Research Article

Inflorescences of the Bromeliad *Vriesea friburgensis* as Nest Sites and Food Resources for Ants and Other Arthropods in Brazil

Volker S. Schmid,[1] Simone Langner,[2] Josefina Steiner,[3] and Anne Zillikens[3,4]

[1] Department of Evolution, Behavior and Genetics, University of Regensburg, 93040 Regensburg, Germany
[2] Justus-Liebig-Universität Gießen, Karl-Glöckner-Straße 21 C, 35394 Gießen, Germany
[3] Departamento de Biologia Celular, Embriologia e Genética, CCB, Campus Universitário Trindade,
  Universidade Federal de Santa Catarina, 88040-900 Florianópolis, SC, Brazil
[4] Med.-Naturwissenschaftliches Forschungszentrum, Universität Tübingen, Ob dem Himmelreich 7, 72074 Tübingen, Germany

Correspondence should be addressed to Volker S. Schmid; volker.schmid@biologie.uni-regensburg.de

For the first time, the usage of bromeliad inflorescences as nesting sites for ants and other arthropods was studied. Frequencies of occurrence of nests were recorded from hollow stems of dried infructescences of the bromeliad *Vriesea friburgensis* on Santa Catarina Island, southern Brazil. Three habitat types were studied: miconietum and two types of restinga, one with low (restinga-low) and one with high vegetation cover (restinga-high). Additionally, flower visitation by ants was examined in restinga-low. Out of 619 infructescences, 33% contained nests. Ants were the most frequent occupants (82–96% of nests), followed by termites (3–18%) and bees (0–0.6%). Species accumulation curves and diversity indices indicate that the diversity of stem-occupying ant species is highest in restinga-low (eight species observed, 18 predicted) and lowest in restinga-high (four observed and predicted). Highest similarity of compositions of infructescence-inhabiting ant species was recorded between miconietum and restinga-high, lowest between restinga-low and restinga-high. Similarity between compositions of inflorescence-visiting and infructescence-inhabiting species in restinga-low was even higher (compared with the cases described in the previous sentence) although 50% of the involved species were present in only one of the samples. Altogether, our results indicate that inflorescences are important resources for ants and other nest-building insects from flowering season to past-fruiting season.

1. Introduction

Bromeliads (Bromeliaceae) are monocot plants occurring almost exclusively in the neotropics [1]. Animal-bromeliad interactions are highly diverse and have been in the focus of intensive research during the last decades [2]. Consequently, several aspects of these associations are well studied, for example, pollinator systems [3–5] or usage of bromeliad rosettes as nest sites by ants [6, 7] and bees [8]. Additionally, bud and fruit capsules are known to nourish and shelter developmental stages of wasps [9] and butterflies [10].

The stalks of bromeliad inflorescences or infructescences have mainly been reported as subjects of insect larval herbivory. For example, inflorescence stems may be infested by several species of Curculionidae (Coleoptera) [2]. In the bromeliad species *Vriesea friburgensis* Mez var. *paludosa* (L. B. Smith) L. B. Smith 1952, flower buds are sterilized by the feeding behavior of a eurytomid wasp larva. Affected flowers do not open and eventually dry up forming a resistant pupal chamber for the developing larva [9]. A similar case is that of *Strymon serapio* (Godman and Salvin 1887) [10] whose larvae attack the ripening fruit capsule of *V. friburgensis*. During feeding, the larva enters the capsule and finally pupates within. In both cases, the imagines emerge from their pupal chambers after weeks or even months. This is enabled by the fact that the stalk of the drying infructescence usually remains standing erect in the rosettes for one year or longer,

instead of wilting and decomposing rapidly (pers. obs.). This feature is typical for many species in the genus *Vriesea* which has an anemogamous seed dispersal syndrome, and allows the small seeds provided with pappi to take flight with the wind. This is in sharp contrast to other bromeliads in the subfamily Bromelioideae whose seeds are embedded into a fleshy pulp and whose infructescence stalks wilt and collapse soon after the colorful berries have been eaten by birds and small mammals.

In the course of a study on the diversity and interactions of flower visitors of bromeliads in the Atlantic rainforest of southern Brazil, we discovered stems of old infructescences of *V. friburgensis* to be inhabited by ant species. This, together with the other mentioned characteristics of the infructescence stalk, suggests that it might play another important role in the ecosystem by providing shelter or nest sites with a beneficial environment for perennial arthropods and social insects. Among the latter, ants constitute the dominant animal group in most terrestrial ecosystems [11], and numerous species that are unspecialized nesters could benefit from the properties of infructescence stems. Therefore, assessing the use of stalks as nesting sites was the main purpose of our study.

Not only infructescences but also inflorescences are, at least during flowering, attractive to ants: in a preliminary census, about 50% of 159 open flowers (distributed over 68 inflorescences) were visited by at least one ant (S. Langner, unpubl. data). The inflorescences are visited by a high diversity of animals, mainly bees [12]. Yet, ants have not been systematically registered so far; hence, an additional goal of our study was to survey the spectrum of ant species associated with inflorescences and infructescences.

In particular, we determined frequencies of occurrence as well as alpha and beta diversity (i.e., diversity within and among habitats) of ants and other arthropods in old infructescence stems of *V. friburgensis*. We expected differences in ant species richness (which is one component of diversity) and composition among habitat types due to different species communities as was reported for inflorescence-visiting ants of other bromeliad species [13]. At one site, we also recorded ants visiting inflorescences for comparison with the stem-inhabiting ants, testing the hypothesis that species richness and composition should be similar because ants living within the bromeliads can be expected to visit nearby flowers.

