

UNIVERSIDADE VILA VELHA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DE ECOSISTEMAS

**DISTRIBUTION OF SHREDDERS IN ATLANTIC FOREST
STREAMS: ARE THEY IN EVERYWHERE?**

KAROLINE VICTOR SERPA

VILA VELHA
MARÇO/2019

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KAROLINE VICTOR SERPA

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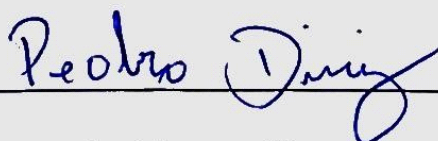
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Orientador

À astronauta que, mesmo de longe, guia meu coração.

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Se tem uma coisa que descobrimos quando entramos no mestrado é que tudo (eu disse TUDO) o que pode acontecer de complicado na nossa vida acontece nesse período (e ao mesmo tempo). São os dois anos mais corridos que podemos imaginar. Daí a presença de algumas almas são imprescindíveis para a sobrevivência de qualquer ser. Então, queridos, vamos lá:

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Vocês foram fundamentais.

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RESUMO

SERPA, Karoline Serpa, M. Sc., Universidade Vila Velha – ES, março de 2019.

Distribution of shredders in Atlantic Forest streams: Are they in everywhere?

Orientador: Marcelo da Silva Moretti.

Apesar da importância dos fragmentadores no processamento de matéria orgânica em riachos, a informação sobre as especificidades do habitat de diferentes taxa é escassa. Aqui, nós avaliamos as preferências de habitat de invertebrados fragmentadores em riachos de florestas tropicais. Nossa hipótese é que, embora os fragmentadores sejam comumente associados a manchas de folhas, os taxa difeririam na amplitude de nicho e nas especificidades do habitat. Um total de 72 bancos foliares foram amostrados sistematicamente na Mata Atlântica (SE Brasil). Para cada amostra, 20 parâmetros ambientais foram medidos, incluindo propriedades da água e características do banco foliar. Utilizamos uma análise do Índice de Média Externa (OMI) para avaliar a amplitude de nicho e a sobreposição de cada táxon encontrado, bem como as preferências de habitat. No total, encontramos 14 táxons fragmentadores em 68 manchas de folhas, e o gradiente de condições ambientais influenciou a distribuição da maioria dos taxa. Considerando os taxa que ocorreram em nichos atípicos, *Blaberidae* e *Trichodactylus fluviatilis* apresentaram segregação de nicho, enquanto *Macrobrachium potiuna*, *Tupiperla* e *Nectopsyche* apresentaram sobreposição de nicho. Por outro lado, *Heterelmis*, *Stenochironomus*, *Phylloicus major* e *Triplectides gracilis* ocorreram em bancos foliares comuns. Estes resultados corroboram a hipótese proposta e sugerem que as diferenças na amplitude de nicho e nas especificidades de habitats entre os táxons provavelmente contribuem para a diversidade de fragmentadores em riachos tropicais.

Palavras-chave: Bancos foliares; Detritívoros; Sobreposição de nicho; Análise OMI; Riachos de Mata Atlântica.

ABSTRACT

SERPA, Karoline Serpa, M. Sc., Universidade Vila Velha – ES, março de 2019.

Distribution of shredders in Atlantic Forest streams: Are they in everywhere?

Orientador: Marcelo da Silva Moretti.

Despite the importance of shredders in organic matter processing in streams, information about the habitat specificities of different taxa is scarce. Herein, we evaluated the habitat preferences of invertebrate shredders in tropical forest streams. We hypothesized that, although shredders are commonly associated with leaf patches, taxa would differ in niche breadth and habitat specificities. A total of 72 leaf patches were randomly sampled in the Atlantic Forest (SE Brazil). For each sample, 20 environmental parameters were measured, including water properties and characteristics of the leaf patch. We used an Outlying Mean Index (OMI) analysis to evaluate the niche breadth and overlap of each taxon found as well as habitat preferences. In total, we found 14 shredder taxa in 68 leaf patches, and the gradient of environmental conditions influenced the distribution of most taxa. Considering taxa that occurred in atypical niches, Blaberidae and *Trichodactylus fluviatilis* showed niche segregation, while *Macrobrachium potiuna*, *Tupiperla* and *Nectopsyche* showed niche overlap. On the other hand, *Heterelmis*, *Stenochironomus*, *Phylloicus major* and *Triplectides gracilis* occurred in common leaf patches. These results support the proposed hypothesis and suggest that differences in niche breadths and habitat specificities among taxa probably contribute to the diversity of shredders in tropical streams.

Keywords: Leaf patches, Detritivores, Niche overlap, OMI analysis, Atlantic Forest streams.

Distribution of shredders in Atlantic Forest streams: Are they in everywhere?

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Manuscrito apresentado nas normas do periódico Hydrobiologia

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Distribution of shredders in Atlantic Forest streams: Are they in everywhere?

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Introduction

The range of habitats colonized by aquatic invertebrates is spatially and temporally determined by both environmental and biological factors (Mathers et al., 2014; Árvá et al., 2015). In this context, the distribution of taxa in stream ecosystems results from the interaction among the physical and chemical properties of the aquatic environment (Nguyen et al., 2018), hydrological conditions (Matlou et al., 2017; Rasifudi et al., 2018), substrate composition (Fu et al., 2016), biological interactions (Boyero et al., 2012), and historical constraints that act at different scales (Heino et al., 2003). Aquatic invertebrates have morphological, physiological and behavioral adaptations that allow them to colonize several microhabitats in different environmental conditions (Allan & Castillo, 2007). Therefore, within-stream factors are considered especially important in determining taxa niche breadth and distribution patterns (Heino, 2009).

In low-order forest streams, leaf litter from riparian vegetation is an important energy source for aquatic consumers (Vannote et al., 1980). After entering streams, this organic material is retained along the stream channel, forming leaf patches that differ in size and species composition (Palmer et al., 2000). These leaf patches can be used as shelter and food sources by a high number of invertebrate taxa (Graça, 2001; Moretti et al., 2007). The amount of organic material available on the streambed is determined by both the allochthonous inputs provided by the riparian vegetation and the stream retention capacity (Cummins et al., 1989). The diversity and biomass of leaf patches (Presa Abos et al., 2006) and the hydraulic and environmental conditions where they are formed (Costa & Melo, 2008; Hoover et al., 2010) determine the taxonomic composition of the assemblages associated with this type of substrate. Kobayashi & Kagaya (2002, 2004) identified four categories of leaf patches in stream ecosystems, one formed in riffles and three formed in pools, that differed in the composition of associated invertebrates.

