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Littoral chironomids of a large Alpine lake: spatial variation and variables supporting diversity

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Abstract – Chironomidae are a major group of littoral secondary producers whose spatial changes in assemblage structures are shaped by diverse variables. Using their subfossil remains, we aimed at disentangling the relative impact of environmental, topographic, littoral occupation and hydrodynamic variables on the littoral assemblages as well as identifying taxa and sites of primary importance for the β-diversity in a large lake (Lake Bourget). A redundancy analysis coupled with a variance partitioning indicated that 22% of the assemblage variability was explained by slope, carbonate concentration and littoral occupation. A non-negligible fraction of non-separable variance among these variables likely highlights the topographic constraint on anthropogenic development and environmental conditions. Taxonomic turnover overwhelmingly (93.2%) dominated the assemblage changes indicating site-specific taxonomic composition. The taxa contribution to β-diversity was positively correlated with their mean abundances. The local abundances were either positively or negatively correlated with local contribution of sites to β-diversity (LCBD) providing evidence for different contributions of taxa to β-diversity. A couple of taxa (*i.e. Cricotopus* spp., *Microtendipes* sp. and *Cladotanytarsus* sp.) and sites (*i.e.* LB57, LB31, LB2) clearly supported the major variations of β-diversity and are therefore identified as being of primary importance regarding conservation programs. Both LCBD variations and taxa spatial autocorrelations suggest that chironomid assemblages were the most variable at a spatial-scale ranging from 500 m to 1 km, characterizing the spatial successions of littoral contexts. These results illustrate the need for considering short spatial scales to reveal the extent of the benthic diversity in the littoral areas of large lakes.

Keywords: lakes / littoral / β-diversity / Chironomidae / spatial variability /

Résumé – Les Chironomes littoraux d'un grand lac alpin : variabilité spatiale et variables soutenant la diversité. Les Chironomidae constituent un groupe important de producteurs secondaires littoraux dont les changements spatiaux dans les structures d'assemblage sont façonnés par diverses variables. À partir de leurs restes subfossiles, le rôle relatif des variables environnementales, topographiques, de l'occupation du littoral et de l'hydrodynamisme sur les assemblages littoraux a été recherché avant d'identifier les taxons et les sites de première importance pour la diversité β dans un grand lac alpin (le lac du Bourget). Une analyse de redondance couplée à un partitionnement de la variance a indiqué que 22 % de la variabilité des assemblages était expliquée par la pente, la concentration de carbonate et l'occupation du littoral. Une fraction non négligeable de la variance non séparable parmi ces variables met probablement en évidence l'effet de la contrainte topographique sur le développement anthropique et les conditions environnementales. Le renouvellement taxonomique a dominé les changements d'assemblage (93,2 %) mettant en évidence des compositions taxonomiques spécifiques pour les différents sites. La contribution des taxons à la diversité β était positivement corrélée à leur abondance moyenne, tandis que les abondances locales étaient corrélées positivement ou négativement à la contribution locale des sites à la diversité β (LCBD), suggérant différentes contributions des taxons à la diversité β. Un ensemble de taxons (*Cricotopus* spp., *Microtendipes* sp. et *Cladotanytarsus* sp.) et des sites (LB57, LB31, LB2) supportaient clairement les variations majeures de la diversité β et sont donc identifiés comme étant d'intérêt prioritaire pour des actions de conservation. Les variations de LCBD et les autocorrélations spatiales des taxons

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suggèrent que les assemblages de chironomes étaient les plus variables à une échelle spatiale allant de 500 m à 1 km, caractérisant les successions spatiales des contextes littoraux. Ces résultats illustrent la nécessité d'envisager de courtes échelles spatiales pour appréhender la diversité benthique dans les zones littorales des grands lacs alpins.

Mots-clés : lacs / littoral / β-diversité / Chironomidae / variabilité spatiale

1 Introduction

The littoral areas of lakes are defined as the lake fringe where at least 1% of the solar light can reach the substrate allowing benthic primary production to be supported (Wetzel, 2001). These areas are characterised by diverse mosaics of substrates (*e.g.*: rocks, sand, macrophytes) exposed to significant hydrodynamic constraints (Hofmann *et al.*, 2010; Stoll *et al.*, 2010). Consequently, despite representing minor areas relative to total lake surface, the littoral areas shelter a large fraction of the total biodiversity in lakes (Vadeboncoeur *et al.*, 2011). Over the last 50 years, numerous programs implemented to mitigate eutrophication have led to an increase in water transparency supporting the expansion of these littoral areas, which is expected to increase their contribution to the whole-lake energy flows (Vadeboncoeur *et al.*, 2001). These areas are also promptly exposed to anthropogenic development, which can locally induce both chemical and physical alterations. These changes could lessen the ecological wealth of littoral areas (Matthey *et al.*, 2004; Rivera *et al.*, 2017) and may cascade at the lake level.

Benthic macroinvertebrates play key functional roles in littoral areas, being actively involved in organic matter recycling and supporting fish production (Goedkoop and Johnson, 1996; Nogaro *et al.*, 2008; Wagner *et al.*, 2012). Consequently, they were shown to be a crucial link at coupling benthic and pelagic compartments (Vander Zanden *et al.*, 2006; Wagner *et al.*, 2012). Chironomidae is a highly diverse family of littoral macroinvertebrates (Wiederholm, 1983; Moller Pillot 2009) and can represent a major fraction of the littoral secondary production (Drake and Arias, 1995; Anderson *et al.*, 2012). The cephalic part of the moults of chironomid larvae, the head capsule (HC), is highly chitinised and well preserved in lake sediments (Brodersen and Quinlan 2006; Millet *et al.*, 2014). Recent studies have shown that subfossil remains such as HC can be representative of macrofauna at a local scale (*i.e.* ~1 ha, van Hardenbroek *et al.*, 2011) and can be suitable to describe contemporary biodiversity (Cao *et al.*, 2012; Cakiroglu *et al.*, 2014). Therefore, their use can be a valuable trade-off in order to circumvent field limitations related to the aggregative distribution and temporal variability of the abundances of living benthic organisms (Ali *et al.*, 1998; Lobinske *et al.*, 2002).

The settlement and growth of chironomid species were found to be constrained by different environmental variables such as dissolved oxygen, sediment organic matter or macrophyte coverage (*e.g.*: Wiederholm, 1980; Verneaux and Aleya 1998; Nyman and Korhola 2005; Árva *et al.*, 2015). Nonetheless, such environmental filtering only partly explains variations of littoral chironomid assemblages at the lake level. The influence of topography (*e.g.* slope, Free *et al.*, 2009) as well as hydrodynamic constraints (*i.e.* turbulence, Lienesch and Matthews, 2000; Kozarek *et al.*, 2018) may also exert additional controls on chironomid assemblages, especially in large and deep lakes that are characterized by strong depth variability over a short spatial scale and long fetched distances (*i.e.* the distance on the lake over which the wind can blow without encountering obstacles). Consequently, the interplay between environmental and physical controls likely conditions the differential occurrence of chironomid species in the littoral areas, affecting each species' contribution to the local diversity (*i.e.* α-diversity) and its variation over space (*i.e.* β-diversity).

In this study, we used the chironomid HC preserved in surficial sediment to depict at a short spatial scale the littoral chironomid assemblages of a large pre-Alpine lake, Lake Bourget (France). The candidate variables considered to possibly structure the chironomid assemblages were related to environmental conditions (*i.e.* sediment organic matter and carbonates), littoral anthropisation (*i.e.* littoral land use, littoral occupation), topography (*i.e.* local slope) and hydrodynamic conditions (*i.e.* local wave energy). We expected that these different variables would differently affect the settlement and growth of chironomid species leading to spatial differences in assemblage compositions. Specifically, we hypothesized that littoral anthropisation, topography and hydrodynamic conditions may act as primary drivers for chironomid assemblages as compared to the environmental variables in this large lake. Two complementary methodologies were applied to characterise chironomid β-diversity (Baselga, 2012; Legendre and De Cáceres, 2013) and to provide relevant insights regarding the spatial variations of chironomid assemblages. Specifically, the analysis of β-diversity was conducted to both characterise the spatial structure of chironomid assemblages and support the identification of species and sites of primary interest regarding their originality at the whole-lake level. These results consequently provide a basis for the implementation of future conservation and restoration programs.

