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Preference for different prey allows the coexistence of several land planarians in areas of the Atlantic Forest

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A B S T R A C T

Land planarians are recognized as important predators, yet studies on their feeding habits are usually restricted to invasive species. Thus, it is difficult to determine the real ecological role of this group in ecosystems and how their communities are structured. In the present study, we analyzed the diet of six co-occurring Neotropical land planarians and their success in capturing prey, based on experiments in the laboratory, in order to determine how they share resources in the same environment. We also calculated indices of food niche breadth and food niche overlap for land planarians for the first time. The diet of *Luteostriata abundans* comprises only woodlice and the diets of *Obama ficki* and *Obama ladislavii* are composed only of gastropods, while *Paraba multicolor* and *Obama anthropophila* feed on both gastropods and other land planarians. An invasive species recently found in Western Europe, *Obama nungara*, showed the highest food niche breadth, feeding on gastropods, earthworms and planarians. We found the highest niche overlap between *O. anthropophila* and *P. multicolor*. The results suggest that land planarians are frequent predators of woodlice and land gastropods in the Neotropical ecozone and thus are important for the maintenance of native ecosystems and for the control of invasive species. The coexistence of several species in the same habitat is possible due to the use of different species as main prey, which reduces interspecific competition.

1. Introduction

Trophic interactions are an important factor affecting the structure of communities (Brännström et al., 2012) and the function of the ecosystem as a whole (Rodríguez-Lozano et al., 2015). Therefore, knowing a predator's life history is essential to understand the dynamics of ecosystems (Schmitz, 2007). Unfortunately, such information is still lacking for many important, yet neglected, predators, such as land planarians (Ogren, 1995; Sluys, 1999).

Land planarians are invertebrate predators having high species richness in the Neotropical Ecozone, especially in areas of the Atlantic Forest in Brazil. They are usually seen as top predators due to the limited number of species known to feed on them (Sluys, 1999). Vertebrates, for example, seem to find them unpalatable (Ducey et al., 1999). Their ecological importance as predators is highlighted by the impact caused by some invasive species on invertebrate populations in areas where they have been introduced (Boag and Yeates, 2001; Sugiura et al., 2006). Most studies on the feeding ecology of land planarians focus on those invasive species, as they may threaten ecosystems as well as human activities such as earthworm culture (Ogren, 1995; Winsor et al., 2004), and aim to understand their life history in order to assist in management programs (Ducey et al., 2007; Sugiura and Yamaura, 2009). Europe is a continent particularly affected by invasive land planarians, with several introduced species, most of them posing a threat to populations of earthworms (Santoro and Jones, 2001; Breugelmans et al., 2012; Murchie and Gordon, 2013; Álvarez-Presas et al., 2014).

Meanwhile, non-invasive species are usually neglected, making it difficult to ascertain their actual ecological role in ecosystems. For example, despite the high diversity of land planarians in the Neotropical region (Sluys, 1999), only two species, *Luteostriata abundans* and *Obama ladislavii*, had their feeding habits consistently examined (Prasniski and Leal-Zanchet, 2009; Boll and Leal-Zanchet, 2015), the first feeding on woodlice and the second on land gastropods. Assumptions on the diet of some other species are based on sporadic observations in the field or in the laboratory (Froehlich, 1955). This lack of knowledge on non-invasive species also limits the understanding of the phenotypic aspects that make invasive species successful, as there are no comparative parameters (Ducey et al., 2005).

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But apart from the diet of an organism, quantitative measures are important to understand the ecological significance of species in their environment. Measurements of food niche breadth and food niche overlap help to clarify the organism's impact on prey populations, its ability to withstand environmental changes and colonize new areas, and the potential competition with similar species (Krebs, 1999).

Competition is, in fact, a factor usually considered important for the structure of communities. Classical ecological theory predicts that species phylogenetically close to each other rarely share the same environment, as they have very similar niches, which leads to competitive exclusion (MacArthur and Levins, 1967). On the other hand, the concept of environmental filtering predicts that similar species will co-occur, as their similarities increase their probability of colonizing the same environments (Mayfield and Levine, 2010).

Land planarian communities in areas of the Atlantic Forest in Brazil contain species closely related to each other, as well as more distantly related ones, all occurring sympatrically (Amaral et al., 2014; Negrete et al., 2014). They almost exclusively inhabit the leaf litter layer, where they remain protected from dehydration, as they do not have water-retaining mechanisms (Sluys, 1998). Since their niche requirements remain almost completely unknown, it is not possible to determine whether interspecific competition is important in structuring their communities.

