herbivores. Bromeliads did not alter the overall behavioural profile of arboreal invertebrates, but did lead to more positive interactions in the day than at night, with a reverse pattern on trees without bromeliads. In particular, tending behaviours were influenced by bromeliad-associated predators. These results indicate that detailed examination of the functional affiliations and behaviour of organisms can reveal complex effects of habitat-forming species like bromeliads, even when total densities of trophic groups are insensitive.

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By comparing abundance and behavioural patterns, we innovate in quantifying community shifts. We detect subtle changes that are contingent on time, and that may be missed by classical trophic studies.

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Introduction

Individual species can have profound effects upon the interacting network of species in which they are embedded (Hairston et al. 1960; Fretwell 1987; Abrams 1995). The importance of species on ecological networks has been demonstrated by either manipulating the density of particular species (Paine 1980; Peacor and Werner 2001), or by comparing communities where one species is naturally absent (Cox and Ricklefs 1977; Strong 1992). Such studies have shown that ecological networks have a predominance of relatively weak interactions, but a few species with disproportionate effects on other species. In some cases, changes in the density of a single species can ripple through the network of species interactions, indirectly affecting a large number of species (Srivastava and Bell 2009). Quantifying the effect of individual species on an entire ecological network can be challenging. Simply demonstrating a change in taxonomic composition may not help in understanding the underlying ecological mechanisms, because there is no information on

the type of species most affected. This may be a particular problem in ecological networks with a large number of species, such as those that typify tropical systems.

A classic approach to quantifying effects of species in entire food webs is to categorize species into trophic levels, such as predators and herbivores, and to examine changes in the total abundance or biomass of these trophic levels. Manipulations of entire trophic levels have revealed the importance of indirect pathways mediated by multiple species, such as trophic cascades: the indirect and alternating top-down effect of higher trophic levels on lower trophic levels (Fretwell 1987; Schmitz et al. 2000; Ripple et al. 2016). Such manipulations of trophic levels can be effective in ecological networks with strong top-down effects of predator consumption on lower trophic levels, or strong bottom-up effects of resource production on higher trophic levels. However, this approach is limited in several ways. First, predators not only affect their prey through direct consumption, reducing their density, but also by inducing phenotypic changes in their prey, including morphological or chemical defenses and behaviour (Jeffries and Lawton 1984; Abrams 1995; Verdolin 2006) as prey attempt to reduce the chances of being eaten (Schmitz et al. 2004; Bestion et al. 2015; Buchanan et al. 2017). Second, negative trophic interactions are not the only important ecological interactions that can affect predator density. Positive interactions can have far-reaching impacts on the density and traits of other species in ecological networks (Boucher 1982; Peacor and Werner 2001; Leclerc et al. 2016). A common example is the facilitative ant-homopteran system, where ants tend honeydew-producing insects, securing this source of energy-rich food by defending the homopterans against predators, including other ants (Dejean et al. 1997; Blüthgen et al. 2000; Styrsky and Eubanks 2007), resulting in a change in the overall ecological community (Styrsky and Eubanks 2007). Third, categorizing species by trophic groups is complicated by the prevalence of omnivory in many food webs (Thompson et al. 2007), and the specialization of herbivores on different parts of their host plant (e.g., phloem feeders and leaf chewers only indirectly compete, Carrillo et al. 2012).

In response to the limitations of the trophic level approach, ecological networks have often been more finely characterized in terms of functional groups. Feeding functional groups aggregate species that exploit a similar resource in a similar way (e.g., leaf chewer), and provide a characterization of the community that is both simple and mechanistic (Blondel 2003). There may be substantial changes in functional group composition even in the absence of changes in the abundance of a trophic level, for example when the presence of a predator alters the relative abundance of edible to non-edible prey (Piovia-Scott et al. 2017). However, functional groups are ultimately based on categorizing one or two traits of species, and traits may be better characterized as both continuous and multivariate. A third approach is therefore to describe ecological networks of species not in terms of abundances of individuals at all, but instead in terms of the abundance of traits. The rationale here is that the trait structure of communities should relate closely to the underlying niche mechanisms, and so may be more sensitive to any perturbations to the community than taxonomic composition (McGill et al. 2006). Even though the role of traits in mediating ecological interactions is increasingly understood, their inclusion in conceptual studies of ecological networks is relatively recent (e.g., Solé and Bascompte 2006; Mora et al. 2018). To date, most trait-based studies of community structure have considered morphological or chemical traits. However, in the context of examining how an individual species affects an ecological network of interacting species, behaviour may be one of the most relevant traits. The behavioural profile of a community can encapsulate both positive (facilitative) and negative (consumptive and non-consumptive) interactions between individuals, allows for interspecific and intraspecific interactions, and can be affected by both individual decisions (e.g., predator escape behaviour) and species turnover (e.g., replacement of diurnally active species by nocturnally active species). Changes in prey behaviour can indirectly influence other species. For example, epigeous predators induce burrowing detritivores to move deeper into the soil, increasing nutrient availability at greater depths and thus indirectly increasing aboveground plant biomass (Wu et al. 2015). Nonetheless, surprisingly few studies have considered how the presence of a particular species may affect the behavioural profile of the rest of a community (Touchton and Smith 2011). Here we examine how bromeliad presence on orange trees affects the invertebrate community on the tree, comparing the effects on taxonomic composition, the relative abundance of trophic levels, the composition of feeding functional groups, and the behavioural profile of the invertebrate community. We also evaluate if such changes reflect a shift in the strength of negative (consumptive and non-consumptive) or positive (facilitative) interspecific interactions between invertebrates on the support tree.