2 Material and methods

2.1 Lake Bourget

Lake Bourget is the largest natural lake in France ($44.5\,km^2$, 45°699 N–5°873 E) and is especially deep due to its glacial origin with a maximal depth of 145 m. It is located between the limestone mountains of the Epine and Bauges. The two main towns close to the lake are Chambéry (220,000 inhabitants) and Aix-les-Bains (30,000 inhabitants). The lake experienced significant nutrient intakes during the first half of the twentieth century, leading to eutrophication (Berthon *et al.*, 2013). A remediation plan consisting in the construction of a collector channel surrounding the lake was implemented during the 1970s and the 1980s, leading to a gradual reduction

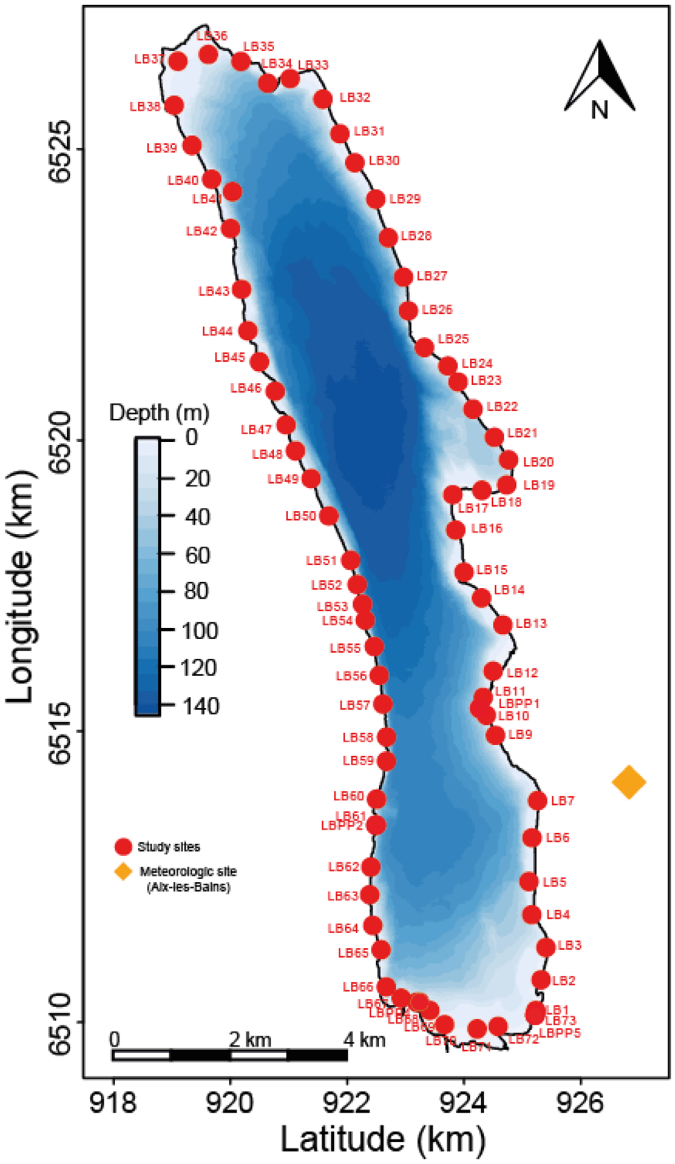

Fig. 1. Geographical location of the study sites distributed along the shoreline of Lake Bourget. The red dots and the associated numbers indicate the sampling sites. The orange square represents the Météo-France station in Aix-les-Bains.

in total phosphorus in the water column over the last decades, from ~120 μg L^{-1} in the 1980s to ~10 μg l^{-1} since 2010 (Jacquet *et al.*, 2017). The main fish species in the lake are perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), lavaret (*Coregonus lavaretus*), pike (*Esox luscius*).

2.2 Study sites and sampling

Sampling took place from 3 to 7 August 2015. A total of 76 samples were collected covering the entire littoral shoreline of the lake (Fig. 1). The median distance between two successive sites is ~655 ± 410 m. At each sampling site, surface sediments (*i.e.* ~5 first centimetres) were collected by scuba diving using a modified 4 cm diameter syringe. Depending on the bathymetry of the site, the samples were taken from several meters to a few dozen metres from the shoreline at depths between 80 cm and 6.5 m.

2.3 Laboratory treatment

The samples were sieved using a sieve with a mesh size of 100 μm. For each sample, the sieve residue was treated at room temperature by two successive baths of hydrochloric acid (10%) and potassium hydroxide (10%) for 1 h each in order to remove carbonates and residues of organic matter that could alter identification of HC (Walker, 1987). The HC were then thoroughly collected using thin forceps under a binocular (magnification ×5 to ×60) and subsequently mounted between slides and coverslips using semiconservative Aquatex® liquid. The individual determination of the HC was finally performed under a microscope (magnification ×100 to ×1000) using the identification guide of Brooks *et al.* (2007). Most identification was made at a genus-level, except for Pentaneurini and Procladiini for which the tribe was considered to prevent misidentification.

2.4 Variables characterising sites

To characterise environmental conditions within the sediment at each site, a fraction of the sediment sample was used to estimate the proportion of organic matter in the sediment (%) as well as the proportion of carbonate (%) according to the protocol in Heiri *et al.* (2001). The slope (%) of each site was calculated as the change in depth along a 100 m segment perpendicular to the shoreline and passing through the geographical location of the site, using the bathymetric data (spatial resolution = 10 m) of Ledoux *et al.* (2010). The littoral anthropization was measured by two different variables. First, the watershed land use was estimated semiquantitatively by extracting values from the CORINE Land Cover database in a 500-m buffer surrounding the sampling site. Three levels of watershed anthropization were considered; (1) ≤25% of watershed anthropization, (2) ≤25% to <75% of watershed anthropization and (3) ≥75% of watershed anthropization. Then, a qualitative typology was considered in relation to the type of habitats dominating the littoral shoreline during the sampling session by distinguishing beaches, reedbeds, natural rock and artificial rock. The slope as well as the littoral anthropization metrics was retrieved from Rivera *et al.* (2017), which is based on the same sampling sites as the present study. The hydrodynamic variable considered was the wave energy (watt m^{-1} of shoreline). This metric was calculated for each sampling site by coupling bathymetric data (Ledoux *et al.*, 2010) with wind direction and speed records from the Météo-France station in Aix-les-Bains (*i.e.* hourly data over three annual cycles, see Appendix 1 for the wind rose of the lake). Briefly, for each cell of the bathymetry layer within 100 m of the shore, the fetch (distance to shore) was estimated for 16 directions at regular 22.5° increments. For more robust estimates, each of the 16 fetched values represents the average of 9 subbearings spread at 2.5° angles (from −10° to 10°) around the main bearing. For each hourly time step, the wave energy was calculated from the recorded wind speed, the local depth and the local fetch at the angle closest to the wind direction. The details of the hydrodynamic calculations are described in Resio *et al.* (2003) and Rohweder *et al.* (2008). The wave energy was averaged over the full 3-year time series for each cell, and the mean wave energy for a sampling site was obtained by averaging the wave energy of cells in a 50-m radius around the site. The wave energy raster for the 100 m shoreline and the estimated values for each sampling site are shown in Appendix 2.

