

Succession of the richness, abundance and species composition of frugivorous insects in *Psidium guajava* (L.)

Mudanças sucessionais na composição, riqueza e abundância de insetos frugívoros associados a frutos de *Psidium guajava* (L.)

Marconi Souza Silva¹
marconisouza@unilavras.edu.br

Rodrigo Lopes Ferreira²
drops@uffa.br

Abstract

The maintenance of species diversity is a complex phenomenon whose determinant factors can act in many spatial scales from local habitats to the regional level. We analyzed the habitat use by frugivorous insects in three categories of *Psidium guajava* fruits. We found 2,140 individuals of 22 morphospecies, of which Diptera (6 spp.), Hymenoptera (6 spp.), and Coleoptera (5 spp.) were the richest orders. Diptera was the most abundant order, with 93% of the total collected individuals (1,986 ind.). The greatest richness occurred in the fruits on the litter: 19 spp., contrasting with 7 spp. in ripe fruits and 2 spp. in unripe fruits on the tree. Diversity was significantly higher in fruits on the litter. Similarity was greatest between unripe and ripe fruits on the tree (0.50). Abundance ($r^2 = 0.08$; $r = 0.29$, $p = 0.00$) show a positive and significant relation with total volume of the all fruit categories Abundance (Log_{10}) in unripe fruits correlated positive and significantly with total diameter of these fruits ($r^2 = 0.12$; $r = 0.35$, $p = 0.04$). Variations in invertebrate richness, abundance, diversity, and density in the three fruit categories suggest different community establishment restriction levels. The physical and biological change gradients in the *P. guajava* fruits represent a heterotrophic succession. The temporal and spatial position of the fruits promotes variations in their physical and chemical properties. This variation in resource quality creates microhabitat heterogeneity and makes the presence and co-existence of many species of frugivorous invertebrates possible.

Key words: diversity, microhabitat heterogeneity, heterotrophic succession, *Psidium guajava*

Resumo

A manutenção da diversidade de espécies é um fenômeno complexo cujos fatores determinantes podem atuar em muitas escalas espaciais, sejam elas locais ou regionais. Foram analisadas neste estudo o uso de três categorias de frutos de *Psidium guajava* como habitats para insetos frugívoros. Foram encontrados 2.140 indivíduos de 22 morfo-espécies. Díptera (6 spp.), Hymenoptera (6 spp.), e Coleoptera (5 spp.) foram as ordens mais ricas. Díptera foi a ordem mais abundante, contribuindo com 93% o total dos indivíduos coletados (1.986 ind.). A maior riqueza (19 spp) foi encontrada em frutos presentes no chão (serrapilheira), contrastando com frutos maduros presentes nas árvores, onde foram encontradas 7 spp. e frutos verdes 2 spp. A diversidade foi significativamente mais elevada nos frutos na serrapilheira. A similaridade foi maior entre frutos maduros e verdes presentes na árvore (0.50). A abundância ($r^2 = 0.08$; $r = 0.29$, $p = 0.00$) relacionou-se positiva e significativamente com o volume do conjunto de frutos. A abundância (Log_{10}) encontrada nos frutos verdes foi correlacionada positiva e significativamente com o diâmetro total ($r^2 = 0.12$; $r = 0.35$, $p = 0.04$). As variações na riqueza, na abundância, na diversidade, e na densidade dos insetos nas três categorias de frutos sugerem níveis diferentes de limitação ao estabelecimento

¹ Núcleo de Pesquisa em Ciências Biológicas, Centro Universitário de Lavras (UNILAVRAS), Fundação Educacional de Lavras Rua Padre José Poggel, 506, Centenário, 37200-000, Lavras, MG, Brazil.

² Departamento de Biologia/Setor de Zoologia. Universidade Federal de Lavras. CP. 3037, 37200-000, Lavras, MG, Brazil.

destas comunidades. O gradiente de mudanças físicas e biológicas nos frutos de *P. guajava*, representa uma sucessão heterotrófica. A posição temporal e espacial dos frutos promove variações em suas propriedades físicas e químicas. Esta variação interfere na qualidade do recurso criando uma heterogeneidade de microhabitats que possibilita a presença e a coexistência de muitas espécies de insetos frugívoros.

Palavras-chave: diversidade, heterogeneidade de microhabitats, sucessão heterotrófica, *Psidium guajava*.

