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HETEROTROPHIC SUCCESSION IN *ALIBERTIA EDULIS* FRUITS: VARIATION IN RESOURCE AVAILABILITY AND TEMPORAL HETEROGENEITY OF MICROHABITATS FOR INVERTEBRATES

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Abstract. Gradual changes in the composition of invertebrate communities associated with ephemeral resources are called heterotrophic succession. We analyzed succession changes in species richness and diversity of frugivorous invertebrates in four categories of *Alibertia edulis* (Rubiaceae) fruits. Of 119 morphospecies of invertebrates, 19 morphospecies occurred on unripe fruits, 60 on ripe fruits in the tree, 68 on intact ripe fruits on the litter, and 64 on split fruits on the litter. Coleoptera (53 spp.), Hymenoptera (22 spp.), and Diptera (14 spp.) were the richest orders. Coleoptera (980 ind.), Hymenoptera (805 ind.), Isoptera (593 ind.), and Diptera (264 ind.) were the most abundant groups. Variations in species richness, abundance, diversity, and density of invertebrates may be due to different levels of constraint on colonization and establishment of species in the fruit categories. The gradients of physical and biological changes found in the fruits of *Alibertia edulis* represent a distinct degradative model in which colonization starts on unripe fruits, with herbivorous species, and ends on ripe fruits on the litter, with scavenger species. The succession process shown here may be common in tropical systems, in which the diversity of many invertebrate communities may be associated with fruit diversity. *Accepted 15 January 2004.*

Key words: *Diversity*, *heterogeneity of microhabitats*, *invertebrates-fruit interaction*, *heterotrophic succession*.

INTRODUCTION

Many species of invertebrates exploit ephemeral resources distributed in discrete patches, such as feces, carcasses, and fruits (Shorrocks 1990, Arndt *et al.* 1996, Paarmann *et al.* 2002). Such resource categories are discontinuous in space and persist for a short time interval before being degraded (Zuben 2000). Such substrates are frequently colonized by a great number of species (Lane 1975, Shorrocks 1990). Nevertheless, since on such resources only heterotrophic organisms are found the communities persist in dynamic changes until the available energy is consumed (Zuben 2000). So with ephemeral resources the main processes involved are colonization, assimilation of the organic matter, and dispersal. The gradual changes observed in these communities are called heterotrophic succession (Gee & Giller 1987).

The coexistence of species in such substrates is possible because of their different ecological needs, especially regarding the use of food resources (Tilman 1982). Differences in choice and use of resources result from specialization on different resources fractions with spatial or temporal partitioning (Ives 1991, Greene & Stamps 2001). Various authors assume that habitat selection by a species involves factors such as species density in the habitat, the intrinsic quality of the habitat, and the energetic costs of establishment in the habitat (Horne 1983, Vickery *et al.* 1992).

There are many studies on the spatial and temporal organization of invertebrate communities in discrete and ephemeral habitats (Ferreira *et al.* 2000, Paarmann *et al.* 2001, Arti 2001). Nevertheless, little attention has been given to invertebrate communities in fruits principally in Brazilian ecosystems (Paarmann *et al.* 2001, Paarmann *et al.* 2002). As they have a high nutritive value, fruits are important components of the diets of many invertebrates (DeVries & Walla 2001, Larned *et al.* 2001).

Knowledge of the succession dynamics in *Alibertia edulis* (Rubiaceae) fruits can reveal a distinct model that describes succession on fruits, and also shows the diversity of invertebrates and ecological interactions on these substrates during succession. For this purpose, we aimed to answer the following questions:

1. What is the structure of the invertebrate community associated with *Alibertia edulis* fruits?

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2. Do the spatial and temporal variations in the physical properties of *Alibertia edulis* fruits promote changes in the structure of the associated invertebrate community?
3. What are the trophic interactions in the invertebrate communities associated with *Alibertia edulis* fruits?

METHODS

Study site. The study was carried out in the ecological reserve of Pirapitinga, Minas Gerais state, Brazil. Located in the reservoir of the hydroelectric power station of Três Marias (18°23'S, 45°17'W), this area has been preserved for environmental conservation since 1962, when the reserve became an island. Its approximate surface area is 1000 ha (Azevedo 1987). Two general vegetation types can be distinguished in Pirapitinga: a forest, formed by trees up to 20 m high, and *cerrado* vegetation, the Brazilian savanna (Azevedo 1987). Samples were collected close to the edge of a semi-deciduous seasonal forest, in an area of *cerrado*. This vegetation is located on the upper limit of the depletion margin of the Três Marias reservoir (Azevedo 1987).