2.5 Data analysis

The associations between different taxa and sites as well as the influence of the variables characterising the sites were evaluated through a redundancy analysis (RDA; Borcard *et al.*, 2011). The significant variables were selected by forward selection with 9999 permutations. The contribution of each variable to chironomid assemblage variability was estimated through variance partitioning and plotted as a Venn diagram. The HC abundances were Hellinger-transformed prior to the analyses, as suggested by Legendre and Gallagher (2001), and only taxa with a total abundance higher than 5 HC were considered. In addition, sites with fewer than 20 HC were excluded from the analyses as those samples might not constitute representative assemblages (Larocque, 2001).

For each sampling site, chironomid assemblages were characterised by their taxonomic richness (*i.e.* the number of taxa identified) and their diversity (*i.e.* α-diversity) by means of the Simpson Index interpreted as the effective number of dominant taxa in the assemblages. The methodology recently proposed by Hsieh *et al.* (2016) was applied to compute asymptotic estimates of these two metrics to prevent biased estimations due to different sample sizes. The influence of environmental variables on the taxonomic richness and α-diversity was assessed through linear models.

The variation in chironomid assemblages between sites (*i.e.* β-diversity) was estimated using the approach proposed by Legendre and De Cáceres (2013). This approach considers total assemblage diversity as the total variance of the site/taxa matrix of all sites. Hellinger similarity was used to obtain the similarity matrix required for β-diversity calculations between two sites. This approach allows for partitioning β-diversity between sites and taxa in order to classify their contribution to the total β-diversity. The two metrics, contributions of taxa to β-diversity (SCBD) and contributions of sites to β-diversity (LCBD), thus support the identification of taxa and sites of primary importance regarding the changes of chironomid assemblages at the whole-lake scale. Complementarily, the approach proposed by Baselga (2012) was followed to characterise the changes of chironomid assemblages between sites. This approach first considers the distance between sites, calculated as the Jaccard Index, as a measure of β-diversity. In the second step, the distance between sites is decomposed into two components: (1) the nestedness, where species found at sites with lower richness are a subset of those present at high richness sites, and (2) the turnover, where assemblages of a site include species unique to that site.

The spatial autocorrelation of the taxa distribution was estimated using Moran's I index (Moran, 1950), considering 20 classes of spatial distances ranging from 708 m to 17 km. This index varies from −1 to 1, indicating the strength of positive or negative correlation in taxa abundances for sites separated by each distance class. The significance of the autocorrelation was estimated by a randomization test.

All statistical analyses and graphical representations were performed using R.3.4.1. (R Development Core Team, 2017) and the following packages: *waver* (Marchand and Gill, 2017), *Inext* (Hsieh *et al.*, 2016), *vegan* (Oksanen *et al.*, 2015), *betapart* (Baselga and Orme, 2012), *pgirmess* (Giraudoux, 2013), as well as the R codes provided by Legendre and De Cáceres (2013).

3 Results

3.1 Characteristics of assemblages and structuring variables

A total of 7464 HC from 35 taxa were identified at 76 sampling sites from which 19 taxa and 65 sites were selected for the analyses according to the criteria described in the "Data Analysis" section. More than 75% of the sites had a sum of identified HC greater than 40 with an average (±sd) of 112 ± 42 HC. The retained taxa showed important differences in total abundance with *Cricotopus* spp., *Microtendipes* sp., *Tanytarsus* spp. and *Psectrocladius* spp. as dominant taxa and *Cladopelma* sp., *Parachironomus* sp., *Endochironomus* sp., *Thienemaniella* sp. and *Stenochironomus* sp. as rare taxa. Other taxa exhibited intermediate abundances.

The RDA highlighted the associations between the sites and the different taxa (Fig. 2). The two first axes of the RDA support 22 and 3% of the overall chironomid variability, but only the first RDA axis supported a significant proportion of constraint information. *Cricotopus* spp. was the taxon with the highest score on axis 1 (RDA1) and was therefore typical of different sites such as LB53, LB58 and LB60. Conversely, *Tanytarsus* spp. had the most negative RDA1 score and was mainly associated with sites LB32 and LB2. Site LB43, and to a lesser extent LB42, LB45 and LB16, were characterised by the presence of Tanypodinae and *Cryptochironomus* sp. LB33 differed from the other sites by the high representation of *Cladotanytarsus* sp. LB54 and LB55 differed from the other sites by being associated with *Microtendipes* sp. and *Paratendipes* sp. *Psectrocladius* spp. as well as *Chironomus* spp., Pentaneurini and *Corynoneura* sp. were highly represented at different sites such as LB48, LB24 and LB35. Most other sampling sites were not characterised by a particular taxon or taxon association (Figs. 2a and 2b).

Among the different environmental variables considered to explain the variation of chironomid assemblages, the slope, carbonate and shoreline habitat were significant and explained 22% of the total variation in chironomid assemblages (Fig. 2c). The carbonate and the slope influenced the two axes of the RDA although the first axis was more constrained. *Cricotopus* spp. was the most associated with high percentages of carbonate and slope. *Microtendipes* sp. and *Paratendipes* sp. were the two taxa mostly related to steep slopes. In contrast, *Tanytarsus* spp., *Cladotanytarsus* sp. and to a lesser extent *Polypedilum* sp. and *Cryptochironomus* sp. were mainly associated with sites with gentle slopes and low carbonate. Beaches and reedbeds were the two littoral habitats associated with low slopes and low carbonate and

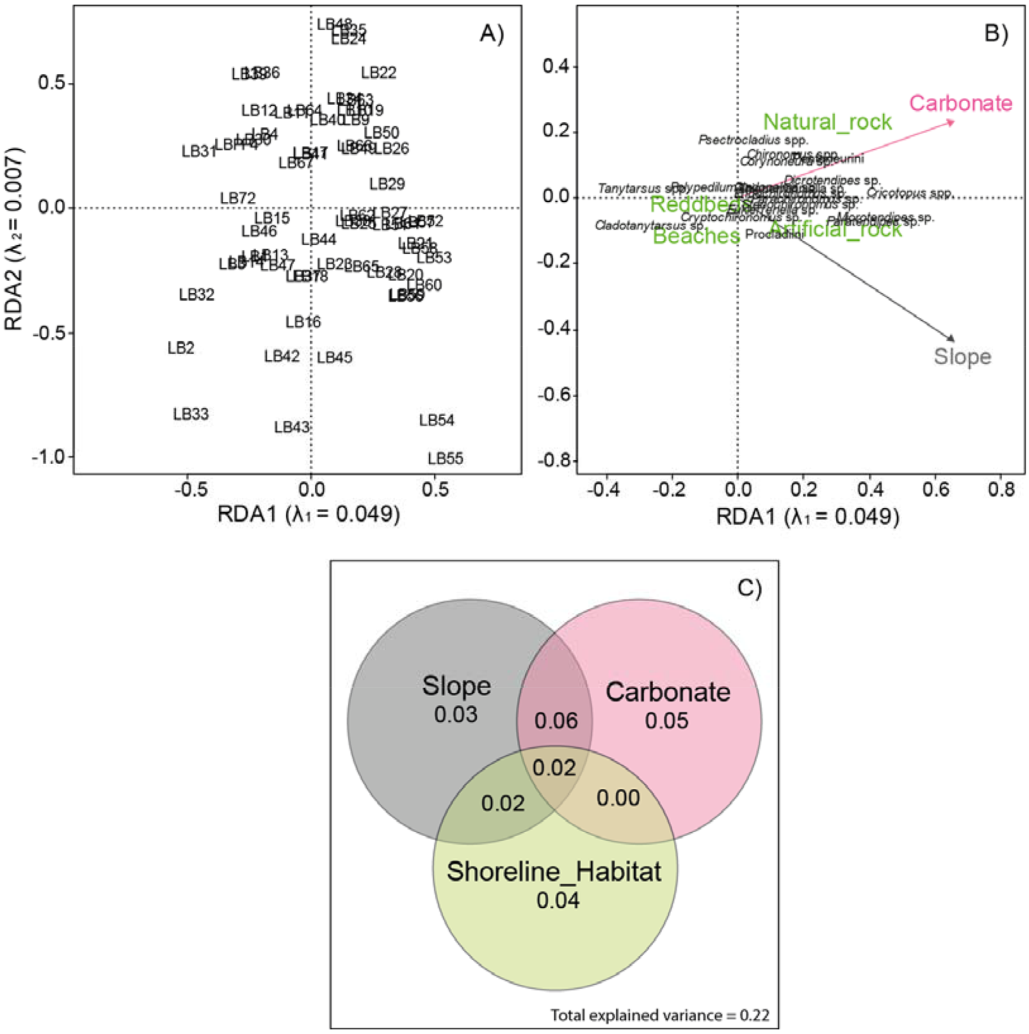

Fig. 2. Summary of the redundancy analysis (RDA). (a) RDA-biplot representing the distribution of the sampling sites on the first two axes of the RDA. (b) RDA-biplot representing the association between the three significant variables (slope, carbonate, shoreline habitat) and the different taxa on the first two axes of the RDA. (c) Venn diagram summarising the variance partitioning for the three significant variables.