Epiphytic tank bromeliads, members of the diverse Bromeliaceae family, are ubiquitous plants throughout most of the Neotropics, both in natural and agricultural settings (Benzing 2000; Toledo-Aceves et al. 2012). Their epiphytic lifestyle relies on the trapping of water and detritus by their leaf rosette, and extraction of nutrients by specialised trichomes (Wittman 2000). Bromeliads are considered ecosystem engineers (Linder et al. 2012), as they create terrestrial microhabitats that are opportunistically occupied by a diverse array of species (Benzig 2000; Angelini and Silliman 2014). More precisely, the bromeliad leaf rosette is utilized by a variety of predatory terrestrial arthropods, such as ants or spiders (Gutierrez Ochoa et al. 1993; Dejean et al. 1995;

Stuntz et al. 2002; Castaño-Meneses 2016). This increase in predator microhabitat in trees bearing bromeliads is known to impact species and functional group densities in support trees (Cruz-Angón et al. 2009; Yanoviak et al. 2011; Rogy et al. 2019; Rost-Komiya et al. in press), with some studies suggesting that, by harbouring predators, epiphytic tank bromeliads may provide indirect protection against herbivorous insects to their support tree (Dejean et al. 1995; Hammill et al. 2014; but see Rogy et al. 2019 and Rost-Komiya et al. in press). However, to the best of our knowledge, there has been no study that has examined if bromeliads, by harbouring predatory insects, impact invertebrates on their support trees through consumptive or non-consumptive processes, or if facilitative mechanisms play an important role in community shifts. In other words, it remains unknown if the effects of bromeliad-associated predators on the support tree stems primarily from direct consumption of arboreal prey, modification of prey behaviour, or, in the case of ants, through symbiosis with other organisms, such as aphids. If bromeliad-associated predators affect arboreal communities through non-consumptive or facilitative mechanisms, it would highlight a new pathway through which community structure may be altered.

We hypothesize that: (1) trees with bromeliads will harbour higher predator abundances and lower herbivore abundances than trees without bromeliads because bromeliads provide increased habitat for predators; (2) invertebrate communities in trees with bromeliads will have a different taxonomic and functional group composition, and behavioural profile, than in trees without bromeliads because of modified interspecific interactions in the ecological network; (3) there will be differences in the number of positive and negative species interactions in trees with bromeliads versus without bromeliads given that bromeliads harbour ants and ants are involved in both predation and homopteran honeydew-tending. We also examine the temporal context dependence of the above effects, hypothesizing that (4) bromeliad effects on the arboreal invertebrate communities will differ with time of the day, as bromeliad inhabitants may exhibit differing diurnal and nocturnal activity patterns (Way 1963).

Materials and methods

Site description and observation design

In this study, we observed the behaviour, abundance, and composition of invertebrates on the leaves and branches of orange trees, comparing trees with and without bromeliads. As predation pressure and facilitative interactions may vary with diel cycles of organisms (Way 1963; Kohl et al. 2018), we performed observations both during the day and at night. These observations took place in June 2017 in two orange

plantations near Santa Cecilia, northern Guanacaste Province, Costa Rica (11° 03′51″ N–85° 25′06″ W). The first plantation, hereafter CP (named after the owners, Calixto Moraga and Petrona Ríos), consisted of about a hundred lightly maintained trees in a 10 × 12 matrix, separated by rows of tall fodder plants, and located in a matrix of human settlements, pasture, and forest fragments. The other plantation, hereafter DO (named after the owner, the company Del Oro S.A.), is an intensively managed parcel of many thousand trees, located at the edge of the Area de Conservación Guanacaste, and isolated from the rest of the company's operations by forested areas. Unlike CP, DO was intensively sprayed with pesticides until September 2016, but is now used as an experimental parcel to develop sustainable agricultural techniques by the company agronomists. The between-tree rows consisted of a diverse matrix of short grasses and bushes.

Due to the large differences in the abundance of trees between our sites, and because of difficulties in traversing the dense fodder plants at CP, our study design differed between the two sites (Fig. S1). At CP, where there were a limited number of trees, we selected three blocks of 12 trees. Within each block, six trees bore bromeliads and six did not. Here, blocks did not consist of spatially distinct groups of trees, but rather a temporally distinct group. Each block consisted of a random set of 12 trees selected across the entire parcel sampled at the same time. At set hours, two observers separately conducted either two diurnal or two nocturnal observations on each tree of a block. Each observation consisted of a researcher carefully approaching the edge of the orange tree—so as to minimize disturbance of behaviour—and recording all invertebrate activity in a randomly selected, eye-level 50*50*50 cm volume of leaves and branches for five minutes. We classified behaviour into one of 11 categories (Table 1b) and recorded the duration of the activity to the nearest 5 seconds. When interspecific interactions were observed during the behavioural observations, we categorized these as positive or negative (Table 1c). We repeated the same design a second time on each block, but with time of observation (day or night) switched for observers to reduce any observer bias. Due to the relative isolation of DO, it was not possible to safely perform nighttime observations; therefore, the two observers synchronously performed diurnal observations on opposite sides of each tree. However, because the abundance of trees was not limiting in this site, we did not need to repeat observations on blocks of trees, but rather observed a different random, relatively close (within a 50 m radius) set of 12 trees each day of observation. Observations lasted for 13 days overall: 6 days at CP (36 trees, three blocks observed twice) and 7 days at DO (84 trees, seven groups observed once). For both sites, we recorded invertebrate activity four times on six trees with bromeliads and six trees without bromeliads

Table 1 List of **a** functional and taxonomic groups, **b** behaviours, and **c** interspecific interaction types used in the analysis, and their abbreviations for Figs. 2, 3

