



The relationship between zooplankton occupancy and abundance in a floodplain is mediated by the hydrological regime

A relação entre distribuição regional e abundância de espécies zooplanctônicas numa planície de inundação é mediada pelo regime hidrológico

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Abstract: Aim: Positive relationships between occupancy and abundance are often found for different groups of organisms and ecosystem types. However, to our knowledge, no study has sought to assess this relationship considering a context in which a particular mechanism is the most likely explanation. In this study, in addition to the positive relationship with abundance, we tested the hypothesis that occupancy of zooplankton species should be greater during the flood season because in this period the hydrological connectivity is greater than in the dry season, facilitating passive dispersal between floodplain environments. **Methods:** Our study was carried out at 52 sites - including lakes and rivers - on the Araguaia River floodplain. We used an analysis of covariance to test the effects of abundance and hydrological period on zooplankton occupancy. **Results:** We found, as expected, a positive relationship between occupancy and abundance of zooplankton species in each hydrological period. Our results also indicated that, with the increase in abundance, species occupancies were higher in the flood than in the dry season. **Conclusions:** The positive effect of the flood on zooplankton occupancy can be explained by the increase in water level that increases the hydrological connectivity and the potential for plankton passive dispersal.

Keywords: Araguaia river; spatial distribution; flood pulse; hydrological connectivity; mechanisms.

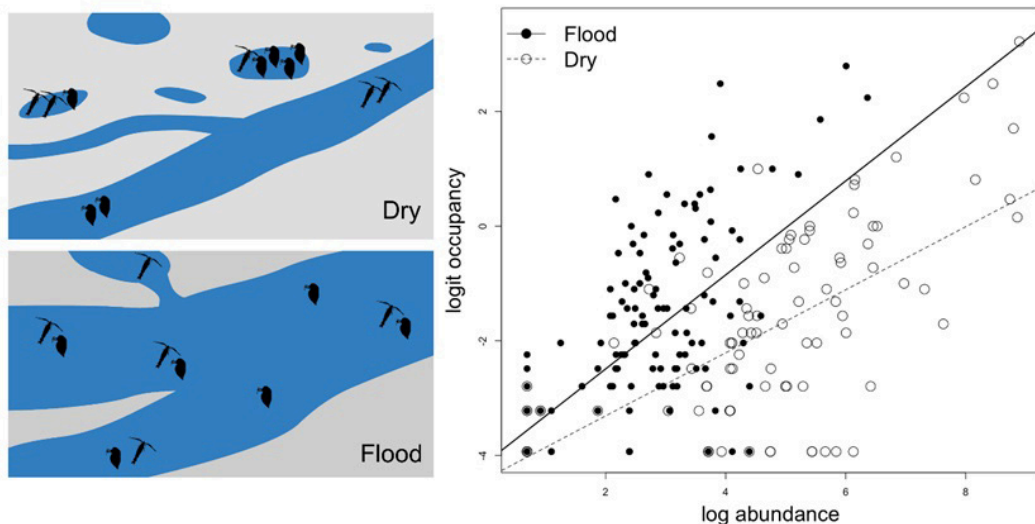
Resumo: Objetivo: Relações positivas entre distribuição regional e abundância são frequentemente encontradas para diferentes grupos de organismos e tipos de ecossistemas. No entanto, até onde



sabemos, nenhum estudo buscou avaliar essa relação considerando um contexto no qual um determinado mecanismo fosse a explicação mais provável. Neste estudo, além da relação positiva com a abundância, nós testamos a hipótese de que a distribuição regional de espécies zooplancônicas deveria ser maior durante o período de cheia uma vez que neste período a conectividade hidrológica é maior que no período de seca, facilitando a dispersão passiva entre os ambientes de uma planície de inundação. **Métodos:** Nosso estudo foi realizado em 52 locais - incluindo lagoas e rios - na planície de inundação do rio Araguaia. Nós utilizamos uma análise de covariância para testar os efeitos da abundância e do período hidrológico sobre a distribuição regional. **Resultados:** Encontramos, como esperado, uma relação positiva entre distribuição regional e abundância de espécies zooplancônicas em cada período hidrológico. Nossos resultados também indicaram que, com o aumento da abundância, as distribuições regionais das espécies foram maiores no período de cheia. **Conclusões:** O efeito positivo da cheia sobre a distribuição regional pode ser explicado pelo aumento do nível de água, que aumenta a conectividade hidrológica e o potencial de dispersão passiva do plâncton.

Palavras-chave: rio Araguaia; distribuição espacial; pulso de inundação; conectividade hidrológica; mecanismos.