were therefore also characterised by the presence of the last mentioned taxa. The second axis of the RDA (RDA2) reinforces the segregation of sites and taxa according to the slope and carbonates as well as shoreline habitats. Sites with natural rock tend to exhibit high carbonate and were characterised by *Psectrocladius* spp. and to a lesser extent *Chironomus* spp., Pentaneurini and *Corynoneura* sp. Different sites with artificial rock tend to have steeper slopes and are characterized by the presence of *Microtendipes* sp. and *Paratendipes* sp. The overall results of the RDA are corroborated by the linear relationships between taxon abundances and the slope and carbonate (Appendices 2a and 2b) as well as variations in mean abundances between sites with different shoreline occupations (Appendix 3c).

The partition of variance (Fig. 3c) suggests that the three significant variables had a similar influence on chironomid assemblages (*i.e.* between 3 and 5% each). The relatively large fraction of non-separable variance among the variables (*e.g.* 6% for the slope and carbonate) is likely evidence of the covariations between these different variables within the lake.

3.2 Taxonomic richness/diversity α and environmental influence

The average richness of the sites was 13 ± 4 taxa with a maximum of 25 taxa at LB57. Simpson's diversity had an average value of 5.7 ± 1.6 and a maximum value of 9 at LB49. These two metrics were weakly, though significantly, correlated (R^2adj = 0.08, p-value = 0.01), indicating that they would allow a different characterisation of the assemblages of the study sites. Further, these metrics were not correlated with the total number of HC (p-value > 0.05), suggesting that these metrics were not influenced by the sample size. Both richness and diversity showed short-scale spatial variations between sites (Fig. 3) that may explain the absence of simple linear relationships with latitude or longitude (p-values > 0.05).

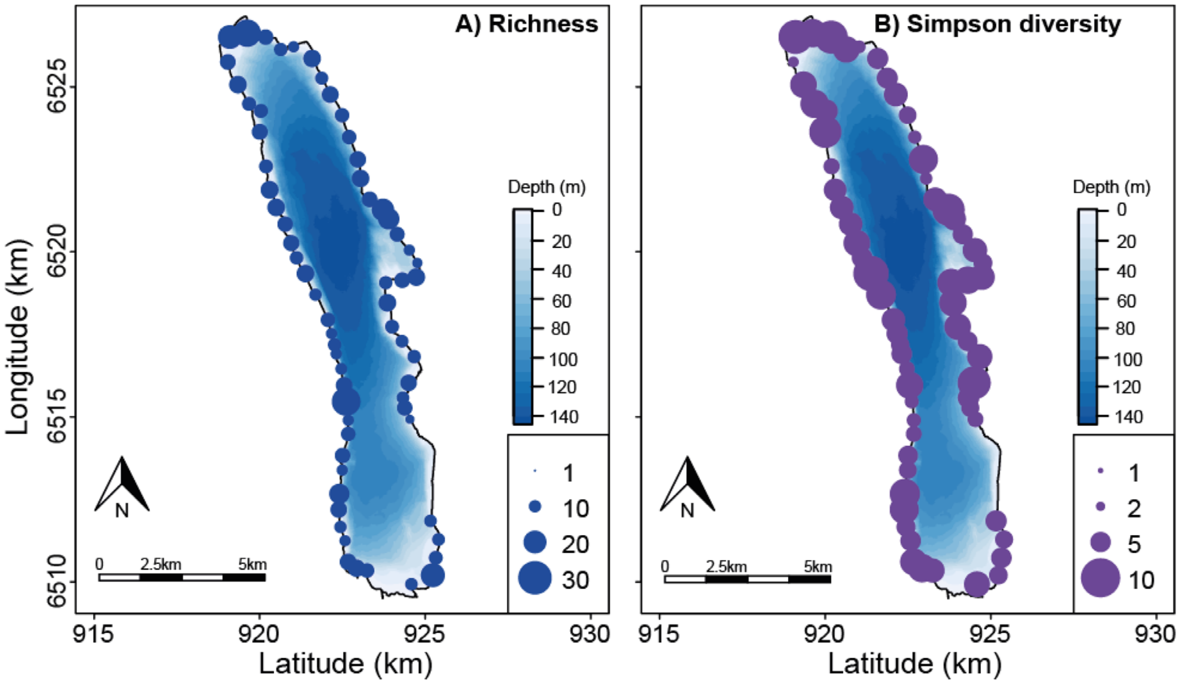

Fig. 3. Representation of the spatial variability of (a) the taxonomic richness, and (b) the Simpson Index diversity for the different sampling sites.

Neither richness nor Simpson's diversity exhibited significant linear relationships with the environmental variables (p-values > 0.05).

3.3 Contribution of sites and species to β-diversity

The partition of the Jaccard similarity over sampling sites indicated that 93.2% of the Jaccard similarity would be due to the turnover of taxa through a renewal of species between sites. Thus, different taxa were associated with subsets of sites probably related to different environmental conditions. The analysis of β-diversity according to the approach of Legendre and De Cáceres (2013) allows for classifying the sites relatively to their implication in the variability of the assemblages (LCBD) as well as for evaluating the implication of the taxa in these variations (SCBD). A high inter-site spatial variability can be identified for LCBD (Fig. 4a). The highest LCBD were associated with sites at different ends of the lake such as LB57, LB31, LB2, LB33, LB43. This high intersite spatial variability can probably explain the lack of linear spatial trend at the lake scale ($p > 0.6$). The LCBD appear to be negatively correlated with two of the environmental variables characterising the sites, organic matter and carbonate ($p < 0.05$). However, the linear relationships are both weak, accounting for 6 and 11% of the variance of the LCBD for organic matter and carbonates, respectively. For these two variables, the relationships were negative, indicating that the contribution of the sites to the β-diversity decreases as the percentages of organic matter and carbonate increase.

SCBD differ strongly among the different taxa (Fig. 4b). *Cricotopus* spp., *Microtendipes* sp. and *Cladotanytarsus* sp. were the most involved in β-diversity variations since they accumulate 40% of the total SCBD. The SCBD of the different taxa was strongly correlated with their mean abundances ($R^2adj = 0.64$, Fig. 5a). In order to clarify the influence of taxa on β-diversity, taxon abundance was related to LCBD using linear models. Among the 19 taxa selected for analysis, only 5 exhibited significant linear relationships. The slope differences of linear models (Fig 5b) indicated that taxa could be either positively or negatively related to LCBD. Taxa with a positive relationship to the LCBD of the sites were characterised by a low percentage in the assemblages as well as a low occurrence, whereas taxa with negative relationships were characterised by significantly higher proportions in the assemblages as well as a greater occurrence among sites (Fig. 6). At the lake scale, the variations in both abundance and occurrence support the differences between these two groups of taxa (Appendix 4). For instance, *Cricotopus* spp. and *Dicrotendipes* sp. are present in more than 90% of sites and contribute to a high proportion of the total HC (Appendices 4a and 4b). In contrast, *Cladotanytarsus* sp., *Cryptochironomus* sp. and *Eukiefferiella* sp. are present only in certain areas of the lake. *Cladotanytarsus* sp. and *Cryptochironomus* sp. are mainly present in the North-West and South-West areas near the reedbeds (Appendices 4c–4e). If their mean representation at the lake level is low for some sites, they may represent more than 50% of the HC identified. *Eukiefferiella* sp. presents an atypical profile with a strong representation at a single site with 40% cephalic capsules identified.