Trophic level	Functional groups	Taxonomic groups (or lowest taxonomic unit)
(a)		
Predator	Predator (Prd) (includes scavengers (Scv) and omnivores (Omn) with predatory behaviours in univariate analyses)	Ants (excluding leaf-cutter ants), predatory heteropterans (Pbu), hunting spiders (Hsp), lacewings (Lac), mantids, predatory beetles (Pbt), predatory flies (Pfl), wasps, web-weaving spiders (Wsp), cockroaches (Coc), opiliones (Opl)
Herbivore	Leaf chewers (Chw)	*Atta* sp. (leaf-cutter ants), herbivorous beetles (Hbt), herbivorous lepidopterans, herbivorous orthopterans (Ort), herbivorous snails (Snl)
	Phloem feeders (Phl)	herbivorous heteropterans (Hbu), hoppers (mobile homopterans, Hop), scales/aphids (Dew, includes mealybugs, and the Asian citrus psyllid *Diaphorina citri* Kuwayama (Psy))
	Leaf miners (Min)	All leaf miners (Min), including *Phyllocnistis citrella*
Others	Detritivore (Det)	Collembola, Diplopoda, Psocoptera
	Granivore (Gra)	Rhyparochromidae
	Mycophagous (Myc)	Lauxaniidae
	Non-feeder (Non)	Chironomidae, Psychodidae, Sciaridae
	Omnivore without predatory behaviours (Omn)	Ensifera, earwigs
	Parasitoid (Par)	Parasitoids (Par)
	Palynivore/Nectarivore (Pol)	Syrphidae, Apoidea, Lepidoptera
	Xylophagous (Xyl)	Scolytinae
	Unknown feeding behaviour (Unk)	Acari, Apocrita, Brachycera, Coleoptera, Diptera, Hemiptera, Lepidoptera, Nematocera, Orthoptera, Polyphaga, Sternorrhyncha, Thysanoptera

Behaviour category	Description
(b)	
Stationary (Sta)	Specimen stationary, including spiders in their web, and phloem feeding herbivores with no evidence of feeding
Detritivory (Det)	Detritivore sponging leaf or eating debris
Leaf chewing (Chw)	Herbivore chewing leaf
Phloem feeding (Phl)	Herbivore feeding on phloem. Includes scale insects and mealybugs
Leaf mining (Min)	Leaf miner present inside tunnel
Predation/parasitism (PPr)	Predators feeding, parasitism, and attack attempts on other organisms
Defense (Def)	Response of an organism to an attack by a predator
Mobile (Mob)	Exploring the environment
Tending (Ten)	Ants tending honeydew-producers, such as scale insects, mealybugs, or aphids
Reproduction (Rep)	Mating or oviposition, excluding parasitism
Development (Dev)	Molting or pupation
Transporting (Tra)	Organism carrying food, dead material. Largely concerns ants

Interaction type	Description
(c)	
Negative	Predator or parasitoid attack on an organism
Positive	Tending

each day ($n = 4$ observations for each tree; total $n = 288$ at CP and total $n = 336$ at DO). All trees with bromeliads had 1–4 bromeliads of average size for each site, except for three trees at CP. These threes trees bore 8–11 bromeliads, and are included in the present analyses because their exclusion did not significantly change the results.

Categorization of invertebrates

We identified invertebrates to morphospecies, or to 'near-morphospecies' (identification approximate, or slight morphological differences present). Because in situ identification of arthropods can be challenging, we relied on morphospecies identified in Rogy et al. (2019), a study conducted concomitantly at the same sites, in which we compared abundances of invertebrate species within bromeliads versus in vacuum samples of the surrounding tree leaves. Rogy et al. (2019) also dissected 117 bromeliads growing on orange trees in both sites, 50 of which were on trees we observed for this study, providing information on the local bromeliad fauna. We categorized specimens into taxonomic groups (Table 1a) and, if identification was certain, we inferred trophic level from taxonomy (see Rogy et al. 2019). However, if identification was approximate, or the taxon includes a range of feeding behaviour, trophic level was considered unknown. As ants are key arthropod predators in agroecosystems (Schmitz et al. 2000), we assigned our ant morphospecies to existing species or taxa with both morphological and genetic methods (Smith et al. 2014). We also classified our morphospecies of invertebrates as bromeliad-associated or not, based on Rogy et al. (2019). Specifically, we defined bromeliad-associated predators as those that preferentially occurred in bromeliads, discounting "tourist" species.

In our classification, we did not consider parasitoids as predators because, as we did not dissect specimens to assess parasitism rate, their impact can only be detected after the larvae emerge from hosts. Finally, herbivores were further classified into functional groups based on their feeding behaviours, namely leaf chewers, phloem feeders, and leaf miners.

Statistical analyses

The study design differed between the two sites, so we analyzed each site separately, using the R programming language version 3.5.1 (R Core Team 2018). We separately examined the effects of bromeliads and of bromeliad-associated predators on the invertebrate community.

Community abundance and composition

To separately test the associations between bromeliads, all predators, bromeliad-associated predators and herbivore functional groups, we used generalized linear models with Poisson or negative binomial error distributions as appropriate. We pooled all four observations for each tree, as bromeliad presence or absence was recorded at the tree level. At CP, to control for the repeated measures of our block design, we used generalized linear mixed-effect models with tree nested within block as random effect, using the 'glmer'

function of the 'lme4' package (Bates et al. 2015). We tested model outputs with likelihood ratio tests, using the 'mixed' function of the 'afex' package (Singmann et al. 2018). At DO, which did not have a random block design, we instead used generalized linear models, and tested model outputs with the same method, using the 'Anova' function of the 'MASS' package (Venables and Ripley 2002). We assessed fit of all models with the 'DHARMa' package (Hartig 2018) and plotted model outputs using the 'ggeffects' package (Lüdecke 2018). To avoid any circularity, we removed abundances and behaviours of the bromeliad-associated predators from the response matrix when bromeliad-associated predators were the explanatory variable. We also removed from analyses of herbivores one CP tree with > 200 aphids, as this was the only instance of such infestation, and more than five times the abundance of herbivores in the next most abundant quadrat. Finally, leaf miners were not numerous enough to be analyzed separately in univariate analyses, but were still included in multivariate analyses.