Graphical Abstract



1. Introduction

More abundant species generally occur in a greater number of local communities (i.e., they have higher occupancies) than less abundant ones. This positive relationship between occupancy and local abundance is one of the most ubiquitous patterns in ecology (Gaston et al., 2000; Gaston & Blackburn, 2003; Borregaard & Rahbek, 2010). Different mechanisms can generate this relationship. For example, species that use widely distributed resources tend to have higher abundances and occupancies (Hanski et al., 1993; Ten Caten et al., 2022). Occupancy and abundance would also increase with the niche breadth and dispersal capacity of the species (Gaston et al., 1997; Ten Caten et al., 2022). However, the positive relationship between occupancy and abundance could emerge from sampling artifacts as less

abundant species are more difficult to sample (Gaston et al., 1997; Ten Caten et al., 2022). Finally, other factors such as habitat heterogeneity and biotic interactions can influence the strength of observed occupancy-abundance relationships (Holt et al., 2004).

Studies on the relationship between occupancy and abundance are variable in methodological terms. Even the choice of the response variable (abundance or occupancy) and, consequently, of the explanatory variable, can vary between studies (Gaston et al., 2000). Also, there is a variation in how models are specified. For example, in analyzes that consider occupancy as a response variable, species-specific attributes (e.g., dispersal ability and niche breadth), in addition to abundance, can be used as explanatory variables in multiple regression models (Gaston & Blackburn, 2003; Webb et al., 2009). There are also

examples of studies that analyze the relationship between occupancy and abundance and, later, the relationship between each of these variables and species-specific traits (e.g., Siqueira et al., 2009; Vilmi et al., 2019). However, no study – to the best of our knowledge – has sought to assess the relationship between occupancy and abundance considering a context in which a particular mechanism (related to the environmental characteristics) to explain the relationship is more likely. For example, water level fluctuations in floodplain systems can alter hydrological connectivity and, therefore, the ease with which organisms can disperse between the different environments of these systems. Specifically, during flood periods, the increase in water level can increase the connectivity among aquatic ecosystems (Thomaz et al., 2007; Bozelli et al., 2015). As the water level rises, the transport of plankton may be more intense (e.g., Bonecker et al., 2005) and, therefore, it is expected that the species will have a higher occupancy. On the other hand, environments may be hydrologically less favorable for planktonic communities during flood periods, decreasing their abundance (Bozelli, 1992).

Here, we aimed to test the relationship between occupancy and abundance of zooplankton species in the dry and flood seasons in the Araguaia River floodplain. Specifically, we tested whether, in addition to a relationship with abundance, the regional distribution (occupancy) of zooplankton species was higher during the flood season than during the dry season. This expectation is justified considering that the hydrological connectivity among the floodplain environments increases during the flood season. Thus, compared to the dry season, when the environments are more isolated, the species could reach (mainly by drift) a larger number of sites during the flood season.

2. Methods

We used a dataset obtained by Vieira (2008) for this study. Data on zooplankton species densities (individuals/m³) were obtained from 52 sites distributed in 30 environments (22 lakes with two sampling sites - one in the deepest zone and other near the shoreline of the lake - and 8 rivers, including two sampling sites in the Vermelho River and six sampling sites in the main stem of the Araguaia River (Figure 1), between the municipalities of Aruaná and São Miguel do Araguaia (Goiás, Brazil). The same sites were sampled during the flood (January) and dry (July) periods of 2006 (for details of the field and laboratory work, see Vieira, 2008).

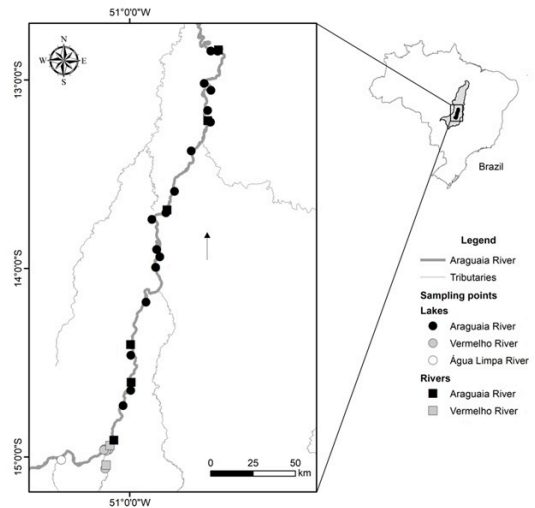


Figure 1. Sampling locations in the Araguaia River floodplain. The same environments (lakes or rivers) were sampled in two periods (January 2006 and July 2006). Two sites were sampled in each lake.

