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Penatti Pinese, Olívia; da Silva Casseiro, Fernanda Aparecida; Pinese, José Fernando; Felizola
Diniz-Filho, José Alexandre

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Metabolic Theory of Ecology and diversity of continental zooplankton in Brazil

Olívia Penatti Pinese^{1*}, Fernanda Aparecida da Silva Cassemiro¹, José Fernando Pinese² and José Alexandre Felizola Diniz-Filho¹

¹Instituto de Ciências Biológicas, Laboratório de Ecologia Teórica e Síntese, Programa de Pós-graduação em Ecologia e Evolução, Universidade Federal de Goiás, Av. Samambaia, Cx. Postal, 131, 74001-970, Goiânia, Goiás, Brazil. ²Instituto de Biologia, Programa de Pós-graduação em Ecologia e Conservação de Recursos Naturais, Universidade Federal de Uberlândia, Uberlândia, Minas Gerais, Brazil. *Author for correspondence: oliviapp@gmail.com

ABSTRACT. Several ecological hypotheses try to explain geographical patterns in biodiversity. The Metabolic Theory of Ecology (MTE) predicts that temperature is the main determinant of richness patterns for ectothermic organisms and that the relationship between richness ($\ln S$) and temperature ($1/kT$) is a linear relationship with angular coefficient (b) near -0.65 . This study tested the MTE for continental zooplankton diversity in 63 lakes in Brazil. Copepoda, Cladocera and Rotifera, as well as the three groups combined, showed different patterns from that predicted by MTE, with b values equal to 0.871, 0.516, 0.720 and 0.901, respectively. Temperature explains 12.7% of the richness of Copepoda, 5.3% of Cladocera, 6.7% of Rotifera, and 11.4% of all zooplankton groups together. Several studies have shown that the MTE does not apply to many terrestrial groups, perhaps because the model does not consider variances generated by other factors such as environmental spatial range, body size and other variables. The present study confirms this point of view, expanding it to continental aquatic invertebrates as well.

Keywords: macroecology, biodiversity, Copepoda, Cladocera, Rotifera, temperature gradients.

A Teoria Metabólica da Ecologia e a diversidade do zooplâncton continental no Brasil

RESUMO. Várias hipóteses ecológicas tentam explicar os padrões geográficos de biodiversidade. A Teoria Metabólica da Ecologia (*Metabolic Theory of Ecology* - MTE) prediz que a temperatura é o principal determinante dos padrões de riqueza de organismos ectotérmicos e que a relação entre riqueza ($\ln S$) e temperatura ($1/kT$) é uma reta com coeficiente angular (b) próximo a $-0,65$. O presente estudo testou a MTE para a diversidade zooplancônica continental em 63 lagos brasileiros. Copepoda, Cladocera e Rotifera, assim como os três grupos analisados em conjunto, apresentaram padrões diferentes do previsto pela MTE, com os valores de b iguais a 0,871; 0,516; 0,720 e 0,901, respectivamente. A temperatura explicou 12,7% da riqueza de Copepoda, 5,3% de Cladocera, 6,7% de Rotifera e 11,4% do zooplâncton total. Diversos trabalhos têm demonstrado que a MTE não se aplica a muitos grupos terrestres, talvez porque o modelo não prevê desvios ocasionados por fatores como a variação espacial no ambiente, o tamanho corporal e outras variáveis. O presente trabalho corrobora este ponto de vista, expandindo-o também para invertebrados aquáticos continentais.

Palavras-chave: macroecologia, biodiversidade, Copepoda, Cladocera, Rotifera, gradientes de temperatura.

Introduction

Describing patterns of diversity gradients across the latitude is a fundamental goal of ecologists, because this kind of information provides an important picture of the environments and guides applied actions for species conservation (BLACKBURN; GASTON, 2003). Thus, several ecological hypotheses try to explain the current geographical patterns of biodiversity observed in the world through a macroecological approach.