A total of 141 semi-fleshy fruits of the Rubiaceae *Alibertia edulis* (A. Rich.), with different spatial and temporal distributions, was collected in September 2001: 34 unripe fruits, 33 ripe fruits, both in the trees, 35 intact ripe fruits, and 39 split ripe fruits, both on the litter.

The fruits considered as unripe were those with a green color; the ripe ones were those totally dark (brown). All the fruits collected from the litter were ripe. The color is a good indicator to determine if fruits of Myrtaceae are ripe or unripe, for instance, in *Psidium guajava* (L). (Mercado-Silva *et al.* 1998).

To investigate the influence of tree height and distance from the forest edge on abundance and species richness of invertebrates associated with fruits, the samplings were done at 15 trees with different locations in relation to the border of the forest and distributed along a linear distance of 750 m, so that the closest individuals sampled were separated by 50 m. The distance of each fruit sampled to the ground was measured. Total height of each tree and its distance from the forest boundary were also measured. Fruits were put in individual plastic bags and labeled. In the laboratory, we measured their maximum diameter and area of fissures when this was the case. We also counted the number of "injuries". Such "injuries" are defined as small holes made by invertebrates that hatched in the fruit when leaving it. The volume of the fruits was estimated using the formula for the calculation of the volume of a sphere ($4/3(\pi R^3)$). These methods were used to test the influence of the above environmental variables on the abundance and species richness of invertebrates associated with fruits.

The invertebrates associated with fruits were extracted using tweezers and brushes, and with stereoscopic microscopes were identified to the lowest taxonomic level possible, then assigned to morphospecies. Voucher specimens of the invertebrates are deposited in the Laboratory of Ecology and Behavior of Insects, Department of General Biology, within the Institute of Biological Sciences (ICB) at the Federal University of Minas Gerais (UFMG).

Data analysis. The mean density of organisms (ind/cm^3) per fruit was calculated, as well as the standard deviation for each fruit category. The correlations of abundance and species richness of invertebrates with total height and distance of the trees to the forest edge, number of injures in the fruit, fruit volume, height, and area of fissures were done using linear regressions (Zar 1996). Data sets that did not have normal distribution were log-transformed ($\log_{10}$). The calculations of diversity for each fruit category were performed using the Shannon-Wiener index, and similarity was estimated using the Sorenson index (Magurran 1988). The significance of differences between diversity values was evaluated using the *t*-test of Hutcheson (Magurran 1988).

RESULTS

A total of 2.760 invertebrates representing 119 morphospecies was obtained from 141 fruits. Most species belong to Coleoptera (53 spp.), Hymenoptera (22 spp.) and Diptera (14 spp.); Coleoptera (980 ind.), Hymenoptera (805 ind.), Isoptera (593 ind.), and Diptera (264 ind.) were the most abundant orders (Tab. 1). Species richness, abundance, diversity, and density were greatest in intact and ripe fruits located on the litter under the trees (Tab. 1). The taxonomic composition, abundance and species richness of the invertebrates and diversity, equitability and density in different fruit categories (unripe and ripe on tree; intact and split in ground) are also given in Table 1.

TABLE 1. Taxonomic composition, number of individuals, richness of morphospecies, diversity, equitability and density of the invertebrates in different fruit categories (unripe and ripe on tree; intact and split in ground).