2. Material and Methods

2.1. Study Plant. *Vriesea friburgensis* is a common, mostly soil-growing but facultatively epiphytic tank bromeliad occurring in forest and restinga habitats in southern Brazil [12, 14, 15]. Its inflorescences, flowering from November to March [9, 12], reach a height of about 0.5–1.5 m (for habitus see Supplementary Figures S1 and S2 in Supplementary Material available online at http://dx.doi.org/10.1155/2014/396095). The dry infructescences frequently remain standing erect in the rosettes for one year or longer, and even when bent or broken, they may stay more or less intact for a long period

of time (pers. obs.). Only terrestrially growing plants were examined.

2.2. Study Sites and Period. The study was conducted from January 2006 to January 2009 in the municipality of Florianópolis on Santa Catarina Island, southern Brazil. Infructescence occupation was examined between August and February, inflorescence visitation in December and January. Observations and sampling were performed in the two habitat types "miconietum" (a pre-forest succession stage, [8]) and "restinga" (a xerophilous vegetation formation on sand dunes, [16]). Four sites were studied: (i) a mountainside in Santo Antônio de Lisboa (miconietum; 27°30′26″S, 48°30′28″W); (ii) Joaquina beach (27°37′37″S, 48°26′59″W) (see Supplementary Figure S2) and (iii) Campeche beach (27°40′38″S, 48°28′48″W), both similar low-vegetation restingas and pooled as "restinga-low"; (iv) Reserva Ecológica do Morro das Aranhas (high-vegetation restinga, termed "restinga-high"; 27°28′11″S, 48°23′06″W). An overview of most samples described in the following subsections is provided in Supplementary Figure S3.

2.3. Assessing Infructescence Occupation. We examined a total of 619 infructescences (defined as the stem and remains of buds and fruits above the level of the water reservoir in the rosette) for nests of ants and other social insects by breaking them apart. Criterion for the record of a nest was the presence of brood. Other arthropods were occasionally registered too.

From a subset of 131 infructescences (restinga-low: 54; restinga-high: 28; miconietum: 49), inhabitants of the interior of the stem as well as of cavities under bracts were hand-collected and identified in the laboratory. For the other fraction (488 infructescences, only restinga-low), we identified the inhabitants directly in the field and additionally noted whether the stems were solid or hollow. Cavities under bracts were not examined in this case. To estimate cavity volume, five hollow infructescences were randomly chosen and the lengths and inner diameters (at base and apex) of their cavities were measured.

In addition to the samples described above, we recorded arthropods in infructescences during occasional field trips that were not specifically associated with this study. Sometimes, we also examined the most basal, humid part of the stems. Those findings are separately presented in the results section and Supplementary Table S9 but were not taken into account for the remaining data presentation and analysis. Generally, sets of infructescence stems that served as references for calculation of percentages included those that were not hollow. This is because we regard massive stems to be a resource for ants too, at least for those that are capable of gnawing holes into the plant material themselves.

Three samples of non-social insect brood were taken to the laboratory and reared to adult stages for identification. Voucher specimens of all collected species were deposited in the entomological collection of the Native Bee Laboratory, BEG, Federal University of Santa Catarina, Florianópolis, Santa Catarina, Brazil.

2.4. Inflorescence Visitation by Ants. For identification of ants foraging on inflorescences, specimens were hand-collected from a set of 33 flowering inflorescences (from flower-bearing branches or the nearby stalk; see Supplementary Figure S1) at Joaquina. In two cases, ants were present but could not be identified because they escaped collection. Moreover, the presence of ants within flowers was recorded at the same site, where a further sample of 101 randomly chosen inflorescences was defined. On five days in weekly intervals, all available open flowers on these inflorescences were examined for ants. Because inflorescence lifetime of *V. friburgensis* usually includes days without open flowers [12], the number of inflorescences with open flowers varied between 40 and 79 (out of 101).

For investigating whether the attractiveness of inflorescences begins with the emergence of open flowers or earlier, we assessed ant presence for a separate set of 26 inflorescences with buds only.

2.5. Species Richness and Diversity. We compared the diversity of ants occupying infructescences among habitats (three comparisons) as well as infructescence occupation with inflorescence visitation in restinga-low. Alpha diversity (diversity within each locality) was assessed by computing species accumulation curves (generated with the "Mao Tau" binomial mixture model by Colwell et al. [17]), the Chao2 species richness estimator, and the reciprocal Simpson index. Since Simpson diversity is a measure that combines species richness with the evenness of the species abundance distribution, we also calculated Simpson evenness by dividing the Simpson index by the number of observed species (as given by the species accumulation curves) [18]. Accumulation curves and means (obtained by 1000-fold resampling) of estimators and indices were plotted against the cumulative number of species occurrences as a measure of sampling effort [19]. If such a curve reached a plateau over a logarithmically scaled x-axis, we regarded the corresponding index or species richness as stable [19]; if not, then it was expected to change with increased sampling.

For evaluating beta diversity (i.e., complementarity between sites, [18]) of ant species inhabiting infructescences and visiting inflorescences among the three habitats we calculated Chao's estimator for the Jaccard similarity index ("Chao-Jaccard") with 95% confidence intervals for statistical comparisons. Since similarity is reciprocally related to beta diversity [18], a low similarity index indicates high beta diversity among the sites compared. All species richness and diversity computations were performed with the software package EstimateS 8.2 [20].