Recently, Brown et al. (2004) described the Metabolic Theory of Ecology (MTE), based on the principles of biochemical kinetics and thermodynamics at a cellular level. MTE predicts that patterns of species

richness on broad spatial scales result from the dependence of metabolic rates of organisms in relation to temperature. This metabolic hypothesis (ALLEN et al., 2002) is part of the MTE, which in addition argues that the metabolic rate of an individual can be understood as a fundamental biological principle that drives all the processes of individuals involved with energy allocation, such as daily activities, survival, reproduction and interactions. Thus, a major premise underlying this theory is that the individual metabolism is quite important for ecology, because it is through these activities that the organisms interact with other organisms and with their environment (BROWN et al., 2004).

Allen et al. (2002) first proposed a simplified mathematical model to describe the general relationship between latitudinal diversity gradients and the global environmental parameters, in this case represented by temperature. Thus, Allen's model, subsequently rewritten by Brown et al. (2004), basically gives an accurate quantitative prediction of how species richness should range with environmental temperature: linearly with a slope (b) of approximately -0.65 (ALLEN et al., 2002). However, this model has assumptions that prevent its widespread use, as it should only be used to predict the distribution of ectothermic organisms, whose body size and abundance do not vary across geographical space. According to Hawkins et al. (2007a), the necessary knowledge to meet these assumptions is still very scarce for many biological groups, making difficult an important initial step to implement the model.

Several authors have questioned the adequacy of Allen's equation for some ectothermic organisms, including zooplankton (CASTRO; GAEDKE, 2008). Recently, Hawkins et al. (2007a and b) tested the model for a large dataset of terrestrial organisms around the planet, including plants, invertebrates and ectothermic vertebrates and concluded that the metabolic theory, as currently proposed, is still an ineffective tool to satisfactorily demonstrate distribution patterns of species around the globe. According to these authors, the hypothesis that species richness can be predicted as a function of temperature is an oversimplification of the global diversity patterns, because it does not consider other environmental standards.

Due to the fact that zooplanktonic organisms are ectothermic and show wide geographical distribution, they are appropriate to test the hypothesis that temperature drives the latitudinal patterns of zooplankton richness. In this context, the present study aimed to test the model of Allen et al. (2002) with zooplankton data of Brazilian freshwater lakes, considering the major groups of zooplankton individually (Copepoda, Cladocera and Rotifera), as well as all zooplankton combined. Therefore, this work aims to extend the empirical knowledge on the applicability of the MTE to freshwater invertebrates, which are important organisms on the bottom of the food chain in freshwater ecosystems.

Material and methods

The collection of biological information was conducted through published literature, with a compilation of data on zooplankton richness in 63 Brazilian freshwater lakes. The papers used in this search are listed in Table 1. We included in the list freshwater lentic environments, such as natural and artificial lakes, as well as marginal lagoons.

Table 1. References used for testing the model of Allen about MTE, number of environments in each study, kind of environment and region.

References	N	Environment	Region
Almeida (2005)	1	Artificial	Pernambuco
Azevedo; Bonecker (2003)	3	Marginal pond	Paraná
Branco et al. (2007)	1	Natural	Rio de Janeiro
Eskinazi-Sant'Anna et al. (2005)	17	Artificial	Minas Gerais
Espíndola et al. (2000)	3	Artificial	Pará
Hardy (1980)	5	Natural	Amazonas
Keppeler and Hardy (2004)	1	Natural	Acre
Keppeler (2003)	2	Natural	Acre/Amazonas
Lopes et al. (1997)	1	Artificial	Paraná
Melo et al. (2006)	3	Natural	Pará
Moschini-Carlos et al. (2008)	10	Natural	Maranhão
Nogueira (2001)	1	Artificial	São Paulo
Pinese et al. (2008)	1	Artificial	Minas Gerais
Pinese (2008)	2	Artificial	Minas Gerais
Sampaio et al. (2002)	7	Artificial	São Paulo-Paraná
Starling (2000)	6	Artificial/natural	Minas Gerais

The dataset were organized considering the geographic coordinates of each place, richness by zooplankton group (Copepoda, Cladocera and Rotifera), richness by total zooplankton (sum of all groups) and local climate data (average of annual air temperature) in each geographic point.