Order	Family	Unripe		Ripe		intact		Split	
		N° indiv.	N° species	N° indiv.	N° species	N° indiv.	N° species	N° indiv.	N° species
Acarina	Unidentified							9	6
Araneida	Gnaphosidae					1	1		
	Oonopidae							1	1
	Salticidae					1	1	1	1
	Theridiidae					1	1	1	1
	Unidentified							1	1
Coleoptera	Anthicidae							3	2
	Bostrichidae					2	1	1	1
	Carabidae							1	1
	Chrysomelidae			1	1				
	Cucujidae			1	1			1	1
	Lathridiidae					1	1		
	Nitidulidae	5	4	201	21	404	26	58	14
	Staphylinidae	2	2	2	1	21	3	5	2
	Unidentified	4	3	77	6	49	4	168	5
Collembola	Unidentified							6	5
Copepopda	Unidentified					1	1		
Dermaptera	Unidentified							1	1
Diptera	Anthomyidae			16	2		1		
	Cecidomyiidae					2	2	1	1
	Ceratopogonidae					1	1		
	Chironomidae							1	1
	Culicidae			1	1				
	Drosophilidae			2	1	27	4	12	2
	Mycetophilidade					1	1		
	Unidentified			52	1	108	2	33	3
Dictyoptera	Unidentified					1	1		
Heteroptera	Miridae					1	1	1	1
	Pyrrhochoridae			1	1				
Homoptera	Unidentified					1	1		
Hymenoptera	Apidae					2	2	1	1
	Formicidae	7	4	11	4	300	5	45	6
	Eurytomidae	327	2	72	2	21	2	13	1
	Torymidae	4	1	8	1	2	1		
	Unidentified					1	1		
Isoptera	Nasutitermitidade	1	1					480	1
	Rhinothermitidae							112	1
Lepidoptera	Unidentified	2	1	14	1	30	2	14	1
Polyxenida	Polyxenidae					1	1		
Pseudoscorpiones	Chernetidae	1	1						
Psocoptera	Liposcelidae			5	1			4	2
	Unidentified					1	1	1	1
	Total	353	19	450	60	980	68	976	64
	Diversity	1.27		2.70		3.60		2.20	
	Equitability	0.43		0.71		0.75		0.53	
	Density*	0.01		0.03		0.06		0.04	