In the present work, based on experiments in the laboratory, we investigate the diet of six Neotropical land planarians indigenous to areas originally covered by Atlantic Forest, which show habitat overlap. We aimed to identify their prey, analyze their success in capturing different food items, and determine their food niche breadth and food niche overlap. As most land planarians inhabit the leaf litter layer, we predict that they avoid competition by specializing in, or showing preference for, different prey rather than by occupying different spatial layers in the environment.

2. Materials and methods

2.1. Capture and maintenance

We captured specimens of land planarians in the field and took them to the laboratory, where we kept them in small plastic terraria containing moist soil, leaves and log fragments to simulate their natural environment. The terraria remained in the dark at a temperature ranging between 18 and 20 °C and a relative air humidity of about 90%. We used terraria of four different sizes according to the size of the planarian maintained in each one: (1) 9 cm × 5.5 cm × 2.6 cm, for specimens less than 20 mm in length; (2) 13 cm × 6.6 cm × 3.5 cm or (3) 11.2 cm × 7.2 cm × 4 cm, for specimens between 20 and 100 mm in length; and (4) 15.5 cm × 10.7 cm × 6 cm for specimens more than 100 mm in length.

Planarians were captured in the state of Rio Grande do Sul, southern Brazil, in areas of different forest formations which belong to the Atlantic Forest biome, viz. Araucaria moist forest (AMF), subtropical Atlantic Forest (SAF), deciduous seasonal forest (DSF) and semi-deciduous seasonal forest (SSF), as well as human-disturbed areas (HDA).

We selected the following six species (N = number of individuals; areas of capture) according to their availability: *Luteostriata abundans* (N = 35; HDA, DSF, SSF); *Obama anthropophila* (N = 41; HDA, AMF, DSF, SSF); *Obama ficki* (N = 12; SSF, DSF, AMF, SAF); *Obama ladislavii* (N = 27; HDA, AMF, SAF, DSF); *Obama nungara* (N = 13; HDA); *Paraba multicolor* (N = 22; HDA). Fig. 1 shows a schematic overview of how the species co-occur.

We captured several other invertebrate species in the same areas in order to test them as potential prey. The following list

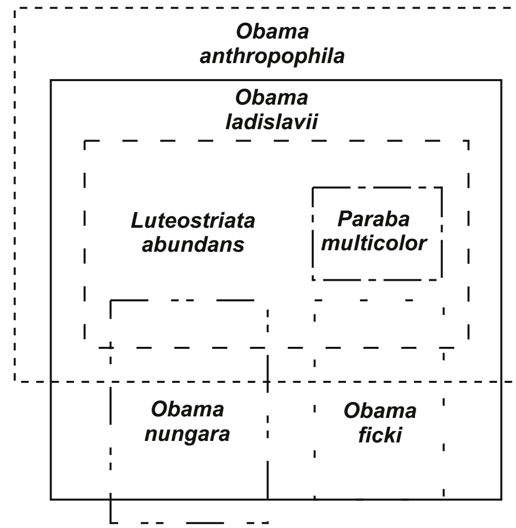

Fig. 1. Co-occurrence of six species of land planarians. Each rectangle represents one species. Overlapping rectangles indicate that the species may co-occur.

presents the selected invertebrate prey species (asterisk indicates exotic species):

- land gastropods: snails *Bradybaena similaris** and *Helix aspersa**; slugs *Deroceras laeve**, *Sarasinula plebeia* and *Belocaulus* sp.;
- earthworms: *Eisenia andrei**, *Metaphire schmardae**, *Amynthas gracilis**;
- land planarians: *Endeavouria septemlineata**, *Dolichoplana carvalhoi**;
- woodlice: *Atlantoscia floridana*, *Balloniscus glaber*, *Benthana cairensis*, *Porcellio scaber**, *Armadillidium vulgare**;
- harvestmen: *Discocyrtus* cf. *dilatatus*, Gonyleptidae sp. 1, Gonyleptidae sp. 2;
- termites: *Nasutitermes* sp.;
- ants: *Camponotus* sp., *Solenopsis* sp.;
- millipedes: *Rhinocricus* sp. 1; *Rhinocricus* sp. 2., *Obiricodesmus* sp.;
- unidentified species of Hirudinea, Entomobryidae, Hypogastruridae, Blattaria, Dermaptera and larvae of Elateridae, Passalidae and Mycetophilidae;

We also offered the four planarian species of the genus *Obama* to each other, and *Luteostriata abundans* to the other five species.

