Relationship between invertebrate fauna and bromeliad size

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(With 4 Figures)

Abstract

Several bromeliads species store water and organic substrates, allowing the establishment of phytotelmata and associated fauna on their leaves. In this study, we sampled 70 individuals of *Vriesea* sp. (Carrière) (Bromeliaceae), in rupestrian fields in the Serra de Ouro Branco-MG, Brazil. The relationships between invertebrate species richness and abundance and size of bromeliads were tested using multiple regression. We found 19 species associated with bromeliads, mainly Diptera larvae. The abundance of the phytotelmate fauna increased principally in relation to the volume of water in the bromeliad reservoir. Phytotelmata richness was affected principally by diameter of the reservoir. There was a significant relationship between the abundance and richness of invertebrates associated with leaves with diameter and height of the plant. Invertebrate richness was better explained by abundance of individuals. These results suggest that the increase of richness was attended by higher numbers of microhabitats and more space for colonization of bigger bromeliads. Additionally, there was more chance of sampling different species in locales with greater abundance of individuals.

Keywords: species-area relationship, phytotelmata fauna, insects, Bromeliaceae.

Relação entre a fauna de invertebrados e o tamanho da bromélia

Resumo

Muitas espécies de bromélias são capazes de armazenar água e detritos, permitindo o estabelecimento de comunidades associadas aos seus tanques de água e às suas folhas. Neste trabalho, foram amostrados 70 indivíduos de *Vriesea* sp. (Carrière) (Bromeliaceae), em uma área de campo rupestre na Serra de Ouro Branco-MG, Brasil. Foi testada a relação entre a riqueza e a abundância das comunidades de invertebrados associados e o tamanho da bromélia. Em todos os casos foram utilizadas análises de regressão linear múltipla. Foram amostradas 19 espécies, principalmente larvas de Diptera associadas à bromélia. A abundância da fauna fitotelmata aumentou principalmente com o volume de água no reservatório da bromélia. Já a riqueza de fitotelmata foi relacionada principalmente com o diâmetro da planta. No entanto, a abundância e riqueza dos invertebrados associados às folhas apresentaram relação significativa com a altura e o diâmetro da planta. A riqueza de invertebrados foi mais bem explicada pela abundância de indivíduos do que pelo tamanho da bromélia. Estes resultados sugerem que o aumento da riqueza pode ter sido resultante do maior número de microhabitats e de espaço para colonização em bromélia de maior tamanho. Além disso, houve maior chance de amostrar espécies diferentes em locais com maior abundância de indivíduos.

Palavras-chave: relação espécie-área, fauna fitotelmata, insetos, Bromeliaceae.

1. Introduction

In ecology, one of the most studied patterns is the relationship between species and area (Connor and McCoy, 1979; May, 1981), showing an increase in the number of species with increased size of the area. Larger areas are heterogeneous and support larger populations, thus reducing the probability of species extinction (Willig et al., 2003). The species-area relationship has been studied on a variety of spatial scales (Rosenzweig, 1995), and is used to explain species richness patterns of insects associated with plants (Strong et al., 1984). Larger bodied plants contain a higher quantity of resources and a higher number of microhabitats, thus increasing the probability of insect permanence, as well as increasing the possibilities to find refuge to escape natural enemies (Lawton and Schröder, 1977).

Bromeliads have an important ecological role (Cathcart, 1995) because they have phytotelmata, small bodies of water held by the plant in which many organisms live. Thus, bromeliads do not only increase the number of habitats for invertebrates associated with their leaves, as other plants do, but they also provide habitats for aquatic organisms (Ratsirarson and Silander, 1996). Generally, such water reservoirs harbour a low number of species. This relative simplicity facilitates the study of feeding relationships; hence, the communities inside phytotelmata can be used as models for ecological studies of colonization and community structure (Marguire, 1971).

In this study, we analyzed the effects of the epiphyt bromeliad *Vriesea* sp. (Bromeliaceae) size on the richness (number of species) and abundance (number of individuals) of the phytotelmata fauna, as well as of the invertebrate fauna associated with the bromeliad leaves. Larger bromeliads have larger reservoirs with a higher water volume increasing the space and site of oviposition (Richardson, 1999). We tested whether species richness and abundance of phytotelmata fauna as well as that of invertebrate fauna associated with the bromeliad leaves increased with size of the plant.