Invertebrate shredders play a fundamental role in streams shaded by riparian vegetation. Because individuals within this functional feeding group are able to feed on coarse particulate organic matter (CPOM) (Cummins, 1974; Graça et al., 2001), they reduce these particles in size, making them available to other consumers, and convert the organic material into biomass and CO₂ (Chung & Suberkropp, 2009; Boyero et al., 2011; Graça et al., 2015). In the tropical region, shredders are represented by a diverse and polyphyletic group, including immature stages of aquatic insects, semiaquatic roaches and macroconsumers, i.e., large, nonspecialist and omnivorous taxa, such as freshwater decapods (crabs and shrimp) and fishes (Pringle & Hamazaki, 1998; Moulton et al., 2010; Costa et al., 2016; Poi et al., 2017). However, the distribution of shredders in tropical streams varies widely across regions and

biomes. While a high abundance of these individuals has been found in streams of South America, Africa and Oceania (see Cheshire et al., 2005; Chara-Serna et al., 2012; Masese et al., 2014a; Mendes et al., 2017), some streams in Kenya and in the Brazilian Cerrado were characterized by a scarcity of shredders (Dobson et al., 2002; Gonçalves et al., 2007; Rezende et al., 2016).

Despite their importance to stream nutrient cycling and energy flow, information about the habitat specificities of different taxa of shredders in tropical streams is still scarce. This may be attributed to the low number of studies (Rezende et al., 2016; Biasi et al., 2019) and imprecise methods used for invertebrate sampling and assignment into functional feeding groups (Boyero et al., 2009; Camacho et al., 2009). In the Atlantic Forest, most of the current knowledge about the habitat preferences of shredders in streams is based on personal observations during field surveys. For example, larvae of the caddisfly shredders *Triplectides gracilis* (Burmeister, 1839) (Trichoptera: Leptoceridae) and *Phylloicus major* Müller, 1880 (Trichoptera: Calamoceratidae) are easily found in leaf patches formed in shallow stream pools. On the other hand, the freshwater crab *Trichodactylus fluviatilis* Latreille, 1828 (Crustacea: Trichodactylidae) is normally found in gaps under rocks and pebbles (adults) or in deep and large leaf patches (juveniles). The shrimp *Macrobrachium potiuna* (Müller, 1880) (Crustacea: Palaemonidae) is found on leaf patches formed close to the stream banks and under the marginal vegetation. Therefore, understanding the factors that influence the distribution of different taxa of shredders in streams is important to maintaining the diversity of this functional feeding group and ecosystem functioning.

In this study, we aimed to evaluate the habitat preferences of invertebrate shredders in tropical forest streams. For this, we randomly sampled 72 leaf patches found in different environmental conditions on the streambed of 3 streams of the Atlantic Forest and determined the abundance of all taxa of shredders found. For each sample, we measured 20 environmental parameters, including water properties and characteristics of the leaf patch and riparian zone. We hypothesized that, although shredders are commonly associated with leaf patches in Atlantic Forest streams, taxa would differ in niche breadth and habitat specificities.

Methods

Study area

The streams studied (Banana: 20°02'22.1" S – 40°31'53.9" W, 585 m a.s.l.; Macuco: 20°01'23.1" S – 40°32'58.6" W, 593 m a.s.l.; Santa Clara: 20°00'37.6" S – 40°32'41.2" O, 621 m a.s.l.) belong to the headwaters of the Prata River and are located inside fragments of the Atlantic Forest in the municipality of Santa Leopoldina (Espírito Santo, SE Brazil). The

riparian vegetation of the three streams is well developed, shading approximately 90% of the streambed, and the substrate is very heterogeneous, composed of pebbles, gravel and leaf patches formed in riffle and pool reaches. More information about the study area can be found in Casotti et al. (2015b).

Field survey

A total of 72 leaf patches were sampled with a Surber sampler (0.09 m², 250 µm mesh) during a 3-day field survey conducted in August 2017 (dry season). In each stream, we systematically sampled well-defined leaf patches of different sizes formed in a wide range of environmental conditions, e.g., varying in depth, submersion level (totally or partially submerged), stream bank distance, mesohabitat (riffles or pools), and streambed type (rocky or sandy). The samples were placed individually in plastic bags and were labeled and transported to the laboratory on the same day in an ice box.

Before sampling, the environmental conditions of the exact place where the leaf patch was formed were determined by evaluation of the water properties and the characteristics of the leaf patch and the riparian zone. In addition to the determination of stream width and mean depth, measurements of leaf patch size, distance to the margin, depth to the stream bottom and depth to the most superficial leaf were performed with a retractable measuring tape (cm). The values of water temperature, pH, oxidation-reduction potential (ORP), conductivity, turbidity, total dissolved solids, and dissolved oxygen (immediately above and inside the leaf patch) were determined with a multiprobe (YSI-57, Yellow Springs, Ohio) and a portable oximeter (HI 9146, HANNA Instruments, Rhode Island). Water velocity was determined with a flow meter (Flowatch, JDC Electronic SA, Yverdon-les-Bains, Switzerland). The percentages of canopy coverage were determined by the analysis of photographs taken with a digital camera (GoPro HERO 3 Silver Edition, GoPro Inc., California) positioned parallel to the water surface and immediately above the leaf patch using ImageJ Software (US National Institutes of Health, Bethesda, Maryland). Later, the dry mass of the entire leaf patch, including leaves and leaf fragments, and the number of leaf morphospecies in each sample were also determined (see laboratory procedures below). Table 1 shows the descriptions and the abbreviations of each environmental parameter used in the data analysis and the range of variation among samples.

Laboratory procedures

The leaves and leaf fragments of each sample were washed in tap water over a sieve (250 µm mesh). The material retained in the sieve was then sorted using a stereoscope (Bel Photonics

STMPro – 20x), and the invertebrates found were preserved in 70% ethanol. The invertebrates were identified up to the genus or species level (except for Blattaria) using neotropical specific taxonomic keys (Mugnai et al., 2010; Hamada et al., 2014) and the assistance of specialists when needed. The identification effort at the genus level is very useful for biodiversity studies with aquatic invertebrates (Heino & Soininen, 2007). However, some genera identified in our study, such as *Stenochironomus*, *Nectopsyche* and *Tupiperla*, have more than one species found in our study area.