Introduction

The maintenance of species diversity is a complex phenomenon whose determinant factors can act in many spatial scales from local habitats to the regional level (Hengeveld, 1996). Species co-existence has been considered possible due to different ecological needs (Rosenzweig, 1981; Shorrocks, 1990; Haslett, 1994), especially regarding resource use (Tilman, 1982; Shorrocks, 1990). Differences in resource use may occur through specialization in different kinds or fractions of the resource or temporal partitioning (Ives, 1991). In habitats where the resource is present in a scattered and ephemeral way, other habitat options may appear mainly due to the spatial aggregation of competitors (Shorrocks, 1990). Species aggregation can be caused by qualitative differences in the substrate, making some more attractive than others (Ives, 1991; Hansen and Coleman, 1998).

Many invertebrates explore resources distributed in small separated ephemeral patches, such as feces, carcasses, fruits, leaves, shelter under rocks, and trunks on the litter. Such places can frequently shelter aggregations of many species. Since such habitats shelter only heterotrophic organisms, their communities persist under dynamic changes because all the available energy is consumed (Gee and Giller, 1987). Thus, in ephemeral resources, the main processes involved are colonization, organic matter assimilation, and dispersion, so that the gradual changes observed in the communities present are called heterotrophic succession (Doubt 1986).

Many fruit species are used by insects as food and/or shelter, resulting in changes in the fruit structure. Diptera, Heteroptera, and Coleoptera, that use ripe fruits for feeding or oviposition, are examples of those that cause the greatest damage in cultivated fruits throughout the world (Uchôa-Fernandes and Zucchi, 1999; Panizzi, 2000; Larned *et al.*, 2001; Souza-Silva and Ferreira, 2004).

Many authors assume a relationship between resource heterogeneity and richness and the diversity of different taxa (Hooper *et al.*, 2000). As a result, there are many studies of the effects of resource variability on diversity (Diamond and Case, 1986; Gee and Giller, 1987; Ives, 1991; Hansen and Coleman, 1998; Hooper *et al.*, 2000). Nevertheless, little attention has been given to invertebrate communities associated to fruits (Atkinson and Shorrocks, 1984; Pizzo and Oliveira, 2000; Devries and Walla, 2001; Souza-Silva and Ferreira, 2004). As they have high nutritive value, fruits are important dietary components of many animals (Devries and Walla, 2001; Larned *et al.*, 2001).

Fruit in different categories (unripe, ripe on tree and fallen on the litter) offer a great opportunity to test this paradigm in ecology. Here we are assuming the prediction that spatial and temporal variation caused by fruit maturation promotes habitat complexity and interactions that prevent diversity reduction due to competitive exclusion.

Psidium guajava is a tree species broadly distributed in tropical America (Tanaka *et al.*, 1992; Joly, 1998). Its fruits occur from January to March and many species of frugivorous in-

vertebrates can associate to its fruits. The analysis of insect communities associated to *Psidium guajava* fruits is essential to understand the use patterns of such habitats and provide evidence of the role of spatial variability in maintaining frugivorous insect diversity. For this purpose, we aimed to answer the following question:

- (i) What is the structure of the insects community associated to *Psidium guajava* fruits?
- (ii) Do total volume, endocarp diameter, and mesocarp and epicarp thickness of *Psidium guajava* fruits influence richness, diversity, and density in the associated communities?
- (iii) Do spatial and temporal variations in *Psidium guajava* fruits promote changes in the structure of the associated communities?

Material and Methods

Study site

This work was conducted at the Ecological Station of Universidade Federal de Minas Gerais (UFMG), Belo Horizonte (19° 52' S, 43° 58' W), Minas Gerais State, Brazil. The dry and rainy seasons are well defined, the dry (and cold) season receive less than 50mm average monthly rainfall (May through August), and the rainy (and hot) season receive 300mm average monthly rainfall (November through January). The Ecological Station is a restricted area within the UFMG campus, covering an area of 150 ha, and limited externally by major urban avenues. It is covered by a secondary growth vegetation, where herbs and bushes predominate, and a few secondary growth semideciduous

forest areas, where trees are medium to large size, reaching less than 25 m. Additionally there are field areas with shrubs, vines, various grasses (*Melinis minutiflora* P. Beauv., *Pennisetum purpureum* Schum.), swamps, and small streams (Souza-Silva *et al.*, 2001).

