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Taxonomic sufficiency in detecting hydrological changes and reproducing ordination patterns: A test using planktonic ciliates

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ABSTRACT

Ciliates are commonly and successfully used as bioindicators in marine ecosystems, even at low levels of taxonomic resolution. However, the use of these organisms in biomonitoring programs of freshwater ecosystems is less common. Evidence showing the reliability of the taxonomic sufficiency approach for freshwater ciliates is also limited. Demonstrating taxonomic sufficiency would be important to foster the use of ciliates in freshwater biomonitoring programs in a cost-effective way. Here we tested whether richness and multivariate patterns generated by ciliate community data, at species level, were retrieved by analyses carried out with data at lower taxonomic resolutions. Community and environmental datasets were gathered at 36 sites in the Upper Paraná River floodplain (Brazil), during high and low water levels periods of the years 2010 and 2011. We found that, in comparison with species-level data, genus-level identification was sufficient to detect the effects of the environmental changes caused by floods, to retrieve the ordination patterns generated during each hydrological period and to detect relationships with environmental and spatial gradients. We also showed that the use of coarser taxonomic resolutions was not advisable because high relationships with species-level data were found only with genus-level data. We encourage the use of ciliates in biomonitoring programs of freshwater ecosystems and, according to our results, the use of genus-level identification is a reliable strategy, not only to increase cost-efficiency, but also to guarantee temporal comparability of data.

1. Introduction

Eukaryotic microorganisms are rarely used in biomonitoring programs of freshwater systems. This scarcity of studies can be related especially to the lack of experts and to the difficulty of taxonomic determination. For instance, ciliate identification requires *in vivo* observation of the samples and it must be performed quickly after sampling (Madoni, 1984; Foissner et al., 1999). Moreover, for accurate identification at species level, the use of impregnation techniques is indispensable, allowing the observation of the infraciliature and nuclear apparatus (Ma et al., 2003; Foissner et al., 1999). The use of these methods requires skilled experts, demanding years of training (Stoeck et al., 2014). On the other hand, the use of ciliate communities in biomonitoring/bioassessment programs of marine ecosystems is common and highly successful in terms of impact detection (Jiang et al., 2013). This is mainly so due to the high sensitivity of ciliates to environmental changes (Zhang et al., 2012). Thus, we believe that freshwater biomonitoring programs would benefit from expanding the use of these organisms.

Despite criticism, the use of the taxonomic sufficiency approach would be an alternative to promote the inclusion of ciliated protozoa in biomonitoring programs of freshwater systems. However, this possibility must be placed in a context. First, we emphasize that the taxonomic sufficiency approach should be tested and not aprioristically assumed. Specifically, the use this approach (e.g., genera instead of species) in a biomonitoring program would be defensible only when the patterns depicted with the species level data are reproduced with the genus level data. Second, even when a high potential of this approach in biomonitoring is found, this does not mean that higher taxa data are enough for basic ecological studies.

Taxonomic sufficiency has been reported in several groups of organisms (Marshall et al., 2006; Heino and Soininen, 2007; Bertasi et al., 2009; Smale et al., 2010; Landeiro et al., 2012). However, there is no agreement on the levels of taxonomic resolution suitable for

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biomonitoring studies (Bailey et al., 2001; Jones, 2008). Some authors suggest that the use of higher taxonomic levels would lead to significant information losses, and that the identification to the specific level would be required to ensure the reliability of the results in terms of bioassessment (Moog and Chovanec, 2000; Lenat and Resh, 2001; Schmidt-Kloiber and Nijboer, 2004; Lavoie et al., 2009; Heino, 2014). Other authors argue that the use of higher taxonomic levels would be enough to identify differences among samples distributed along a gradient of environment impacts (Chessman et al., 1999; Heino and Soininen, 2007; Melo, 2005; Terlizzi et al., 2009).