To analyse the effect of bromeliad and bromeliad-associated predators on community composition on orange trees, we used permutational analysis of variance (PERMANOVA), a method to detect changes in community composition associated with ecological parameters (Anderson 2001). We performed PERMANOVA on a Bray–Curtis dissimilarity matrix with 2000 permutations, which were either restricted at the block level for CP, or unrestricted for DO, using the 'adonis' function of the 'vegan' package (Oksanen et al. 2018). We first performed this analysis on a community matrix of abundance within each functional group (Table 1a). We then performed the same taxonomic analysis on the subset of herbivore and predators that could be confidently assigned to a taxonomic group (Table 1a, "Restricted taxonomic groups"). To ensure that removing specimens with low taxonomic resolution did not affect our analyses, we also repeated the PERMANOVA analyses with these specimens included (left at order or suborder, "Overall taxonomic groups"). Inclusion of all taxonomic groups did not change the results, and can be found in Online Resource 1. In all three matrices, functional or taxonomic groups with less than five recorded individuals were excluded from the analyses. Relevant PERMANOVA outputs for this paper were visualized in ordination space using Principal Coordinate Analysis (PCoA), with the weighted averages score of relevant groups calculated using the 'add.spec.scores' function in the 'BiodiversityR' package (Kindt and Coe 2005).

Behavioural analysis

We conducted further PERMANOVAs with the goal of assessing the possible impact of bromeliads and bromeliad-associated predators on invertebrate behaviour, using behaviour categories (Table 1b) instead of functional or taxonomic

groups in the community matrix. We examined two aspects of community behaviour: behaviour duration (in seconds) in a Hellinger-transformed matrix, and raw behaviour frequency. Here we generated the dissimilarity matrix using Euclidean distances, rather than Bray–Curtis dissimilarity, due to the non-integer nature of the data. Looking at these two aspects of behaviour allows us to understand if behavioural responses to either bromeliads or bromeliad-associated predators are mediated by strong (change in behaviour frequency) or weaker behavioural modifications (change in behaviour duration). The behavioural profile of each tree was visualized using PCoA analyses, and the vector for the bromeliad-associated predators was plotted using the 'envfit' function in 'vegan' (Oksanen et al. 2018).

To assess if bromeliads influence negative or positive interspecific interactions in their host trees, we used the same site-dependent model structure as aforementioned. However, we added total number of observed invertebrates per tree as a covariate, to account for the dependence of interaction frequency on invertebrate abundance.

Diurnal analysis

As the impacts of bromeliads on their host tree communities may be dependent on diurnal patterns of bromeliad-associated invertebrates, we separated diurnal and nocturnal observations at CP before repeating the same regression models and diet, taxonomic and behavioural PERMANOVAs. In other words, instead of pooling all observations per tree for each replicate, we only pooled at the time of observation level (day or night per tree for each replicate). In addition, we added time of observation (day or night) as an interaction term in the same CP generalized-mixed effect model and PERMANOVA structure.

Results

During the study, we observed a total of 3269 individual invertebrates (1874 at CP and 1395 at DO) and witnessed 174 interactions (99 at CP and 75 at DO; Table 1c). At DO, negative interactions were more numerous than positive interactions (51 vs. 24, respectively); at CP, positive interactions were more numerous than negative interactions (81 vs. 18, respectively). Three ant species account for most of these positive interactions (tending): *Solenopsis sp.* and *Camponotus sp.*, both bromeliad-associated, and *Ectatomma sp.*, not bromeliad associated. The bromeliad-associated *C. atriceps* and *Azteca sp.*, and the non-bromeliad associated *C. planatus* accounted for the remainder.

Predator and herbivore abundance—overall analysis

There was no effect of bromeliad presence on the abundance of predators (Fig. S2a for CP), bromeliad-associated predators (i.e., predators encountered during bromeliad dissection, Fig. S2c for CP) or herbivore abundances at either of the two sites (Table S1). Similarly, bromeliads did not affect abundances of either leaf chewers or phloem feeders (Table S1).

Predator and herbivore abundance—diel analysis

On average, predators and bromeliad-associated predators were, respectively, 30% and 50% more abundant during the day than at night (Table S4, Fig. S2b, S2d), while herbivores, including as functional groups, remained unaffected by time of observation (Table S4). Even when accounting for this diel pattern, bromeliads still had no effect on abundances of these three invertebrate groups (Table S4, Fig. S2b, S2d).

Community composition—overall analysis

At CP, bromeliads and their associated predators consistently impacted the taxonomic structure of the invertebrate community on the support tree when we examined taxonomic structure in a high-confidence but restricted set of taxa (respectively, $F_{1, 69} = 2.18$, $P = 0.026$, $r^2 = 0.0311$, and $F_{1, 68} = 4.66$, $P = 0.065$, $r^2 = 0.0005$, Fig. S2b). Bromeliads and bromeliad-associated predators also modified the functional group structure of invertebrates on orange trees at CP (respectively, $F_{1, 69} = 3.02$, $P = 0.007$, $r^2 = 0.0425$, and $F_{1, 68} = 7.81$, $P = 0.0005$, $r^2 = 0.103$, Fig. 1a). The effects of either bromeliads or bromeliad-associated predators on these compositional groups were minor, explaining between 3.11% and 10.3% of the observed variation. By contrast, at DO, neither bromeliads nor their associated predators had a detectable impact on taxonomic (respectively, $F_{1, 82} = 0.393$, $P = 0.91$, $r^2 = 0.0048$, and $F_{1, 82} = 1.32$, $P = 0.0161$, $r^2 = 0.022$) or functional group composition (respectively, $F_{1, 82} = 0.689$, $P = 0.66$, $r^2 = 0.0084$, and $F_{1, 82} = 1.53$, $P = 0.15$, $r^2 = 0.0185$).

Community composition—diel analysis

Time of day affected the composition of functional groups, and taxonomic groups, explaining 1.8–3% of the observed variation (Table 2a; Fig. 2a–d, Table S5). However, accounting for time of day only lowered the amount of variance explained (to 2% and less) by bromeliads or bromeliad-associated predators, without changing the qualitative results. Indeed, bromeliads still altered the taxonomic and functional structure of the invertebrate community on orange trees, and bromeliad-associated predators again altered only

the functional structure (Table 2a; Fig. 2a–d). However, the interaction of bromeliads and time altered the functional structure of the invertebrate community on orange trees (Fig. 2a–b), but not the taxonomic structure (Table 2a) unless taxa with low taxonomic resolution were included (Table S5).

