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Relationship between turbidity and the benthic community in the preserved Montebello Lakes in Chiapas, Mexico

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Abstract. One of the consequences of increased turbidity in lakes is the modification of the structure of the benthic macroinvertebrate community. To understand this relationship, we evaluated 13 lakes in the Montebello Lakes National Park in Chiapas. The lakes have been affected by gradual eutrophication over decades, producing variable transparency values among lakes. Macroinvertebrates were sampled from each lake in the rainy and dry seasons, and species richness and abundance were calculated and related to Secchi disc transparency. Cluster analysis showed that community composition was similar in pristine and semitransparent lakes, in contrast with turbid lakes. Considering macroinvertebrate groups, hyalellids were dominant in pristine and semiturbid lakes, whereas chironomids were dominant in turbid lakes. A significant quadratic relationship between richness and Secchi disc depth values was found, which is consistent with the intermediate production hypothesis. This study shows how a gradual change in Secchi disc depth can markedly modify benthic communities.

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Introduction

Benthic macroinvertebrates are indicators of aquatic system dynamics; their community composition changes rapidly as water physicochemical conditions are altered. In lakes affected by anthropogenic processes, benthic communities can reflect the dynamics of the whole aquatic system and indicate the trophic status of the lake (Alonso and Camargo 2005; Vian *et al.* 2018).

In most cases, anthropogenic actions increase turbidity, which promotes marked ecological changes over short periods of time. This phenomenon has been explained by theories such as the theory of alternative stable states in shallow lakes (Scheffer *et al.* 2001), which argues that turbidity in shallow lakes is the response variable of the nutrient–zooplankton–phytoplankton interaction and indicates that lakes can move from a pristine stable state to a turbid stable state over a short period of time. In lentic systems, turbidity can provide information about nutrient concentrations and eutrophication state (Doña *et al.* 2011; Haggag *et al.* 2018). Nutrient enrichment favours turbid stable states because nutrients are the algal and bacterial resources that promote blooms. Such blooms cause physicochemical changes in ecosystem variables, such as reducing the dissolved oxygen concentration and water transparency (Smith *et al.* 1999). Once the ecosystem conditions change to a turbid state, macrophytes, benthic macroinvertebrates, and fish are affected (Persson *et al.* 1991; Scheffer *et al.* 2001; Suikkanen *et al.* 2013).

Several studies have evaluated how the invertebrate community is modified by increases in anthropogenic pollution and nutrients. Macroinvertebrate abundance increases with nutrients, although not all species exhibit increases in abundance at the same rate (Barbour *et al.* 1996; Arimoro *et al.* 2007; Miserendino *et al.* 2008). Furthermore, the relationship between lake perturbation and invertebrate richness appears to be nonlinear and has a low prediction capacity. Some studies have shown that species richness increases with nutrient concentrations (Spieles and Mitsch 2000; Arimoro *et al.* 2007), whereas others have reported that species richness decreases with increases in nutrient concentrations (Barbour *et al.* 1996; Battle and Golladay 2001; Miserendino *et al.* 2008).

One of the hypotheses that can explain this interaction is the intermediate productivity hypothesis, which proposes that a unimodal relationship exists between species richness and productivity. Therefore, a lake with low productivity values yields fairly low species richness, which can increase as productivity increases. However, high values of productivity can deplete species richness, and maximum richness is found when productivity levels are intermediate (Rosenzweig and Abramsky 1993; Kondoh 2001). The first part of the interaction can be explained by a lack of resources in the low-productivity system, which can only be used by a few organisms and species. At higher nutrient levels, there are more resources for more species (Rosenzweig and Abramsky 1993). However, the mechanism responsible for the decrease in richness in systems with high productivity levels remains undetermined. High levels of productivity may favour superior competitors and promote competitive exclusion, in which one species tends to monopolise all resources (Kondoh 2001).

Evaluating this interaction is not an easy task because it requires different study lakes with similar conditions that also have a nutrient concentration gradient. Lakes in the Parque Nacional Lagunas de Montebello (PNLM) in Chiapas, Mexico, fit these criteria. A heterogeneous eutrophication process has produced a transparency gradient among the PNLM lakes (Olea-Olea and Escolero 2018). The lakes serve as a model in which to evaluate the bistable hypothesis in a tropical lake system and the intermediate productivity hypothesis with benthic organisms. The present study investigated how the benthic macroinvertebrate communities of the PNLM lakes have been affected by the eutrophication process.