In order to specify at which spatial scale β-diversity varies, the absolute variations of LCBD between successive sites were compared with between-site distances (Fig. 7a). No significant linear relationship was identified ($p > 0.7$). Nonetheless, it was possible to notice that at a distance of ~550 m, absolute differences in LCBD exhibited the greatest variability (Fig. 7a, vertical dotted line). Similarly, while spatial autocorrelations in abundances may be relatively low overall (Fig. 7b), most of

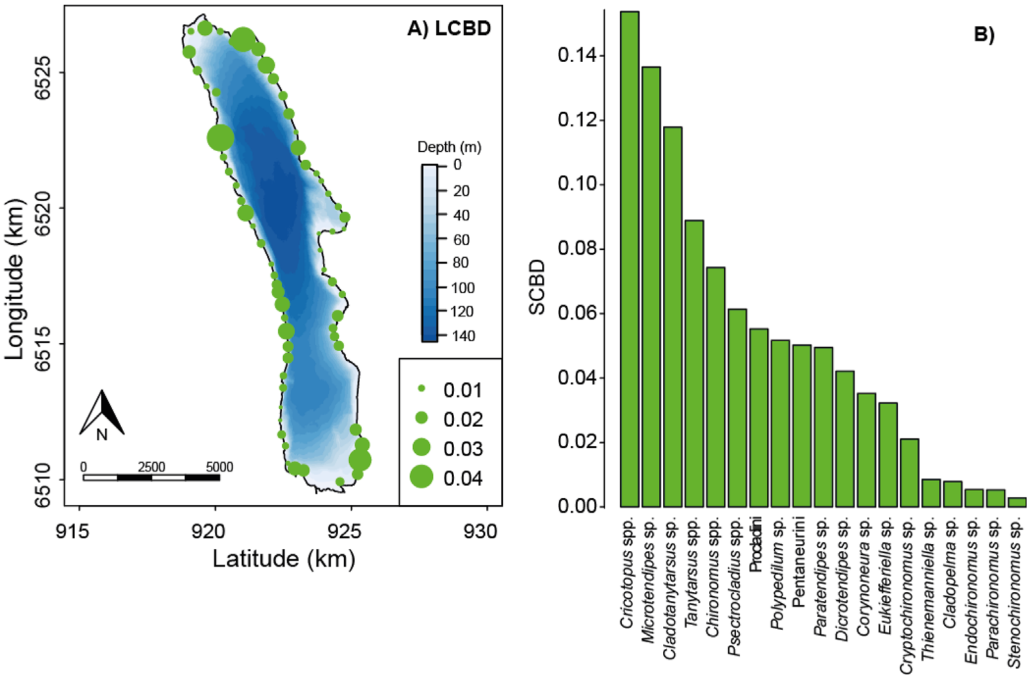

Fig. 4. Synthesis of β diversity analysis: (a) Spatial variability of the contribution of sampling sites to β diversity (LCBD) and (b) Contribution of the different taxa to β diversity (SCBD).

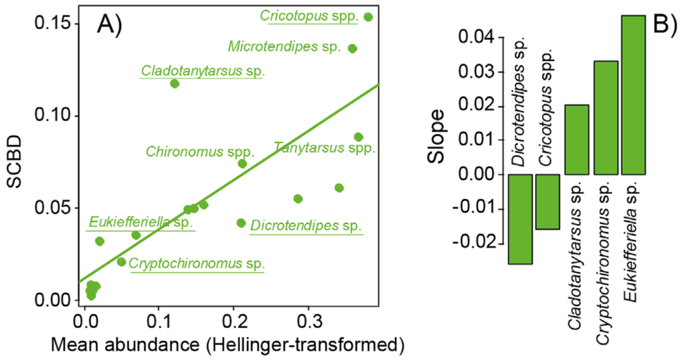

Fig. 5. (a) Relationship between the contribution of taxa to β diversity (SCBD) and the mean abundance of taxa. The names of the underlined taxa correspond to those whose mean abundance is significantly correlated with the LCBDs of the sites. (b) Slopes of significant linear relationships between mean taxon abundance (Hellinger transformation) and site LCBDs

them were detected in the first distance class (*i.e.* 708 m) (Fig. 7c; Appendix 5). Consequently, the greatest variations in LCBD appear at a similar spatial scale than the dominant spatial autocorrelation for the different taxa, suggesting that it is at a spatial scale ranging from 500 m to 1 km that the variations of assemblages were the most important.

4 Discussion

4.1 Characteristics of chironomid assemblages

A total of 35 different chironomid taxa were identified within the littoral area of Lake Bourget. This taxonomic

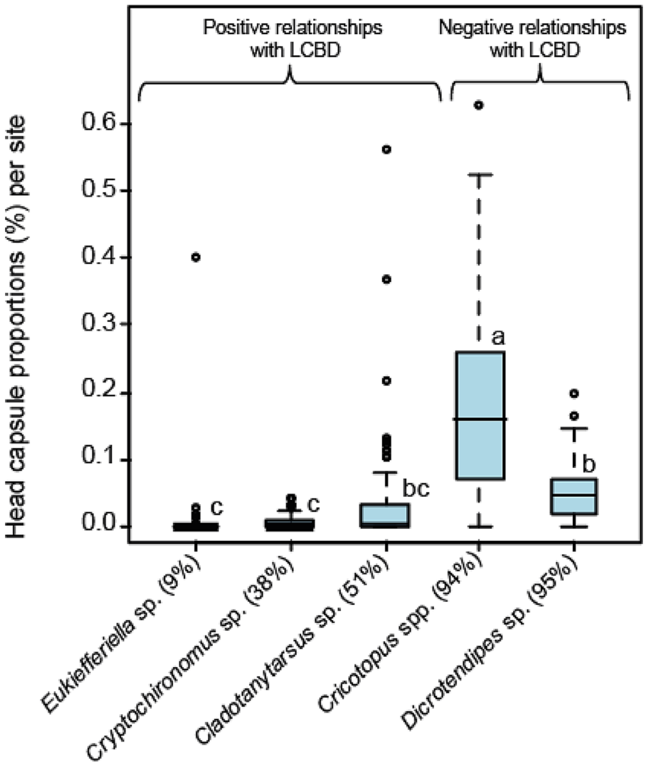

Fig. 6. Boxplots showing the variability of the percentages of each taxon in the assemblages for the different sampling sites. The different letters represent taxa with significant different percentages. The percentages in parentheses indicate the frequency of occurrence of the taxa at the different sampling sites.