Procedures

A total of 251 *Psidium guajava* fleshy fruits were randomly collected. These fruits had scattered distribution and were in different senescence stages: 75 fruits were unripe, 100 fruits were ripe, all located on the tree, and 76 ripe fruits were laying on the litter under the *P. guajava* trees.

Fruits were visually attributed to three senescence categories: smaller and dark-greenish fruits were considered as unripe. Completely yellow fruits were considered as ripe. All the fruits collected on the litter were yellow. Fruits with intermediate color pattern or senescence stage were not collected. The color is the best parameter to evaluate the maturation level of *P. guajava* fruits (Mercao-Silva *et al.*, 1998). Fruits were put in individual plastic bags and labeled. In the laboratory, they were weighed and the meso-epicarp thickness and endocarp diameter measured (Gerhart *et al.*, 1997).

To analyze the influence of fruit size on abundance and richness of associated invertebrates, each fruit was put in graduated test tubes containing 100 ml of water, and fruit volume was given by the displaced water volume. The invertebrates associated to the fruits were extracted using tweezers, brushes, and a stereoscopic microscope was used for identification to the lowest taxonomic level possible. Afterwards, they were separated into morphospecies. Individuals at different developmental stages were considered as distinct morphospecies (Ferreira and Marques, 1998). All the specimens are deposited in the laboratory of *Ecologia e Comportamento de Insetos* of the *Universidade Federal de Minas Gerais* (UFMG).

Data analysis

Mean organism density (ind/cm³) per fruit and standard deviation were calculated for each fruit set. The correlations between invertebrate richness, abundance and density with meso-epicarp thickness, endocarp diameter, injuries and fruit volume were performed using linear regression (Zar, 1986). The data sets without normal distribution were log-transformed (log₁₀). Diversity calculations for each fruit category were performed using the Shannon-Wiener index and the similarity calculations were performed using the Sorenson index (Magurran, 2004). The significance of the differences among the diversity values was evaluated using the *t* test of Huntchinson (Magurran, 2004).

Results

Associated invertebrates

A total of 2,140 invertebrates of 22 morphospecies from at least 11 families distributed in seven insect and Acari orders, were found to be associated to *P. guajava* fruits (Table 1). Diptera (6 spp.), Hymenoptera (6 spp.), and Coleoptera (5 spp.) were the richest orders. Diptera was the most abundant order, contributing 93% of the total individuals collected (1,986 ind.), whereas Coleoptera contributed with nearly 6% of total abundance (128 ind.) and Hymenoptera, with about 1% (22 ind.) (Figure 1). The orders Acari, Dermoptera, Dictyoptera, Heteroptera, and Isoptera had a single individual each, jointly contributing with only 0.2% of total abundance. The orders Dictyoptera and Heteroptera were restricted to ripe fruits on the tree, whereas Acari, Dermoptera, and Isoptera were restricted to fruits on the litter (Table 1). Hymenoptera were richer and more abundant in ripe fruits on the litter (5 species and 21 individuals versus 1 species and 1 individual in ripe fruits on the tree).

The greatest richness was found in fruits on the litter, which had 19 morphospecies, versus seven in ripe fruits and two in the unripe (Table 1, Figures 2 and 3). Only the species *Anastrepha fraterculus* (Diptera: Tephritidae) and *Conothrachelus* sp. (Coleoptera: Curculionidae) were present in the three fruit categories analyzed.

Diversity was estimated as 0.24 (E = 0.14) in ripe fruits, 0.57 (E = 0.83) in unripe fruits and 0.98 (E = 0.33) in fruits on the litter. Differences among fruit categories were significant according to Hutchinson *t* test ($p < 0.001$; Table 1). The fauna similarity was 0.50 between unripe and ripe fruits on the tree, 0.24 between ripe fruits on the tree and ripe fruits on the litter, and 0.19 between unripe fruits and ripe fruits on the litter. The difference among the three data sets was significant according to Hutchinson's *t* test ($p > 0.001$). The estimated densities varied among the three fruit categories analyzed, and the differences observed were significant ($p > 0.001$; Figure 4).

Among the variables correlated through linear regression, richness abundance (Log₁₀) ($r^2 = 0.12$; $r = 0.36$, $p = 0.00$) showed a significant relation with total volume of the all fruit categories Abundance (Log₁₀) in unripe fruits showed a significant relation with total diameter of these fruits ($r^2 = 0.12$; $r = 0.35$, $p = 0.04$).