Materials and methods

Study site

PNLM is located in the south-east of the state of Chiapas in Mexico. The region has a subhumid climate with a monthly mean temperature of 23.6°C. The annual total precipitation of 1862 mm is distributed in two defined rainy and dry seasons (Ramírez-Marcial *et al.* 2007). The PNLM has more than 50 lakes that share the same karstic origins and ecotones, which makes them highly similar in their ecosystem effects, such as the type of vegetation that surrounds them, and consequently their limnological characteristics (Alcocer *et al.* 2016). These lakes vary in their surface area (ranging from 306.6 to 1.1 ha) and depth (ranging from 198 to 3 m). Previous studies have classified these aquatic systems into four groups based on their morphology: (1) large and deep; (2) large and shallow; (3) small and deep; and (4) small and shallow (Alcocer *et al.* 2016).

Since 1986, some lakes in the PNLM have experienced eutrophication caused by agricultural intensification in the region (Olea-Olea and Escolero 2018) and waste pollution from surrounding towns. All lakes are fed by groundwater. The karstic system facilitates water movement, connecting and feeding lakes and causing them to have similar water quality (Ramsar 2003). The highland lakes (Comisión Nacional de Áreas Naturales Protegidas 2011) receive water with no pollution source (Comisión Nacional de Áreas Naturales Protegidas and Consultorías Integrales para el Desarrollo Rural Sustentable 2009). However, the lakes in the lower part of the basin are also fed by the Río Grande de Comitán, which carries wastewater discharges from several towns in the upper part of the basin. Consequently, these lakes have been the most affected by eutrophication (Comisión Nacional de Áreas Naturales Protegidas 2011).

Because of the particular geomorphology of the system, these lakes have been differently affected by agricultural waste pollution from the groundwater that discharges into the lacustrine system. This process of eutrophication has altered the transparency and colour of the water in some of the lakes, causing them to change from crystalline blue to yellowish-green (Melo and Cervantes 1986; Alcocer *et al.* 2016; Olea-Olea and Escolero 2018).

The contrast in pollution sources between the lowland and highland groups of lakes can be seen each year, because the water in the lowland lakes becomes green, whereas the highland lakes keep their pristine blue appearance (Alcocer *et al.* 2016). The separation between turbid and pristine lakes can be as small as a distance of only 10 m of land.

Sample collection

Two sampling sessions were undertaken in 2013, the first in April (dry season) and the second in September (rainy season). In both seasons, samples were collected from the same ecotone in 13 representative lakes (with less than 13 km between the most distant lakes) based on morphological classification (Alcocer *et al.* 2016; Table 1). The 13 lakes were divided into three transparency categories based on Secchi disc values: turbid (<2 m), semitransparent (2–8 m) and pristine (>8 m). These categories are consistent with the categories of eutrophic, mesotrophic and oligotrophic lakes based on the eutrophication index of Carlson and Simpson (1996). Using this system resulted in six lakes being classified as turbid, four lakes being classified as semitransparent and three lakes being classified as pristine (Fig. 1).

Secchi disc values were used as a measure of water transparency according to the mean of three measurements in the centre of each lake, which was established as the point of intersection of two lines drawn in Google Earth representing the maximum width and length. All Secchi disc measurements were taken by the same person between 1100 and 1400 hours under sunny conditions at the same distance above the water.

Benthic macroinvertebrates were sampled with a standard 30.5-cm D-frame aquatic net (mesh size 0.25 mm). Samples were taken from different points along the lakeshore. In the dry season, samples were taken at four different points. Owing to logistical constraints, in the rainy season samples were taken from six to nine points. In all cases, the sampling points were selected *in situ* depending on their accessibility and microhabitat: (1) rocks and sand with adhered epiphytic algae; (2) submersed vegetation; and (3) sedge. Because sedge was the most abundant microhabitat, in the dry season this microhabitat was sampled twice, whereas the other two microhabitats were sampled only once. For similar reasons, in the rainy season submerged vegetation and sand and rocks were only sampled twice, whereas the rest of the points were established in the sedge. At each point, macroinvertebrates were sampled at depths of ~0.5–1 m under the water with six swings of the net in an attempt to shake and scrape the roots, stems and leaves of the plants. All samples were fixed in 80% alcohol for later identification in the laboratory. Individuals were identified to family level using the taxonomic keys of Merritt and Cummins (1996) and Burch and Cruz-Reyes (1987). Family level was considered adequate to characterise the macroinvertebrate community because it reduces the costs of identification, and only a small amount of information is lost (Marshall *et al.* 2006). In the study of Marshall *et al.*, they found that only 6% or less of the information was lost using the family level rather than species level.