3. Results

3.1. Infructescence Occupation. Overall, 205 of all 619 examined infructescences (33%) were occupied by nests of ants (Supplementary Figure S4), termites, or bees. Depending on habitat, ant nests were found in at least 18% of the stems (Figure 1) and made up the majority of nesting occupants (miconietum: 82%; restinga-low: 97%; restinga-high: 94%).
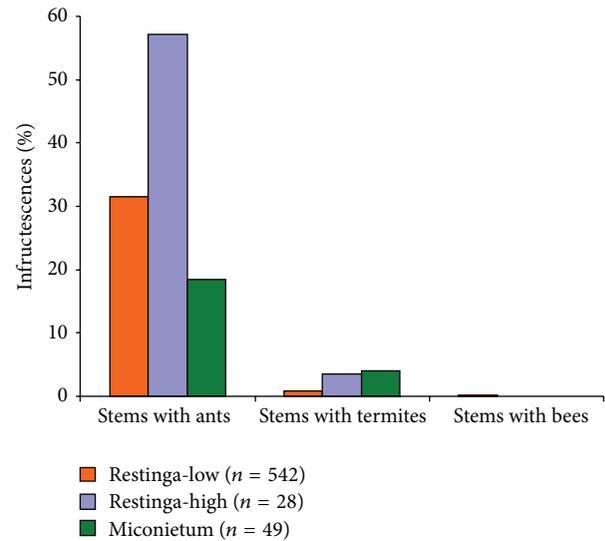

Figure 1: Percentages of infructescences of *Vriesea friburgensis* occupied by ant, termite, or bee nests in different habitat types (whole dataset, $n = 619$) on Santa Catarina Island, southern Brazil.

Under bracts, ant nests were present on 4–11% of infructescences (Supplementary Table S7). The most frequent stem inhabitants were ants of the genera *Camponotus*, *Pseudomyrmex*, and *Solenopsis* (Tables 1 and 2). During regular collections, we found nests of 14 ant species, at least two termite species (Termitidae: Nasutitermitinae: *Cortaritermes* sp. and *Velocitermes* sp.; habitat types miconietum and restinga-low; all nests occupied stem and rosette), and one bee species (Tables 1 and 2). Ant species composition differed among the habitat types (Table 1). We encountered eight cases of two social insect species occupying different sections of the same infructescence stem (Supplementary Table S8). Occasional findings outside of the regular dataset comprised nests of further ant species; brood of a megachilid bee, a castniid moth, and syrphid flies; several coleopterans, pseudoscorpions, collembolans, and spiders (Supplementary Table S9).

Out of 488 infructescence stems collected at restinga-low sites, 402 (82%) were hollow, and of these, 161 (40%) were occupied by ants, termites, or bees (Table 2). Length of cavities in infructescences was 92 ± 22 cm (mean $\pm$ SD, $n = 5$), and inner diameter was 1.9 ± 1.3 mm at apex and 4.6 ± 0.9 mm at base, yielding an estimated volume of 37 ± 30 cm^3 (assuming a truncated-cone shape).

3.2. Inflorescence Visitation by Ants. We found ants foraging on 22 of 33 (67%) flowering inflorescences. Furthermore, at 36–70% (median 55%, $n = 5$) of the weekly examined flowering inflorescences ($40 \leq n \leq 79$), ants were observed inside flowers. In contrast, ants were present at one of 26 (4%) inflorescences with buds only. Nine ant species/morphospecies were identified; most species and visitor records belonged to the genera *Camponotus* and *Pseudomyrmex* (Table 1).

TABLE 1: Absolute frequencies of occurrence of ant species recorded at 33 flowering inflorescences as well as of ant nests in infructescence stems (subset of 131 infructescences) of *Vriesea friburgensis* in three habitat types on Santa Catarina Island, southern Brazil. Differences between sum of ant records and number of occupied infructescences are due to occupations of stems with two ant species.

Ant species	At inflorescences (restinga-low)	Nests in infructescences		
		Restinga-low	Restinga-high	Miconietum
Acromyrmex rugosus (Smith 1858)	1			
Camponotus arboreus (F. Smith 1858)		1		
Camponotus bonariensis Mayr 1868		4		
Camponotus novogranadensis Mayr 1870	11	1		
Camponotus rufipes (Fabricius 1775)	2			
Camponotus sexguttatus (Fabricius 1793)	4	1		
Camponotus trapezoideus Mayr 1870			1	2
Camponotus sp. 13	1			
Camponotus sp. 14		1		
Cephalotes minutus (Fabricius 1804)				1
Crematogaster curvispinosa Mayr 1862			3	
Crematogaster limata F. Smith 1858			4	3
Nesomyrmex spininodis (Mayr 1887)				2
Procryptocerus convergens (Mayr 1887)				2
Pseudomyrmex gracilis (Fabricius 1804)	6	6		1
Pseudomyrmex phyllophilus (F. Smith 1858)	6	4		
Pseudomyrmex sp. PSW05[a]	1			
Solenopsis sp. 2	2	1	10[b]	1
Sum of ant records	34	19	18	11
Number of occupied stems	—	18	17	9
Number of examined stems	33	54	28	49

[a]A species of the *P. flavidulus* species complex which "might actually correspond to *P. flavidulus* itself" (Philip Ward, pers. comm.).

[b]Once three stems very close to each other were occupied by this species, so it was presumably the same colony, resulting in eight independent findings in restinga-high. Therefore, the value "8" was used for computation of similarity and diversity indices.

3.3. Species Richness and Diversity. The species accumulation curve of the restinga-high habitat reached a plateau (Supplementary Figure S5) and was significantly lower than the curve of miconietum, indicated by non-overlapping 95% confidence limits at the end of the shorter curve (Figure 2(a)). Moreover, the confidence limits of the restinga-high curve almost fell below those of the restinga-low curve. The other three curves lay near to each other without significant differences and without stabilizing. The Chao2 species richness estimator predicted highest (and even rising) richness for restinga-low and (according to the 95% confidence limits) significantly lowest for restinga-high (Figure 2(b)). The Simpson diversity index showed the same trend as the species accumulation curves (Figure 2(c)): highest diversity in miconietum and lowest in restinga-high. Finally, evenness was highest for miconietum (Figure 2(d)).

Comparing the ant communities that nested in infructescences, the Chao-Jaccard similarity index was highest for the habitat type pair restinga-high/miconietum (0.58), followed by restinga-low/miconietum (0.19) and restinga-low/restinga-high (0.05) (the latter significantly different from the first, according to 95% CIs), that is, beta diversity ascended in that order (Figure 3). Similarity between the inflorescence and infructescence samples in restinga-low was highest overall and significantly higher than between infructescence occupation in restinga-low and the other two habitats (Figure 3).