Unripe fruits

Unripe fruits varied in volume (mean 24.9 cm³ ± 8.9). In these fruits, a total of 88 individuals belonging to only 2 morphospecies of 2 families from the orders Diptera and Coleoptera were collected (Table 1). Diptera had 63 individuals whereas Coleoptera contributed 23 individuals that corresponded to 74% of the total specimens collected in these fruits (Table 1).

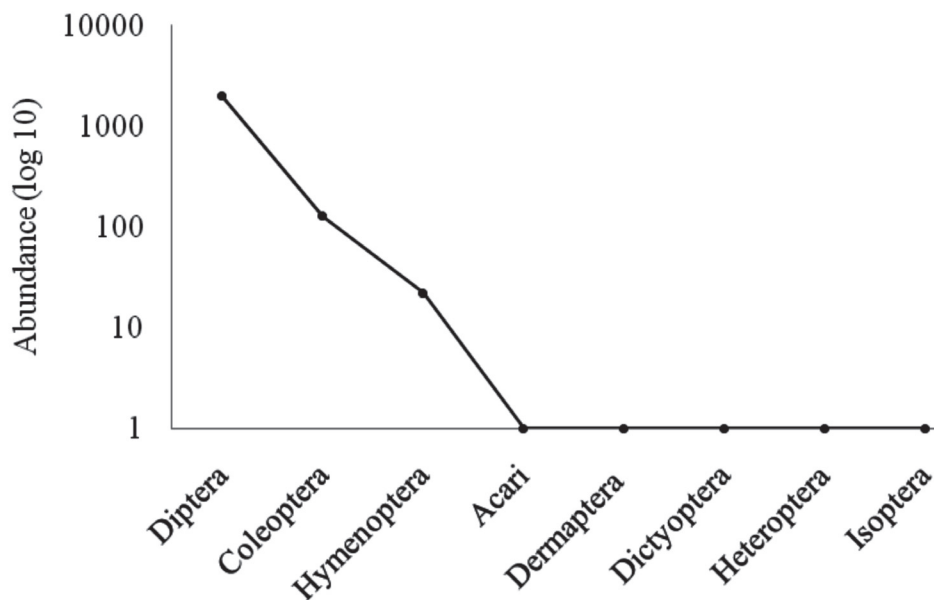


Figure 1. Distribution of abundance of invertebrate orders associated to *P. guajava* fruits.

Table 1. Composition, richness and abundance of the communities associated to *P. guajava* fruits with localized spatial and temporal distribution. L = larvae stage.

Order	Morphospecies/species	Unripe	Ripe	Ripe on the litter
Acari	Acari sp1			1
Coleoptera	<i>Conotrachelus</i> sp1			2
	<i>Conotrachelus</i> spL1	23	36	24
	Curculionidae spL1		1	34
	Scolytidae sp1			7
	Staphilinidae sp1			1
	Forficulidae sp1			1
Dermaptera	Forficulidae sp1			1
Diptera	<i>Anastrepha fraterculus</i> (L)	65	662	1054
	Drosophilidae sp1			45
	Drosophilidae sp2			9
	Drosophilidae spL1		1	64
	Drosophilidae spL2			83
	Lonchaeidae spL1			3
Dictyoptera	Dictyoptera sp1		1	
Heteroptera	Pyrrhocoriade sp1		1	
Hymenoptera	Formicidae sp1			11
	Formicidae sp2			3
	Formicidae sp3		1	
	Braconidae sp3			4
	Eucoilidae sp1			2
	Eucoilidae sp2			1
Isoptera	Termitidae sp1			1
	Abundance	88	702	1350
	Richness	2	7	19
	Equitability	0.83	0.14	0.33
	Diversity	0.57	0.24	0.98

Ripe fruits on the tree

This fruit category had an average volume larger than that of unripe fruits ($36 \text{ cm}^3 \pm 15$), but smaller than that of fruits on the litter. Among the 702 specimens associated, seven morphospecies of at least six families distributed in five invertebrate orders were identified (Table 1). Diptera (2 spp.) and Coleoptera (2 spp.) were the richest and most abundant orders (663 and 37 individuals, respectively). *Anastrepha fraterculus* was the dominant species in these fruits, contributing 99.8% of the total abundance in the order Diptera (Table 1).