The data on average annual air temperature for each place were obtained at www.worldclim.org, in the format of ESRI grids, geographically selected through the software Arc View GIS 3.2 and subsequently changed to the Kelvin unit.

The effect of air temperature on species richness was analyzed for each zooplankton group individually (Copepoda, Cladocera and Rotifera) and also for total zooplankton. According to Allen et al. (2002), the relationship between the natural logarithm of species richness ($\ln S$) presents a linear relationship with temperature, denoted by $1/kT$ (with k = Boltzmann's constant = 8.62×10^{-5} ; T = temperature in Kelvin), and generates a negative slope (b), ranging between -0.6 and -0.7. The analyses were performed using the software SAM 4.0 (RANGEL et al., 2010). A map showing the pattern of distribution of total zooplankton was constructed through the program ArcGIS 9.3.

As the places are naturally autocorrelated due to their spatial proximity, much of the observed diversity may reflect the diversity of a nearby

place (DINIZ-FILHO et al., 2003). In order to correct this autocorrelation, the significance test was performed using the number of degrees of freedom estimated by Dutilleul's (1993) approach. The analyses considered the positive part of the correlogram, assuming that overestimation of degree of freedom is mainly due to short distance autocorrelation. This analysis was run in SAM 4.0 (RANGEL et al., 2010).

Results

Copepoda, Cladocera and Rotifera, as well as the three groups analyzed together (total zooplankton) showed different patterns from the predicted by MTE. The b values were equal to 0.871, 0.516, 0.720 and 0.901, respectively. Temperature explains only 12.7% of the richness of Copepoda, 5.3% of Cladocera, 6.7% of Rotifera and 11.4% of total zooplankton. All tests were significant, except for Cladocera. However, using Dutilleul's (1993) method for correcting spatial autocorrelation, all correlations were not significant (Table 2).

Figure 1 presents the linear regressions obtained between richness and temperature for the three groups of zooplankton (Copepoda, Cladocera and Rotifera) and total zooplankton, as well as the equations provided for each one ($y = a + bx$) and the values of p (probability) and r^2 (percentage of explanation for the relationship between richness and temperature).

Table 2. Probabilities of linear regression between temperature and zooplankton richness using simple correlation and Dutilleul's methods.

Group	P	Corrected P
Copepoda	0.004	0.320
Cladocera	0.065	0.391
Rotifera	0.037	0.330
Zooplankton	0.006	0.311

The dataset analyzed concentrated studies in southern and southeastern Brazil, with few works in the North and Northeast. Figure 2 illustrates the distribution of the 63 lakes analyzed in Brazilian territory and the pattern of diversity to continental zooplankton (total zooplankton).