We gathered data on planktonic ciliate communities in the Upper Paraná River floodplain (Brazil) to test the effectiveness of data with low levels of taxonomic resolution (genera, families, classes and orders) in representing species level data. For this task, we proposed a series of critical tests to validate the use of the taxonomic sufficiency approach for planktonic ciliates. First, we evaluated whether analyses carried out with data aggregated to lower levels of taxonomic resolution could detect differences between hydrological periods (i.e., low versus high water periods). Floods represent major drivers of aquatic community structure (Junk et al., 1989) and any scientifically defensible shortcut for biodiversity assessments should be able to detect their impacts. Second, we evaluated whether the ordination patterns detected with species level data were reproduced with data at lower levels of taxonomic resolution. This test aimed to evaluate whether data with lower levels of taxonomic resolution could represent ordination patterns obtained with species level data independently of the sampling period and, therefore, considering lower levels of environmental variability (as compared to the large environmental differences between high and low water periods). Third, we tested whether the relationships between the species level dataset and two sets of predictors (environmental and spatial variables) were maintained after decreasing the taxonomic resolution of the biological dataset. The taxonomic sufficiency approach would be considered as reliable only if the results point to (i) a clear differentiation between hydrological periods, (ii) a strong match between datasets with different taxonomic resolutions during both periods analyzed and (iii) similar patterns of relationships between biological datasets (with different taxonomic resolutions) and environmental and spatial predictors.

2. Materials and methods

2.1. Study area

We conducted this study in the Upper Paraná River floodplain (Brazil). A detailed description of this floodplain can be found elsewhere (Thomaz et al., 2004; Padial et al., 2012). The sampling sites were distributed in three rivers (Paraná, Ivinheima and Baía), four channels, and 29 lakes nearby the Ivinheima, Baía, and Paraná Rivers, which are the three main rivers forming the floodplain. The same 36 sites were sampled during high and low water levels periods (March and September, respectively) of the years 2010 and 2011.

2.2. Biological data

Four liters of water were collected using a Van Dorn bottle at the sub-surface of the pelagic zone in each one of the 36 sampling sites. The samples were stored in polyethylene flasks, which were kept in thermal boxes with ice and transported to the field station of the Maringá State University, in Porto Rico municipality (Paraná state, Brazil).

The samples were concentrated using a 10 μm net until reaching the final volume of 100 mL, following the sedimentation and siphoning principles (Madoni, 1984). Then, we analyzed ten subsamples of 100 μL each for the identification and quantification of the ciliates *in vivo*, under bright-field microscope, following the method proposed by Madoni (1984). The ciliates were identified to species level whenever possible using specialized literature (Corliss, 1979; Dragesco and Dragesco-Kernéis, 1986; Foissner et al., 1991, 1992, 1994, 1995; Foissner and Berger, 1996; Foissner et al., 1999).

2.3. Environmental data

The following environmental variables were measured in the field: water temperature (°C, using a portable thermistor), pH (using a portable pH-meter) and water transparency (cm, Secchi disc). In the laboratory, water samples were analyzed for dissolved oxygen (mg L^{-1}), total phosphorus (μgL^{-1}) and total nitrogen concentrations (μg L^{-1}) using methods described in APHA (2005).

2.4. Data analysis

As a first step in our analyses, we created abundance matrices (p taxa x n samples) with different taxonomic resolutions (species, genera, families, orders, and classes). Second, these matrices were *log* transformed ($Y + 1$) to minimize the influence of highly dominant species (Legendre and Gallagher, 2001). Third, all analyses described below were done by using the Bray-Curtis coefficient (Legendre and Legendre, 2012) as a measure of compositional dissimilarity between samples.

For each sampling year, we tested for differences in community structure between hydrological periods (low and high water periods) using a Permutation Multivariate Analyses of Variance (PERMANOVA; Anderson, 2001), with 999 permutations. The main aim of this analysis was to verify whether the changes in the communities between periods were detectable by analyses done with data at different taxonomic resolutions. We conducted a Principal Coordinate Analysis (PCoA), for each taxonomic resolution, to ordinate samples (sites/months) and visualize the differences in community composition between water levels periods.