The invertebrates found were assigned to functional feeding groups. The assignment of taxa to the group of shredders was based on information available in the literature from tropical and neotropical taxa and laboratory experiments (Table 2). Although there is evidence of the shredding capacity of *Ulmeritoides* and *Hagenulopsis* (Leptophlebiidae) in the available literature (see Shimano et al., 2012; Longo & Blanco, 2014), these genera were not considered in this study because of the low abundances observed (4 and 13 individuals, respectively). On the other hand, the genera *Helichus* (Dryopidae), *Anchycteis* and *Anchytersus* (Ptilodactylidae), which had been reported as shredders in previous studies (see Covich et al., 2006; Oliveira & Nessimian, 2010), were not assigned as shredders because individuals collected in the studied streams were not able to feed on CPOM in the laboratory (*Pers. observation*).

The individuals belonging to the taxa assigned as shredders were counted. The leaves and leaf fragments of each sample were dried (60° C, 72 h) and weighed (0.01 g) to determine the total amount of CPOM. The number of leaf morphospecies in each sample was also determined.

Data analysis

Because we did not find any shredder taxon in 4 leaf patches sampled, these samples were disregarded from our data set, and all statistical analyses were performed with data obtained from 68 samples. We used an Outlying Mean Index (OMI) analysis, a two-table ordination technique that places the sampling units in a multidimensional space as a function of environmental parameters (Dolédec et al., 2000). This analysis was chosen because of the advantage of this method over Canonical Correspondence Analysis (CCA) and Redundancy Analysis (RDA). The advantage of OMI analysis over the other ordination techniques is the good performance in describing either unimodal response curves or linear response curves that are linked to a limiting factor (Dolédec et al., 2000), such as found in this study. The abundance data were log-transformed ($\ln [x + 1]$) to reduce the effect of dominant taxa, and a PCA was performed on the correlation matrix of environmental parameters.

In the OMI analysis, the distribution of taxa in the multidimensional space represents their realized niches and considers two aspects: marginality and tolerance. The marginality measures the distance between the mean habitat conditions used by a taxon and the mean habitat conditions across the study area (origin of the niche hyperspace). Taxa with high values of OMI have marginal niches, i.e., occur in atypical habitats in a study site, and those that get low values have nonmarginal niches, i.e., occur in typical habitats in a study site. The tolerance index estimates the niche breadth, which means the amplitude of the distribution of each taxon along the sampled environmental conditions. Low values mean that a taxon is distributed across a limited range of conditions, i.e., a specialist, while high values imply that a taxon is distributed across habitats with widely varying environmental conditions, i.e., a generalist. The OMI analysis also reports the unexplained variance of the model, i.e., the percentage of residual tolerance (%Rtol), accounting for variability not related to the environmental parameters measured.

The statistical significance of the marginality of each taxon was tested by a Monte Carlo (MC) test with 999 random permutations. The frequency of random permutations with values higher than the observed marginality was used as an estimated probability of rejecting the null hypothesis that the environmental conditions do not constrain the spatial distribution of the taxa. The OMI analysis and MC permutations were performed by the function 'niche' and 'rtest', respectively, within the 'ade4' package (Dray & Dufour, 2007) in R software version 3.5.1 (R Core Team, 2017).

Results

In total, 1392 shredders belonging to 14 taxa were found (Banana: 374 ind., 12 taxa in 38 samples; Macuco: 523 ind., 11 taxa in 15 samples; Santa Clara: 495 ind., 11 taxa in 15 samples). The caddisfly *T. gracilis* was the most abundant and widely distributed taxon (659 ind. found in 52 samples), followed by *P. major* (235 ind. in 43 samples), and the stonefly *Tupiperla* (192 ind. in 25 samples; Table 3). The genera *Stenochironomus* (Diptera) and *Heterelmis* (Coleoptera) were also well distributed but had intermediate values of abundance (108 and 55 ind. in 41 and 28 samples, respectively). All other shredder taxa occurred in low abundances (<3% in <15 samples; Table 3).

In the OMI analysis, the global test of an average marginality of all taxa was significant ($p = 0.04$). Eight of 14 taxa showed a significant deviation in their niche from the mean origin of the computed canonical weights, suggesting a significant influence of the environmental conditions for most of the shredder taxa found. However, the leaf patch size, water velocity, stream flow, pH, and canopy coverage were less important than the other

parameters measured (Fig. 1). The position of samples and the distribution of taxa, which were calculated by the weighted average and the amplitude of the cartesian coordinates, resulted in a clear differentiation among the streams studied (Fig. 2), i.e., the distribution of shredders varied among streams of the same catchment. The three first axes of the OMI analysis accounted for 87% of the marginality (60, 20 and 7%, respectively). Therefore, only these three axes were presented in the subsequent figures.

Nine taxa had high OMI and low tolerance values (*Blaberidae*, *Xenelmis*, *Microcylloepus*, *Hexacylloepus*, *Macrobrachium potiuna*, *T. fluviatilis*, *Perissophlebiodes*, *Tupiperla* and *Nectopsyche*). These taxa occurred in leaf patches with atypical environmental conditions within the study area (i.e., marginal niches) and only tolerated specific leaf patch conditions (i.e., specialists). Regarding the five most abundant taxa of this group, *Blaberidae* and *T. fluviatilis* showed niche segregation, while *M. potiuna*, *Tupiperla* and *Nectopsyche* showed niche overlap (Table 4; Fig. 3A). In contrast, *Heterelmis*, *Stenochironomus*, *P. major*, *Smicridea* and *T. gracilis* had low OMI and high tolerance values. These taxa occurred in typical (or common) leaf patches of the study area (i.e., nonmarginal niches) and tolerated the broad leaf patch conditions (i.e., generalists). With the exception of *Smicridea*, which occurred in low abundance, all these taxa showed niche overlap (Table 4; Fig. 3B). The cooccurrence of at least 2 shredder taxa was observed in 64 samples, and more than 2 taxa were found in 54 samples. The niche marginality plots of the 14 shredder taxa found in this study are presented in the Electronic Supplementary Material (Fig. S1).

Discussion

Invertebrate shredders were found to be associated with leaf patches formed under different conditions, and the environmental gradient influenced most of the taxa. In addition, the wide variation observed in the values of niche marginality and tolerance suggests that shredder taxa had different habitat specificities and niche breadths. As expected, our study showed that the group of shredders was composed of a large variety of taxa, including immature stages of aquatic insects, semiaquatic roaches and decapods, that occupy a wide range of niches. This might be related to the high heterogeneity of leaf patches available on the streambed (Pilotto et al., 2016). Lisboa et al. (2015) suggested that the high richness of leaf species in the organic matter inputs of Atlantic Forest streams results in the formation of leaf patches with different characteristics, which provide food resources and habitat that vary widely in quality and complexity, respectively. The high biomass of leaf litter produced year-round by the riparian vegetation of these streams also support this hypothesis (Gonçalves et al., 2014).