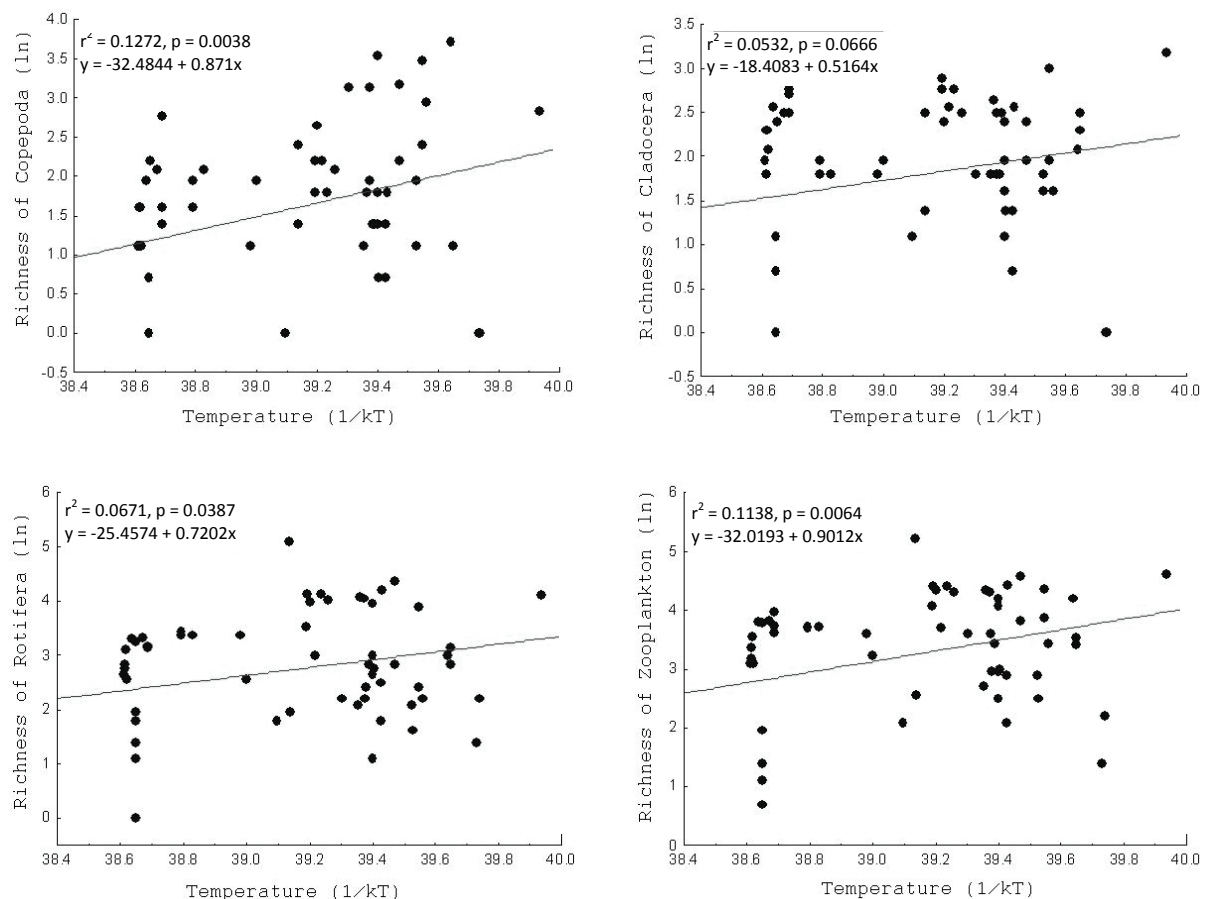


Figure 1. Linear regression between temperature (1/kT) and richness (natural logarithm) of Copepoda, Cladocera, Rotifera and total zooplankton of 63 continental lakes in Brazil.