2. Material and Methods

2.1. Study sites

The Serra de Ouro Branco is situated south of the Espinhaço Mountain (43° 39' 44'' W and 20° 28' 44'' S), with a maximum altitude of 1573 m. The soil was characterized by an area of quartzite (canga), with rupestrian fields as the main vegetation type, with the predominance of Velloziaceae and Poaceae (Alkmim, 1987). The samples were obtained at an average altitude of 1250 m.

2.2. Sampling and analysis

Samples were collected from November 2002 to February 2003. Seventy individuals of *Vriesea* sp. (Carrière E. Morren ex Mez) (Bromeliaceae) were sampled in a 400 m transect, with a minimal distance of two meters between each sample. The sampled bromeliads were epiphytic and were associated with trunks of *Vellozia compacta* (Mart. ex. Schult. f.) (Velloziaceae).

The height (the vertical distance between the plant base and the peak of the highest leaf) and the largest diameter of the body of water, as well as the volume of water, were measured for each *Vriesea* individual. Samples of water were collected using a pipette (Lozovei and Silva, 1999). These measurements are used as estimators of the plant size (Kitching, 1987; Lopez et al., 1998, Richardson, 1999; Araújo et al., 2003). Two numbered recipients were used for each individual, one containing the phytotelmata community preserved in the water from the plant, and the other containing the invertebrate fauna associated with the bromeliad leaves, preserved in 70% alcohol. The invertebrates were collected using an entomological pincer and paintbrushes. Animals were classified into morphospecies.

2.3. Statistical analyses

To investigate the relationship between the abundance and the richness of the phytotelmata fauna with the bromeliad size were performed multiple regressions whose explanatory variables were the surrogates of bromeliad size: bromeliad height, water storage volume, and diameter of the reservoir and their interactions.

All analyses were carried out using generalized linear models followed by residual analyses (Crawley, 2002) and performed under R (R Development Core Team, 2005), followed by residual analyses to verify error distribution and the suitability of the models employed, including checks for overdispersion.

Model simplification was achieved by extracting non-significant terms ($p > 0.05$) from the model according to their respective complexity, starting with the most complex one. When two non-significant terms presented the same complexity, the one explaining less deviance was extracted first. Each term deletion was followed by an ANOVA with F test, in order to recalculate the deviance explained by remaining terms. In order to prevent misinterpretation arising from term redundancy, six models were built and tested, each model comprising all explanatory variables and interactions, but differing from the others by the order in which the variables were included in the model (Crawley, 2002). (Table 1).

To evaluate the relationships between the abundance and the richness of the fauna associated to the bromeliad leaves with plant size, the variable water storage volume was not tested because the leaves associated to fauna is not directly dependent on this variable.

In order to verify a possible effect of passive sampling (Schoereder et al., 2004), a multiple linear regression using Binomial negative errors, was carried out to check the effects of phytotelmata abundance and abundance of invertebrates associated with leaves (x variables) on the phytotelmata richness (y) and richness of the invertebrates associated to leaves (y), respectively.

3. Results

A total of 797 individuals associated with *Vriesea* sp. were sampled, consisting of 19 species (Table 2). Larval Diptera constituted 83.8% of the total catch. The *Chironomidae* sp.1 was the most abundant among the four larvae species, followed by the *Chironomidae* sp.2, *Culicidae* sp. and *Culex* sp. Species of the order Hymenoptera were the second most abundant (12.9%), and the other groups (Coleoptera 1.2%, Arachnida 1.2%, Orthoptera 0.8%, Hemiptera 0.1%, Blattodea 0.1% e Chilopoda 0.2%) were less representative.

All models used to describe the effects of bromeliad size on phytotelmata richness converged to an equation comprising a single explanatory variable (diameter of the reservoir or water volume) that describes a positive relationship (Diameter: $F_{1,68} = 5.964$, $p = 0.014$, $R^2 = 0.10$

Table 1. Models tested to inspect the effects of bromeliad size parameters. Height = bromeliad height, Diameter = diameter of the reservoir and Volume = water storage volume. Full models converge to a simpler equation, depending on the order at which x variables enter the model and the y variable used. * denotes inclusion of single terms plus all possible interactions. † denotes significancy of the terms. See Material and Methods for details.