The monthly average flows registered during these months (January and July) were typical of the flood and dry periods in the Araguaia River floodplain (ca. 2507 m³/s and 519 m³/s, respectively; data from the National Agency of Waters near the city of Nova Crixás, state of Goiás, Brazil).

For each hydrological period, we calculated the occupancy by dividing the number of occurrences of each species (i.e., number of sites in which the species was present) by the total number of sites (52). The local mean abundance of each species consisted of the mean density (individuals/m³) considering only the sites with densities greater than zero. Prior to the analyzes, occupancy and abundance data were transformed using the logit and logarithmic transformations, respectively. These transformations were necessary to satisfy the assumption of normality of the residuals. Finally, to test the relationship between occupancy and the explanatory variables (mean abundance and hydrological period), we used an analysis of covariance (ANCOVA). The hydrological period - with two levels (flood and dry) - was the categorical factor tested, whereas the mean abundance was the quantitative variable (covariate) in our ANCOVA model. All analyses were performed in the R environment (R Core Team, 2020; version 4.0.2) using the package car (Fox & Weisberg, 2019).

3. Results

The numbers of taxa with densities greater than zero in the flood and dry seasons were equal to 145 and

111, respectively (considering a total of 190 taxa in both periods). Young copepods (Diatomidae and Cyclopidae) and Bdelloidea, treated as taxonomic units in our analyzes, showed the highest occupancies (i.e., presence in more than 90% of the sites) in each of the periods studied. In addition to the young forms, the species with the highest occupancies (> 70%) in the flood season were *Bosminopsis deitersi* Richard (1895), *Lecane curvicornis* Murray (1913), *Ceriodaphnia cornuta* Sars (1885), *Moina minuta* Hansen (1899) and *Platyias quadricornis* Ehrenberg (1832). For the dry season, the species with the highest occupancies (> 70%) were *Moina minuta* and *Bosmina hagdmani* Stingelin (1904).

In each hydrological period, we found a positive relationship between occupancy and abundance of zooplankton taxa ($F_{1,143} = 94.6$, $R^2 = 0.40$ for the flood season and $F_{1,109} = 107.8$, $R^2 = 0.50$ for the dry season; Figure 2). In addition, the results of the analysis of covariance (Table 1) indicated that the slopes (b) of the relationship between occupancy and abundance differed between the flood ($b = 0.820 \pm$

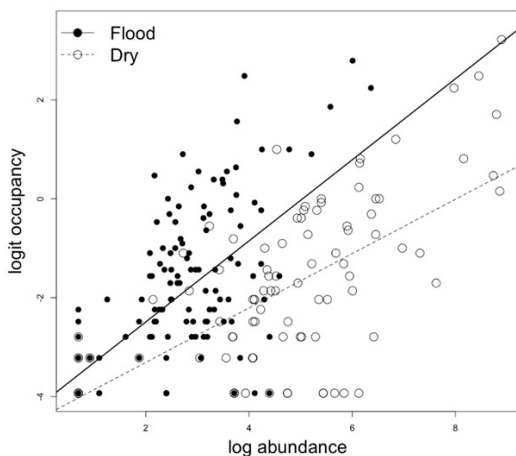


Figure 2. Relationship between occupancy and abundance of zooplankton taxa in the Araguaia River floodplain in two hydrological periods (flood and dry seasons; January 2006 and July 2006, respectively).

0.084 SE) and dry ($b = 0.550 \pm 0.053$ SE) seasons. The lack of parallelism, as evidenced by the significant interaction between abundance and hydrological period, did not allow the direct test of our main hypothesis. However, we found that, with increasing abundance, the occupancy was progressively higher during the flood season than during the dry season (Figure 2). We also performed the analyses with only the taxa that occurred in both hydrological periods (83); however, the results were qualitatively the same.

4. Discussion

We found a positive relationship between occupancy and abundance in the two seasons. However, when compared to the dry season and as abundance increased, the zooplankton taxa progressively showed higher occupancy during the flood season.

The positive relationship between occupancy and abundance has been verified for several groups of organisms, but especially for terrestrial vertebrates and insects (Holt et al., 2002; Blackburn et al., 2006). In this context, our results suggest that the relationship can be generalized to the zooplankton community (see also O'Brien et al., 2004; Ten Caten et al., 2022). However, our results are also consistent with those obtained by Ten Caten et al. (2022) by demonstrating that, despite the ubiquity of the relationship (including over time, as also demonstrated in our study), a substantial part of the variation in occupancy was not explained by abundance (as indicated by the coefficients of non-determination: $1-R^2 = 0.60$ for the flood season and $1-R^2 = 0.50$ for the dry season; see also Blackburn et al., 2006).