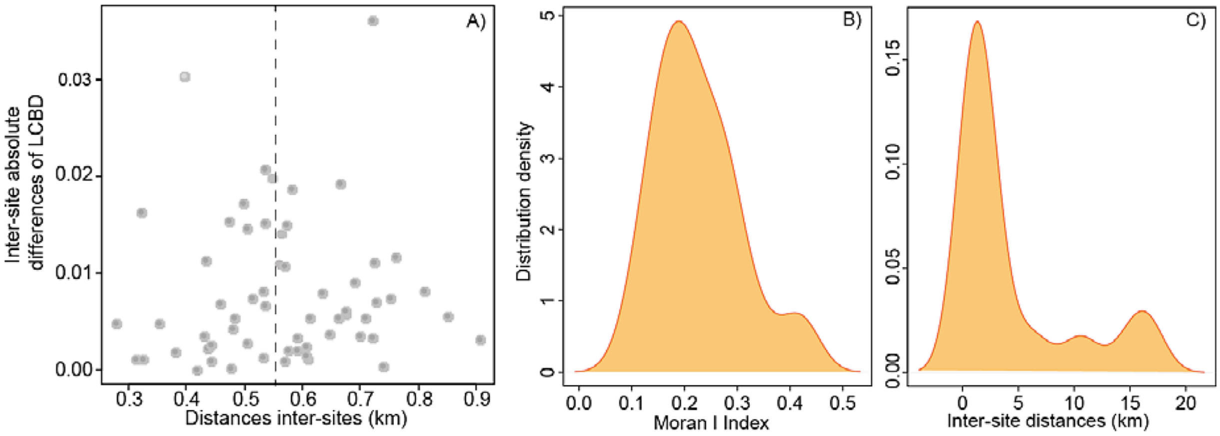

Fig. 7. (a) Relationship between between-site LCBD differences and between-site distances. The dashed line indicates the mode highlighting the distance of the greatest variations of between-site LCBD differences. Kernel densities distributions representing (b) Moran's I and (c) associated intersite distances for which the spatial autocorrelation is significant.

richness was greater than the richness observed in the current monitoring program in which 14 and 23 genera were identified in 2012 and 2013, respectively (Jacquet *et al.*, 2013). This result may be due to the intensive sampling effort but also to the use of subfossil remains which provide temporal integration and lessen aggregative distribution compared to living larvae. Consequently, the use of subfossil remains as a surrogate to living organisms seems to be a fair trade-off when seeking to reveal the biodiversity of benthic organisms, in line with van Hardenbroek *et al.* (2011) and Cakiroglu *et al.* (2014). The most represented taxa belong to three distinct taxonomic groups (*i.e.* Orthocladinae, Chironomini, Tanytarsini) that exhibit different ecological requirements. For instance, *Cricotopus* spp. have been shown to mostly develop in both macrophytes and rocks (Brooks *et al.*, 2007; Árva *et al.*, 2015), while *Tanytarsus* spp. is usually associated with coarse-to-fine sediments (Brooks 2007). In contrast to smaller lakes where single taxa can dominate the chironomid assemblages in association with similar environmental context (*e.g.* Lobinske *et al.*, 2002; Ingvason *et al.*, 2004), the strong variation in taxonomic dominance along the littoral shoreline of the lake (Appendix 4) suggests that the assortment of the assemblages may be constrained by variations of the environmental context.

4.2 Variables interplay as drivers of chironomid assemblages

The variance partitioning performed revealed different implications of topographic (*i.e.* slope), environmental (*i.e.* carbonate) and littoral-occupation variations in structuring chironomid assemblages. Contrary to our initial expectations, the hydrodynamic constraint estimated by a model of the mean wave energy did not explain a significant proportion of the variability in chironomid assemblages. Because of the large size of Lake Bourget that can support relatively long fetches (*i.e.* several km), such forcing may have been especially relevant in structuring littoral chironomids, as wave energy describes wave action inducing relevant ecological implications on chironomids such as sediment transport (Hofmann *et al.*, 2010) or larvae drifting (Lienesch and Matthews, 2000).

This result may be partly explained by the important variation of the littoral topography that originates from the early-Holocene glacier retreat that led to the lake basin formation. Littoral successions of steep to gentle slopes seem to be more structuring than wave action in this lake and could be involved in the significant proportion of non-separable variation among the three significant variables. The non-separable variation between the slope and the littoral occupation may highlight the constraint of the topography on the anthropic development along the littoral shoreline (*e.g.* beaches and reedbeds associated with gentle slopes). The non-separable variation between the slope and the carbonates can be explained by the fact that the sediments present in the first meters of the sites of steeper slope (*i.e.* the west coast of the lake) comprised high proportions of carbonates possibly resulting from lake snow accrual (*i.e.* precipitation carbonates forming long white threads). Lake snow is generally encountered in the deep areas of the lake (E. Lyautey, pers. commun.). Nonetheless, the very steep slopes in these areas could foster the upwelling movements that may explain the presence of these particles not observed in other areas of the lake at the time of sampling.

The influence of littoral occupation on the assemblages does not seem to be explained by a direct causal link. Rather, differences in the occupation of the littoral shoreline could reflect differences in nutrient enrichment possibly inducing differences in trophic contexts at the local scale as recently demonstrated by Rivera *et al.* (2017). However, lake-scale isotope analyses did not clearly identify a nutrient enrichment gradient in the littoral of the lake (unpublished data). The influence of littoral occupation on the diversity of Chironomidae has been demonstrated by Árva *et al.* (2015) in Lake Balaton (Hungary) and could have hydrodynamic consequences not taken into account in our wave energy model, due to differences in the physical structure of littoral habitats (*e.g.* rocks or reedbeds) that could induce different turbulent regimes at a short-spatial scale (*e.g.* m^2). Árva *et al.* (2015) have also highlighted an influence of the type of macrophytes as well as water chemistry on the structuring of Chironomidae assemblages. Those data were not directly available for our study. However, taking into account that the slope could be a surrogate for estimating the richness of macrophytes (F. Arthaud, pers. commun.), the remaining unexplained variability of chironomid assemblages may be related to stochastic dynamics of chironomid populations (Tokeshi, 1992) as well as pure spatial processes (Árva *et al.*, 2015).

4.3 Sites and taxa of importance in the diversity of assemblages

The analyses carried out regarding chironomid β-diversity allowed for thoroughly addressing the way the assemblages changed over sites. According to the approach proposed by Baselga (2012), the very high turnover (*i.e.* >90%) characterizing the similarity between sites highlights that sites tend to shelter specific subsets of taxa, which may be due to different local conditions (*i.e.* the taxa encountered on the beaches are different from those encountered on the rocky slopes) as shown by our previous results. The approach proposed by Legendre and De Cáceres (2013) allowed for the identification of sites that contribute the most to β-diversity, with high LCBD, that may be considered as original sites such as LB57, LB31, LB2, LB33, LB43 (Fig. 4a). These sites were present in different areas of the lake suggesting that no particular area of the lake would be most likely to host original assemblages. The importance of taxa in the LCBD showed that site originality was mainly due both to low abundance of taxa exhibiting a high occurrence throughout the littoral zone (*e.g. Cricotopus* spp.) and high abundance of taxa exhibiting a low occurrence in the littoral zone (*e.g. Cladotanytarsus* sp.).

4.4 Spatial variability of chironomid assemblages

Positive autocorrelations (*i.e.* Moran's I index) for the different taxa were mostly restricted to the first spatial distance tested (*i.e.* up to 708 m), which is also consistent with the distance of greater variability of the LCBDs (*i.e.* 550 m). Together, these results suggest that chironomid assemblages varied importantly at a relatively short spatial scale (*i.e.* <1 km) relative to the size of the lake, which may reflect the habitat successions related to topography. Successions of steep slopes to gentle slopes indeed occurred in the littoral at a scale of ~1 km, supporting the strong environmental constraint on the assemblages, which could have otherwise shown larger scales of positive autocorrelations. Interestingly, spatial autocorrelations beyond 15 km seem to highlight the similarities of habitats between the reedbeds present at the northern and southern ends of the lake, characterised by the high abundances of different taxa such as *Cladotanytarsus* sp. or *Cryptochironomus* sp. This analysis of chironomid spatial variability provided relevant insights regarding the spatial scale at which littoral chironomid biodiversity should be considered for both monitoring and conservation programs.