Statistical analysis

A frequency analysis was conducted with the Secchi disc measurements to group the lakes into different categories. Then, a Kruskal–Wallis test was performed to test this categorisation. Finally, a Mann–Whitney *U*-test was performed to determine which categories differed significantly.

To evaluate the total annual macroinvertebrate family richness in each lake, rarefaction curves (Mao Tau; Colwell *et al.* 2005)

Table 1. Summary of community structure data

Lake morphological groups are according to Alcocer *et al.* (2016; LD, large and deep; LS, large and shallow; SD, small and deep; SS, small and shallow). Unless indicated otherwise, data age given as the mean ± s.d. of the dry and rainy seasons. Rarefied richness and Ephemeroptera, Plecoptera and Trichoptera (EPT) richness data are annual totals. NA, not available

	Morphological group	Secchi disc depth (m)	Rarefied richness	Abundance (number of individuals)	EPT richness	Number of chironomids	Number of hyalellids
Turbid lakes							
Balantetik	LD	0.26 ± 0.20	15	107 ± 52	1	47 ± 21	0
Chaj-Chaj	SS	0.46 ± 0.02	19	247 ± 76	1	161 ± 105	5 ± 6
San Lorenzo	LS	0.66 ± 0.15	17	238 ± 182	1	176 ± 130	0
Liquidámbar	SS	0.68 ± 0.59	20	309 ± 306	1	167 ± 215	0
La Encantada	SD	0.80 ± 0.29	9	833 ± 401	0	778 ± 395	0
Bosque Azul	LD	0.83 ± 0.34	11	790 ± 59	0	738 ± 22	0
Semiturbid lakes							
San José	LS	3.01 ± 1.40	18	101 ± 1	3	15 ± 6	48 ± 9
Península	NA	3.27 ± 1.55	22	216 ± 101	5	10 ± 3	159 ± 95
Esmeralda	SS	4.01 ± 0.41	25	184 ± 115	4	22 ± 1	93 ± 78
Agua Tinta	SS	5.22 ± 0.16	28	332 ± 333	4	2.5 ± 0.7	152 ± 194
Pristine lakes							
Tziscao	LD	9.28 ± 0.96	27	209 ± 65	6	35 ± 43	92 ± 119
Cinco Lagos	SD	13.59 ± 3.31	13	88 ± 63	4	11 ± 8	0
Pojoj	LD	18.08 ± 4.67	11	135 ± 62	3	9.5 ± 0.7	52 ± 45