Larvae of the caddisfly species *T. gracilis* and *P. major* showed low values of OMI, i.e., these taxa were generalists in terms of habitat preferences and exhibited a wide distribution. The genera *Triplectides* Kolenati, 1859 and *Phylloicus* Müller, 1880 are commonly abundant in Neotropical streams (see Oliveira et al., 1999; Nikolcheva et al., 2005; Landeiro et al., 2010; Andrade et al., 2017; Mendes et al., 2017) and are widely used in laboratory and field experiments aiming to evaluate the feeding preferences and consumption rates of typical shredders (Casotti et al., 2015a; Kiffer et al., 2018; Biasi et al., 2019; Reis et al., 2019). Individuals of these genera build cases with organic material: larvae of *Triplectides* build cases with wood sticks (Camargos & Pes, 2011; Kiffer et al., 2016), and larvae of *Phylloicus* build cases with leaf pieces (Wiggins, 1996; Moretti et al., 2009). Because these cases confer a mechanical defense (Otto & Svensson, 1980) or facilitate camouflage (Williams et al., 1987) against predators, the case-building behavior exhibited by these larvae can result in the high abundances and wide distribution observed. Moreover, the use of cases also promotes respiration, allowing these larvae to direct water flow to the gills (Williams et al., 1987). This feature could allow them to live inside the leaf patches or in deep stream pools where the level of dissolved oxygen is low.

The three taxa of macroconsumers found in this study, i.e., the freshwater decapods *T. fluviatilis* and *M. potiuna* and nymphs of semiaquatic roaches (Blaberidae), occurred in low abundances and were restricted to determined environmental conditions. However, these taxa presented high values of biomass (approximately 70% of the total invertebrate biomass; *unshown data*). According to Tonin et al. (2014) and Mendes et al. (2017), values of both abundance and biomass should be used in the evaluation of the role of shredders in streams because taxa assigned to this functional feeding group may differ largely in size. Because of their nocturnal activity (Pringle & Hamazaki, 1998; Magalhães, 2003) and high mobility (Yule et al., 2009; Costa et al., 2016), the observation and sampling of macroconsumers is more difficult than those of aquatic insects (Baumart et al., 2015). Consequently, the contribution of macroconsumer taxa to organic matter processing may have been neglected in most of the studies developed in tropical streams (Boyero et al., 2009; Cogo & Santos, 2013). Although macroconsumers have been commonly assigned as omnivores (Pringle & Hamazaki, 1998; Crowl et al., 2009; Mancinelli et al., 2013; Lima et al., 2014; Costa et al., 2016; Andrade et al., 2017), some studies have shown that these organisms can ingest significant amounts of leaf litter (Joseph et al., 2013; Lima et al., 2014) and produce fine particles of organic matter at the same proportion, or even higher, than typical insect shredders (Costa et al., 2016). Moreover, because they have mouthparts that facilitate maceration (Mendes et al., 2017), gut-associated microbial communities (semiaquatic

roaches; Schauer et al. 2012), and complex stomachs (decapods; Meiss & Norman, 1977), macroconsumers may be able to consume tough or chemically protected leaves that are not processed by typical insect shredders.

Some studies have already demonstrated niche overlap and segregation of different taxa in time and space (Crosa & Buffagni, 2002; Liu & Wang, 2007; Leberfinger et al., 2011), including aquatic invertebrates (Cummins et al., 1989; Muotka, 1990; Winterbourn, 2003). However, information about shredders is scarce in the literature. The coexistence of taxa that depend on similar food resources in limited areas, such as invertebrate shredders associated with leaf patches, is not completely understood. Taxa that depend on irregularly distributed resources could follow the patterns of the aggregation model of coexistence (Presa Abos et al., 2006). In this model, taxa have a tendency to concentrate on resource spots, resulting in a strong intraspecific aggregation (within leaf patches) and in weak interspecific interactions, i.e., a random association with competitors (see Presa Abos et al. 2006). This combination can reduce competition among taxa and act as a coexistence mechanism (Sevenster & Alphen, 1996). The aggregation model is well documented in terrestrial invertebrates (Jaenike & James, 1991; Sevenster & Alphen, 1996; Krijger & Sevenster, 2001; Woodcock et al., 2002; Veech et al., 2003) and in aquatic invertebrates in general (Murphy et al., 1998; Schmera, 2004; Tokeshi & Townsend, 2019). Regarding the group of shredders, taxa specificities result in different food and habitat preferences that, together with the preexisting differences in stream environmental conditions, could support the aggregation model. In addition, aggregation among taxa tends to increase with increasing spatial scale, i.e., with habitat heterogeneity (Presa Abos et al., 2006). Therefore, in streams with high heterogeneity in leaf patches, such as those in the Atlantic Forest, it is plausible to consider the aggregation model as an explanation for the coexistence of different shredder taxa (Heino et al., 2003).

The aggregation of invertebrate shredders has already been observed in temperate streams (Presa Abos et al., 2006). However, the availability of leaf patches may differ substantially between temperate and tropical streams. While litter inputs are relatively constant throughout the year in tropical streams (Tonin et al., 2017), leaf fall presents a strong seasonality in temperate streams (Graça & Canhoto, 2006). Presa Abos et al. (2006) found strong interspecific aggregation during autumn in Swedish streams, a period in which leaf litter was not limited. As these authors highlighted, the aggregation of shredders is not an immediate ecological response to the intensification of interspecific competition but reflects preexisting differences in food or habitat specificities among taxa.

Invertebrate shredders are dependent on the inputs of allochthonous leaf litter for food (Graça, 2001), shelter (Oliveira & Nessimian, 2010), and case-building (Rincón & Martínez,

2006). Therefore, changes in the riparian vegetation that modify the quality and quantity of litter inputs can influence the characteristics of leaf patches available on the streambed and, consequently, the distribution and abundance of associated invertebrates (Arias-Real et al., 2018). Shredders are more sensitive to changes in the environmental conditions (Masese et al., 2014b) and more susceptible to riparian disturbances than other aquatic invertebrates (Casotti et al., 2015b). Therefore, our findings suggest that even small changes that decrease stream heterogeneity, a relevant factor for the taxonomic composition of aquatic communities (Landeiro et al., 2010; Milesi et al., 2016), may result in the local extinction of some shredder taxa.