Community behaviour—overall analysis

At CP, bromeliad-associated predators altered the frequency of different behaviours in the rest of the invertebrate community ($F_{1, 68} = 3.69$, $P = 0.0025$, $r^2 = 0.0515$, Fig. S2c), but not behaviour duration ($F_{1, 68} = 2.5$, $P = 0.06$, $r^2 = 0.0354$). This effect was mainly driven by phloem feeding and tending behaviours (Table 1), which are positively associated with bromeliad-associated predators in the ordination space (Fig. 1c). We note that this association does not reflect tending of herbivores by the bromeliad-associated predators themselves, because the bromeliad-associated predators were removed from the community matrix for this analysis; instead this is a correlational or indirect effect. As with functional structure, only about 5% of the variation in community behaviour was explained by bromeliad-associated predators. On the other hand, there was no effect on behaviour frequency and duration on orange trees of bromeliads at CP (respectively, $F_{1, 69} = 1.78$, $P = 0.11$, $r^2 = 0.0256$ and $F_{1, 69} = 0.934$, $P = 0.4$, $r^2 = 0.0136$), and, at DO, of bromeliads (respectively, $F_{1, 82} = 1.07$, $P = 0.36$, $r^2 = 0.013$, and $F_{1, 82} = 0.586$, $P = 0.73$, $r^2 = 0.0072$), although bromeliad-associated predators displayed marginally non-significant associations (respectively, $F_{1, 82} = 2.01$, $P = 0.079$, $r^2 = 0.0242$, and $F_{1, 82} = 2.23$, $P = 0.059$, $r^2 = 0.0268$). Bromeliads were not associated with the number of positive or negative interactions in the trees at either site (Table 1c, Table S3).

Community behaviour—diel analysis

Time (either day or night) altered the relative frequency of community behaviours, with around 2% variation explained by time of observation (Table 2b, Fig. 2e, f). There was no effect of time of observation on behaviour duration, nor any effect of bromeliads or bromeliad-associated predators, on the behavioural structure of the community (Table 2b).

In diurnal observations, the frequency of positive interspecific interactions (Table 1) was near-zero in the presence of bromeliads, while, in the absence of bromeliads, exponentially increased with the number of observed specimens (Table S6; Fig. 3). In nocturnal observations, this pattern was somewhat reversed: the increase in number of interspecific positive interactions was much stronger in trees with bromeliads than in trees without bromeliads (Table S6; Fig. 3). Negative interspecific interactions, to the contrary,

remained unaffected by bromeliads, time of day, or number of observed invertebrates (Table S6).

Discussion

Our study assessed if ecosystem engineering by bromeliads was associated with an increase in arboreal predator abundances, changing the functional structure and behavioural profile of arboreal invertebrate communities. By separately examining the abundance, composition and behaviour of the community, we can shed light on different ways bromeliads may affect the trait structure of the invertebrate community on their support trees. In this study, bromeliads did not alter the overall abundance of predators or herbivores on orange trees, nor the behavioural structure of the arboreal invertebrate community. Nonetheless, bromeliads altered the taxonomic and functional composition of the arboreal invertebrates, at least at site CP. Although bromeliads did not affect the behavioural structure of the arboreal invertebrate community, bromeliad-associated predators did—suggesting that bromeliad-associated predators are the proximate driver of altered behavioural structure. The community-wide effect of bromeliads and their associated predators was detectable regardless of time of observation (day or night), yet interactive effects between bromeliads and time of observation on interspecific positive interactions suggest that the effects of bromeliad may be mediated by invertebrate activity patterns. In summary, bromeliads tend to modify several aspects of the invertebrate communities on their support tree, which, coupled with a lack of numerical impact on broad trophic groups, suggests subtle responses in invertebrate communities that may be missed by classic trophic approaches.

There were some stark site-level differences in our results, with all detected associations of bromeliads occurring at CP. The qualitative differences in invertebrate responses are likely a consequence of fundamental differences between small-scale farming (CP) and intensive commercial operations (DO). Bromeliads at DO are removed from trees on a regular basis, as part of the management routine. Even though DO managers agreed to stop removing bromeliads 7 months before the start of the experiment, the long generation time of bromeliads meant they were generally smaller and less abundant than at CP (Rogy, pers. obs.). Moreover, these smaller bromeliads tended to be near or at the top of the tree crown, hence many of our observation quadrats were relatively far from the bromeliads. An alternative explanation would be that differences in the experimental designs between sites led to site differences, however, both the total numbers of samples and the accumulation of species with samples were relatively similar between sites.