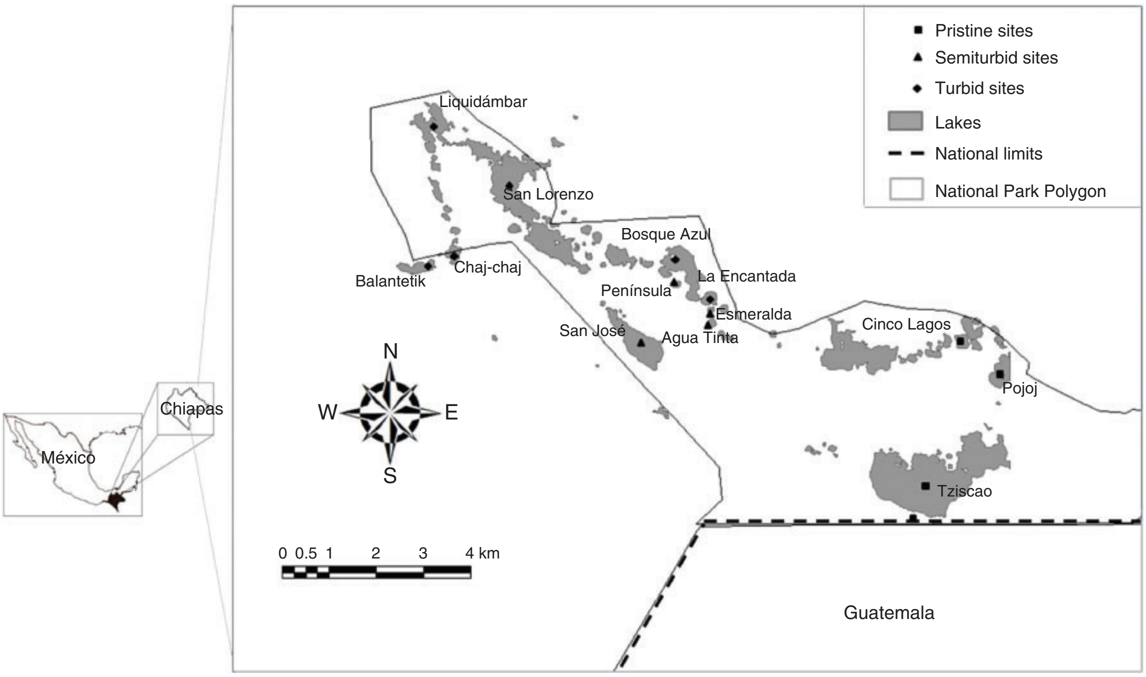

Fig. 1. Map of the lake system in the Parque Nacional Lagunas de Montebello (PNLM). Sampled lakes are shown according to the category to which they belong: turbid, semiturbid or pristine lakes.

were generated using EstimateS (ver. 9.1.0, R. K. Colwell, see http://viceroy.eeb.uconn.edu/estimates, accessed 30 October 2019). Other curves were created for each category of lakes by grouping all the lakes in the same category. The significance of differences in invertebrate richness and abundance between seasons was analysed with paired *t*-tests. In addition, to evaluate dominance, a comparison of the relative abundance of the two most abundant families among the three groups of lakes was performed using the Kruskal–Wallis test, with the Mann–Whitney *U*-test as a post hoc test.

Subsequently, we performed linear regression analysis between Secchi disc depth values and species richness. Linear regression analysis was also conducted between Secchi disc values and mean annual abundance (number of individuals). Given the different numbers of samples collected per lake in the rainy season, the abundance data were standardised to 10 samples per lake. Taxa sensitive to different types of water pollution (Ephemeroptera, Plecoptera and Trichoptera, EPT) were used to assess EPT taxa richness as an important indicator of water conditions in our study system. The effects of microhabitat on abundance and richness were evaluated using a Welch test because the data were heteroscedastic. A *t*-test for non-equal variances was used as a post hoc test. Welch tests were used to compare the abundance and richness of the different lake categories according to microhabitat.

Finally, cluster analysis was performed using PAST software (ver. 3.0, Ø. Hammer, Palaeontological Association, see https://folk.uio.no/ohammer/past/; Hammer *et al.* 2001) to test similarities in the composition of the macroinvertebrate community among lakes. This analysis was conducted using the unweighted pair group method with arithmetic mean (UPGMA) method and the Bray–Curtis algorithm, which are widely used in ecology to evaluate the similarity in community structure at different sites (Clarke *et al.* 2006).

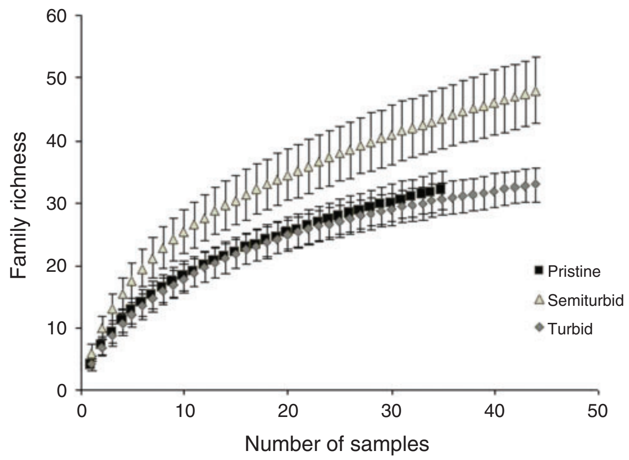

Fig. 2. Rarefaction curves of benthic family richness in lakes grouped by turbidity category. Data are the estimated richness ± s.d.

Results

Lake classification

Based on Secchi disc depth, the lakes were divided into three categories: turbid lakes, semitransparent lakes, and pristine lakes. The Kruskal–Wallis test showed that there were significant differences in Secchi disc depth values among the different categories ($P < 0.05$), and the Mann–Whitney *U*-test showed that all three categories differed from one another ($P < 0.05$).