For each sampling year and hydrological period, we also applied a Principal Coordinate Analysis (PCoA) to ordinate sites according to the community datasets at different taxonomic resolutions. We then used a Procrustes analysis (Peres-Neto and Jackson, 2001) to quantify and test the levels of concordance between PCoA scores generated with species abundance matrices and those scores generated from matrices with lower taxonomic resolutions. As a measure of association between the ordinations, we used the Procrustes' r_P, which is derived from the symmetric Procrustes sum of squares (m^2): $r_P = \sqrt{1 - m^2}$

We also estimated the correlation between species richness and richness of higher taxa using the Spearman's correlation coefficient (r_S). After, both r_P and r_S were correlated with the species to higher taxa ratio (SHR). This was done because many studies have shown that SHR is one of the main predictors of the level of taxonomic sufficiency (following Rosser, 2017 and references therein).

To summarize the limnological dataset, we used a Principal Component Analysis (PCA) from the correlation matrix between variables (Legendre and Legendre, 2012). We used a technique called Moran's Eigenvector Maps (MEM) to create spatial variables using the spatial coordinates of the sites (latitude and longitude). The eigenvectors (scores) obtained with this technique are much more efficient than simple geographical coordinates in representing spatial relationship between sampling sites (Borcard and Legendre, 2002; Borcard et al., 2004; Dray et al., 2006). We selected only the significant MEMs according to the selection method proposed by Blanchet et al. (2008). Finally, we also applied the Procrustes analysis to test the concordance between PCoA scores obtained with the matrices organized at different taxonomic resolutions (species, genus, family, order and class) and PCA (summarizing environmental variation) and MEM (summarizing spatial relationships) scores. The statistical significance of each comparison was determined by a Monte Carlo permutation test using 999 permutations (Jackson, 1995; Peres-Neto and Jackson, 2001).

All statistical analyses were performed in R, using the packages *vegan* (Oksanen et al., 2010) and *packfor* (Dray et al., 2007).

Table 1
PERMANOVA results testing the differences in the structure of the ciliate communities between hydrological periods (low versus high water periods), considering data with different taxonomic resolutions. *F* values in bold were significant.

Resolution	2010		2011	
	F	*P*	*F*	*P*
Species	**9.21**	< 0.001	**9.04**	< 0.001
Genus	**9.35**	< 0.001	**9.20**	< 0.001
Family	**6.73**	< 0.001	**9.11**	< 0.001
Order	1.73	0.09	1.44	0.53
Class	0.91	0.72	1.86	0.4

3. Results

We recorded 126 ciliate species, belonging to 87 genera, 61 families, and eight classes. The highest values of species richness and species abundance were registered during the high water periods of 2010 and 2011. Thirty-two species were exclusive of the high water period, while 17 species were recorded only during the low water period (see Supplementary Material). The most abundant species during the high water periods were *Vorticella aquadulcis, Rimostrombidium humile, Actinobolina vorax, Halteria grandinella,* and *Urotricha farcta*. During the low water periods, the most abundant species were *Microthorax pusilus, Urocentrum turbo,* and *Stokesia vernalis* (see Supplementary Material).

Using species level data, we found significant differences in ciliate community structure between hydrological periods (Table 1). Similar results were detected for data grouped into genera and families. However, no differences were observed between periods for data grouped into orders or classes (Table 1; Fig. 1).

The ordination patterns generated with lower levels of taxonomic resolution, in general, significantly matched those generated with species level data (used as reference). However, the levels of concordance between the ordination scores generated with datasets amalgamated at orders or classes and those with species data were conspicuously lower and, in some cases, not significant (Table 2). The multivariate correlation between species level and higher taxa datasets (as given by the Procrustes' r_P) declined markedly with SHR (Pearson's $r = -0.82$, -0.99, -0.78, and -0.99 for the high and low water periods of the years 2010 and 2011, respectively). We also found significant correlations between species richness and richness of higher taxa (Table 3). Low correlations (i.e. $r_S < 0.7$) between species and class richness were, however, obtained for the year 2010. We found a marked decline in the correlation between species richness and richness of higher taxa (r_S) with SHR ($r = -0.99$; -0.98; -0.82; -0.97, for the high and low water periods of the years 2010 and 2011, respectively). Thus, the strong (and negative) relationships between both r_P and SHR and r_S and SHR indicate that the higher the species richness within higher taxa the poorer the performance of the higher taxa approach.