*(ind/cm^3)/fruit

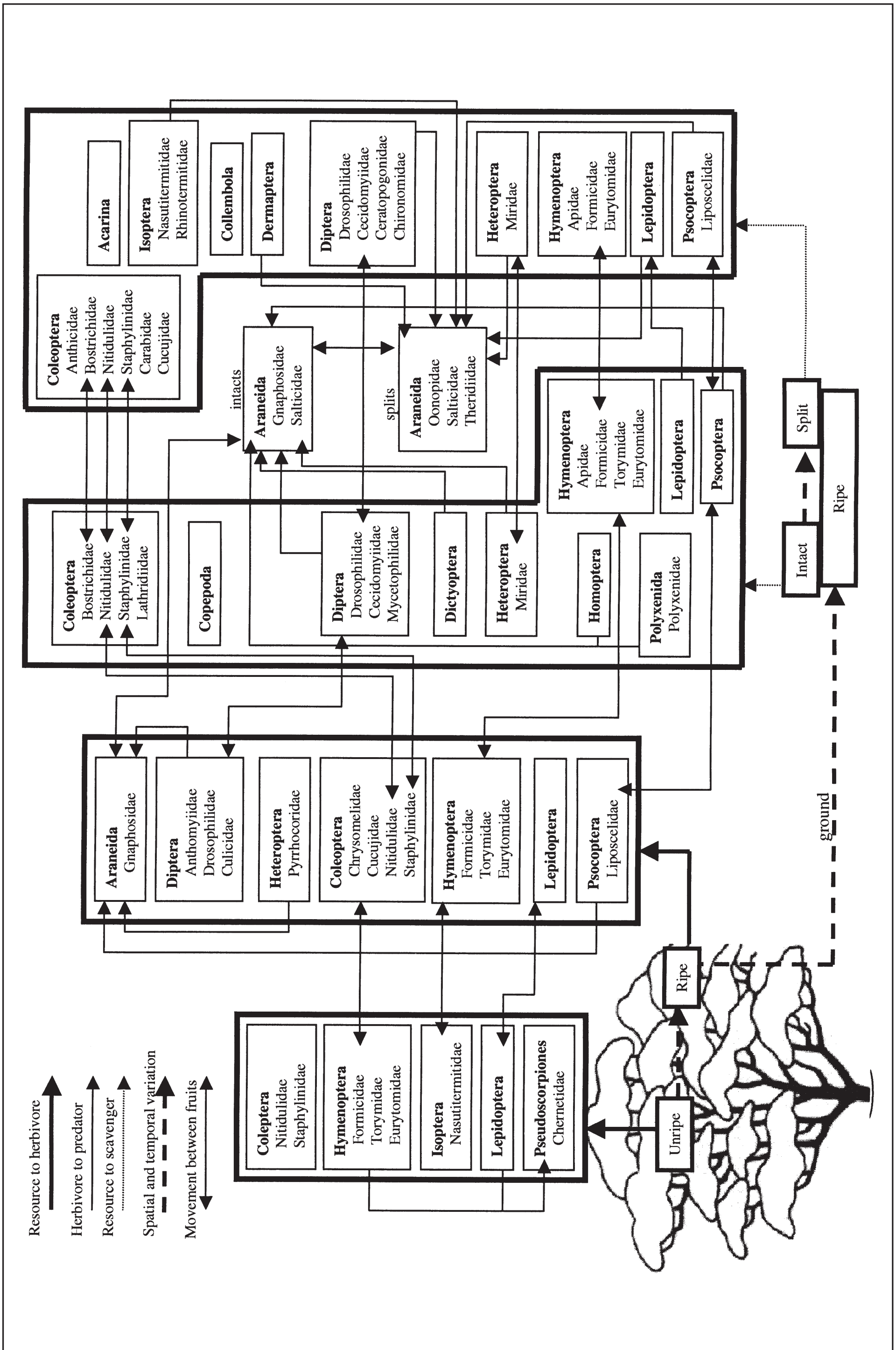

FIG. 1. Successional changes and trophic interactions of frugivorous invertebrates in *Alibertia edulis* fruits.

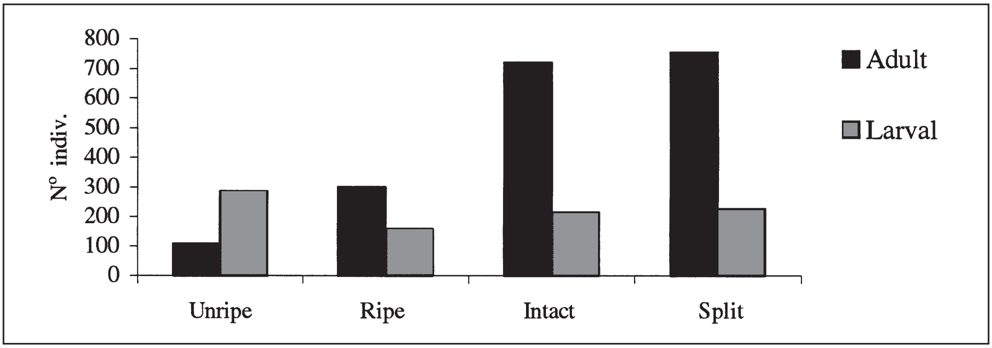

FIG. 2. Comparison of larval and adult abundance of the invertebrates associated with *Alibertia edulis* fruit categories.

The successional sequence and trophic interactions, assumed through comparison of presence/absence data of the taxa, showed the trophic, spatial, and temporal complexity of the system (Fig. 1). Coleoptera and Hymenoptera were the richest groups in unripe fruits. The species richness of these taxa increased in the remaining fruit categories. Ants and termites were associated especially with split and dry fruits. The abundance of invertebrates in the larval stage was higher than in the adult stage only in unripe fruits (Fig. 2).

The diversities calculated beteween all the fruit categories were significantly different ($p < 0.001$) (Tab. 2). Ripe fruits in the tree and intact ripe fruits on the litter were the most similar in species composition (Tab. 3).

The physical and biological factors here measured that were significantly correlated to richness and diversity of the invertebrate communities are shown in Table 4.

DISCUSSION

Fruits are frequently used by invertebrates as a food resource and/or shelter. Diptera, Heteroptera, and Coleoptera usually use ripe fruits for feeding or egg-laying (Panizzi 2000, Zerm *et al.* 2001, Paarmann *et al.* 2002). The developmental stages of pioneer species and the general abundance pattern of species look similar to those found in other ephemeral systems, such as carcasses and feces, that present a few abundant species (Gee & Giller 1987, Tilman 1982). In this study, the first ones to colonize the fruits are the Coleoptera, Hymenoptera and Lepidoptera larvae, that consume the material for a long time (unripe, ripe and fallen fruits, on the litter). The Hymenoptera and Coleoptera species exploit mainly the seeds of the fruits. Secondary colonizers were mainly Diptera, Psocoptera, and Heteroptera. Such groups feed on the mesocarp of ripe fruits, accelerating their fragmentation

TABLE 2. significance values between the compared diversity values in four fruit categories, calculated by the *t*-test of Hutcheson (Magurran 1988).