Benthic community structure in different lakes

Rarefaction curves of the benthos richness values for the three different types of lakes showed that semitransparent lakes had higher family richness values (predicted to be close to 45; 47 collected) than turbid and pristine lakes, which had similar richness values (predicted to be close to 30; 34 and 32 collected in turbid and pristine lakes respectively; Fig. 2). The benthic richness and abundance varied among lakes. Agua Tinta, a semiturbid lake, was the most family-rich lake, with 28 predicted families, whereas La Encantada, a turbid lake, had the lowest richness, with only nine predicted families. Interestingly, La Encantada was the lake with the highest mean abundance (832.5 individuals on average annually); however, the lake with the lowest abundance was the pristine lake Cinco Lagos, with 88 individuals on average annually (Table 1). No significant differences were found between seasons in terms of abundance ($t = 0.75$, $P = 0.47$, $n = 13$) or family richness ($t = -1.58$, $P = 0.14$, $n = 13$).

A significant quadratic relationship was found between lake Secchi disc depth and family richness ($R^2 = 0.58$, $P < 0.05$, $n = 13$; Fig. 3*a*). The relationship between lake Secchi disc depth and abundance was not significant ($R^2 = 0.22$, $P = 0.195$, $n = 13$; Fig. 3*b*), but seemed to increase with reductions in Secchi disc depth. Interestingly, the abundance in lakes classified as turbid was highly variable, ranging from fewer than 100 to ~800 individuals.

There were significant differences in abundance and family richness among microhabitats ($F = 8.31$ ($P < 0.05$) and

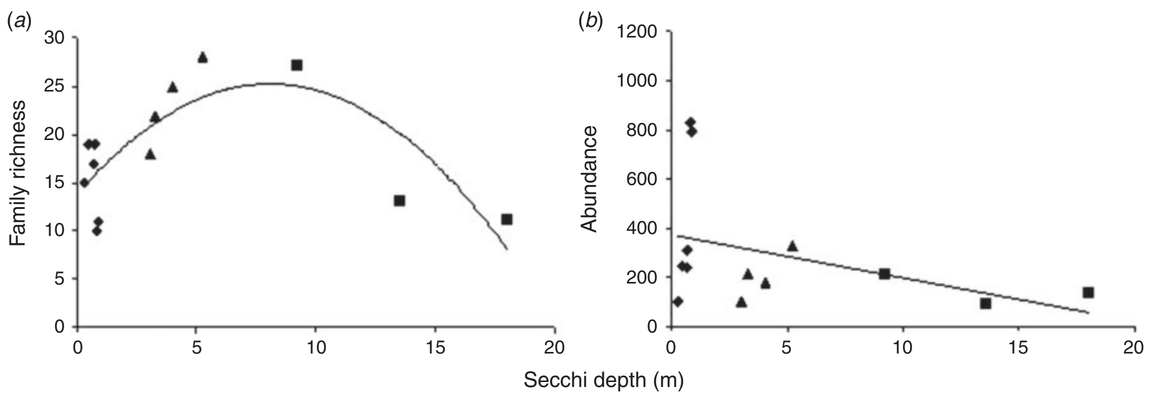

Fig. 3. Relationship between Secchi disc values and (*a*) benthic macroinvertebrate family richness and (*b*) annual mean abundance of benthic macroinvertebrates. Diamonds represent turbid lakes, triangles semi-turbid lakes and squares represent pristine lakes.

$F = 7.28$ ($P < 0.05$) respectively). Rocks and sand microhabitats had less abundance and lower richness than the other two microhabitats (t-test, $P < 0.05$). The abundance by microhabitat pattern was consistent with the overall pattern; there was higher abundance in turbid lakes in both sedge and rocks and sand microhabitats ($F = 4.55$ ($P < 0.05$) and $F = 4.50$ ($P < 0.05$) respectively). However, there were no significant differences in abundance among lake categories in the submerged vegetation ($F = 2.15$, $P = 0.14$). For richness, significant differences among lake categories were found only for the sedge microhabitat ($F = 3.55$, $P < 0.05$). In this microhabitat, higher richness was found in the semitransparent lakes.