2.2. Prey preference identification and capture success

For the identification of each planarian species' prey, we put one planarian and one other invertebrate together in a Petri dish under low diffuse daylight entering through a window. We covered the dish with its lid and let both the planarian and the other invertebrate move around freely until they contacted each other. If both specimens entered in a resting state in different places in the dish before contacting each other, we induced them to resume moving through the dish by slight touches with a soft brush. While left undisturbed, we observed the specimens continually from a distance of ca. 30 cm. We considered prey those species that the planarian captured and consumed. If the planarian did not capture and ingest the invertebrate inside the Petri dish, we left one individual of that invertebrate species in the terrarium with the planarian for three or four days in order to determine whether or not the planarian had rejected the invertebrate due to the artificial conditions of substrate and luminosity in the Petri dish.

We offered a different invertebrate to each planarian every three or four days. If the planarian consumed the invertebrate, we offered a different species one week later. The sequence in which we offered each invertebrate to each planarian was random, thus reducing the influence of previous experiments on the results (Lehner, 1979). We offered each invertebrate species 15 times to each planarian species.

Once we had identified the prey species, we calculated the feeding preference for each planarian species and their capture success for each prey. For this purpose, we offered each identified prey 15 additional times and added the results to the previous 15 offers for identification, totaling 30 trials with each prey. We determined the feeding preference by comparing the rate of attacks on different prey species. Sugiura (2010) determined prey preference by comparing the rate of successful predation among different prey. Here, we define capture success as the number of captures divided by the number of attacks (modified from Lemos et al., 2012). We subjected the data to chi-square tests using the program SPSS Statistics 21 (IBM Corp., Armonk, NY, USA) in order to determine whether there were statistically significant differences in the feeding preference and the capture success of different prey species. When necessary, we performed an approximation by the Monte Carlo method using 1000 permutations.

2.3. Indices of food niche breadth and food niche overlap

We calculated food niche breadth using the standardized Levins' index (Krebs, 1999):

$$B_A = \frac{\left(1/\sum {p_i}^2\right) - 1}{n - 1},$$

where B_A is the standardized Levins' index, p_i is the prevalence of each consumed prey in the diet, and n is the number of species available as prey (in this case, the number of invertebrate species offered to the planarian). The index is expressed on a scale from 0 to 1, where lower values indicate a smaller food niche (more specialized diet) and higher values a larger food niche (more generalist diet).

The prevalence of each food item in the diet is usually determined by the proportion of each item in the animal's stomach contents or feces (Krebs, 1999). Since this method is inefficient for identifying prey items in planarians (Reynoldson and Davies, 1970), we determined the prevalence by offering each prey species an equal amount of times (in this case, 30) to the planarian species. We calculated the prevalence of each item by dividing the number of consumed individuals of a specific prey item by the total number of prey items consumed.

Levins' index assumes that all food items are available in the same proportion in the environment. While this situation rarely occurs in the wild, the fact that we offered all items in the same proportion in the experiments justifies the use of this index in the present study.

We calculated the food niche overlap between each pair of species using Pianka's index (Pianka, 1973):

$$O_{jk} = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum {p_{ij}}^2 {p_{ik}}^2}},$$

where O_{jk} is Pianka's food niche overlap index between species j and k, p_{ij} is the proportion of the food item i compared to the number of all items consumed by species j and p_{ik} is the proportion of the food item i compared to the number of all items consumed by species k. This index is also expressed on a scale from 0 to 1, with higher values indicating a greater niche overlap. Thus, a value of 0 indicates that both species do not share any food item, while a value of 1 represents identical food niches and both species would consume the same food items in the same proportion.