Fruit categories	t-value	Freedom of degree	Probability
Unripe × Ripe	16.72	803.93	P < 0.001
Unripe × Intact	24.41	730.7	P < 0.001
Unripe × Split	10.8	980.53	P < 0.001
Ripe × Intact	6.58	970.98	P < 0.001
Ripe × Split	6.318	1261	P < 0.001
Intact × Split	13.63	1789.6	P < 0.001

TABLE 3. Similarity (Soreson index) of the invertebrate communities associated with the four fruit categories of *Alibertia edulis*.

Fruit categories	Unripe	Ripe	Intact	Split
Unripe	1	0.413	0.273	0.024
Ripe		1	0.566	0.355
Intact			1	0.439
Split				1

TABLE 4. Physical and biological parameters of the invertebrate communities associated with *Alibertia edulis* fruits, significantly related by linear regression.

Fruit categories	Parameters	Significance
Unripe	Density (log_{10}) × Height of the tree	$F_{1,14}$ = 11,376; R = 0,665; P < 0,01
Unripe	Species richness (log_{10}) × Injuries (log_{10})	$F_{1,9}$ = 15,056; R = 0791; P < 0,01
Ripe	Species richness (log_{10}) × Distance to the forest edge	$F_{1,19}$ = 4,863; R = – 0,451; P < 0,05
Ripe	Density (log_{10}) × Distance to the forest edge	$F_{1,18}$ = 5,033; R = – 0,467; P < 0,05
Intact	Species richness (log_{10}) × Volume (log_{10})	$F_{1,23}$ = 7,052; R = 0,484; P < 0,01
All categories	Species richness (log_{10}) × Volume (log_{10})	$F_{1,87}$ = 6,374; R = 0,261; P < 0,01
All categories	Species richness (log_{10}) × Injuries (log_{10})	$F_{1,57}$ = 10,812; R = 0,399; P < 0,01
All categories	Density (log_{10}) × Distance to the forest edge	$F_{1,87}$ = 8,855; R = – 0,303; P < 0,01

and decomposition. Other colonizers were Acarina, Araneida, Collembola, Copepoda, Dermaptera, Dictyoptera, Hymenoptera (Formicidae), Isoptera, and Polyxenida. These organisms colonized mainly fruits on the litter, and are predators, hosts, saprophagous or shredders. In a heterotrophic succession process, many species actively involved in organic matter degradation occur (those that cause fragmentation), while others are passive (hosts and predators) (Price 1975). Formicidae, the most abundant group in this study, usually explore fallen fruits in arid vegetation, thereby causing fragmentation (Pizzo & Oliveira 2000).

General patterns in species richness and diversity: The variations in species richness, abundance, diversity, and density of invertebrates can be caused by different levels of resistence to colonization and establishment of species in the fruit categories. Possibly physical properties of the fruits in each category function as barriers making it more or less difficult for species to colonize and persist (e.g., maturation level, tree height, distance from the forest edge, and fruit volume). The species colonized the fruit categories at different times, so that changes observed in the communities may be due to changes in the resource. The highest similarity values between ripe fruits in the tree and intact ripe fruits on the litter may suggest microhabitat similarities and/or movement between these categories.

The lowest values of species richness, abundance, diversity, and density observed in the unripe fruits characterize this category as one of the most resistent to colonization. These restrictive features can, though, benefit those invertebrate species able to colonize and use such fruits. Additionally, such a restriction can reduce competition for space or food that usually occurs in resources with a high density of organisms (Bautista & Harris 1996).

The highest values of species richness, abundance, diversity, and density in the ripe fruits reveal the importance of this resource category for invertebrate species, and stresses the how crucial resource variation is in succession of resident species. The highest values of the parameters of fruits sampled on the litter may be due to two main factors: the variation in the resource creating microhabitats available and the proximity to the litter, a rich source from which scavenger invertebrates can come as fruit colonizers. The heterogeneity of the forest litter can lead to a great diversity of scavenger arthropods (Ferreira & Marques 1998, Hansen & Coleman 1998, Hooper *et al.* 2000).

Effects of resource situation on species richness and diversity: Since the forest litter functions as a source of fruit colonizers, larger distances are possibly covered by only a few species, those with a higher dispersal ability. So the decrease in species richness and density in relation to the distance from the forest edge may be related to this fact. Species diversity of different taxa may be correlated across different sites because of island effects resulting from the size of suitable habitat fragments and their distance from sources of colonization (Hooper *et al.* 2000). Many species of beetle use fig fruit falls as alternate hosts or "stepping stones" between fruit falls of their host trees, which can be widely separated both in time and space (Paarmann *et al.* 2001).