The two most abundant families were Chironomidae and Hyalellidae. Comparison of the relative abundance of these families among the three categories of lakes showed significantly higher values of chironomids in turbid lakes and hyalellids in pristine and semitransparent lakes (Kruskal–Wallis, $P < 0.05$; Mann–Whitney U-test, $P < 0.05$; Fig. 4).

Few EPT taxa were found in all lakes; most of these taxa were found in semitransparent and pristine lakes, where the number of EPT families ranged from three to six (Table 1). Baetidae (Ephemeroptera) was the only EPT family found in turbid lakes. Cluster analysis based on benthic macroinvertebrate family composition showed two groups of lakes, leaving only two lakes unclassified. The first group formed matched the classification of turbid lakes, and the second group matched the classification of pristine and semitransparent lakes. The two unclassified lakes represented extremes. The first lake was evaluated as the most turbid lake, and it was closer to the turbid group. The second lake was the most pristine lake, and it was close to the pristine group (Fig. 5).

Discussion

The pattern of transparency in the lakes of the PNLM is consistent with the flux of water within the basin. Pristine lakes are located in the upper part of the basin and do not have superficial connections with other lakes. Semitransparent lakes have superficial connections with turbid lakes, but the semitransparent lakes are geographically more elevated than the turbid lakes; therefore, water seems to move from the former to the latter. Not only are turbid lakes located in the lower part of the basin, but they also have superficial connections with one another throughout the year (Comisión Nacional de Áreas Naturales Protegidas 2011). Therefore, the reduction in transparency, which suggests the occurrence of a eutrophication process, is worst in the lower lakes, and this seems to be related to the discharges of the del Río Grande de Comitán and groundwater polluted with agrochemicals and wastewater (González *et al.* 2013; Olea-Olea and Escolero 2018).

Our analysis showed that Secchi disc depth values are related to changes in macroinvertebrate community family richness, but not in the number of individuals. However, in two microhabitats, abundance was highest in turbid lakes, whereas in only one microhabitat was richness highest in semitransparent lakes. In addition, species composition and dominance varied among lakes with different Secchi disc depth values.

Secchi disc depth values have been used as an indirect indicator of nutrient concentration and perturbation (Lambou *et al.* 1982; Carlson and Simpson 1996; Brown *et al.* 1998; Doña *et al.* 2011). In lake of the PNLM, a decrease in Secchi disc depth values can be associated with anthropic eutrophication.

Family composition

Cluster analysis suggested that even when pristine lakes have the same richness as turbid lakes, their composition is very different. Pristine lakes have a similar composition to semitransparent lakes despite semitransparent lakes being the most family-rich lakes. This suggests the occurrence of a bistable system in which, after certain levels of perturbation, a marked shift in the community occurs (Scheffer *et al.* 2001). This change in composition

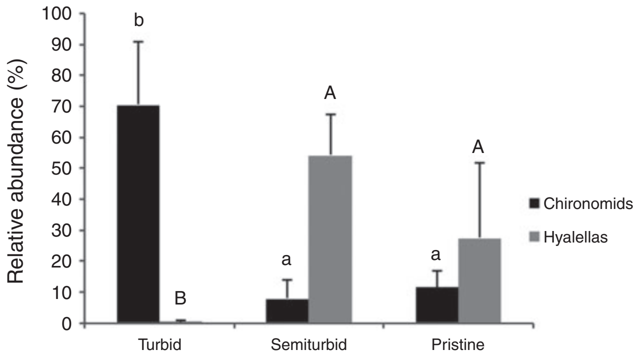

Fig. 4. Mean (±s.d.) abundance of hyalellids and chironomids in the three groups of lakes. Different lowercase and uppercase letters indicate significant differences in chironomids and hyalellids respectively between lake groups.