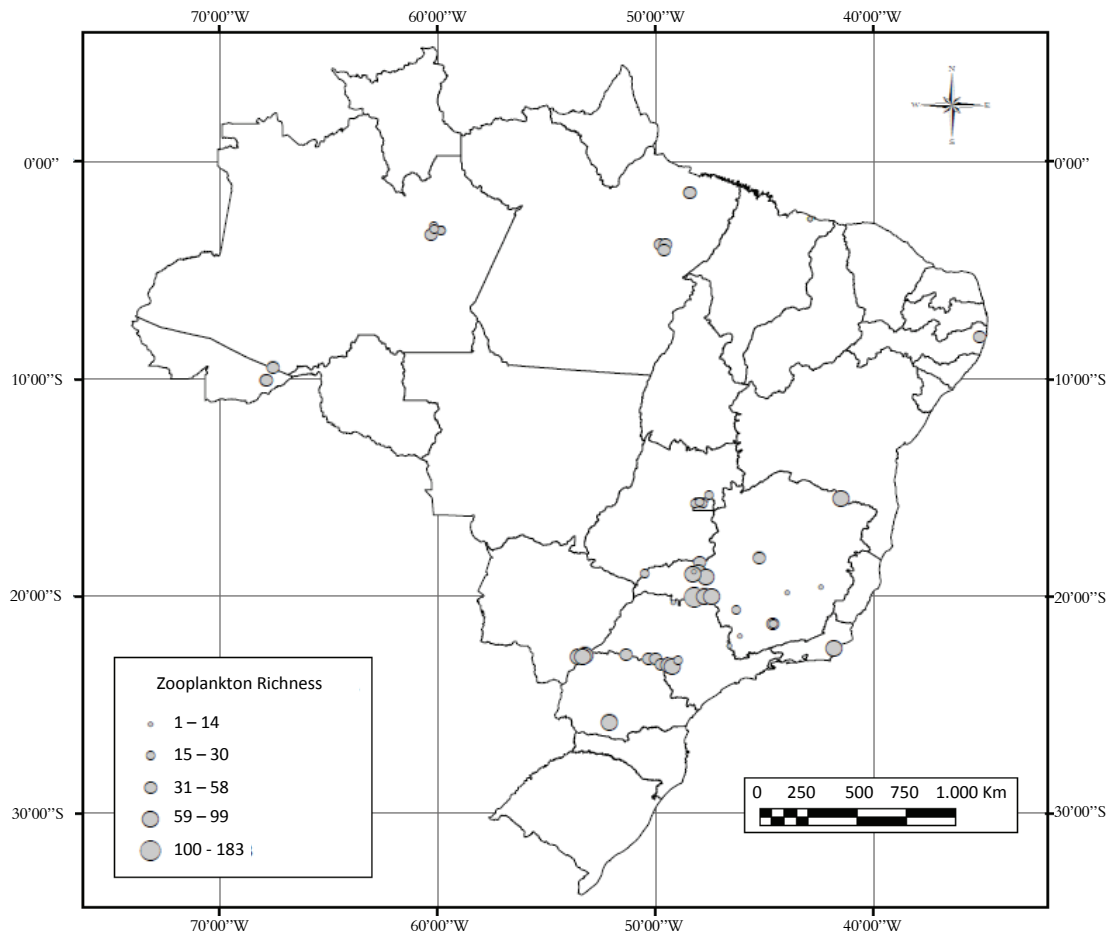


Figure 2. Spatial distribution of total zooplankton richness (sum of Copepoda, Cladocera and Rotifera) of 63 continental lakes in Brazil.

Discussion

The continental zooplankton data used in this study do not support MTE, as predicted by Allen et al. (2002). Several authors have also shown that MTE does not apply to many terrestrial groups, such as birds, amphibians and reptiles (CASSEMIRO et al., 2007a and b; HAWKINS et al., 2007a; TERRIBILE; DINIZ-FILHO, 2009).

Castro and Gaedke (2008), in their studies with plankton in Lake Constance, a temperate lake, also concluded that MTE has low predictive power on the diversity of these organisms, although their studies has been performed for a single environment, and thus with low latitudinal extension. Although the present analysis was conducted in a single country, Brazil has a broad regional scale and the latitudinal variation between study areas is relatively high, according to a macroecological view. This may not have reduced the predictive power of the results, since MTE applies to patterns with wide latitudinal variation that, consequently, varies considerably in metabolic kinetics.

Probably, the deviations predicted by MTE for many groups worldwide may occur because the model of Allen et al. (2002), applied initially to plants, terrestrial and marine animals dataset, does not predict variances in diversity caused by factors other than temperature, such as spatial variation in environment, peculiarities of life-history, body size and another environmental variables acting in the determination of diversity.