4. Discussion

4.1. Species Accounts. Altogether, we recorded 22 ant species (three subfamilies, nine genera) and at least 12 other arthropod species associated with inflorescences and infructescences of *V. friburgensis*. Even these high numbers must still be regarded as underestimations because species richness did not reach saturation in any habitat. Considering this inventory incompleteness and our sampling bias (focusing the search on social insects), there must be a lot more to discover in terms of animal associations with *V. friburgensis*. This is especially true if the view is extended from the inflorescence to the whole plant. The rosettes, which were not systematically examined in this study, might harbor a high diversity of macroinvertebrates as indicated by Zanin and
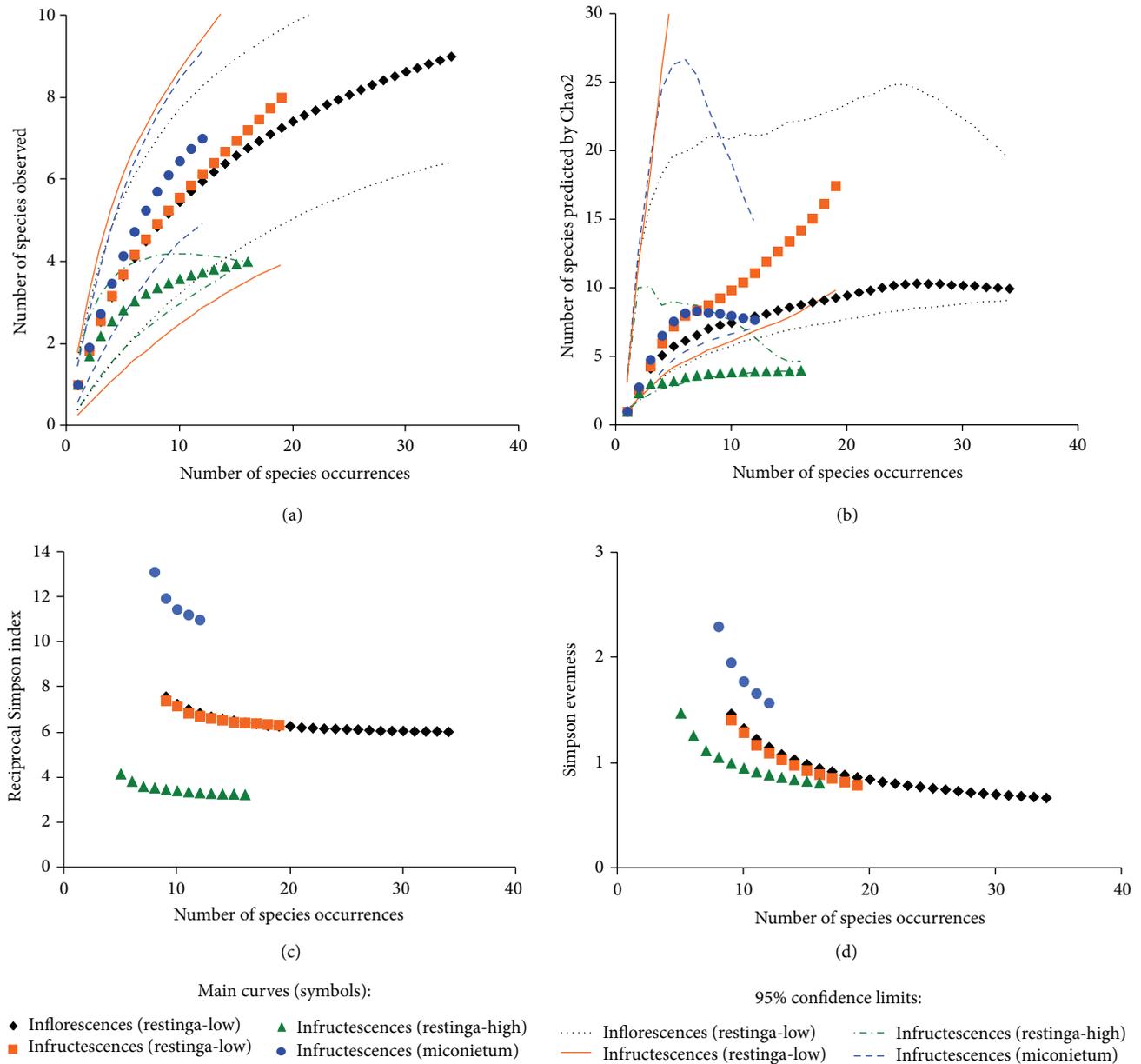
(a)

(b)

(c)

(d)

Main curves (symbols):

♦ Inflorescences (restinga-low)   ▲ Infructescences (restinga-high)
■ Infructescences (restinga-low)   ● Infructescences (miconietum)

95% confidence limits:

.... Inflorescences (restinga-low)   –·–· Infructescences (restinga-high)
——— Infructescences (restinga-low)   – – – Infructescences (miconietum)

FIGURE 2: Diversity of ants inhabiting infructescences or visiting inflorescences of *Vriesea friburgensis*, according to habitat type on Santa Catarina Island, southern Brazil. Plotted against number of species occurrences as measure of sampling effort are (a) species accumulation curves and their 95% confidence limits; (b) Chao2 species richness estimator including 95% confidence limits; (c) rarefaction curves of Simpson diversity index; and (d) Simpson evenness (Simpson diversity divided by the number of species observed). Diagrams with the same data but with logarithmically scaled x-axes are included in the Supplementary Material (Supplementary Figure S5).

Tusset [15] for *V. friburgensis* and as reported for the related bromeliad species *V. inflata* (Wawra 1883) [21].

At least two ant species were for the first time reported for Santa Catarina Island (*Procryptocerus convergens*) or even Santa Catarina state (*Cephalotes minutus*) since they do not appear in previous inventories [7, 13, 22–30].