Ripe fruits on the litter

The fruits collected on the litter had small injuries and holes, possibly a result of the activity of ants, beetles, and termites found at the site (Table 1). Nevertheless, no fruits presented alterations that could make the volume and diameter measurements unfeasible. The mean volume of these fruits was estimated as $40 \text{ cm}^3 \pm 14.6$. The fruits in this category had 63% of the total insect abundance (1,350 ind.). From the 19 morphospecies present, 15 were collected only in this fruit category. Only the orders Heteroptera and Dictyoptera did not occur associated to fruits on the litter (Table 1). Diptera (6 spp., 1,258 ind.), Coleoptera (5 spp., 61 ind.), and Hymenoptera (5 spp., 21 ind.) were the richest and most abundant orders. Diptera contributed 93% of the total of individuals collected in this fruit category. *Anastrepha fraterculus* was the most abundant species, representing 78% of the individuals collected in these fruits.

Discussion

The community composition in *P. guajava* fruits and its relationship with the resource seem to be similar to that found in other ephemeral systems (Souza-Silva and Ferreira, 2004). The colonizers that first ar-

rive at the habitat are larvae (Diptera and Coleoptera). As they colonize the fruit while it is still unripe, they can use this resource for a long time. The secondary colonizers are mainly from the orders Hymenoptera, Dictyoptera, and Heteroptera. Tertiary colonizers were the Acari, Isoptera, and Dermaptera. The abundance pattern of species is also similar to the pattern found in other ephemeral resources, with a few very abundant species (Doube, 1986; Souza-Silva and Ferreira, 2004).

Nevertheless, variations in richness, abundance, diversity, and density of insects in the three fruit categories suggest different restriction levels for the establishment of their communities. It is possible that physical and chemical features of the different senescence stages function as barriers for species colonization and persistence. Physical and chemical variations of *P. guajava* fruits at different senescence stages are described by many authors, corroborating our hypothesis (Elzoghbi, 1994; Mercado-Silva *et al.*, 1998; Ruby *et al.*, 2000). Souza-Silva and Ferreira (2004), described changes in invertebrate communities probably in consequence of the physical and chemical variations of *Alibertia edulis* fruits also at different senescence stages.

Fruits containing unripe seeds can be often toxic and immature fruits have high concentrations of tannins and cyanogenic glycosides in the pulp. On maturation, the concentration of these compounds in the pulp declines rapidly and the glycosides are concentrated in the seeds (Crawley, 1983). When reduced food quality is due to an increase in the concentration of toxins, continued feeding would be clearly debilitating. At high levels of food availability, intake is limited by the rate at which the herbivore can process the food (Crawley, 1983). Mercado-Silva *et al.* (1998), observed a reduction in acidity and an increase in cellulase activity with consequent reduction in fiber concentration and

hardness with the advance of maturation level in *P. guajava* fruits.

The lowest richness and abundance values observed in unripe fruits characterize this kind of habitat as one of the most restrictive. Even if concentration of secondary compounds, hardness, and distance of the fruit from the ground – a possible colonizer source – were not quantified, it is reasonable to assume that these variables may determine the richness and abundance values found here.

The physical and chemical features of the unripe fruits can benefit invertebrates able to colonize and use these fruits, protecting them from parasitoid attacks and predators not adapted to these habitat features (Souza-Silva and Ferreira, 2004). Besides, competition for space and food is reduced since invertebrate density in unripe fruits is lower than in the other fruit categories (Janzen, 1977; Bautista and Harris, 1996).

The physical and chemical composition of a habitat determines richness and abundance of pioneer species in many organic deposits (Gadgil, 1971; Kuusela and Hanski, 1982; Kneidel, 1984; Souza-Silva and Ferreira, 2004). The highest richness and abundance values found in ripe fruits on the tree and on the litter show the importance of these stages of the resource for many invertebrate groups and give evidence for importance of temporal and spatial changes in *Psidium guajava* fruits in the structure of associated insect communities.

According to Hutchinson (1961), gradual changes in the environment may allow the co-existence among species, assuming that different species can be competitively superior at different times. A species will have its abundance altered by other species when its competitive ability is altered by environmental changes.