We found significant concordance between biological and environmental ordinations during the high water periods of both years. On the other hand, during the low water period, no significant concordance between biological and environmental ordinations was detected independently of the year, hydrological period and taxonomic resolution (Table 4). In general, ordinations of sampling sites according to the biological matrices with different taxonomic resolutions were significantly concordant with spatial variables (MEMs) for all, but two comparisons (Table 5).

4. Discussion

Given the strong effects of water level variation on the ecology of floodplain systems (Junk et al., 1989), a natural step to test the taxonomic sufficiency approach in these systems would consist in evaluating whether these effects are detectable using biological data matrices at low levels of taxonomic resolution. We found that the difference between hydrological periods was also detected when genera and families were used instead of species level data (Table 6). This is an

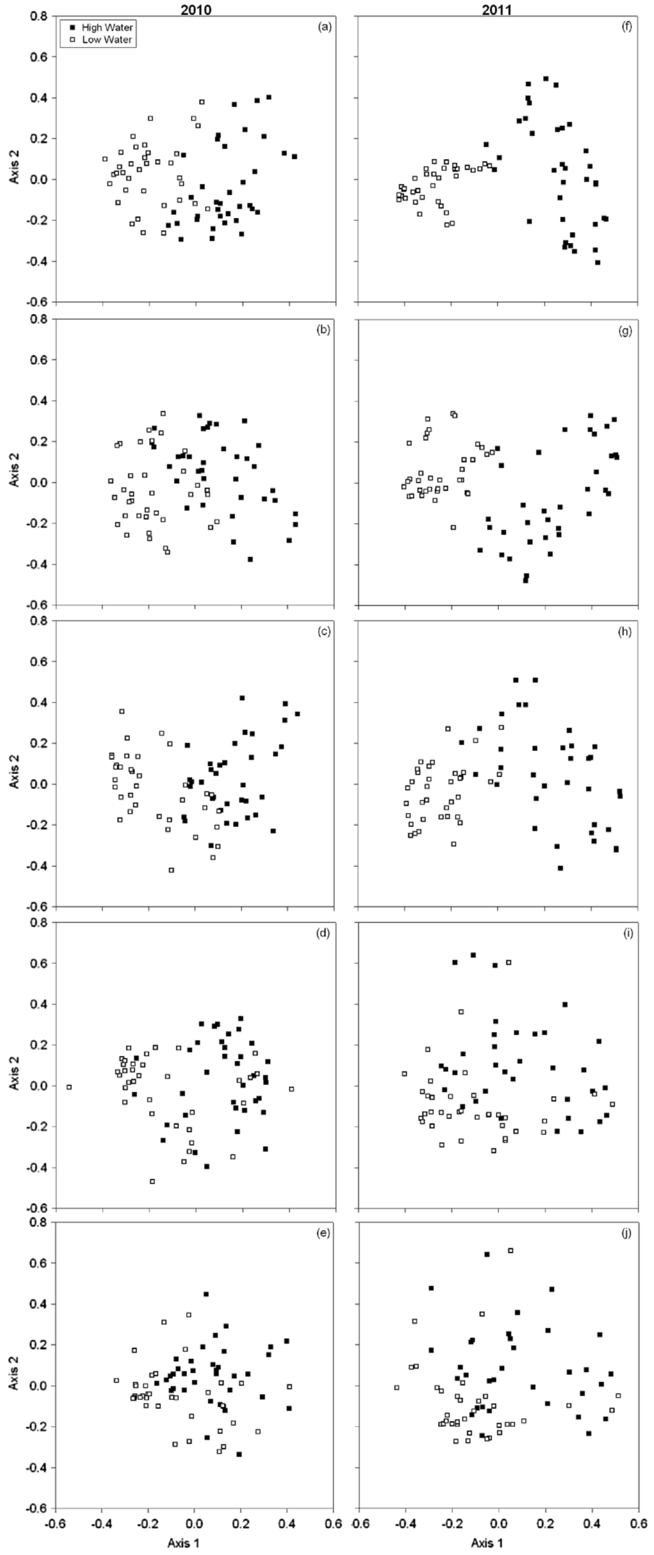

Fig. 1. Ordination plots by Principal Coordinate Analysis (PCoA) contrasting the low and high water periods. Data were based on different taxonomic levels. (a) species/2010; (b) genus/2010; (c) family/2010; (d) order/2010; (e) class/2010; (f) species/2011; (g) genus/2011; (h) family/2011; (i) order/2011; (j) class/2011.