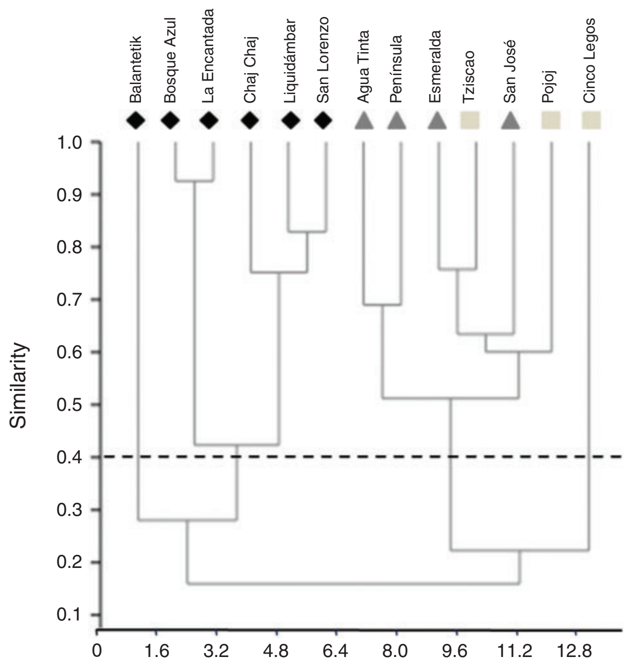

Fig. 5. Cluster analysis based on benthic macroinvertebrate family composition. The dashed line indicates the similarity threshold. Diamonds represent turbid lakes, triangles semi-turbid lakes and squares represent pristine lakes.

suggests a reduction in water quality because families used as indicators of good water quality (six families of the Order Trichoptera, three families of the Order Ephemeroptera and Family Dugesiidae of the Order Tricladida) were found only in pristine and semitransparent lakes. All these families are indicators of good water quality and have narrow tolerances to perturbation and eutrophication (Hilsenhoff 1988; González *et al.* 2012; Rios-Touma *et al.* 2014; Zhang *et al.* 2018). Families with wide tolerances were abundant in turbid lakes.

The most important difference in composition between turbid lakes and the other two types of lakes was the dominant family. In turbid lakes, the Chironomidae family was dominant, whereas in semitransparent and pristine lakes the dominant family was Hyalellidae. Although both families belong to the gatherer functional group, hyalellids are also facultative shredders and have a more important role in recycling organic matter (Cummins and Klug 1979). The shift in the dominant family also modifies the trophic structure in turbid lakes. Chironomids are a family with high tolerance to pollution and low dissolved oxygen concentrations (Barbour *et al.* 1996; Alonso and Camargo 2005). An increase in chironomid relative abundance has been associated with the contamination of waterbodies and high concentrations of organic matter (Alonso and Camargo 2005; Svensson *et al.* 2018).

Hyalellids have narrower tolerances to environmental conditions but represent a family of colonisers that is abundant in both oligotrophic and mesotrophic lakes with macrophytes (Alonso and Camargo 2005; Little and Altermatt 2018). Populations of this family can adapt their fecundity in relation to available nutrients (France 1992). This gives them adaptive advantages over other detritivorous macroinvertebrates, such as chironomids, in lakes with good water quality.

Richness and abundance

We expected to find a positive relationship between abundance and Secchi disc depth values because if the Secchi disc depth values for these lakes can be related to a high nutrient concentration, more nutrients would be available to sustain more individuals (Currie 1991). However, this relationship was not significant; even more in turbid lakes, abundance was reduced when turbidity increased.

This suggests that the relationship of turbidity with abundance could be unimodal. In this case, such relationship seem to be associated with a threshold of water turbidity after which the benthic abundance stops increasing and starts to decrease. An increase in abundance does not always imply that there is a proportional increase in the population of each species. In fact, in several systems, an excess of nutrients leads to the monopolisation of resources by a single species (Voelz and McArthur 2000; Arimoro *et al.* 2007). In freshwater systems, when the excess nutrients are caused by an increase in particulate organic material and are associated with decreases in dissolved oxygen, only some families of detritivore macroinvertebrates and tolerant predators benefit from this increase in nutrients and exhibit an increase in abundance (Miserendino *et al.* 2008; Parsons *et al.* 2010).

In these lakes, species richness does not increase linearly as the transparency of the system decreases, and the transparency–diversity relationship is unimodal (Huston 1979; Kondoh 2001). It is possible that transparency in lakes is related to an excess of nutrients (Olea-Olea and Escolero 2018); therefore, few benthic families can monopolise the available resources, and richness is reduced. Although unimodal relationships between abundance and productivity have been reported by Kassen *et al.* (2000), more data are needed to support this idea.

Conclusions

The results of this study suggest that the benthic macroinvertebrate community is highly correlated with Secchi disc depth values. Semitransparent lakes still support a rich and equitable community, but these lakes can quickly reach a state of low benthic diversity if they become progressively more turbid by eutrophication.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

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