In terms of trophic levels, bromeliads did not affect densities of all predators, predators normally associated
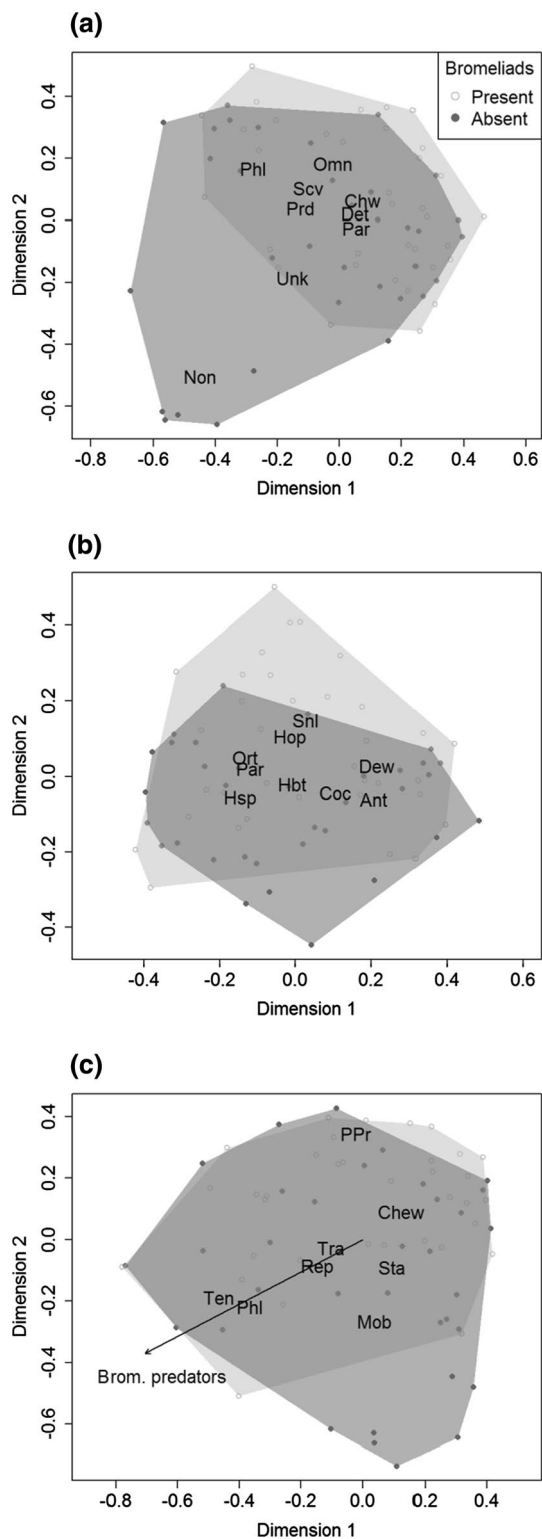
Fig. 1 Principal Coordinate Analysis (PCoA) plots of the effect of bromeliads on **a** functional and **b** restricted taxonomic groups, and **c** of bromeliad-associated predators ("Brom. predators") on behaviour frequencies at CP. To avoid cluttering the graphs, the least abundant groups are not plotted, specifically leaf miners, mycophagous and pollen-feeders in **a**, and herbivorous and predatory heteropterans, lacewings, lepidopterans, predatory beetles and flies, and web-weaving spiders in **b**. Abbreviations as in Table 1

with bromeliads, or herbivores, including herbivore functional groups. We found the opposite pattern in a vacuum-sampling study conducted concurrently at CP (Rogy et al. 2019), where the presence of bromeliads was associated with increased abundance of predators during the dry season, and increased abundance of herbivores in the wet season. As the current study took place in the transitional phase between the dry and wet season, our experiment may have coincided with a seasonal reorganization of invertebrate communities, resulting in no clear effect on either predators or herbivores. Alternatively, differences in sampling intensity (and methods) may contribute to the difference between studies: we observed in this study only half the individuals that we captured with vacuum sampling in Rogy et al. (2019). In addition, while vacuum sampling can collect specimens hiding in leaf curls, for example, observation is inherently biased towards conspicuous, active specimens.

Although bromeliads did not affect arboreal predator and herbivore abundances, the presence of bromeliads in a tree nonetheless altered the distribution of both functional and taxonomic groups in the food web. This suggests that there are subtle changes in invertebrate composition at the level of diet, coarse taxonomy, and feeding guilds, which do not appear in the broader categories of trophic levels. In ordination space, bromeliads tended to be associated with detritivores, omnivores (mainly opiliones) and scavengers (cockroaches). In fact, bromeliads can house a substantial detritivore community (Castaño-Meneses 2016), and are used by numerous cockroaches and opiliones, including juveniles (Rogy, pers. obs.). Moreover, subdividing functional groups into predatory and herbivorous feeding guilds ('Restricted taxonomic groups'), showed that bromeliads increased snail and hopper (Homopterans excluding aphids and scales) presence in their support tree. Snails were commonly encountered inside bromeliads, suggesting that bromeliads acted as a source habitat or microhabitat refuge for these species. Hoppers, by contrast, are not known to be bromeliad-associated (Rogy, pers. obs.), so the mechanism for their increased abundance on bromeliad-bearing trees remains unclear. In short, bromeliads tend to promote organisms that are either associated with detrital food webs within bromeliads, or with the moist microhabitats provided by bromeliads.

There were minor effects of bromeliad-associated predators on the community-wide frequency of particular behaviours, even if we were not able to detect effects of bromeliads themselves on the entire behavioural profile of the arboreal community. In particular, phloem-feeding and tending behaviours were promoted by bromeliad-associated predators. Predation events are rare and very rapid (Nentwig 1986), unlike tending events, so our study may have underestimated their true occurrence. In this experiment, most observed bromeliad-associated predators were ants, many of

Table 2 Effects of bromeliad presence ("Bromeliads) and bromeliad-associated predator abundance on **a** functional or taxonomic composition, and **b** behavioural structure of the arboreal invertebrate community, in conjunction with time of observation (day/night)

	Bromeliads (B)	Time of observation (T)	B × T	Bromeliad-associated predators (BP)	Time of observation (T)	BP × T
(a)						
Functional groups	$F_{1, 139} = 2.26$ $P = 0.025$ $r^2 = 0.0156$	$F_{1, 139} = 4.29$ $P = 0.0005$ $r^2 = 0.0296$	$F_{1, 139} = 2.34$ $P = 0.018$ $r^2 = 0.0162$	$F_{1, 138} = 0.945$ $P = 0.49$ $R^2 = 0.0067$	$F_{1, 138} = 3.21$ $P = 0.0025$ $r^2 = 0.0229$	$F_{1, 138} = 1.13$ $P = 0.32$ $r^2 = 0.0081$
Restricted taxonomic groups	$F_{1, 139} = 2.26$ $P = 0.0235$ $r^2 = 0.0158$	$F_{1, 139} = 4.24$ $P = 0.0005$ $r^2 = 0.0296$	$F_{1, 139} = 0.859$ $P = 0.55$ $r^2 = 0.006$	$F_{1, 138} = 2.88$ $P = 0.004$ $r^2 = 0.0206$	$F_{1, 138} = 2.5$ $P = 0.0105$ $R^2 = 0.0178$	$F_{1, 138} = 1.55$ $P = 0.15$ $r^2 = 0.011$
(b)						
Behaviour duration	$F_{1, 139} = 0.373$ $P = 0.81$ $r^2 = 0.0027$	$F_{1, 139} = 3.14$ $P = 0.019$ $r^2 = 0.0224$	$F_{1, 139} = 0.642$ $P = 0.607$ $r^2 = 0.0046$	$F_{1, 138} = 0.979$ $P = 0.38$ $r^2 = 0.007$	$F_{1, 138} = 2.09$ $P = 0.093$ $r^2 = 0.0149$	$F_{1, 138} = 1.91$ $P = 0.15$ $r^2 = 0.0137$
Behaviour frequency	$F_{1, 139} = 1.38$ $P = 0.23$ $r^2 = 0.0097$	$F_{1, 139} = 3.4$ $P = 0.008$ $r^2 = 0.0239$	$F_{1, 139} = 1.41$ $P = 0.22$ $r^2 = 0.0099$	$F_{1, 138} = 2.25$ $P = 0.055$ $r^2 = 0.0158$	$F_{1, 138} = 3.23$ $P = 0.0105$ $r^2 = 0.0228$	$F_{1, 138} = 1.39$ $P = 0.24$ $r^2 = 0.0098$