The termites we found living in the bromeliads probably belong to two undescribed species (E. Marques Cancello, pers. comm.). Since their nests were mostly located both in the rosettes and infructescence stems, their relation to

the bromeliads might be similar to the association between the termite *Cortaritermes silvestrii* (Holmgren 1910) and the bromeliad *Dyckia maritima* Baker where the plants appear to grow on termite nests because of beneficial nutrition [31]. But this assumption needs further investigation to be confirmed.

4.2. Arthropods Living in Infructescences. We consider infructescences of *V. friburgensis* to be attractive nest sites for certain groups of arthropods (e.g., small ant colonies and small, serially nesting bees) because they

TABLE 2: Nests of ants and other insects in 488 infructescences (161 occupied) of *Vriesea friburgensis* in Joaquina (habitat type restinga-low) on Santa Catarina Island, southern Brazil. *n*: number of findings (total of 164 due to three cases with two nests in the same stem); % (occ.): percent fraction of the number of occupied stems; % (total): percent fraction of the number of examined infructescences.

Taxon	*n*	% (occ.)	% (total)
Apidae			
Ceratina (*Rhyssoceratina*) sp. (Xylocopinae)[a]	1	0.6	0.2
Formicidae			
Brachymyrmex	3	1.9	0.6
Pseudomyrmex	63	39.1	12.9
Pseudomyrmex gracilis	57	35.4	11.7
Pseudomyrmex sp. PSW05	6	3.7	1.2
Camponotus	68	42.2	13.9
Myrmelachista	1	0.6	0.2
Solenopsis	24[b]	14.9	4.1
Small yellow formicine or dolichoderine ants	1	0.6	0.2
Isoptera[c]	3	1.9	0.6

[a]Three females reared from brood cells.
[b]Once, five stems very close to each other were occupied by this species, so it was presumably the same colony, resulting in 20 independent findings.
[c]Probably *Cortaritermes* sp. according to another termite sample from the same location.
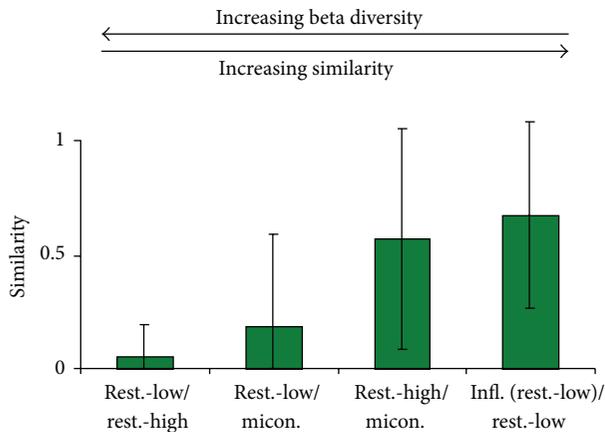

FIGURE 3: Chao-Jaccard similarity index for comparisons of infructescence occupation of *Vriesea friburgensis* by ants among habitats and of infructescence- with inflorescence-associated ants in restinga-low. Whiskers represent 95% confidence intervals; for convenience their lower bounds were cut when crossing the *x*-axis. Calculations were based on the data given in Table 1.

(1) provide a long, narrow space which can be used and defended more efficiently than a compact space of the same volume;

(2) dry up and frequently remain stable for more than a year, a feature which is important for bees and wasps with annual or bivoltine life cycles [9, 32];

(3) are mostly connected to a water reservoir in the leaf rosette, building kind of an oasis especially in well drained sandy habitats such as restingas;

(4) grow near to food sources, such as future inflorescences emerging from adjacent rosettes of the same bromeliad clone, providing floral nectar and flower visitors.

Not only can arthropods profit from nest space provided by *V. friburgensis* but also the plant may gain benefits. As known from former studies, ants frequently protect the plants they live in from herbivores (e.g. [33–36]). Whether *V. friburgensis* actually is protected from its inflorescence herbivores (e.g. *Eurytoma* sp. [9], *Strymon serapio* [10]) is unclear since many of them might already be active before the first flowers open; that is, when ants are not present yet. This might be assessed with exclusion experiments (e.g., [37]).

In most of the habitats studied, *Vriesea* infructescences appear to support a similar alpha diversity of ants. Whereas all diversity measures employed accord that restinga-high had lowest alpha diversity, with no more than four species predicted, species accumulation curves do not allow distinguishing among the other habitat types because they were too close to each other and did not stabilize. Moreover, the habitat ranking derived from the species richness estimator contradicts that indicated by the Simpson diversity index. Since the latter is influenced by species abundance distributions [18] we assume that restinga-low contains more species but with a rather uneven distribution in contrast to miconietum. This is indeed confirmed by estimated evenness.

The restinga-high habitat, in spite of its relatively low species richness, complements the ant species composition of the other habitats, especially low-vegetation restinga, demonstrated by the low similarity index value. Hence, occurring in such different habitats, *V. friburgensis* also supports a high beta diversity of ants.

We do not expect ants to be exclusively dependent on the infructescence stems as nest sites because similar cavities can also be found in other plants. For example, we discovered nests of *Pseudomyrmex gracilis* and *Ps.* sp. PSW05 in twigs of *Epidendrum fulgens* Brongn. 1834 (Orchidaceae) as well as *Nesomyrmex spininodis* in twigs of shrubs (V. S. Schmid, unpubl. data), and Cereto et al. [38] collected, at another restinga-low site on Santa Catarina Island, nests of eight ant species from postreproductive plants of *Actinocephalus polyanthus* (Bong.) Sano (Eriocaulaceae), a plant with a habitus similar to bromeliads and occurring sympatrically with *Vriesea* at our restinga-low study sites.