Full Model	Minimum adequate model
y = Phytotelmata richness	
y ~ height * volume * diameter	y ~ diameter
y ~ height * diameter * volume	y ~ diameter
y ~ diameter * height * volume	y ~ diameter
y ~ diameter * volume * height	y ~ diameter
y ~ volume * height * diameter	y ~ volume
y ~ volume * diameter * height	y ~ volume
y = Phytotelmata abundance	
y ~ height * volume * diameter	y ~ height + volume† + diameter + height:diameter†
y ~ height * diameter * volume	y ~ height + diameter† + volume† + height:diameter†
y ~ diameter * height * volume	y ~ diameter† + height + volume† + diameter:height†
y ~ diameter * volume * height	y ~ diameter† + volume† + height + diameter:height†
y ~ volume * height * diameter	y ~ volume† + height + diameter + height:diameter†
y ~ volume * diameter * height	y ~ volume† + diameter + height + diameter:height†
y = Invertebrate richness associated with leaves	
y ~ height * diameter	y ~ height† +diameter† + height:diameter†
y ~ diameter * height	y ~ height† +diameter† + height:diameter†
y = Invertebrate abundance associated with leaves	
y ~ height * diameter	y ~ height +diameter + height:diameter†
y ~ diameter * height	y ~ height +diameter + height:diameter†

Table 2. Richness and abundance of the invertebrates sampled in *Vriesea* sp.

Order	Species	Abundance
Araneae	*Phelodromidae* sp.	4
	Salticidae sp.1	1
	Salticidae sp.2	1
	Gnophosidae sp.	1
	Corinnidae sp.1	1
	Corinnidae sp.2	1
Blattodea	*Blattodea* sp.1	1
Scolopendromorpha (Chilopoda)	*Scolopendromorpha* sp.1	2
Coleoptera	*Alleculidae* sp.	1
	Staphylinidae sp.1	2
	Staphylinidae sp.2	1
	Curculionidae sp.1	1
	Curculionidae sp.2	4
Diptera (larvae)	*Culicidae* sp.	65
	Culex sp.	59
	Chironomidae sp.1	339
	Chironomidae sp.2	209
Hemiptera	*Reduviidae* sp.1	1
Hymenoptera	*Crematogaster* sp.	103
Total	19	797

and Volume: $F_{1.68} = 5.492$, $p = 0.019$, $R^2 = 0.09$). This result denounces redundant effects of both variables on phytotelmata richness, however the diameter of the reservoir seems more suitable to explain phytotelmata richness since it presents lower Akaike Information Criterion (AIC = 226.66) than the one comprising water volume (AIC = 227.13).

On the other hand, a different result was presented by the models explaining the effects of plant size on phytotelmata abundance. The variables water volume, diameter of the reservoir, and interaction between height and diameter showed positive relationship with phytotelmata abundance depending on the order at with it has been included in the full model. Furthermore, the AIC value was the same for all the models (AIC = 451.39), what prevent the separation the more suitable model to explain phytotelmata abundance. However, the water volume was the unique variable that presented significance in all the models independent of the order at which it was included (Table 1). The results were grouped in two groups: in one of them (y = height*v olume*diameter; y = volume*height*diameter; and y = volume*diameter*height) volume (F = 18.099, $p < 0.001$) and interaction between diameter and height (F = 6.467, $p = 0.010$) were determinants of phytotelmata abundance ($\chi^2_{1.65} = 23.170$, $p < 0.001$, $R^2 = 0.25$). In the other group (y=height*diameter*volume; y = di ameter*height*volume; y = diameter*volume*height) volume (F = 7.989, $p = 0.004$), diameter (F = 12.895, $p < 0.001$) and interaction between diameter and height (F = 6.467, $p = 0.010$) were positively related to phytotelmata abundance ($\chi^2_{1.65} = 24.073$, $p = 0.001$, $R^2 = 0.25$). The variable diameter just was significant when included before volume.

All the models used to test the relationship between bromeliad size and richness of insects associated with leaves presented the same results (AIC = 157.55). The richness was explained by interaction between height and diameter of reservoir ($F_{1.66} = 3.427$, $p = 0.016$, $R^2 = 0.153$). The abundance of the invertebrates associated to leaves was positively related to height, diameter and interaction between these variables ($\chi^2_{1.66} = 16.664$, $p < 0.001$, $R^2 = 0.21$), in the two models used (AIC = 255.22).

