

A paleolimnological perspective on aquatic biodiversity in Austrian mountain lakes

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Received: 21 May 2014 / Accepted: 15 July 2014
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Abstract We assessed long-term aquatic biodiversity patterns, with a focus on functional diversity (FD), by using sedimentary Chironomidae and Cladocera assemblages in four mountain lakes in the Austrian Alps. The objectives were to detect whether the invertebrate communities exhibited similar recent diversity trends in climate-sensitive alpine lakes, to observe how lake-specific limnological shifts affect biodiversity, and to test the relationship between taxonomic diversity (TD) and FD for paleolimnological biodiversity evaluations. We applied traditional TD indices to the sedimentary assemblages and used an FD index that was based on functional traits of the encountered taxa of both invertebrate groups. There were some similar long-term trends in invertebrate FD and TD among the lakes; e.g. chironomid diversity increased in two lakes and cladoceran diversity in three lakes toward the twentieth and twenty-first century, but in general the diversity patterns were variable between lakes. Overall, FD had a positive relationship with TD suggesting that

functionality can be used in paleolimnological studies as a measure of biodiversity. However, cladoceran taxon richness did not correlate with FD in two lakes suggesting that TD is not always a surrogate for FD. Furthermore, TD of chironomids tended to increase more pronouncedly than FD in the top core sections indicating that increasing TD does not necessarily enhance FD and that different taxonomic entities may play similar functional roles in ecosystems. Accordingly, when evaluating biodiversity and ecological redundancy, functionality of the species pool should be carefully considered and highlighted also in paleolimnological research.

Keywords Alpine lakes · Chironomidae · Cladocera · Ecological redundancy · Ecosystem functioning · Functional diversity

Introduction

Since anthropogenic environmental pressure almost always has a negative influence on biological diversity, biodiversity science has emerged to tackle ecological questions related to biodiversity conservation, loss, and restoration (Thomas et al. 2004; Thuiller 2007; Moss et al. 2009). These considerations also have influenced paleolimnological research because fossil biological assemblages of aquatic organisms in lake sediments retain the information on long-term biodiversity trends in lake ecosystems (Willis et al. 2010; Gregory-Eaves and Beisner 2011). Accordingly, a paleolimnological perspective and long-term community data can give deeper insights into biodiversity dynamics than traditional community data from ecological monitoring, which usually does not cover wide geographic or temporal ranges (Nevalainen 2010; Gregory-Eaves and

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Beisner 2011; Velghe et al. 2012). In fact, biodiversity over long time scales has been attributed as a priority research question in paleoecology (Seddon et al. 2014).

Temporal and spatial biodiversity trends in lake ecosystems may be evaluated through using fossil biotic assemblages of aquatic organisms, such as Cladocera (Crustacea) and Chironomidae (Diptera) larvae. These aquatic invertebrate groups are commonly used in paleolimnological studies because their remains are preserved abundantly and with high diversity in lake sediments and they are sensitive to environmental changes (Brooks et al. 2007; Rautio and Nevalainen 2013). Although their modern (surface sediment) and past (sediment core) community structure and diversity can be estimated from fossil assemblages, counting sum (Quinlan and Smol 2001), taphonomic processes (Nykänen et al. 2009; Alric and Perga 2011), sampling site (Luoto 2012; Nevalainen 2012), and taxonomic resolution of identification and selective preservation of the remains (Brooks et al. 2007; Szeroczyńska and Sarmaja-Korjonen 2007), may hamper their indicator value in biodiversity evaluations. Yet, paleolimnological datasets can contribute largely to biodiversity studies, for example, by examining relationships between diversity and lake productivity (Vogt et al. 2010) or food web complexity (Rawcliffe et al. 2010), impacts of climate change on biodiversity (Willis et al. 2010), and functional trait-environment linkages (Luoto and Nevalainen 2014).

Biodiversity has traditionally been treated as equivalent to species diversity, i.e. taxonomic diversity (TD), although for the description of ecosystem functioning, taxonomic identity may not always be relevant because community and ecosystem processes are dependent on functional characteristics of species. Functional diversity (FD) is a biodiversity measure based on functional traits of species (Tilman 2001; Hooper et al. 2002) and it may enable us to assess ecosystem functioning and resilience more comprehensively than traditional species diversity measures. For example, the concept of FD may be important in understanding abrupt community changes and the success (or failure) of species invasions. This aspect of biodiversity should also give new insights for paleolimnological research. Functional diversity indices assess diversity according to specific ecological roles of species, for example by using their inter-specific relationships and habitat, movement, feeding, or reproduction types (Barnett et al. 2007). Community functioning and FD in aquatic ecosystems has gained attention also in paleolimnological research (e.g. Chen et al. 2010; Vogt et al. 2010; Nevalainen and Luoto 2013; Luoto and Nevalainen 2014) and, as stated by Gregory-Eaves and Beisner (2011), the use of palaeolimnological data in functional diversity analyses has only recently begun.

A paleolimnological perspective on FD in aquatic ecosystems may add consistent new knowledge to long-term ecosystem functioning under environmental changes because ecosystem functions are strongly determined by biological processes of the regional species pool. Accordingly, paleolimnological research may provide useful answers to the question whether TD is a surrogate for FD or not, and what is the role of ecological redundancy in ecosystem resilience under environmental perturbations at different time scales. The objectives of the current study were to investigate the relationship between FD and TD, to detect recent regional trends in FD in alpine lakes, and to explicate how local climate-driven limnological shifts affect the functional component of aquatic biodiversity. To answer these specific objectives and, additionally, to highlight the potential of paleolimnological approaches in biodiversity evaluations and promote the use of FD as a biodiversity measure in paleolimnological research, we applied traditional taxonomic biodiversity indices and an FD index to sedimentary invertebrate assemblages of four climate-sensitive tree-line lakes in the Austrian Alps. These lakes have been previously examined by paleolimnological methods and they have shown individual responses to post Little Ice Age (LIA, ca. 1850 AD onward) and twentieth century climate changes. We hypothesized that twentieth century climate warming has decreased functional diversity in the ecotonal lakes by diminishing niche space due to more coherent environmental conditions among the lakes, e.g. in water temperature, habitat structure, and primary production. We, however, presume that in a long-term perspective, aquatic biodiversity and functionality is driven by lake-specific limnological shifts that alter habitat and food resources.