Cereto et al. [38] reported that 79.1% of *A. polyanthus* plants contained ant nests with up to four species living in the same plant. On the one hand, comparison with our study is difficult because sample sizes greatly differ, no accumulation curves were provided by Cereto et al. [38], and they examined whole plants while we only systematically examined the infructescence stems. It is well known that bromeliad rosettes are frequently used by ants as nest sites [6, 7, 13], so the percentage of *V. friburgensis* plants containing ant nests will most likely be higher than the occupation ratio of infructescence stems. On the other hand, both

Cereto et al. [38] and we report the occurrence of several ant species sharing the same plant, indicating that there might be high competition for nest sites in the restingas (see also Livingston and Philpott [39] arguing for generally high competition among ants). If this is true, it seems strange that a high proportion (61%) of hollow *V. friburgensis* infructescence stems was found unoccupied. The causes of this phenomenon remain to be studied in more detail, taking into account aspects such as dynamics of cavity development in plants and of ant colony movements, that is, turnover of site occupation.

4.3. Ants Visiting Inflorescences. Simpson diversity of ants inhabiting infructescence stems in restinga-low was similar to that of those visiting inflorescences in the same habitat type, although the estimated species richness differed significantly. Similarity in alpha diversity goes in line with the compositional similarity between these samples being higher than among the habitats, thus supporting our hypothesis that there is a great overlap between ant species that live in the bromeliads and those that visit their flowers.

However, individuals of some ant species visited the inflorescences, whereas the same species were not found living in infructescences. This may be due to nesting preferences; for example, *Camponotus rufipes* has large workers and colonies that construct nest mounds using plant material, sometimes within groups of *Vriesea* rosettes but apparently not extending into infructescence stems emerging from those rosettes; and *Acromyrmex* species generally nest in the soil [40].

Three *Camponotus* species nested in infructescence stems but were not observed on inflorescences. It might turn out interesting to find out the causes for this pattern, that is, whether it was mere chance owing to low sample size or whether these ants systematically avoid inflorescences, be it due to interspecific competition or because of their foraging habits.

We found five ant genera at inflorescences of *V. friburgensis*. However, within flowers, almost exclusively *Camponotus* ants were present (mainly *Ca. novogranadensis* and *Ca. rufipes*, probably also *Ca. sexguttatus*; V. S. Schmid, pers. obs.). They do not entirely monopolize the inflorescences since we mostly found unoccupied flowers near the occupied ones on the same inflorescences. Occasional behavioral observations indicate that *Camponotus* workers visit flowers to take up floral nectar, sometimes apparently guarded by a conspecific worker (Supplementary Figure S6). They might additionally hunt flower mites which we found along our examinations within flowers of 29 out of 32 (91%) inflorescences in Joaquina and also recorded them in miconietum (V. S. Schmid, unpubl. data), as similarly reported by Schmid et al. [13] for the bromeliad species *Aechmea lindenii* (E. Morren) Baker and *Ae. nudicaulis* (L.) Grisebach. We expect the mites in *V. friburgensis* to belong to the same species (*Proctolaelaps* sp. and *Tropicoseius* sp.) as in *Ae. lindenii* because they are phoretically transported by hummingbirds (see Video S6 in [13]) which occur on the whole island and visit flowers of species of *Aechmea* [3–5, 41] and *Vriesea* [4, 12].

As for infructescence occupation, we regard it as unlikely that any of the ant species reported here is specifically associated with inflorescences of *V. friburgensis*. Its flowers are accessible only during a limited period throughout the year and are not completely monopolized by one or a few ant species; thus ants do not completely depend on the floral resources.

The presence of ants on plants is frequently accompanied by a mutually beneficial association where the ants are attracted by food and/or shelter and in turn provide protection to the plant by deterring herbivores and/or cutting other vegetation that competes with the host plant for resources (e.g., [33–36]). In bromeliads, such a mutualism was reported for *Dyckia floribunda* where exclusion of ants yielded a significant decrease in total seed production per plant [37]. Unlike *D. floribunda*, *V. friburgensis* does not produce extrafloral nectar on its inflorescences (V. S. Schmid, unpubl. data: six plastic-bagged inflorescences inaccessible to animals did not show signs of secreted fluids). The ants are apparently attracted mainly by the nectar contained inside the flowers. They might have both positive and negative effects on the plants' reproductive success by interfering with herbivores and/or pollinators, respectively. Hence, whether *V. friburgensis* benefits from the presence of the ants cannot be judged without appropriate manipulative experiments.

5. Conclusion

Even though there are probably no specific associations with *V. friburgensis*, this bromeliad species does support a high level of alpha and beta diversity of arthropods, mainly ants. Regarding the high potential for competition for nest sites among ant species [39], *V. friburgensis* likely plays an important role for the species communities of the Atlantic Forest region, confirming former studies which stressed the ecological significance of bromeliads (e.g., [10, 13, 42, 43]; see also [2] and references therein). Beyond the scope of our study, there are certainly other bromeliad species (e.g., *Dyckia* spp.; *Hohenbergia* spp.; other *Vriesea* spp.) whose infructescences are worth a closer examination with respect to inhabiting arthropods. Concluding, we recommend that bromeliads should be taken into special consideration for biodiversity conservation efforts.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.
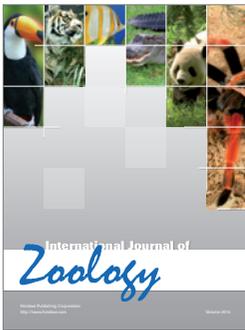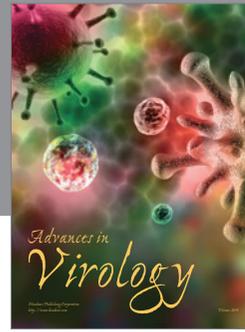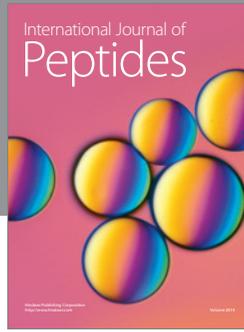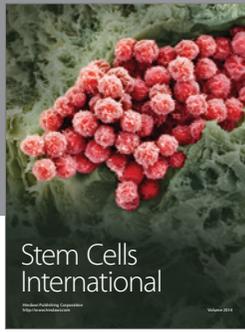
Acknowledgments

References

[1] D. H. Benzing, *Bromeliaceae—Profile of an Adaptive Radiation*, Cambridge University Press, Cambridge, UK.