In summary, this study showed that invertebrate shredders can be found in leaf patches formed under different environmental conditions in Atlantic Forest streams. However, taxa differed in habitat specificities and niche breadths, and this probably contributes to their coexistence. These findings suggest that field surveys aiming to evaluate the abundance and taxa composition of invertebrate shredders in tropical forest streams should consider the sampling of leaf patches formed in the most varied habitats and environmental conditions. Because different taxa may process leaves with contrasting characteristics, e.g., nutrient content and toughness, our results also suggest that changes in the riparian zones that result in stream homogenization can affect the distribution of shredders and, consequently, the role that these decomposers play in the detritus-based food web of forest streams.

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Table 1 Description, abbreviation used in data analysis and range (minimum and maximum values) of the environmental parameters measured in the exact location where sampled leaf patches were formed in Atlantic Forest streams. Only samples containing at least one shredder individual were considered (n = 68).

Parameters	Abbreviation	Description	Range
Width (m)	Wid	Width of the reach where the leaf patch was formed.	2.74-3.26
Depth (cm)	Dep	Mean depth of the reach where the leaf patch was formed. Measurements were done at 50 cm intervals along a perpendicular transect.	5.0-32.3
Distance to margin (cm)	Mar_d	Distance of the leaf patch to the nearest stream margin.	0.0-103.0
Leaf patch size (m ²)	Pat_siz	Product of the values of width and length of the leaf patch.	0.02-2.00
Depth to bottom (cm)	Dep_gr	Depth until stream the bottom.	0.0-35.0
Depth to leaf (cm)	Dep_le	Depth until to the most superficial leaf of the leaf patch.	0.0-25.0
Canopy coverage (%)	Shad	Percentage of canopy coverage in the reach where the leaf patch was formed.	56.95-87.42
Temperature (°C)	Temp	Temperature of the water.	17.2-20.5
pH	pH	pH of the water.	3.69-8.05
ORP (mV)	ORP	Oxidation reduction potential of the water.	119-275
Conductivity (mS.cm ⁻¹)	Cond	Conductivity of the water.	0.02-0.04
Turbidity (NTU)	NTU	Turbidity of the water.	0.60-42.10
Dissolved oxygen (mg.L ⁻¹)	Dis_Ox	Concentration of dissolved oxygen in the water.	2.27-10.07
Dissolved oxygen inside (mg.L ⁻¹)	Ox_ins	Concentration of dissolved oxygen inside the leaf patches.	1.20-9.34
TDS (ppm)	TDS	Total dissolved solids in the water.	0.01-0.02
Water velocity (m.s ⁻¹)	Wat_vel	Water velocity immediately above the leaf patches.	0.00-0.40
Stream flow (m ³ .s ⁻¹)	Flo_rat	Water flow in the reach where the leaf patches were formed.	0.00-0.38
Leaves biomass (g)	Lea_bio	Dry mass of the whole leaves in the leaf patches.	0.00-44.11
Leaf fragments (mg)	Frag	Dry mass of fragments in leaf patches.	1.61-104.49
Leaf morphospecies	Mor_sp	Number of morphospecies in leaf patches.	1-37

Table 2 Invertebrate taxa considered in this study, development stage, and criteria used for their assignment into the functional feeding group of shredders.

Taxa	Develop. Stage	Criteria	Reference
Blattaria			
Blaberidae	Nymph	Feeding experiment	<i>Pers. observation</i>
Coleoptera			
<i>Heterelmis</i> Sharp, 1882	Larvae	Gut content	Longo & Blanco (2014)
<i>Xenelmis</i> Hinton, 1936	Larvae	Feeding experiment	<i>Pers. observation</i>
<i>Microcylloepus</i> Hinton, 1935	Larvae	Feeding experiment	<i>Pers. observation</i>
<i>Hexacylloepus</i> Hinton, 1940	Larvae	Feeding experiment	<i>Pers. observation</i>
Decapoda			
<i>Macrobrachium potiuana</i> (Müller, 1880)	Adult	Gut content, feeding experiment	Longo & Blanco (2014); <i>Pers. observation</i>
<i>Trichodactylus fluviatilis</i> Latreille, 1828	Immature	Gut content, feeding experiment	Costa et al. (2016); <i>Pers. observation</i>
Diptera			
<i>Stenochironomus</i> Kieffer, 1919	Larvae	Gut content	Longo & Blanco (2014)
Ephemeroptera			
<i>Perissophlebiodes</i> Savage, 1983	Nymph	Feeding experiment	<i>Pers. observation</i>
Plecoptera			
<i>Tupiperla</i> Froehlich, 1969	Nymph	Morphology and behavior	Cummins et al. (2005)
Trichoptera			
<i>Phylloicus major</i> Müller	Larvae	Gut content, feeding experiment	Chara-Serna et al. (2012); Longo & Blanco (2014); <i>Pers. observation</i>
<i>Smicridea</i> McLachlan, 1871	Larvae	Gut content	Tomanova et al. (2006); Chara-Serna et al. (2012); Longo & Blanco (2014)
<i>Nectopsyche</i> Mueller, 1879	Larvae	Gut content	Chara-Serna et al. (2012); Longo & Blanco (2014)
<i>Triplectides gracilis</i> (Burmeister, 1839)	Larvae	Gut content, feeding experiment	Casotti et al. (2015a); Chara-Serna et al. (2012); Kiffer Jr et al. (2016)

Table 3 Total and relative abundances of shredder taxa found associated with the leaf patches sampled in Banana (n = 38), Macuco (n = 15) and Santa Clara (n = 15) streams.