An increase in the density of invertebrates in relation to the ecological parameter tree height, found in unripe fruits, could be due mainly to the ease of location of colonization targets. The highest trees can be more exposed to wind than the lowest ones, which can affect the maximum reach of the specific chemical attractive (e.g., aromatic compounds). The highest trees are in addition accessed more easily than the lowest ones as they are "more easily seen". Several airborne volatiles produced by peaches at three ripeness stages gave a greater response when they were at the green-ripe stage (Hernandez *et al.* 1999).

The increase in species richness related in the increase of fruit volume found here may be due to greater resource availability in fruits of larger volume. Larger fruits can keep richer communities simply due to the greater availability of space and food. Herbivorous insects that frequently lay their eggs in the largest fruits do so in response to the higher food resource availability for their offspring, or to the protection that such fruits can offer against natural enemies (Hoffmeister *et al.* 1999).

The increase in species richness in relation to the number of injuries could be mainly due to the facilitation of colonization resulting from herbivore interactions. The presence of holes caused by herbivores is of fundamental importance to invertebrates unable to perforate the exocarp of the fruits (e.g., pseudoscorpions, spiders, bark lice, polyxenids, springtails, copepods, and earwigs).

Heterotrophic succession in Alibertia edulis *fruits*: Heterotrophic succession begins in the green fruit of *Alibertia edulis* with a marked presence of herbivores and galling invertebrates that degrade fruits during ripening (Fig. 3).

After the ripe fruits fall from the tree on to the ground, the next stage in the degradation period of succession begins, as no resource consumed by invertebrates can be replaced in fruits in this category. During this period the marked presence of scavengers and predators can be noted, as well as the decrease in herbivore abundance. So, after fruit formation, these fruits will be available for colonization, but few species

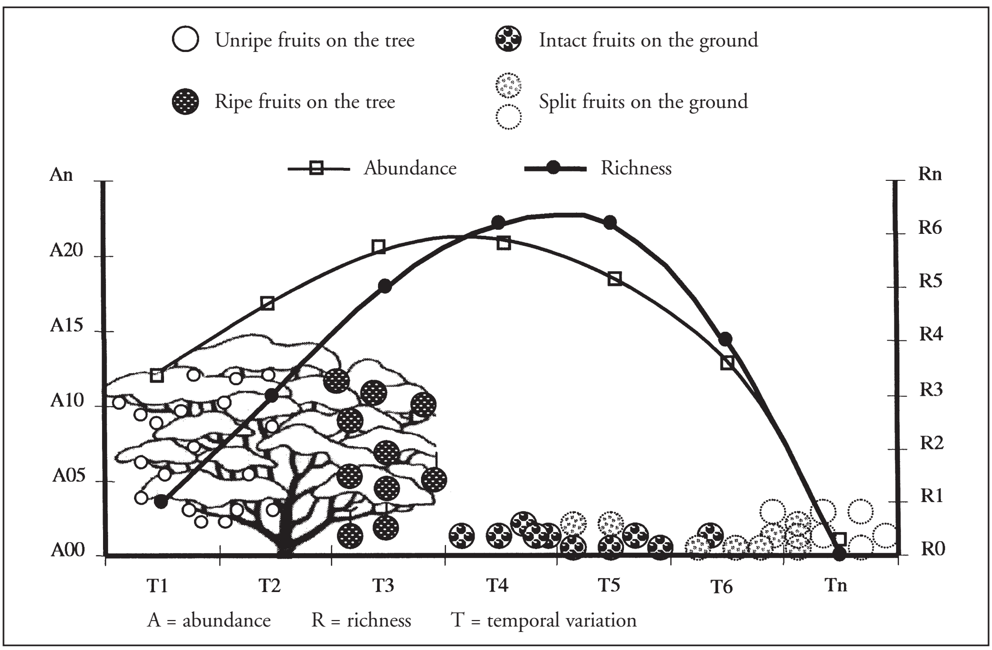

FIG. 3. Representation of the heterotrophic succession in fruits shows a chronological sequence of number of individuals and species richness of invertebrates associated with fruits, separated in space and time, in the tropical region. Communities colonize the resource promptly after its formation (green fruits). Gradual changes occur in relation to exposition, time, biological and physical modification of fruits. The communities remain at the site until there are no resources available for different trophic levels.