Table 2
Procrustes results (r_P = square-root of 1-m^2 and associated P-values) comparing ordinations generated with species level data and different taxonomic resolutions. The data were gathered in two years and two hydrological periods (HW: high water; LW: low water). The number of sites was equal to 36 for each comparison.

Year	Period	Genus		Family		Order		Class	
		r_P	P	r_P	P	r_P	P	r_P	P
2010	HW	0.97	0.001	0.86	0.001	0.89	0.001	0.17	0.240
	LW	0.91	0.001	0.90	0.001	0.59	0.020	0.36	0.040
2011	HW	0.93	0.001	0.67	0.001	0.83	0.020	0.20	0.140
	LW	0.97	0.001	0.92	0.001	0.66	0.020	0.42	0.020

Table 3
Spearman's correlation coefficients between species richness and richness of higher taxa. The data were gathered in two years and two hydrological periods (HW: high water; LW: low water). The number of sites was equal to 36 for each comparison. All coefficients are significant at $P \leq 0.001$.

Year	Period	Genus	Family	Order	Class
2010	HW	0.98	0.95	0.76	0.60
	LW	0.97	0.91	0.80	0.64
2011	HW	0.95	0.89	0.86	0.85
	LW	0.93	0.90	0.85	0.81

encouraging result as it implies that the planktonic ciliate community could be cost-effectively monitored, using the higher taxa approach (genus or at most family), to detect human activities impacting hydrological variation.

We emphasize that in the discussion that follows we are also taking the consistency of the results among the different comparisons into account. Thus, we consider the taxonomic sufficiency approach as reliable only when the patterns were consistent among the different hydrological periods and years (for a similar discussion on the need of temporally invariable cross-taxon congruency, see Padial et al., 2012). We also look for a taxonomic level that would be deemed sufficient to achieve different purposes (i.e., detect hydrological changes, reproduce ordination patterns and relationships with environmental and spatial variables; see Table 6). As discussed below, only genus level identification fulfilled these different purposes.

Table 6
Summary of the results obtained in this study. Tests: (1) Difference between hydrological periods; (2) Community spatial patterns during each hydrological period; (3) Relationship between community data at different taxonomic resolutions and environmental data; (4) Relationship between community data at different taxonomic resolutions and spatial variables. The column "TR" indicates the taxonomic resolution supported by each test.

Tests	Evidence	TR	Results
(1)	Independently of the year, data at family level were able to detect a flood effect	Family	Table 1
(2)	Significant and high relationships (≥ 0.7) with species-level data were found only with genus-level data	Genus	Table 2
(4)	The relationships between species-level data and environmental variables were similar to those detected with the use order-level data	Order	Table 4
(5)	The relationship between species-level data and spatial variables were similar to those detected with the use order-level data	Order	Table 5

The success of the taxonomic sufficiency approach likely increases with the range of environmental gradients (Vilmi et al., 2016 and references therein). Thus, for the reliability of the taxonomic sufficiency approach, we need to "raise the bar" by testing the congruency between data at different taxonomic resolutions considering subtle environmental gradients. In this context, beyond testing the soundness of the taxonomic sufficiency approach to detect the effects of a strong disturbance (i.e., floods), we evaluated the congruency between ordination patterns generated by data at different taxonomic resolutions. Given that these analyses were conducted within each hydrological period, the ranges of the environmental gradients (across the space) were reduced when compared to the strong environmental changes caused by floods. Our results suggest that the ordination of the sites generated by species-level data were maintained even when order-level data were used. However, beyond statistical significance, we should also consider the magnitude of the effect size (see Lovell et al., 2007, Heino, 2010 and Vieira et al., 2015 for a similar discussion on cross-taxon congruency). If we adopt an r value ≥ 0.7, then the taxonomic sufficiency approach would be defensible only when the analyses are carried out with data at genus-level (see Table 2 and Table 6). Also, as recently shown by Rosser (2017 and references therein), we found support for the assertion that the performance of higher taxa strongly depends on the species to higher taxon ratio (SHR). In general, our results indicates that high values of r_P or r_S, measuring the congruence between results derived from species and higher taxa data, were found