Phytotelmata richness and richness of invertebrates associated to leaves were positively related with the abundance of phytotelmata fauna ($F_{1.68} = 15.331$, $p < 0.001$, $R^2 = 0.26$; AIC = 219.30) and with abundance of invertebrates associated to leaves ($F_{1.68} = 10.442$, $p < 0.001$; $R^2 = 0.15$ AIC = 155.40) respectively. Considering the lower value of AIC, phytotelmata richness, as well as richness of invertebrates associated to leaves, were more explained by abundance of individuals than by bromeliad size.

4. Discussion

In rupestrian fields, animals that need aquatic environments to complete their life cycles, use the phytotelmic environment as sites for nesting and foraging, since these reservoirs contain water, even in dry seasons (Picado, 1913; Frank and Curtis, 1977). Our results show that bromeliad size was an important predictor of abundance and richness of invertebrates associated with *Vriesea* sp. However, it is important to point out that the spatial autocorrelation of the samples are not considered in this work. Thus, these results are insufficient to describe the variation along the spatial scale due to spatial localization of the samples not being considered in the sampling (Taylor, 1961, 1984). An alternative would the utilization of geostatistic to describe spatial patterns using autocorrelation between value and distance of the samples (Liebhold et al., 1991). Geostatistic includes the utilization of correlation methods, covariance and semivariance functions to describe spatial patterns of the individuals (Liebhold et al., 1993). This analyses tests if the value of the one variable observed is dependent on the value neighbors (Sokal and Oden, 1978). So, such results must be viewed with the necessary caution because an effect of autocorrelation cannot be dismissed.

Within the Diptera species sampled, two belonged to the Culicidae family. Several species of this family are vectors of diseases and use the water reservoir as natural breeding sites (Pittendrigh, 1948; Forattini et al., 1998; Forattini and Marques, 2000). Together with species of Chironomidae, the Culicidae are the most common organisms in phytotelmata (Fish, 1983).

We observed that the increases in phytotelmata richness and of the invertebrates associated to leaves were more related with an increase in abundance of individuals than bromeliad size. These relationships suggest an effect of passive sampling (Schoereder et al., 2004). On the other hand, the parameters of bromeliad size also affected the abundance and richness of invertebrate fauna in bromelia.

Several studies show that larger bromeliads contain higher amounts of detritus (Richardson, 1999) and this may cause higher abundance of fauna (Jenkins et al., 1992; Richardson, 1999; Richardson et al., 2000). Therefore, larger plants contain more resources, and more water, which allows them to shelter a larger quantity of organisms (Figures 1-4). Additionally space for colonization can be a result of the interaction between bromeliad height and diameter of the reservoir which determined greater abundance of phytotelmata and increase of abundance and richness of the invertebrates associated to leaves. Srivastava and Lawton (1998) observed that the taller plants, besides supporting a larger volume of water, also contained more nutrients. Therefore, larger bromeliads can contain higher numbers of organisms (Figure 2). Our results are in agreement with earlier results, showing a positive relationship between species abundance and water volume (Sota, 1996; Yanoviak, 1999).

In rupestrian fields, the relationships between plant size and invertebrate abundance can be more pronounced, since bromeliads contain a low quantity of nutrients (Leme and Marigo, 1993). In these environments, the distribution and the contents of organic detritus in

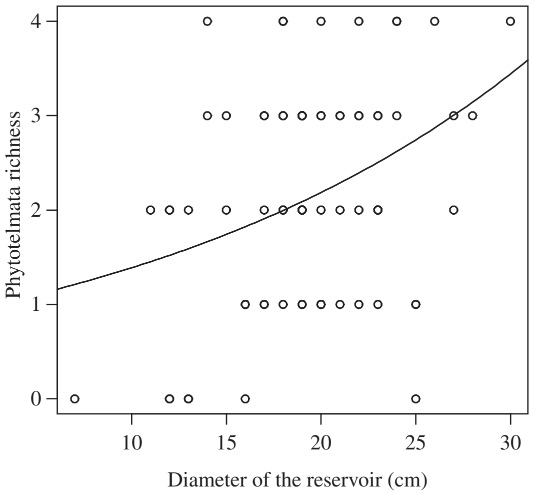

Figure 1. Relationship between phytotelmata richness and diameter of the reservoir (y = –0.126 + 0.045x, P = 0.0151, $R^2 = 0.10$).