Taxa	Abundance (ind.)				Relative Abundance (%)
	Banana	Macuco	Santa Clara	Total	
<i>Blaberidae</i>	6	4	11	21	1.34
<i>Heterelmis</i>	22	11	22	55	3.52
<i>Xenelmis</i>	8	1	1	10	0.64
<i>Microcylloepus</i>	0	4	0	4	0.26
<i>Hexacylloepus</i>	0	0	3	3	0.19
<i>Macrobrachium potiuna</i>	23	0	0	23	1.47
<i>Trichodactylus fluviatilis</i>	10	3	1	14	0.90
<i>Stenochironomus</i>	48	7	53	108	6.91
<i>Perissophlebiodes</i>	12	0	0	12	0.77
<i>Tupiperla</i>	1	41	150	192	12.28
<i>Phylloicus major</i>	34	81	120	235	15.04
<i>Smicridea</i>	9	7	10	26	1.66
<i>Nectopsyche</i>	6	21	3	30	1.92
<i>Triplectides gracilis</i>	195	343	121	659	42.16
Total	375	523	495	1393	

Table 4 Niche parameters of 14 shredder taxa found associated with leaf patches in Atlantic Forest streams and abbreviation used in data analysis. The inertia, the outlying mean index (OMI), the tolerance index (Tol), and the residual tolerance index (RTol) were computed for each taxon. Values in italics represent the corresponding percentages of variability. Monte Carlo tests represent the probabilities from random permutations (out of 999) of OMI results. Values of $p \leq 0.05$ are highlighted in bold.

Taxa	Abbreviation	Inertia	OMI	Tol	RTol	OMI (%)	Tol (%)	Rtol (%)	Monte Carlo
Blaberidae	Blab	23.82	7.07	6.11	10.63	<i>39.7</i>	<i>5.7</i>	<i>54.6</i>	0.05
<i>Heterelmis</i>	Het	26.55	2.2	5.26	19.09	<i>8.3</i>	<i>19.8</i>	<i>71.9</i>	0.01
<i>Xenelmis</i>	Xen	19.5	13.94	0.52	5.03	<i>71.5</i>	<i>2.7</i>	<i>25.8</i>	0.18
<i>Microcylloepus</i>	Mic	18.13	17.17	0	0.96	<i>94.7</i>	<i>0</i>	<i>5.3</i>	0.19
<i>Hexacylloepus</i>	Hex	10.4	5.44	0.29	4.68	<i>52.3</i>	<i>2.7</i>	<i>45</i>	0.88
<i>Macrobrachium potiuna</i>	Macr	19.07	5.87	0.98	12.21	<i>30.8</i>	<i>5.2</i>	<i>64</i>	<0.01
<i>Trichodactylus fluviatilis</i>	Tric	16.68	4.43	2.04	10.21	<i>36.6</i>	<i>2.2</i>	<i>61.2</i>	0.15
<i>Stenochironomus</i>	Sten	21.74	1.57	3.6	16.57	<i>7.2</i>	<i>16.6</i>	<i>76.2</i>	<0.01
<i>Perissophlebiodes</i>	Per	13.06	3.65	0.08	9.34	<i>27.9</i>	<i>0.6</i>	<i>71.5</i>	0.58
<i>Tupiperla</i>	Tup	12	3.51	0.56	7.93	<i>29.3</i>	<i>4.6</i>	<i>66.1</i>	<0.01
<i>Phylloicus major</i>	Phy	25.16	2.96	3.88	18.32	<i>11.8</i>	<i>15.4</i>	<i>72.8</i>	<0.01
<i>Smicridea</i>	Smi	23.14	3.37	2.61	17.16	<i>14.6</i>	<i>11.3</i>	<i>74.2</i>	0.01
<i>Nectopsyche</i>	Nec	24.31	16.58	3.81	3.92	<i>68.2</i>	<i>5.7</i>	<i>26.1</i>	0.03
<i>Triplectides gracilis</i>	Trip	17.93	1.87	3.16	12.9	<i>10.5</i>	<i>17.6</i>	<i>71.9</i>	0.07
OMI mean									0.04

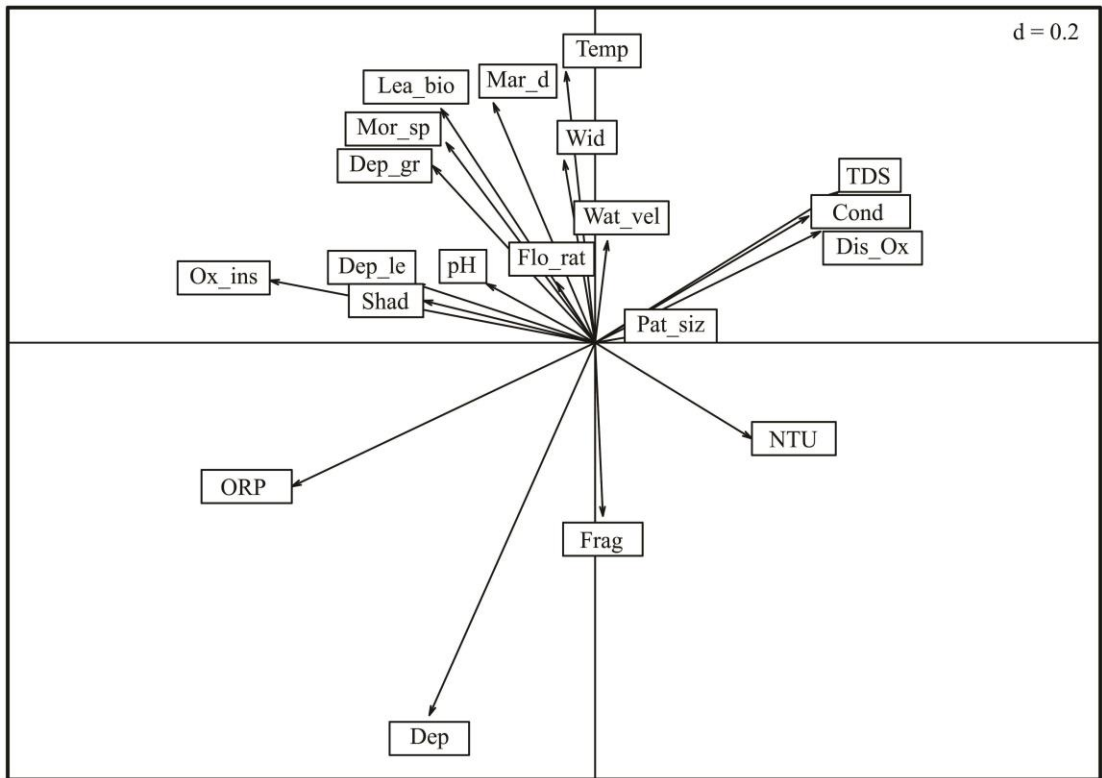


Figure 1.