[2] J. H. Frank and L. P. Lounibos, "Insects and allies associated with bromeliads: a review," *Terrestrial Arthropod Reviews*, vol. 1, pp. 125–153, 2008.

[3] L. L. Dorneles, A. Zillikens, B. Harter-Marques, and J. Steiner, "Effective pollinators among the diverse flower visitors of the bromeliad *Aechmea lindenii* in south Brazilian Atlantic rain forests," *Entomologia Generalis*, vol. 33, no. 3, pp. 149–164, 2011.

[4] R. Kamke, S. Schmid, A. Zillikens, B. C. Lopes, and J. Steiner, "The importance of bees as pollinators in the short corolla bromeliad *Aechmea caudata* in southern Brazil," *Flora*, vol. 206, no. 8, pp. 749–756, 2011.

[5] S. Schmid, V. S. Schmid, A. Zillikens, B. Harter-Marques, and J. Steiner, "Bimodal pollination system of the bromeliad *Aechmea nudicaulis* involving hummingbirds and bees," *Plant Biology*, vol. 13, no. s1, pp. 41–50, 2011.

[6] N. Blüthgen, M. Verhaagh, W. Goitía, and N. Blüthgen, "Ant nests in tank bromeliads—an example of non-specific interaction," *Insectes Sociaux*, vol. 47, no. 4, pp. 313–316, 2000.

[7] F. B. Rosumek, M. A. Ulysséa, B. C. Lopes, J. Steiner, and A. Zillikens, "Formigas de solo e de bromélias em uma área de Mata Atlântica, Ilha de Santa Catarina, sul do Brasil: Levantamento de espécies e novos registros," *Biotemas*, vol. 21, no. 4, pp. 81–89, 2008.

[8] A. Zillikens, J. Steiner, and Z. Mihalkó, "Nests of *Augochlora (A.) esox* in bromeliads, a previously unknown site for sweat bees (Hymenoptera: Halictidae)," *Studies on Neotropical Fauna and Environment*, vol. 36, pp. 137–142, 2001.

[9] S. Grohme, J. Steiner, and A. Zillikens, "Destruction of floral buds in the bromeliad *Vriesea friburgensis* by the phytophagous larvae of the wasp *Eurytoma* sp in southern Brazil (Hymenoptera: Eurytomidae)," *Entomologia Generalis*, vol. 30, no. 2, pp. 167–172, 2007.

[10] S. Schmid, V. S. Schmid, R. Kamke, J. Steiner, and A. Zillikens, "Association of three species of *Strymon* Hübner (Lycaenidae: Theclinae: Eumaeini) with bromeliads in southern Brazil," *Journal of Research on the Lepidoptera*, vol. 42, pp. 50–55, 2010.

[11] B. Hölldobler and E. O. Wilson, *The Ants*, Belknap Press of Harvard University Press, Cambridge, Mass, USA; Springer, Berlin, Germany, 1990.

[12] S. Schmid, V. S. Schmid, A. Zillikens, and J. Steiner, "Diversity of flower visitors and their role for pollination in the ornithophilous bromeliad *Vriesea friburgensis* in two different habitats in Southern Brazil," *Ecotropica*, vol. 17, no. 1, pp. 91–102, 2011.

[13] V. S. Schmid, S. Schmid, J. Steiner, and A. Zillikens, "High diversity of ants foraging on extrafloral nectar of bromeliads in the Atlantic rainforest of southern Brazil," *Studies on Neotropical Fauna and Environment*, vol. 45, no. 1, pp. 39–53, 2010.

[14] R. Reitz, *Bromeliáceas e a Malária-Bromélia Endêmica*, Flora Ilustrada Catarinense, Itajaí, Brazil, 1983.

[15] E. M. Zanin and C. Tusset, "*Vriesia* [sic!] *friburgensis* Mez.: distribuição vertical da espécie e fauna associada," *Revista Brasileira de Biociências*, vol. 5, supplement 1, pp. 138–140, 2007.

[16] M. C. Sampaio, L. E. Perissé, G. A. De Oliveira, and R. I. Rios, "The contrasting clonal architecture of two bromeliads from sandy coastal plains in Brazil," *Flora*, vol. 197, no. 6, pp. 443–451, 2002.

[17] R. K. Colwell, C. X. Mao, and J. Chang, "Interpolating, extrapolating, and comparing incidence-based species accumulation curves," *Ecology*, vol. 85, pp. 2717–2727, 2004.

[18] A. E. Magurran, *Measuring Biological Diversity*, Blackwell Science, Oxford, UK, 2004.

[19] J. T. Longino, J. Coddington, and R. K. Colwell, "The ant fauna of a tropical rain forest: estimating species richness three different ways," *Ecology*, vol. 83, no. 3, pp. 689–702, 2002.

[20] R. K. Colwell, "EstimateS: statistical estimation of species richness and shared species from samples, version 8.2," User's Guide and application, 2009, http://purl.oclc.org/estimates/.

[21] L. A. M. Mestre, J. M. R. Aranha, and M. L. P. Esper, "Macroinvertebrate Fauna Associated to the Bromeliad *Vriesea inflata* of the Atlantic Forest (Paraná State, Southern Brazil)," *Brazilian Archives of Biology and Technology*, vol. 44, no. 1, pp. 89–94, 2001.

[22] A. Bonnet and B. C. Lopes, "Formigas de dunas e restingas da Praia da Joaquina, Ilha de Santa Catarina, SC, (Insecta: Hymenoptera)," *Biotemas*, vol. 6, pp. 107–114, 1993.