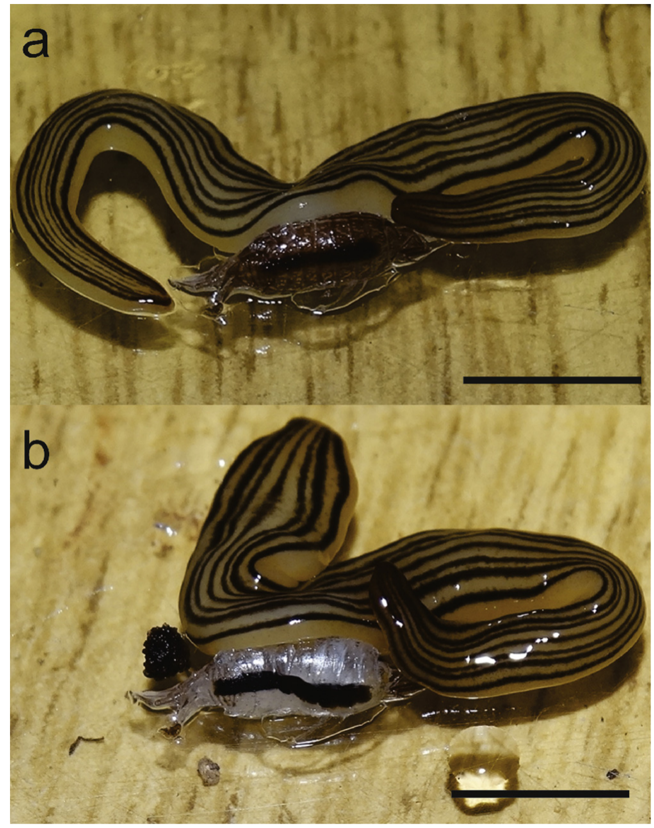

Fig. 2. Dorsal view of *Luteostriata abundans* consuming the woodlouse *Atlantoscia floridana*: (a) beginning of the feeding proccess; (b) woodlouse's empty exoskeleton after the consumption of the internal contents. Scale bars = 10 mm.

3. Results

3.1. Prey identification and capture success

Luteostriata abundans fed exclusively on woodlice (Table 1 and Fig. 2). The number of attacks on *A. vulgare* was lower in relation to the other species and only two individuals were consumed ($\chi^2 = 12.918$; df = 4; $p = 0.012$). The capture success was lower for both of the introduced species, *A. vulgare* and *P. scaber*, in relation to native species ($\chi^2 = 15.399$; df = 4; $p = 0.003$ with the Monte Carlo method).

Paraba multicolor fed on the land planarians *L. abundans, D. carvalhoi* and *E. septemlineata*, as well as on the slug *D. laeve* (Fig. 3a) and the snail *H. aspersa* (Table 1). The three land planarian species were preferred over gastropods and the number of attacks on *H. aspersa* was the lowest ($\chi^2 = 47.676$; df = 4; $p < 0.001$). Capture success was over 80% when attacking both planarians and slugs ($\chi^2 = 5.389$; df = 3; $p = 0.166$ with the Monte Carlo method). Data related to the capture of *H. aspersa* were not included in the comparison of capture success due to the low number of attacks recorded for this species.

Obama ficki fed exclusively on land gastropods (Table 1 and Fig. 3b), consuming all species offered with the exception of *Belocaulus* sp. Slugs were attacked more often than snails ($\chi^2 = 22.933$; df = 4; $p < 0.001$). Capture success was over 85% for all prey species ($\chi^2 = 6.696$; df = 4; $p = 0.110$ with the Monte Carlo method).

The diet of *Obama ladislavii* also included exclusively gastropods (Table 1 and Fig. 4), but there was no consumption of *M. pictum* and *S. plebeia*. Among the four consumed gastropods, there was a greater preference for *B. similaris* and *D. laeve* and a lower preference for *Belocaulus* sp. ($\chi^2 = 17.436$; df = 3; $p = 0.001$). Capture

Table 1
Invertebrate species consumed by the land planarian species under study. Asterisks indicate exotic prey species. Invertebrate prey species that were not eaten are not listed.

Planarian	Prey	Offers	Attack (%)		Success (%)		Consumed
Luteostriata abundans	*Atlantoscia floridana*	30	27	(90.0)	25	(92.6)	25
	Balloniscus glaber	30	25	(83.3)	25	(100)	25
	Benthana cairensis	30	27	(90.0)	26	(92.3)	26
	*Porcellio scaber**	30	26	(86.7)	21	(80.8)	21
	*Armadillidium vulgare**	30	18	(60.0)	13	(72.2)	2
Paraba multicolor	*Helix aspersa**	30	4	(13.3)	3	(75.0)	3
	*Deroceras laeve**	30	16	(53.3)	13	(81.3)	13
	*Endeavouria septemlineata**	30	28	(93.3)	28	(100)	28
	Luteostriata abundans	30	24	(80.0)	20	(83.3)	20
	*Dolichoplana carvalhoi**	30	20	(66.7)	17	(85.0)	17
Obama anthropophila	*Bradybaena similaris**	30	21	(70.0)	8	(38.1)	5
	*Helix aspersa**	30	14	(46.7)	10	(71.4)	10
	*Deroceras laeve**	30	26	(86.7)	20	(76.9)	20
	Belocaulus sp.	30	22	(73.3)	22	(100)	22
	*Endeavouria septemlineata**	30	30	(100)	29	(96.7)	29
	Luteostriata abundans	30	30	(100)	22	(73.3)	22
	*Dolichoplana carvalhoi**	30	28	(93.3)	27	(96.4)	25
	Obama ladislavii	30	5	(16.7)	2	(40.0)	1
Obama ficki	*Bradybaena similaris**	30	10	(33.3)	10	(100)	10
	*Helix aspersa**	30	16	(53.3)	14	(87.5)	14
	*Meghimatium pictum**	30	23	(76.7)	23	(100)	23
	*Deroceras laeve**	30	25	(83.3)	25	(100)	25
	Sarasinula plebeia	30	23	(76.7)	22	(95.7)	22
Obama ladislavii	*Bradybaena similaris**	30	25	(83.3)	23	(92.0)	23
	*Helix aspersa**	30	19	(63.3)	16	(84.2)	16
	*Deroceras laeve**	30	25	(83.3)	24	(96.0)	24
	Belocaulus sp.	30	12	(40.0)	12	(100)	12
Obama nungara	*Bradybaena similaris**	30	21	(70.0)	9	(42.9)	9
	*Helix aspersa**	30	10	(33.3)	4	(40.0)	3
	*Deroceras laeve**	30	12	(40.0)	7	(58.3)	7
	Belocaulus sp.	30	16	(53.3)	14	(87.5)	9
	*Eisenia andrei**	30	23	(76.7)	15	(65.2)	15
	*Amynthas gracilis**	30	21	(70.0)	10	(47.6)	10
	*Metaphire schmardae**	30	23	(76.7)	8	(34.8)	8
	*Endeavouria septemlineata**	30	17	(56.7)	7	(41.2)	4
	Luteostriata abundans	30	14	(46.7)	6	(42.9)	6
	*Dolichoplana carvalhoi**	30	20	(66.7)	13	(65.0)	13