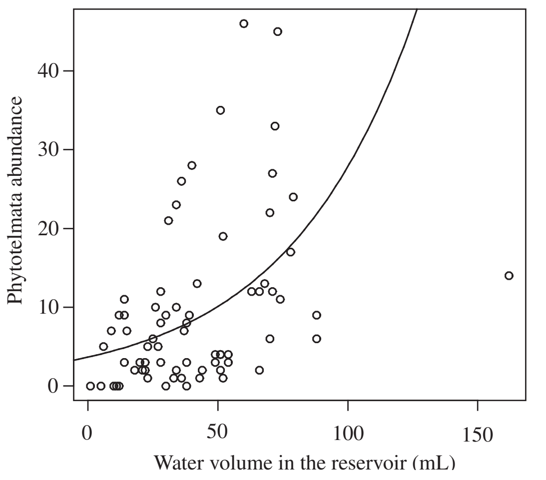

Figure 3. Relationship between phytotelmata abundance and water volume in the bromeliad reservoir (y = 1.66 + 0.012x, P = 0.001, $R^2 = 0.25$).

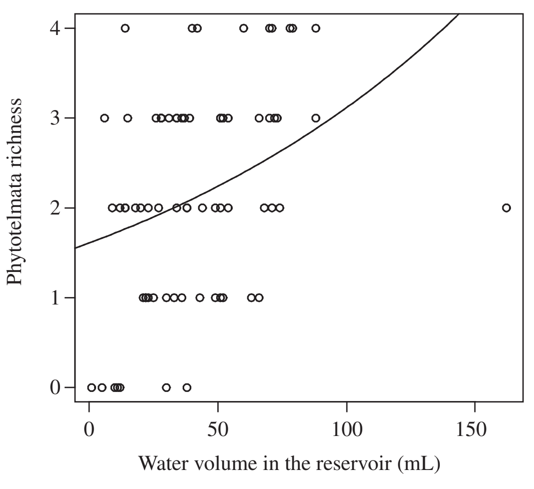

Figure 2. Relationship between phytotelmata richness and water volume in the bromeliad reservoir (y = 0.476 + 0.006x, P = 0.0138, $R^2 = 0.09$).

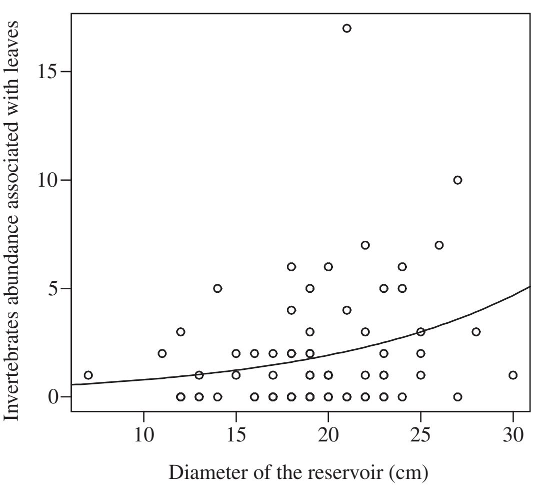

Figure 4. Relationship between invertebrate abundance associated with leaves of the bromeliad (y = –1.070 + 0.086x, P < 0.001, $R^2 = 0.06$).

bromeliad reservoirs depend on physical factors, such as wind. Besides, elevated altitude and occurrence of open fields in these locales can increase the intensity of insolation and, consequently the loss of water by evaporation.

An increase of the area can also generate higher heterogeneity or complexity of the environment. This can result in some advantages such as an increase in the spatial distribution of resources, in sites of oviposition and increased microhabitats in the same plant. Besides, it can supply a higher number of refuges against predators (Strong et al. 1984). This can explain the positive relationship found between the richness of phytotelmata fauna and the volume and diameter of the reservoir (Figures 1-2), since those larger bodied plants make possible the coexistence of species with different ecological necessities.

Species richness increases with the area when this promotes different habitats. Probably, as bromeliad size increased, there was a parallel increase in the availability of resources and microhabitats. Indeed, Richardson (1999) suggested that species richness could be related to the availability of niches in bromeliads because of their simple architecture, while invertebrate abundance can be more dependent on nutritional factors.

This work supports the idea that phytotelmata abundance could be related mainly with the increase of the area for colonization, which could come with an increase in nutrient availability. The probability of sampling more individuals increases with the plant size, and indirectly amplifies the chances of sampling more species.

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