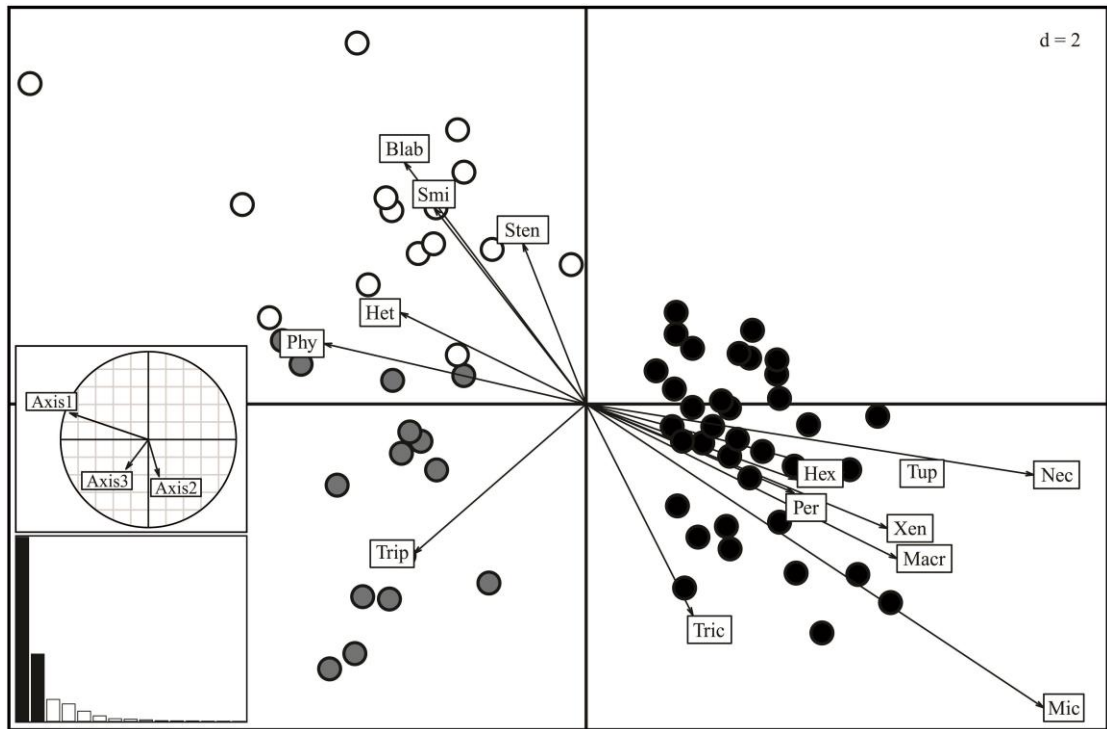


Figure 2.

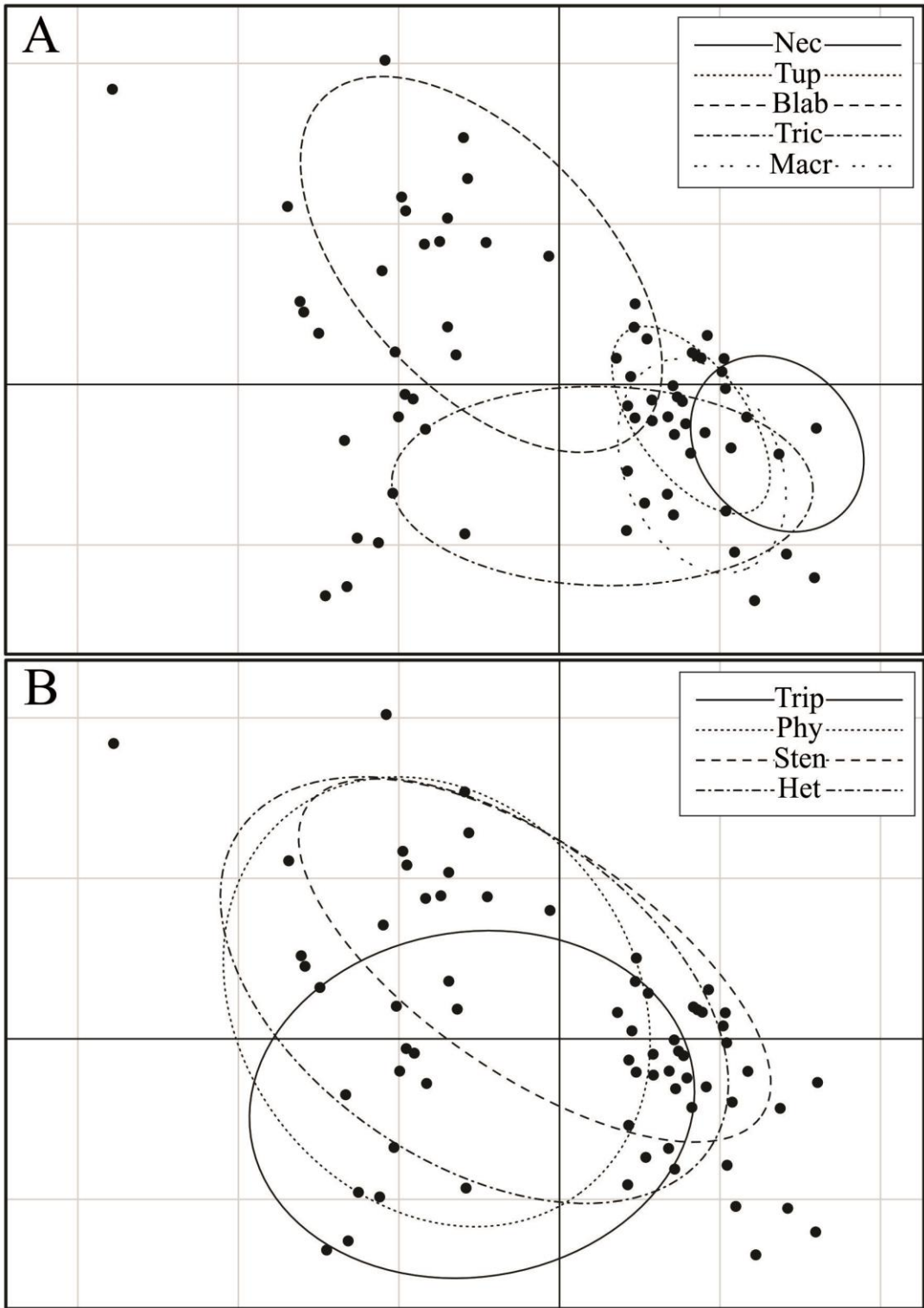


Figure 3.