success was high and similar for all consumed species ($\chi^2 = 3.342$; df = 3; $p = 0.376$ with the Monte Carlo method).

Obama anthropophila consumed the same gastropods as *O. ladislavii*, as well as the land planarians *L. abundans*, *E. septemlineata* and *D. carvalhoi* (Table 1 and Fig. 5a). In a single event, one individual of *O. anthropophila* partially consumed one individual of *O. ladislavii*. There was a lower preference for *H. aspersa* in comparison with other prey species, excluding *O. ladislavii* ($\chi^2 = 91.023$; df = 7; $p < 0.001$) (Fig. 5b). Capture success for *B. similaris* was lower in comparison to that for other species ($\chi^2 = 41.574$; df = 6; $p < 0.001$). Data related to the capture of *O. ladislavii* were not included in the comparison of capture success due to the low number of recorded attacks ($N = 5$).

The diet of *O. nungara* included the three earthworm species and all species consumed by *O. anthropophila* (Fig. 6), except for *O. ladislavii* (Table 1). The number of attacks was higher on all species of earthworms and on the slug *Belocaulus* sp. and lower on the gastropods *H. aspersa* and *D. laeve* ($\chi^2 = 29.854$; df = 9; $p < 0.001$). Capture success was higher on the slug *Belocaulus* sp., the planarian *D. carvalhoi* and the earthworm *E. andrei*. The lowest capture success was recorded on the earthworm *M. schmardae* ($\chi^2 = 16.671$; df = 9; $p = 0.05$).

3.2. Food niche breadth and food niche overlap

Regarding niche breadth, *O. nungara* has the highest index, meaning it is more generalist, while the value for *P. multicolor* is the lowest (Table 2).

Table 2
Levins' index (B_A) for each land planarian species used in this study.

Species	B_A
Luteostriata abundans	0.089
Paraba multicolor	0.050
Obama anthropophila	0.141
Obama ficki	0.099
Obama ladislavii	0.076
Obama nungara	0.208

Table 3
Pianka's index for each pair of land planarian species used in this study.

	Luab	Pamu	Oban	Obfi	Obla	Obnu
Luab	1					
Pamu	0	1				
Oban	0	0.89	1			
Obfi	0	0.208	0.292	1		
Obla	0	0.228	0.481	0.626	1	
Obnu	0	0.471	0.630	0.246	0.479	1

Luab = *Luteostriata abundans*; Pamu = *Paraba multicolor*.; Oban = *Obama anthropophila*; Obfi = *Obama ficki*; Obla = *Obama ladislavii*; Obnu = *Obama nungara*.

The food niche of *L. abundans* does not overlap with those of the species of *Obama* and *Paraba*. Among the species showing niche overlap, the highest value occurs between *O. anthropophila* and *P. multicolor* and the lowest between *O. ficki* and *P. multicolor* (Table 3).