Table 4
Procrustes results comparing ordinations generated with environmental data (PCA) and ordinations generated with data at different taxonomic resolutions (PCoA). The data were gathered in two years and two hydrological periods (Periods (Per): HW − high water; LW − low water). The number of sites was equal to 36 for each comparison.

Year	Per	Species		Genus		Family		Order		Class	
		r_P	P	r_P	P	r_P	P	r_P	P	r_P	P
2010	HW	0.58	0.002	0.48	0.001	0.53	0.002	0.49	0.001	0.46	0.001
	LW	0.24	0.200	0.20	0.300	0.26	0.180	0.26	0.140	0.24	0.140
2011	HW	0.50	0.001	0.46	0.001	0.53	0.002	0.51	0.001	0.47	0.001
	LW	0.17	0.530	0.20	0.570	0.22	0.380	0.20	0.400	0.17	0.620

Table 5
Procrustes results comparing spatial variables (MEMs) and ordinations generated with data at different taxonomic resolutions (PCoA). The data were gathered in two years and two hydrological periods (Periods (Per): HW- high water; LW- low water). The number of sites was equal to 36 for each comparison.

Year	Per	Species		Genus		Family		Order		Class	
		r_P	P	r_P	P	r_P	P	r_P	P	r_P	P
2010	HW	0.53	0.001	0.54	0.001	0.55	0.001	0.75	0.003	0.77	0.060
	LW	0.33	0.010	0.35	0.015	0.41	0.040	0.42	0.040	0.58	0.042
2011	HW	0.51	0.001	0.46	0.003	0.35	0.020	0.37	0.010	0.40	0.010
	LW	0.36	0.010	0.37	0.010	0.37	0.010	0.39	0.010	0.85	0.100

only when SHRs were lower than 2.

We found significant concordance between ciliate communities (at different taxonomic resolutions) and environmental variables during the high water periods of 2010 and 2011 (Table 4). Similar results were obtained between ciliate communities and spatial variables (Table 5). Interestingly, the strengths of the community-environmental relationships were maintained until order-level identification (for similar results using ciliate communities in marine ecosystems, see Xu et al., 2011a,b,c; Xu et al., 2014; Zhang et al., 2015; Jiang et al., 2016). Community spatial patterns were lost when class-level identification was used during the high water period of 2010 and the low water period of 2011. According to Heino (2014), we are far from a consensus on the level of taxonomic resolution needed to test community–environment relationships. However, taken as a whole, our results suggest a potential for the use of genus-level data for monitoring ciliate communities. Obviously, there is a need for further studies on taxonomic sufficiency for freshwater planktonic ciliates; however, the identification of ciliates up to genus-level, would allow one, with some level of expertise, to analyze samples *in vivo* and use a general key to the main groups, without any stain procedure. The guide proposed by Foissner and Berger (1996) presents a general key to those groups and is aimed at non-experts on ciliate identification.

An issue rarely discussed in the context of biomonitoring programs is that community changes can be spurious. For instance, they can be explained by “changes in taxonomic literature and/or taxonomic expertise of the counting personnel” (Straile et al., 2013). Thus, the use of methods (e.g. taxonomic sufficiency) that tend to minimize time and costs, and increase the accuracy and trustworthiness of the results obtained by long-term biomonitoring programs, while minimizing the information losses, would be advantageous. Our results suggest that genus-level identification of planktonic ciliates was sufficient to detect a major environmental perturbation (i.e. floods) and to detect subtler environmental and spatial gradients. At the same time, we believe that the use of this taxonomic resolution would be more robust to spurious changes (ensuring temporal comparability).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2017.07.008.

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