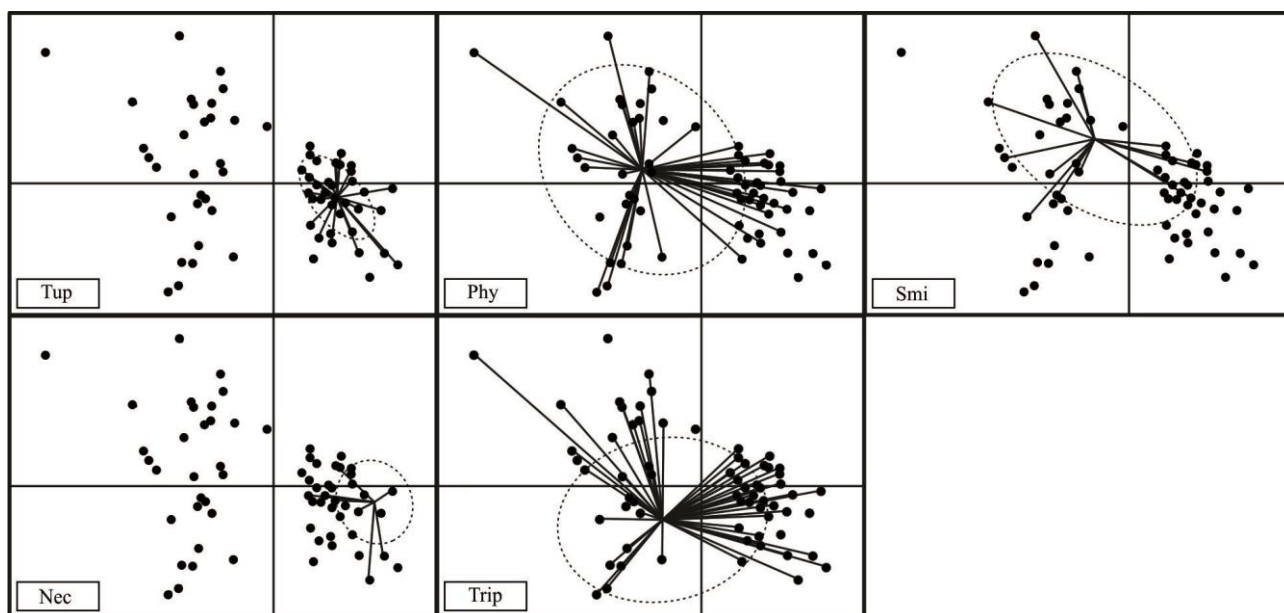


Figura Suplementar 1. Projection of environmental parameters on the axis of OMI analysis with the representation of ecological niches of shredder taxa found associated with leaf patches. Abbreviations of shredder taxa are presented in Table 4. *Continued below.*

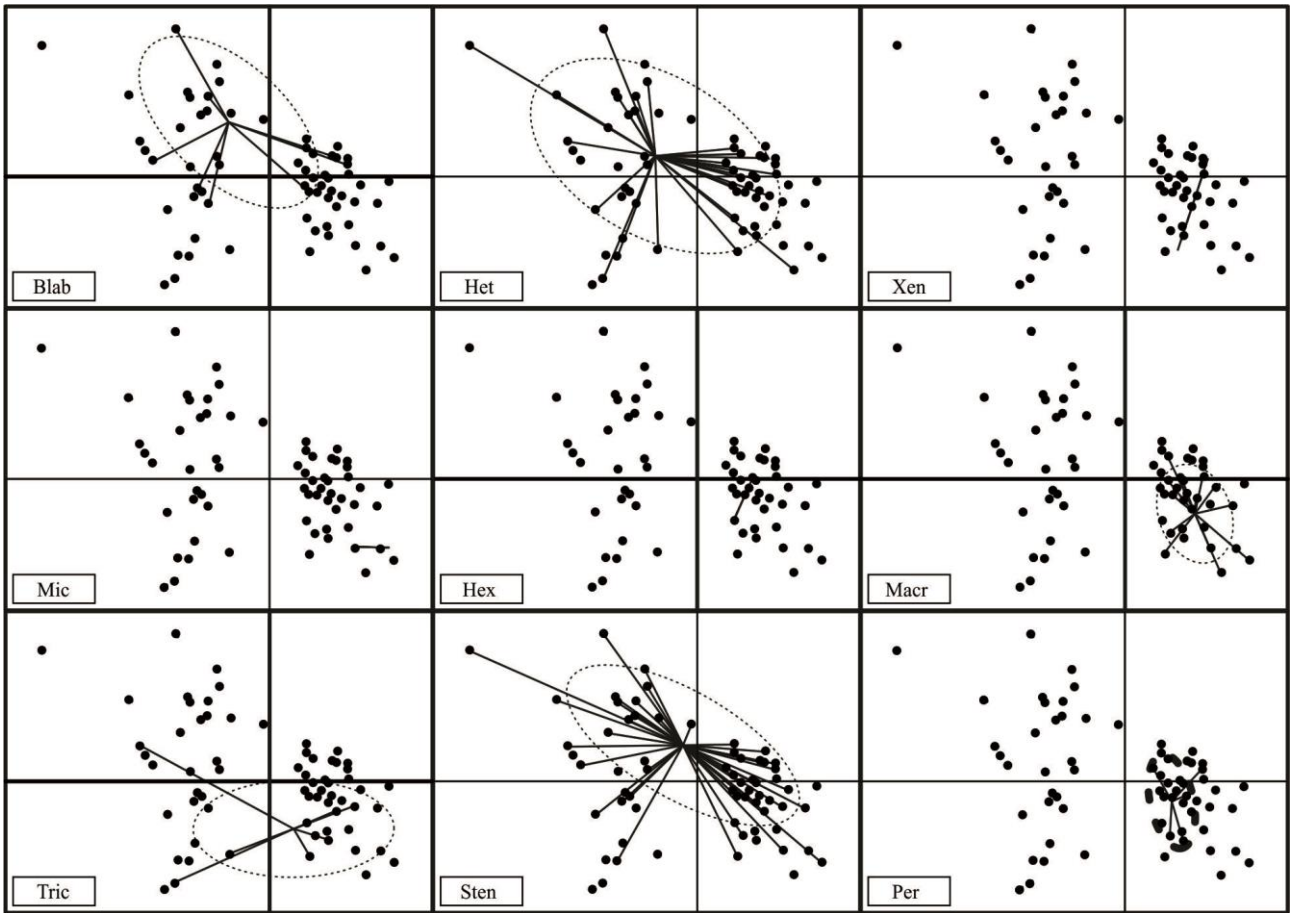


Fig. S1 *Continued.*