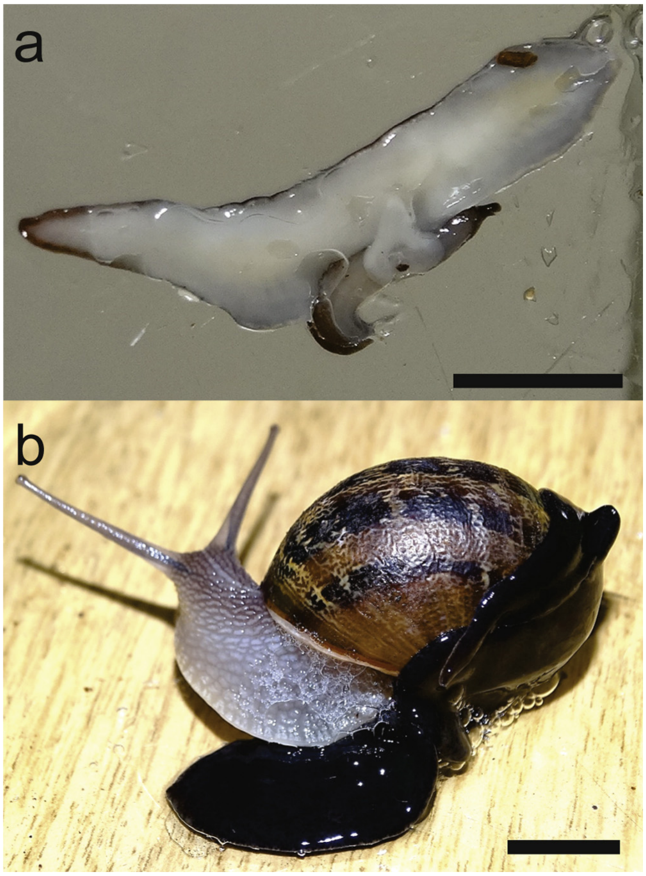

Fig. 3. Land planarians feeding on invertebrates: (a) ventral view of *Paraba multicolor* consuming the slug *Deroceras laeve*; (b) dorsal view of *Obama ficki* capturing the land snail *Helix aspersa*. Scale bars = 10 mm.

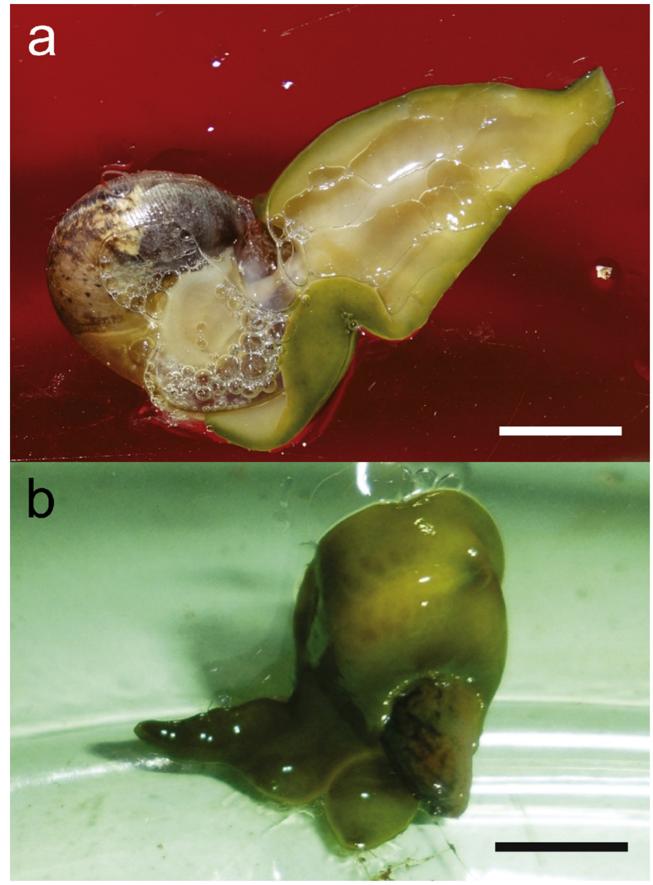

Fig. 4. *Obama ladislavii* consuming land gastropods: (a) ventral view during the consumption of *Helix aspersa*; (b) dorsal view during the consumption of *Deroceras laeve*. Scale bars = 10 mm.

4. Discussion

In the present work, we expand the knowledge on the diet of *L. abundans* and *O. ladislavii* and present the first detailed data related to the behavior of the other four planarian species. Despite some studies comparing the food niches of sympatric freshwater planarians (Reynoldson and Davies, 1970 Young, 1981; Gee and Young, 1993) no other work prior to this one compared the food niches of land planarians. Our results corroborate our predictions, as the six species seem to prefer distinct food items.