The gradient of physical and biological changes in *Psidium guajava* fruits represents a model of heterotrophic succession (Doube, 1986; Souza-Silva and Ferreira, 2004). This model foresees

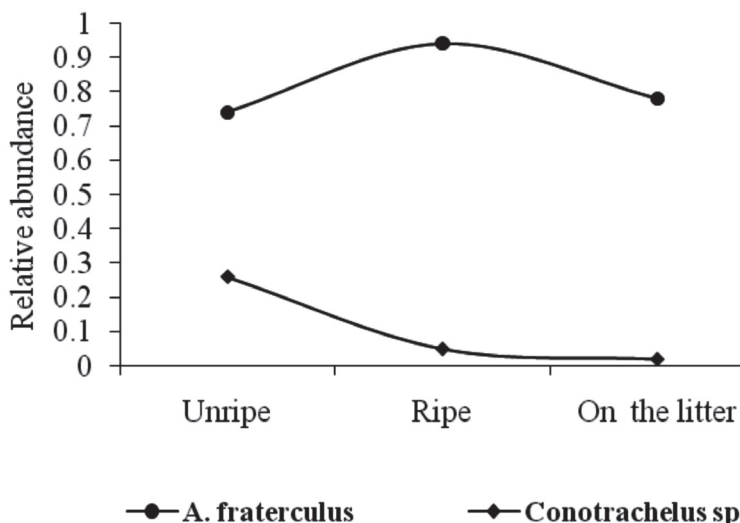


Figure 2. Colonization strategies and differential dominance of the of *Anastrepha fraterculus* and *Conotrachelus sp.* in three senescent stages of the *P. guajava* fruits.

successive changes with time in physical properties, species composition, and the structure of the invertebrate community associated to ephemeral resources. Colonization starts in unripe fruits, with herbivorous species, and ends in ripe fruits on the litter, with scavenger species. After their formation, the systems (fruits) are available for colonization, but few species occur due to the short time available for colonization and the low resource quality, influenced by physical and chemical properties. With maturation, though, the system is modified, making an increase in richness and diversity possible, mainly because some time has passed, allowing colonization by new species and because the physical and chemical changes in the habitat have made the system more accessible (Souza-Silva and Ferreira, 2004).

In the case of species associated to *P. guajava* fruits, it is reasonable to assume that the species able to colonize and cross the barriers present in unripe fruits (pioneers) can benefit from this ability, since they colonize the resource while few species are present and those that are are in low abundance. For instance, only *Anastrepha fraterculus* and *Conotrachelus sp.* coexist in unripe fruits, and *Conotrachelus sp.* has a lower relative abundance

in ripe fruits, suggesting that resource variation can alter the competitive interactions among species. Females of *Anastrepha fraterculus* prefers unripe fruits for visitation and ovoposition activities. Both sexes fed almost exclusively on ripe guava fruits, which had burst naturally or had been injured, and on fruit juice droplets or pieces of fallen fruit (Malavasi *et al.*, 1983).

Ripe fruits, with greater volume, can maintain more abundant populations due to greater resource availability. In ripe fruits, *Anastrepha fraterculus* assumes its highest abundance values. The intra-specific aggregation is well documented for organisms living in ephemeral and localized substrates (Hanski, 1981). This kind of aggregation may increase competition for food and space, but on the other hand, it may improve group survival by increasing defensive ability, success in resource searching or modifying the local microclimate (Inouye, 1999).

The herbivorous insects that frequently lay their eggs in large structures do that in response to the higher food resource availability for their offspring, or to protect them against natural enemies (Hoffmeister *et al.*, 1999). The fruits on the litter represent an intermediate stage in this

heterotrophic succession. The fall may be considered a disturbance that modifies the habitat under succession and makes the colonization by new invertebrates species possible (Tilman, 1982).

The exocarp of ripe fruits on the litter may not offer protection against predators. In their interior, besides food, many terrestrial invertebrates groups that were not observed in other senescence stages can find microhabitats that allow their presence. Colonization and use of the fruits on the litter can be made easier for these invertebrates by physical and biological variations (fruit fall, many fissures, holes, and interactions). In general, interaction among scavengers affecting resource degradation may be positive (e.g. detritus fragmentation by a species facilitates feeding by others) (Larned *et al.*, 2001). Fragmentations in ripe fruit permit colonization by microorganisms and consequently nutrients in fruit juice is increased for scavenger arthropods (e.g. larvae) (Malavasi *et al.*, 1983). Nevertheless, when fruits become very old and there is no more resource available for any trophic level, local richness and abundance can decline due to the dispersion of species that completed their life cy-