Only observations from site CP are included here, as nocturnal observations were not performed at site DO

PERMANOVA analysis performed with 2000 permutations restricted at the block level

Significant associations are in boldface

which were attracted to immobile, feeding aphids or scales (most phloem feeding herbivores) to farm honeydew (tending on the part of the ants). Honeydew-farming ants tend to increase densities of their homopteran partners (Styrsky and Eubanks 2007; Ohgushi 2008), potentially explaining the association between bromeliad-associated predators and phloem feeding in the ordination space. These feeding aphids and scales, in turn, are tended by other ants which may not necessarily be bromeliad-associated, explaining the association between phloem feeding and tending behaviours in ordination space, even when bromeliad-associated predators were removed from the behavioural matrix.

The influence of bromeliads on the composition of the arboreal invertebrate community differed between day and night, a result that we attribute to diel cycles of bromeliad-associated species. For example, at night we observed large, herbivorous katydids feeding in the vicinity of bromeliads whereas we did not see any during the day. In a concomitant study (Rogy et al. 2019), we found many such individuals sheltering within bromeliads (collected during the day), suggesting that bromeliads can be used as a diurnal refuge by large herbivores. These diel patterns in bromeliad occupancy were also reflected in bromeliad-associated predators. In fact, some ant species that nested in bromeliads were only observed on the orange trees during the day, whereas other species were only observed at night. This offers an explanation for why the effects of bromeliads on positive interspecific interactions differed with time of day: nocturnal bromeliad-associated ants may rely more on honeydew than their diurnal counterparts. Similar seasonal differences in

the reliance of ants on honeydew have been documented for at least half a century (Way 1963), which implies that the composition of invertebrates in bromeliads may also differ depending on time of the day, resulting in opposite compositional shifts in their support tree communities. By increasing energy flow to certain ant species, this kind of positive interspecific interaction can radically change ant competitive dynamics, and allow ants that are otherwise subdominant to exclude competitors, indirectly affecting other trophic levels (Dejean et al. 1997; Blüthgen et al. 2000).

We found that, in cases where bromeliads positively influenced the interspecific interactions on their host trees, most of these positive associations were due to the tending activities of species from three genera of ants; *Solenopsis* (Myrmicinae), *Camponotus* (Formicinae) and *Azteca* (Dolichoderinae). Famously, Hölldobler and Wilson (1990) noted that most species from these three sub-families attend—at least to some extent—hemipterans. From *Solenopsis*, we know of many examples of tending hemipterans (Vinson 1997) and in fact, this hemipteran association is widely thought to be a reason for their successful invasion of habitats across the globe (Holway et al. 2002). *Azteca* ants are an arboreal taxon that includes species of generalists which often tend Hemipterans (Longino 2007). Often, Azteca workers tend Hemiptera within, or nearby to, their nest (Davidson et al. 2003). *Camponotus* is one of the largest ant genera in the world and exhibit a variety of life-histories (Bolton et al. 2006). However, one commonly occurring strategy for this group is the tending of hemipteran (Davidson et al. 2003; Wernegreen et al. 2009). In one example, *Camponotus* tending resulted in