Previous studies on *L. abundans* had indicated that this species preys exclusively on woodlice (Hauser and Maurmann, 1959; Prasniski and Leal-Zanchet, 2009), as confirmed here, and observations on *Luteostriata caissara* and *Luteostriata ernesti* suggest that woodlice may be the preferred or exclusive prey group of this genus (Froehlich, 1955; Carbayo, 2010). Areas where *L. abundans* is present usually lack other species of the genus *Luteostriata* (Antunes et al., 2008; Amaral et al., 2014). As the more frequent species of *Obama* and *Paraba* do not show food niche overlap with *L. abundans*, it is likely that it does not have much food competition in its habitat.

The genus *Obama* presents a high interspecific variation in diet, which may explain the fact that many species of this genus coexist (Amaral et al., 2014; Oliveira et al., 2014). Land gastropods are evidently a common prey of this genus (Froehlich, 1955), having been recorded as food for all species studied here. Two of them, *O. ficki* and *O. ladislavii*, feed exclusively on land gastropods but prefer different species, thus reducing their competition. The former feeds more frequently on large snails, possibly having native veronicellid slugs as its main prey, while the latter ignores such species and attacks snails and smaller slugs (Boll and Leal-Zanchet, 2015).

The other two species of *Obama* include other groups beside gastropods in their diet. *O. anthropophila* attacks the same gastropods as *O. ladislavii*, but shows a lesser preference or capture success for snails, preferring and being more efficient at capturing planarians and small slugs. The planarian *L. abundans*, frequently found in the same habitat, is possibly its main native prey (Hauser and Maurmann, 1959). On the other hand, *O. nungara* evidently has earthworms as its main prey, but also feeds on gastropods, especially small slugs, and other land planarians. Therefore, all four species of *Obama* studied here may coexist without much competition, as each one has what Reynoldson and Davies (1970) called a food refuge, i.e., they specialize in different prey, so that part of their food niche does not overlap with those of other species.

We found the highest food niche overlap between two species of different genera, *P. multicolor* and *O. anthropophila*, and both species co-occur in human-disturbed areas. This suggests that a high similarity in niche does not necessarily occur in closely related species as predicted by the hypothesis of competitive exclusion (Mayfield and Levine, 2010).

The presence of *O. nungara* and *O. anthropophila* in highly disturbed areas and their broad food niches suggest a high tolerance to environmental disturbance and a great potential to become invasive species. In fact, *O. nungara* has recently been found in Western Europe, being widely distributed in France, the Iberian Peninsula and Great Britain (Álvarez-Presas et al., 2014; Justine et al., 2014; Lago-Barcia et al., 2015; Carbayo et al., 2016). Observations made in France and Spain revealed that these populations feed on earthworms and snails (Justine et al., 2014; Carbayo et al., 2016). Our

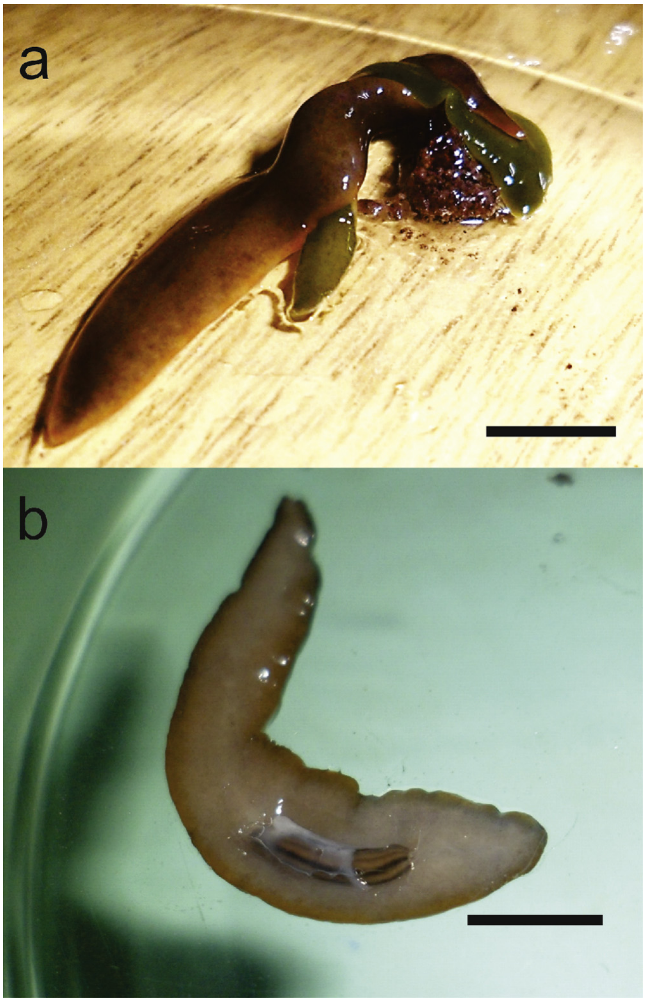

Fig. 5. *Obama anthropophila* capturing and consuming other land planarians: (a) dorsal view of attack on *Obama ladislavii*; (b) ventral view during the consumption of *Dolichoplana carvalhoi*. Scale bars = 10 mm.

experiments partially confirmed these observations, although the consumed species of earthworms and snails were not the same, and extended the knowledge of taxonomic groups in the diet of *O. nungara* by recording the consumption of other land planarians.