[23] D. C. Cardoso and M. P. Cristiano, "Myrmecofauna of the southern Catarinense Restinga Sandy Coastal Plain: new records of species occurrence for the State of Santa Catarina and Brazil," *Sociobiology*, vol. 55, no. 1B, pp. 229–239, 2010.

[24] D. C. Cardoso, T. G. Sobrinho, and J. H. Schoereder, "Ant community composition and its relationship with phytophysiognomies in a Brazilian Restinga," *Insectes Sociaux*, vol. 57, no. 3, pp. 293–301, 2010.

[25] B. C. Lopes and H. G. Fowler, "Fungus-growing ants (Hymenoptera: Formicidae) on Santa Catarina Island, Brazil: patterns of occurrence," *Revista de Biología Tropical*, vol. 48, pp. 643–646, 2000.

[26] J. A. Lutinski and F. R. M. Garcia, "Análise faunística de Formicidae (Hymenoptera: Apocrita) em ecossistema degradado no município de Chapecó, Santa Catarina," *Biotemas*, vol. 18, pp. 73–86, 2005.

[27] J. A. Lutinski, F. R. M. Garcia, C. J. Lutinski, and S. Iop, "Diversidade de formigas na Floresta Nacional de Chapecó, Santa Catarina, Brasil," *Ciência Rural*, vol. 38, pp. 1810–1816, 2008.

[28] R. R. d. Silva, "Formigas (Hymenoptera: Formicidae) do oeste de Santa Catarina: histórico das coletas e lista atualizada das espécies do Estado de Santa Catarina," *Biotemas*, vol. 12, pp. 75–100, 1999.

[29] R. R. d. Silva and R. Silvestre, "Diversidade de formigas (Hymenoptera: Formicidae) em Seara, oeste de Santa Catarina," *Biotemas*, vol. 13, pp. 85–105, 2000.

[30] R. R. d. Silva and R. Silvestre, "Riqueza da fauna de formigas (Hymenoptera: Formicidae) que habita as camadas superficiais do solo em Seara, Santa Catarina," *Papéis Avulsos de Zoologia*, vol. 44, pp. 1–11, 2004.

[31] C. C. Waldemar and B. E. Irgang, "A ocorrência do mutualismo facultativo entre *Dyckia maritima* Backer [sic!] (Bromeliaceae) e o cupim *Cortaritermes silvestrii* (Holmgren), Nasutitermitinae, em afloramentos rochosos no Parque Estadual de Itapuã, Viamão, RS," *Acta Botanica Brasilica*, vol. 17, no. 1, pp. 37–48, 2003.

[32] A. Zillikens and J. Steiner, "Nest architecture, life cycle and cleptoparasite of the neotropical leaf-cutting bee *Megachile* (*Chrysosarus*) *pseudanthidioides* Moure (Hymenoptera: Megachilidae)," *Journal of the Kansas Entomological Society*, vol. 77, no. 3, pp. 193–202, 2004.

[33] B. L. Bentley, "The protective function of ants visiting the extrafloral nectaries of *Bixa orellana*," *The Journal of Ecology*, vol. 65, no. 1, pp. 27–38, 1977.

[34] B. Fiala and U. Maschwitz, "Studies on the south east Asian ant-plant association *Crematogaster borneensis*/*Macaranga*: adaptations of the ant partner," *Insectes Sociaux*, vol. 37, no. 3, pp. 212–231, 1990.

[35] D. H. Janzen, "Coevolution of mutualism between ants and acacias in Central America," *Evolution*, vol. 20, pp. 249–275, 1966.

[36] D. H. Janzen, "Allelopathy by myrmecophytes: the ant *Azteca* as an allelopathic agent of *Cecropia*," *Ecology*, vol. 50, pp. 147–153, 1969.

[37] J. L. Vesprini, L. Galetto, and G. Bernardello, "The beneficial effect of ants on the reproductive success of *Dyckia floribunda* (Bromeliaceae), an extrafloral nectary plant," *Canadian Journal of Botany*, vol. 81, no. 1, pp. 24–27, 2003.

[38] C. E. Cereto, G. O. Schmidt, A. G. Martins, T. T. Castellani, and B. C. Lopes, "Nesting of ants (Hymenoptera, Formicidae) in dead post-reproductive plants of *Actinocephalus polyanthus* (Eriocaulaceae), a herb of coastal dunes in southern Brazil," *Insectes Sociaux*, vol. 58, no. 4, pp. 469–471, 2011.

[39] G. F. Livingston and S. M. Philpott, "A metacommmunity approach to co-occurrence patterns and the core-satellite hypothesis in a community of tropical arboreal ants," *Ecological Research*, vol. 25, no. 6, pp. 1129–1140, 2010.

[40] M. Bollazzi, J. Kronenbitter, and F. Roces, "Soil temperature, digging behaviour, and the adaptive value of nest depth in South American species of *Acromyrmex* leaf-cutting ants," *Oecologia*, vol. 158, no. 1, pp. 165–175, 2008.

[41] M. Lenzi, J. Z. De Matos, and A. I. Orth, "Variação morfológica e reprodutiva de *Aechmea lindenii* (E. Morren) Baker var. *lindenii* (Bromeliaceae)," *Acta Botanica Brasilica*, vol. 20, no. 2, pp. 487–500, 2006.

[42] A. C. Araujo, E. Fischer, and M. Sazima, "As bromélias da região do Rio Verde," in *Estação Ecológica Juréia-Itatins: ambiente físico, flora e fauna*, A. V. Marques and W. Duleba, Eds., pp. 162–171, Holos Editora, Ribeirão Preto, Brazil, 2004.

[43] S. Buzato, M. Sazima, and I. Sazima, "Hummingbird-pollinated floras at three Atlantic forest sites," *Biotropica*, vol. 32, no. 4B, pp. 824–841, 2000.