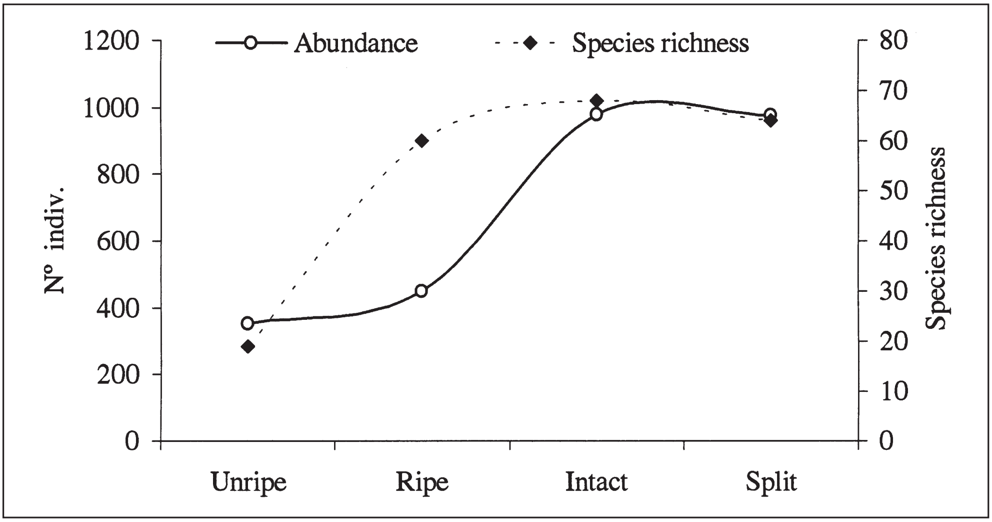

FIG. 4. Individual numbers and species richness of the invertebrates associated with different fruits categories of *Alibertia edulis* (unripe and ripe on tree; intact and split in ground).

occur at this time. In this period species richness is low because too little time has passed for colonization to occur, and only a few species with the greatest dispersal ability will colonize such a system. If the system (fruit) presents restrictions and remains unchanged, the associated community may be poor in species. On the other hand, if the system modifies (fruits ripen and fall), species richness can increase mainly because more time has passed for colonization to occur, including species with low dispersal ability.

In the case of invertebrates associated with the fruits of *Alibertia edulis*, it is reasonable to assume that species able to colonize the unripe fruits (herbivores) can benefit once they use the resource when few species are present and are not abundant. The distribution pattern, and the consequent aggregation level of competing species, can have direct implications on the final result of competition, since the "per capita" resources may be different for each species (Zuben 2000).

The fruits on the litter represent an intermediate succession stage in which the fruits falling can be considered a disturbance. Disturbance through heterotrophic succession modifies the habitat and makes colonization by new invertebrate species possible (Kusela & Hanski 1982, Tilman 1982, Kneidel 1984).

The exocarp of ripe fruits on the litter can offer less protection against predators. Nevertheless in its interior, besides food, microhabitats can be found that allow the occurrence of many invertebrate groups that are not observed in other fruit categories. The opportunities for resource exploitation in these stages can be made easier by physical variations and biological action (fruit-falling, splitting, holes, and interactions). In general, interactions among scavengers affecting detritus processing can be positive (e.g., detritus fragmentation by one species facilitates feeding by others) (Larned *et al.* 2001). But when the fruits become very old and there is no resource available at any trophic level, local species richness and abundance can be reduced by the dispersal of the species that have completed their life cycles, and so the new adults will depart in search of new resources (fruits) (Fig. 4).

The gradient of physical and biological changes found in the *Alibertia edulis* fruits represents a heterotrophic succession. Fruits are ephemeral resources, where the initial successional stages can be seen in unripe fruits and the final stages in ripe fruits on the litter. Variation in resource availability in *Alibertia edulis* fruits structures the associated invertebrate communities, probably promoting a temporal heterogeneity of microhabitats. The diversity of a resource allows a higher number of species to co-exist in a given area, so that the structure of this habitat is an important factor influencing the structure of communities (Price 1975, Hansen & Coleman 1998, Krijger & Sevenster 2001).

In this work we presented additional information on the trophic use of fruits by invertebrate communities. The successional process showed here is especially rich in species and will be common in various tropical systems, in which the diversity of many invertebrates can be related to the diversity of fruits and its variations (Janzen 1980, Jordano 1993, Pizzo & Oliveira 2000).

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