Our results do not allow us to point out the main mechanism that can explain the positive relationship between occupancy and abundance. For example, according to Gaston et al. (1997) and Holt et al. (2004), the metapopulation dynamics hypothesis predicts that more abundant species simultaneously

Table 1. Results of the analysis of covariance (ANCOVA) evaluating the relationship between zooplankton occupancy in the Araguaia River floodplain and the explanatory variables (logarithm of abundance and hydrological period).

	Sum of Squares	df	F	P
Intercept	490.65	1	306.92	< 0.001
Abundance	154.66	1	96.74	< 0.001
Period	1.02	1	0.64	0.425
Abundance×Period	11.85	1	7.41	0.007
Residuals	402.85	252		

Shapiro-Wilk normality test: $W = 0.99$, $P = 0.07$.

have lower extinction rates and higher colonization rates, resulting in higher occupancy. Furthermore, according to the rescue effect, there is a decrease in the probability of local extinction with the increase in the number of habitats colonized (Hanski, 1991; Gaston et al., 1997; Holt et al., 2004). On the other hand, according to the niche breadth hypothesis, the relationship between occupancy and abundance would emerge because there are positive relationships between these variables and niche breadth (Brown, 1984; Gaston et al., 1997). Finally, species can be more abundant and widely distributed when they exploit resources that are also common and widely distributed (Hanski et al., 1993; Holt et al., 2004). Thus, the three mechanisms could explain the positive relationship between occupancy and abundance in each period (flood or dry season). In short, species-specific characteristics (including niche position and breadth, as demonstrated for other aquatic organisms, e.g., Siqueira et al., 2009; Rocha et al., 2018) can be important predictors of occupancy. For example, O'Brien et al. (2004), in a study carried out in 104 lakes in northern North America, hypothesized that the most abundant zooplankton species (and with higher occupancy) were those least vulnerable to fish predation.

After statistically controlling for the effect of abundance (using ANCOVA), however, we observed that the species tended to have higher occupancy during the flood season as compared to the dry season (especially at high abundance). Thus, although species-specific characteristics may explain why some species have higher occupancy than others, our results indicate that the flood pulse (Junk et al., 1989) is fundamental for the occupation of habitats. Probably, the positive effect of flood on the occupancy can be attributed to the increase in water level, which, in turn, simultaneously increased the hydrological connectivity, the similarity of habitats, and the transport of plankton among the different environments in the Araguaia River floodplain (see Havel & Shurin, 2004 for a review of freshwater zooplankton dispersal). It is interesting also to note that despite the commonly negative effect of water velocity (or a positive effect of water residence time) on zooplankton abundance (e.g., Baranyi et al., 2002; but see Ning et al., 2013 for different results), our results show that the occupancies of the taxa were higher in the flood than in the dry season. Our hypothesis of the synergistic effect of species-specific characteristics (e.g., abundance, niche breadth, dispersal ability) and system connectivity (increasing passive dispersal

rates) is reinforced if we consider that the difference in occupancy between the seasons increased with abundance (see the significant interaction between abundance and period, as demonstrated by ANCOVA).

The comparison of the relationships between occupancy and abundance between periods of lower and higher connectivity (dry and flood, respectively), as performed in our study, is similar to that performed by Foggo et al. (2007). These authors compare the relationships between occupancy and abundance after classifying 362 taxa of marine macroinvertebrates collected in the British Isles into planktonic and non-planktonic organisms. Their results clearly demonstrated that, after controlling for abundance, the occupancy was greater for planktonic organisms. Our results also demonstrate the duality of the flood effect on the dynamics of zooplankton species in the floodplain. Although the flood causes a reduction in species abundance (as observed by Vieira, 2008 for the Araguaia River floodplain), in general, occupancies were higher during this period. This observation can be linked to the increase in habitat similarity frequently observed during floods (Thomaz et al., 2007). For instance, an experiment conducted by Holt et al. (2004) with protists and bacteria showed that some species achieved higher occupancies in homogeneous than heterogeneous environments, despite having similar abundances in both habitat conditions.

In conclusion, our study suggests that system characteristics, in terms of facilitating the dispersal among habitats, in addition to species-specific characteristics (as demonstrated in other studies; e.g., Foggo et al., 2007), are key to explaining the distribution of species in floodplains. Considering the increasing human interference in these ecosystems (Pelicice et al., 2021), we also speculate that changes in the hydrological regime (e.g., caused by dams or climate change) may reduce the connectivity of the system and, therefore, the ability of planktonic species to occupy the floodplain environments.

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