Aquatic organisms are strongly influenced by local water conditions, such as temperature, pH, oxygenation, trophic, solutes and biotic interactions and, consequently, many species can be considered sensors of environmental changes (MARGALEF, 1983; MATSUMURA-TUNDISI, 1999). For this reason, the kind of ecosystem is an important factor that also must drive the diversity of plankton.

In the specific case of continental zooplankton, as well as other freshwater organisms, what directly affects their distribution is the water temperature, and not air temperature. The variation in air temperature considered in the present analysis can be very different from water temperature in some cases. The initial idea is that water temperature

should be spatially related to air temperature. However, some local features, such as geology and wind speed can result in a considerable variation of temperature among environments, leading to particular patterns that are detected of different ways in aquatic and terrestrial organisms. Therefore, for continental zooplankton data, this contrast between global patterns of air temperature and local patterns of water temperature may have contributed to the violation of the theory.

MTE does not provide distinctions between the application of the model in aquatic and terrestrial environments, neither in marine and freshwater waters, but the earlier empirical studies on aquatic organisms were carried out on marine ecosystems, a highly established environment (ALLEN et al., 2002). However, oceans and freshwater ecosystems show many ecological differences such as geological age and level of stability and, therefore, these idiosyncrasies are not incorporated by the metabolic model.

As stated above, Allen et al. (2002) in their initial studies tested MTE in aquatic habitats only in marine environments, for fish, prosobranchia and fish ectoparasites. In this situation, they found adequacy to the data with MTE. Older ecosystems usually have greater environmental stability for both abiotic and biotic factors. In this sense, marine ecosystems, the oldest environment on Earth, presumably have high stability and their diversity cannot be compared to freshwater ecosystems. Diversity in stabilized environments can be more resistant to disturbances, as the interactions among species tend to be intrinsically linked, with practically no vacant niches. In this situation, global environmental variations may be more effective in determining diversity gradients than local factors, and this should be the reason for the adequacy of data used by Allen et al. (2002).

In the case of freshwater ecosystems, the stability is lower and it becomes more evident when comparing natural and artificial lakes. In most artificial freshwaters, such as hydroelectric reservoirs, very common in Brazilian waters, colonization by plankton is going on a short period of evolutionary time and, consequently, the local populations show a higher ability to fill vacant niches to succeed. Thus, in unstable environments, the power of global patterns in determining diversity loses importance for biotic and abiotic components acting locally. This may be an important reason for the non adequacy of freshwater zooplankton data to MTE in the present study.

Brazil is a country of large rivers, but natural lakes are scarce, occurring only in floodplains as marginal lagoons, which are strongly affected by seasonal flood cycles. Indeed, the ecosystems included in this study (most of them are artificial reservoirs and marginal lagoons) show great instability, with constant disturbances acting on the environment. These characteristics may also have contributed to the deviations from those predicted by MTE, because of the importance of local features on freshwater zooplankton in these situations.

It is important to stress that some Brazilian regions were not sampled enough – for instance, the Central, Amazon and Southern regions, which should be considered on further tests for MTE in order to increase the acceptability of results. Moreover, future studies like this should also consider the age of the lake studied, as well as the environment category, natural or artificial, thus seeking a better explanation for the applicability of MTE to aquatic the invertebrates of zooplankton.

In addition, it is important to consider that there are some erroneous records of zooplankton species in scientific literature, which may interfere in data richness, which is also presented incorrectly in some papers. As it is difficult to define such wrong identifications, it is important to consider this problem when interpreting the results.

Conclusion

This work does not corroborate with Allen's model, that is, temperature does not drive the zooplankton richness along latitudinal gradient in Brazil. Probably, other factors (e.g., evolutionary and ecological) besides temperature should be influencing the zooplankton distribution. This research also emphasizes the importance of local descriptive studies in freshwater environments, without which there is a great loss in the understanding of aquatic biota diversity on a regional and global scale, which can only be possible through data compilation and spatial analysis approach. Further studies should take account other environmental variables and idiosyncratic characteristics in order to understand the zooplankton's distribution pattern.

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