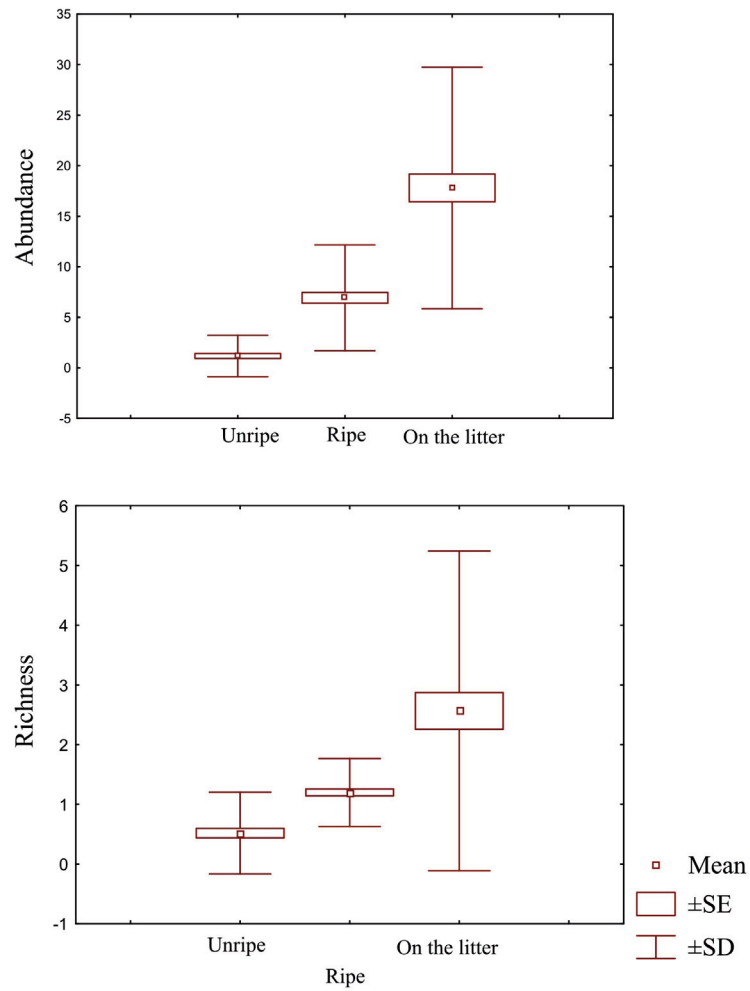


Figure 3. Abundance and richness increase of invertebrate species influenced by senescent stages of the *P. guajava* fruit.

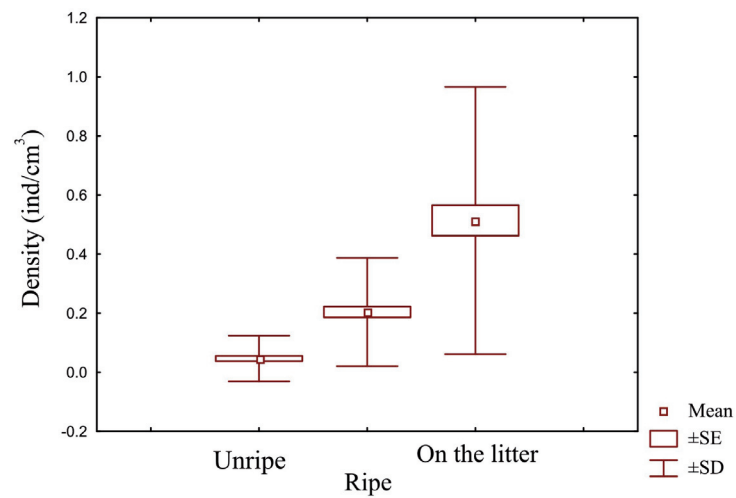


Figure 4. Density increase of invertebrates associated to *P. guajava* fruits with localized spatial distribution and senescence.

cles, when adults leave searching for new resources (fruits). The temporal and spatial positions of *P. guajava* fruits promote variations in physical and chemical properties of fruits with consequent variation in resource quality and availability. Microhabitat heterogeneity makes the co-existence of many frugivorous invertebrate species possible. The diversity of a given resource allows a larger number of species to co-exist in a given area and consequently the structure of this habitat is an important factor influencing community structure (Price, 1975; Janzen, 1980; Pizzo and Oliveira, 2000). Patterns of fruit used provide evidence of the role of spatial variability in maintaining frugivorous communities. The diversity of arthropods in these fruits can be especially high in the tropical biomes, in which the diversity of many invertebrates may be associated to fruit diversity (Janzen, 1980; Malavasi *et al.*, 1983, Souza-Silva and Ferreira, 2004).

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