Obama ficki has not been recorded in highly disturbed areas. Nevertheless, it showed the third largest food niche breadth, as its diet also included several species of invasive gastropods. Interestingly, among these invasive gastropods, *D. laeve* occurs in several conservation areas in Southern Brazil along with *O. ficki*, such as in the São Francisco de Paula National Forest (personal observation). Because of their flexible diet, *O. ficki* may restrict dispersion of invasive gastropods into protected areas and even begin to use them as a main food resource in a situation of competitive exclusion of its native prey (Carlsson et al., 2009).

In contrast, *O. ladislavii*, which also fed exclusively on gastropods, showed the second lowest value of food niche breadth. However, it has a higher tolerance to environmental variation, occurring in both highly disturbed areas and pristine forests (Carbayo et al., 2002; Leal-Zanchet et al., 2011; Amaral et al., 2014; Oliveira et al., 2014), which indicates a high adaptability and therefore a greater potential to become an invasive species (Boll and Leal-Zanchet, 2015).

Land gastropods or woodlice were present in the diet of all land planarians studied here. Considering the high diversity of land planarians in forest environments of the Neotropical ecozone and

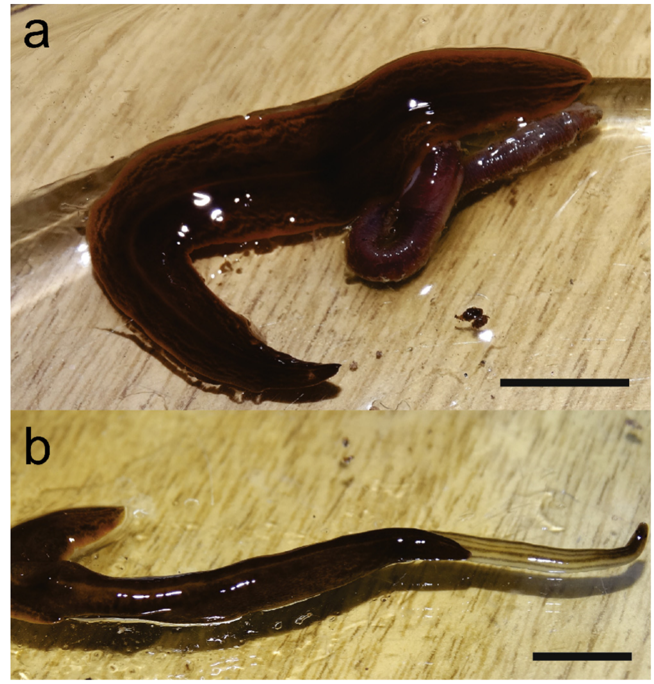

Fig. 6. *Obama nungara* consuming earthworm and land planarian: (a) dorsal view during consumption of the earthworm *Eisenia andrei*; (b) dorsal view of attack on *Dolichoplana carvalhoi*. Scale bars = 10 mm.

how frequently gastropods and woodlice are present in their diet, it becomes evident that land planarians are important predators of such organisms. However, the lack of knowledge regarding the ecology of land planarians leads to their importance as predators of woodlice (Paoletti and Hassall, 1999) being underappreciated. Recognition of land planarians as predators of mollusks occurs almost exclusively when planarians are invasive species and pose a threat to the stability of ecosystems (Winsor et al., 2004; Chiba and Roy, 2011).

Our results also suggest that many Neotropical land planarians are important predators of other land planarians. As a result, invasive land planarians may be less successful in establishing and spreading in South America (Boll et al., 2015) when compared, for example, to Europe, where native land planarians constitute a rare group and many invasive species have established successfully (Álvarez-Presas et al., 2014; Justine et al., 2014).

Because they also constitute a rare group in invertebrate communities in the Holarctic ecozone (Sluys, 1999), land planarians usually have their ecological importance underestimated and European researchers only started to show an interest in this group as a result of the economic and ecological impacts caused by invasive species introduced into Europe (Winsor et al., 1998). Conversely, in the Neotropical ecozone, land planarians make up a highly diverse group and, as reinforced by the results of the present study, may be important for both the maintenance of ecological processes in native ecosystems as well as in the control of the spreading of invasive species.

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