4.5 Concluding remarks

The framework considered in this study highlighted the importance of topography in shaping chironomid assemblages, which may be a characteristic of post-glacial large deep lakes compared to other shallower lakes. Purely spatial processes were not directly taken into account in the multivariate analyses (*e.g.* principal coordinates of neighbour matrices; Borcard *et al.*, 2004) and could provide complementary information regarding the spatial structure of the chironomid assemblages. Nonetheless, the taxa-specific analysis of spatial autocorrelation could partly fill this gap in highlighting the short spatial scale at which taxa abundance varied (*i.e.* <1 km). Both sites and taxa of primary importance of the lake β-diversity could be identified, which can be useful knowledge for lake managers in implementing conservation and restoration programs. In this context, the preservation of littoral habitats such as reedbeds, which declined over the last decades on the shoreline of the lake, could be the first objective as they constitute the original habitat hosting taxa (*e.g. Cladotanytarsus* sp.) positively implicated in the originality of the site (*i.e.* LCBD).

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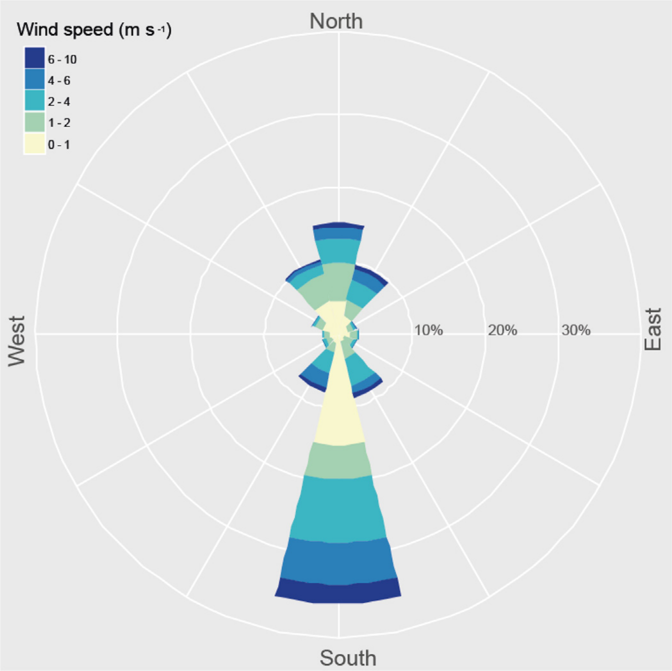
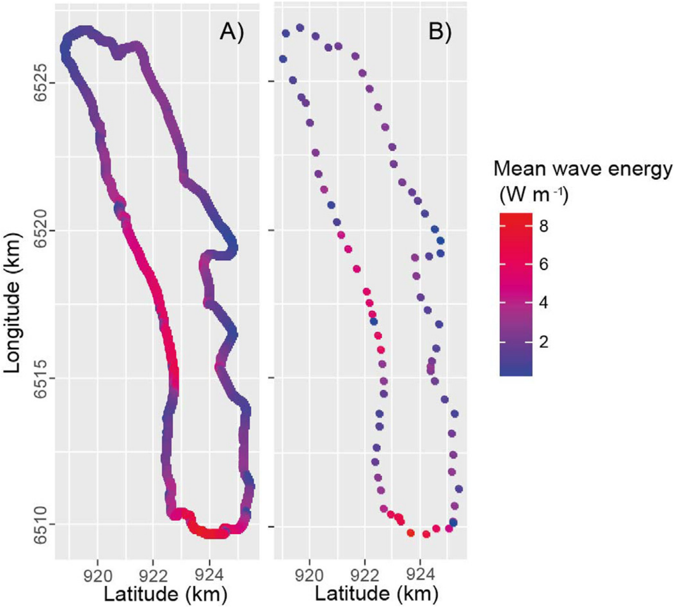
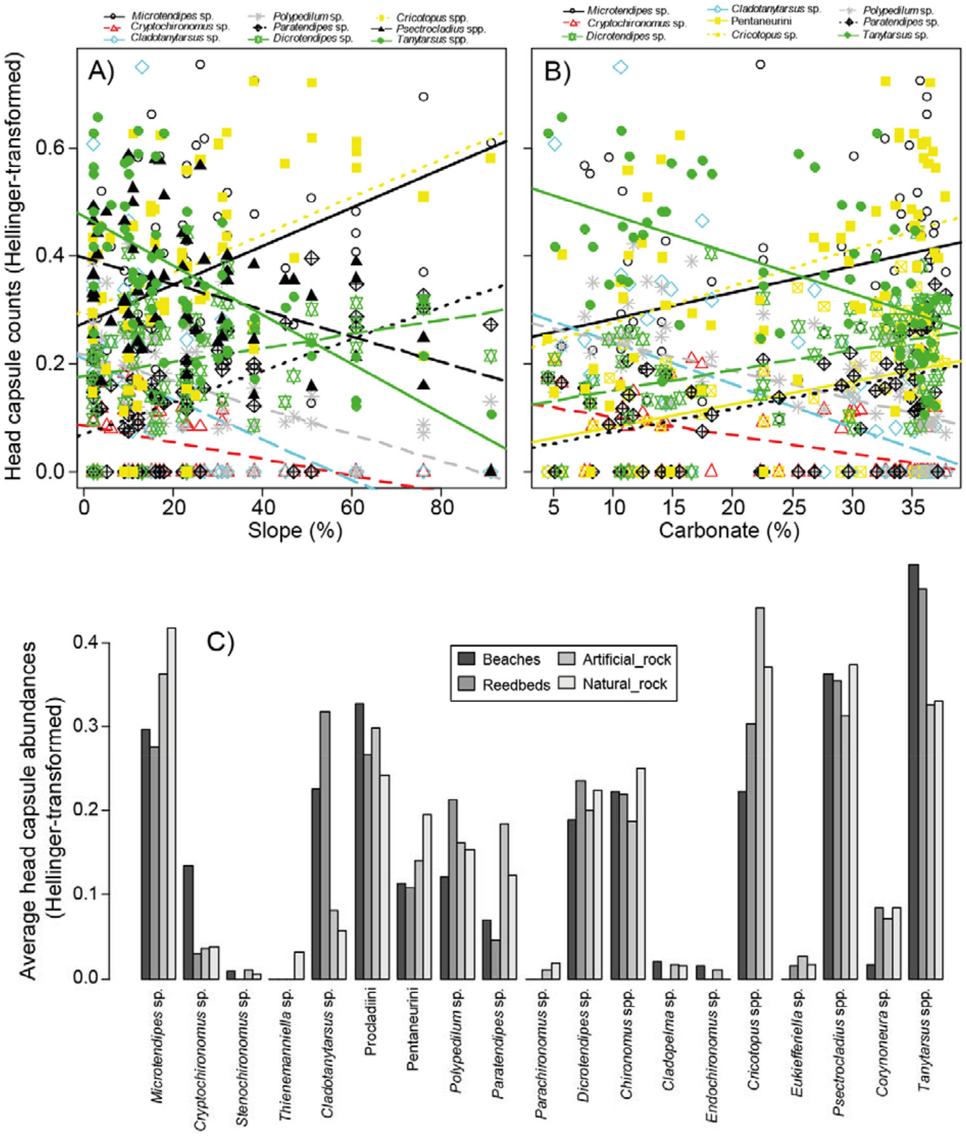
Appendix