Fig. 2 Mean diurnal (left panels) and nocturnal (right panels) abundance of **a**, **c** functional and **b**, **e** taxonomic groups, and **c**, **f** frequency of behaviours on trees with and without bromeliads. Error bars represent standard deviation from the mean. Abbreviations as in Table 1. Ordinate scale differs among panels
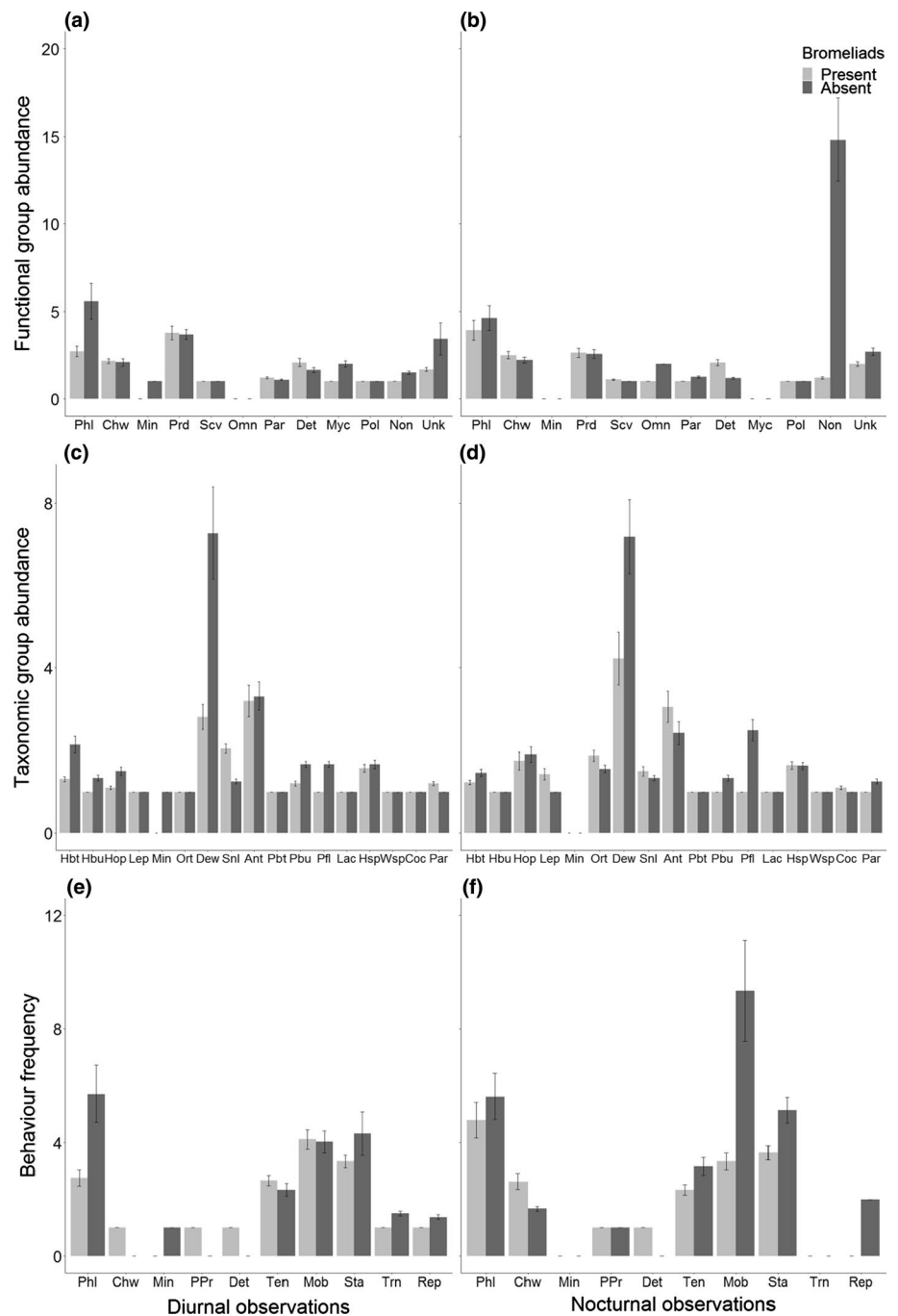
more than a 30% increase in the size of the hemipteran population compared to where tending was prevented (Renault et al. 2005). The presence or absence of ant tending can be a limiting resource to hemipterans (Holway et al. 2002) and such interactions are common in general (Delabie 2001) and in particular in Costa Rica (Espadaler et al. 2012). Such ant tending could explain the association observed in multivariate space between the presence of bromeliads in a tree, and the abundance of hoppers (comprising mobile members of

two hemipteran suborders), but confirming this mechanism would require careful manipulative experiments.

In conclusion, we documented relatively subtle effects of bromeliads or their associated predators on functional and taxonomic composition, as well as on the behavioural profile of the invertebrates on orange trees. This contrasts with the strong negative effects of bromeliads, especially bromeliads with ants, on leaf damage reported in the same area of Costa Rica several years earlier (Hammill et al. 2014). This difference is likely due to the difference in dominant ant species in
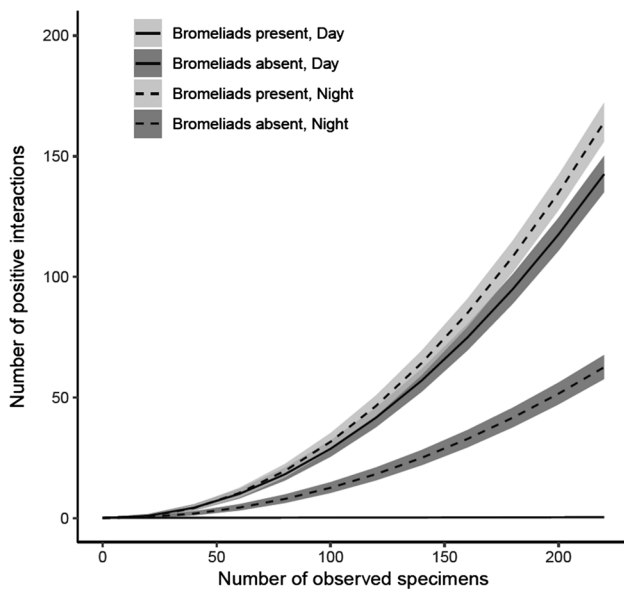
Fig. 3 Estimates of the effect of bromeliad presence, number of observed specimens, and time of observation (day/night) on positive interspecific interactions. Error bars represent 95% confidence interval, and do not include variation captured by random effects. Brown lines represent trees with bromeliads and green lines represent trees without bromeliads. Opaque confidence intervals of each colour represent estimations for nocturnal observations, while transparent ones represent estimates for diurnal observations. The horizontal brown line represents the negligible estimates for diurnal observations of positive interactions on trees with bromeliads

the two systems: while Hammill et al. (2014) recorded many predatory ants in the species *Odontomachus hastatus* Fabricius, the dominant ant species associated with bromeliads in our study were instead found commonly tending aphids and scale insects. As a result, our bromeliad-associated ant species act as much as facilitators as predators, attenuating potential cascading effects. Our study emphasizes that bromeliads can affect invertebrate composition on orange trees, effects that change with diel patterns in invertebrate occupancy of bromeliads versus tree brancShes, and that appear contingent on the agricultural practices in different sites. In conclusion, in line with Paine (1980), detailed observations on how invertebrates behave, coupled with taxonomical and functional information, can help deciphering the complex links between species in ecological communities.

Author contribution statement PR designed the survey. PR collected the data and analyzed it with input from DSS. BRK and MAS identified ant species. PR wrote the first version of the manuscript, and all other co-authors made contributions to manuscript revision.

Data availability statement Data available from the Open Science Framework: https://osf.io/kx7sw/.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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