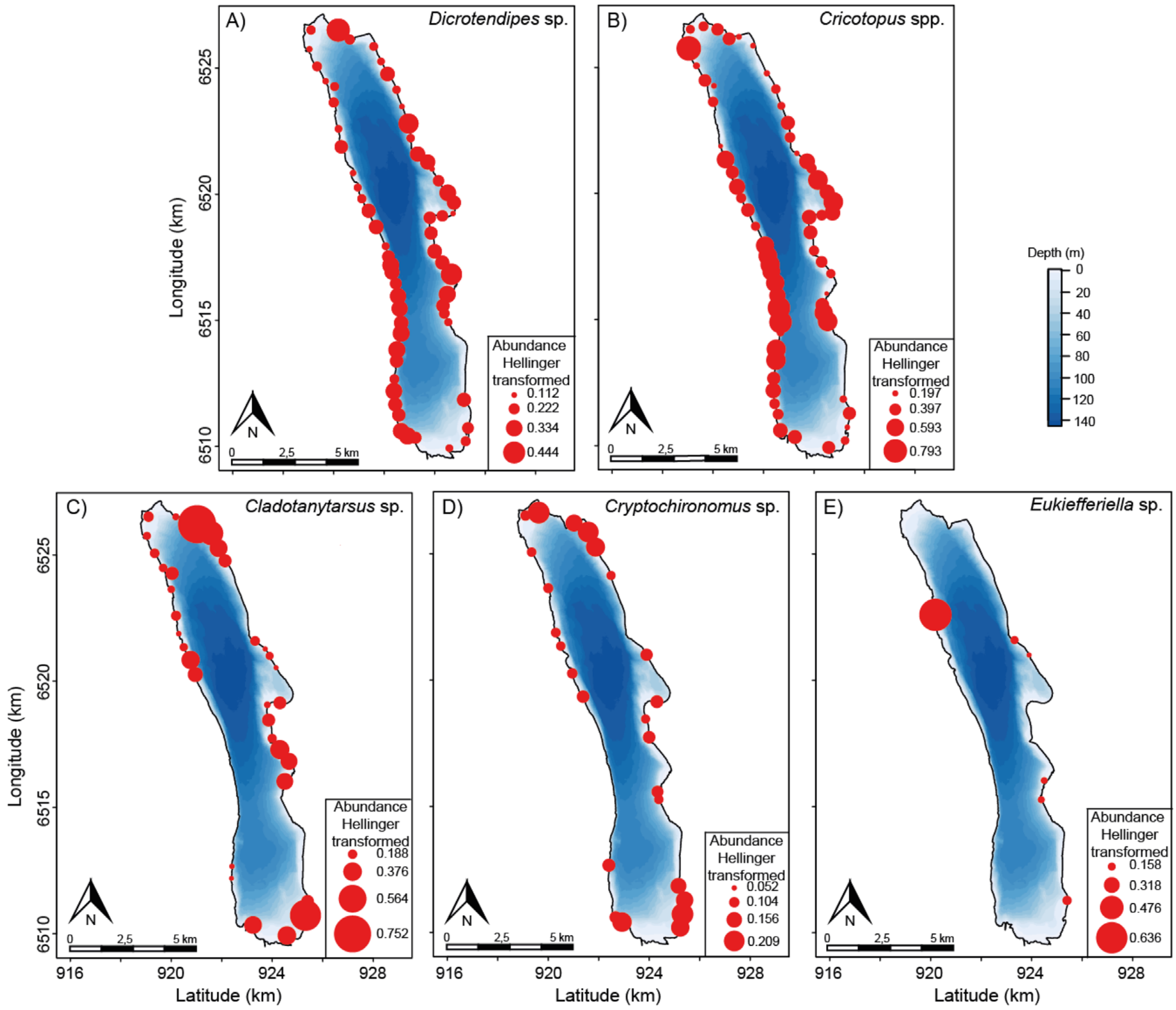
Appendix 1. Wind rose of Lake Bourget produced according to the daily data of the orientation and the intensity of the wind at 10 m of height at the meteorological station of Météo-France at Aix-les-Bains from the 1 January 2013 to 31 December 2015. The wind orientation indicates the direction of wind (i.e. most wind comes from North and goes to the South).



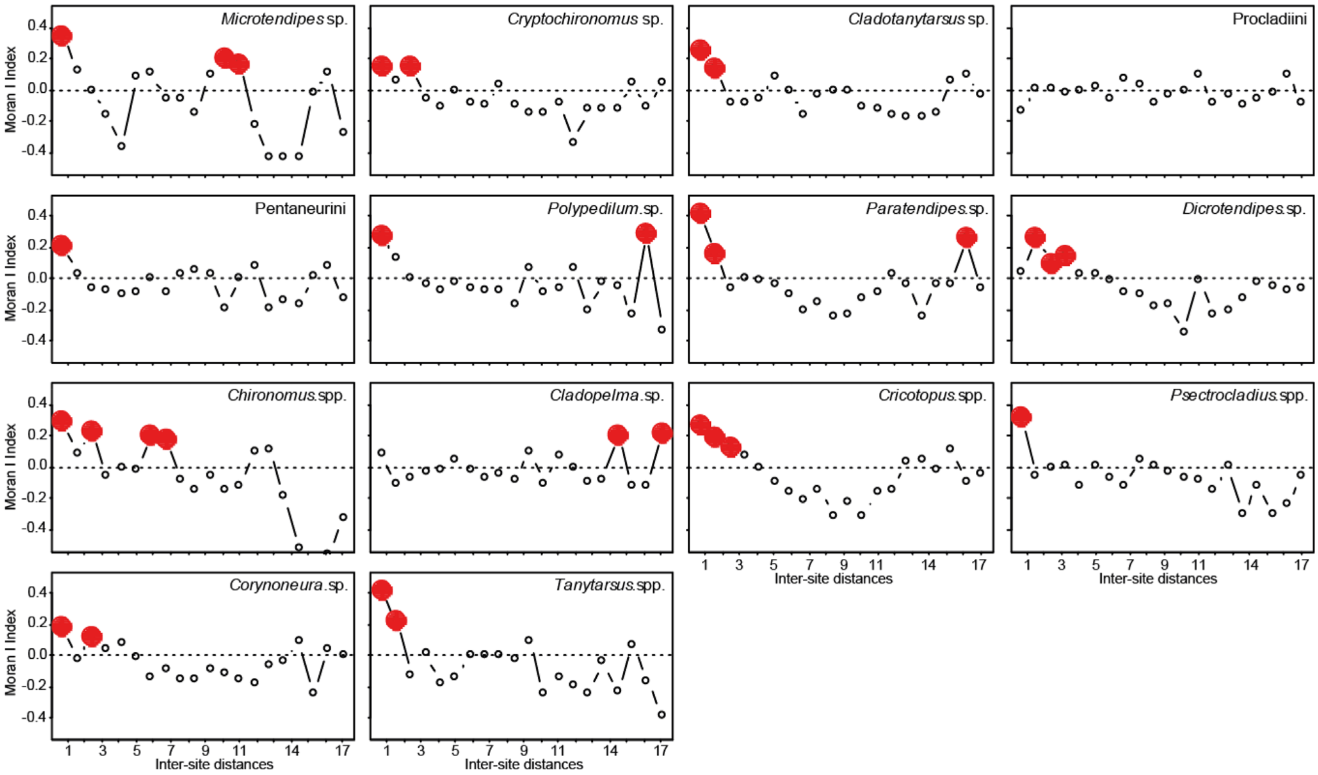
Appendix 2. Spatial variability of wave energy as a quantitative metric of hydrodynamic forces in the littoral zone. (a) Wave energy is represented for the first 100 m littoral shoreline. (b) For each sampling point, the wave energy is the average of the energies calculated for all spatial points included in a buffer of 50 m around the sampling point.



Appendix 3. Significant linear relationships between abundances (Hellinger Transformation) and (a) slopes and (b) carbonate percentage of the sampling sites. Variations of the average abundances of the principal taxa (Hellinger Transformation) among the different shoreline habitats.



Appendix 4. Spatial distributions of abundances (Hellinger transformation) of the five taxa significantly correlated with site-specific local contribution to β-diversity (LCBD). (a) *Dicrotendipes* sp., (b) *Cricotopus* spp., (c) *Cladotanytarsus* sp., (d) *Cryptochironomus* sp. and (e) *Eukiefferiella* sp.



Appendix 5. Spatial autocorrelation of the abundances estimated from Moran's I for the 14 most abundant taxa over 20 different distance classes. Circles in red represent significant autocorrelations.