Materials and methods

Previously analyzed fossil assemblages of Chironomidae and Cladocera from short sediment cores (16–24 cm) of four alpine lakes (Moaralmsee, Oberer Landschitzsee, Unterer Giglachsee and Twenger Almsee) were used in the present study. These oligotrophic, clear-water, and circum-neutral lakes vary in size, depth, and water temperature and are located close to the tree-line in the Niedere Tauern region of the Austrian Alps (Table 1). The bioassemblage data (Chironomidae and Cladocera) and dating (^{210}Pb) of the sediment cores were originally published and discussed in Luoto and Nevalainen (2012) for Moaralmsee, Nevalainen and Luoto (2012) for Oberer Landschitzsee, and Luoto and Nevalainen (2013a, b) for lakes Unterer Giglachsee and Twenger Almsee, respectively. The previous studies have emphasized the sensitivity of these lakes and

Table 1 Location and environmental characteristics of the four study lakes located in the Niedere Tauern region of the central Austrian Alps

	Moaralmsee	Oberer Landschitzsee	Unterer Giglachsee	Twenger Almsee
Latitude (N)	47°21'28"	47°14'49"	47°14'00"	47°13'13"
Longitude (E)	13°47'32"	13°51'33"	13°39'00"	13°36'05"
Altitude (m a.s.l.)	1,825	2,067	1,922	2,118
Area (ha)	2.13	8.8	16.8	3.11
Depth (m)	5.9	13.6	18.0	33.6
pH	7.0	6.3	7.5	7.3
Conductivity ($\mu\text{S cm}^{-1}$)	29	14.5	73	69
Total phosphorus ($\mu\text{g L}^{-1}$)	3.7	2.5	4.5	3.3
NO ₃ ($\mu\text{g L}^{-1}$)	182	64	20	7
Dissolved organic carbon ($\mu\text{g L}^{-1}$)	1,142	623	601	649
Ca ²⁺ ($\mu\text{eq L}^{-1}$)	224	104	533	431
T _{WATER} August (°C)	8.2	12.8	14	11.6

their invertebrate communities to climate-driven limnological changes.

Ecologically relevant functional traits were determined for all encountered taxa from the four sediment cores to separate functional groups. The characterization of traits was based on faunistic literature (Flössner 1972, 2000; Merritt and Cummins 1996; Mandaville 2002), although the characterization is not completely straightforward due to wide and overlapping habitat preferences and feeding mechanisms of the organisms. For chironomids, traits included head capsule size (small, intermediate, large), morphology of mouth parts (mentum, ligula), feeding type (collector-filterer, collector-gatherer, shredder, scraper, predator), habitat (open-water, bottom, vegetation) and trophic position (herbivore, detritivore, carnivore). For cladocerans, body size (small, intermediate, large), body shape (globular, oval), feeding type (filterer, scraper), and habitat (open-water, bottom, vegetation) were considered. The functional traits were treated as binary codes (1 present, 0 absent). A functional dendrogram for the regional species pool was generated using hierarchical clustering analysis with average linkage clustering, unweighted pair grouping, and Euclidean distances following Barnett et al. (2007). The dendrogram was generated with the Paleontological Statistics (PAST) software (Hammer et al. 2001).

A community-based weighted functional diversity index (wFDc), which is based on the total branch length of the functional dendrogram taking into account the species community pool with weights of species abundances (Pla et al. 2008), was applied to the down-core chironomid and cladoceran assemblages. In addition, taxon richness S (total number of taxa present) and taxon diversity H (Shannon's diversity index) were determined. The diversity indices were generated with the FDiversity software (Casanoves et al. 2011).

A *t* test was used to test for significant differences in chironomid and cladoceran FD values in each lake and one-way ANOVA was used to test the differences in FD among the four lakes. Bivariate data normality was tested with Mardia's multivariate skewness, and kurtosis and relationships between FD and TD in each study site were evaluated with Pearson's correlation coefficient (*r*) and statistical significance of the correlation (*p*). These tests were performed with PAST.

Results

The functional dendrogram separated chironomids and cladocerans into functional groups (Fig. 1), which followed taxonomic (genus-based) grouping. Among chironomids, the major separation followed feeding type, habitat, and trophic position, since open-water predators (carnivores, group 1), vegetation-associated shredders and scrapers (herbivores, group 3), and others (collector-filterers and collector gatherers, i.e. detritivores, group 2) clustered separately. Among cladocerans, habitat and feeding type principally separated open-water filterers (groups 1–2) from bottom- and vegetation-associated scrapers (group 3). In the pelagic group, further separation was based on body size and shape; small and intermediate globular (group 1) versus large oval (group 2).

The stratigraphic variation of chironomid diversity in Moaralmsee showed a decreasing trend between ca. 1,600–1,800 AD but a mostly stable diversity in cladocerans (Fig. 2). There was a short-term drop in cladoceran wFDc and H during the mid twentieth century and a slight increase in chironomid H in the core top sample. In Moaralmsee, wFDc correlated strongly with H and S in chironomids, but in cladocerans, where data had non-

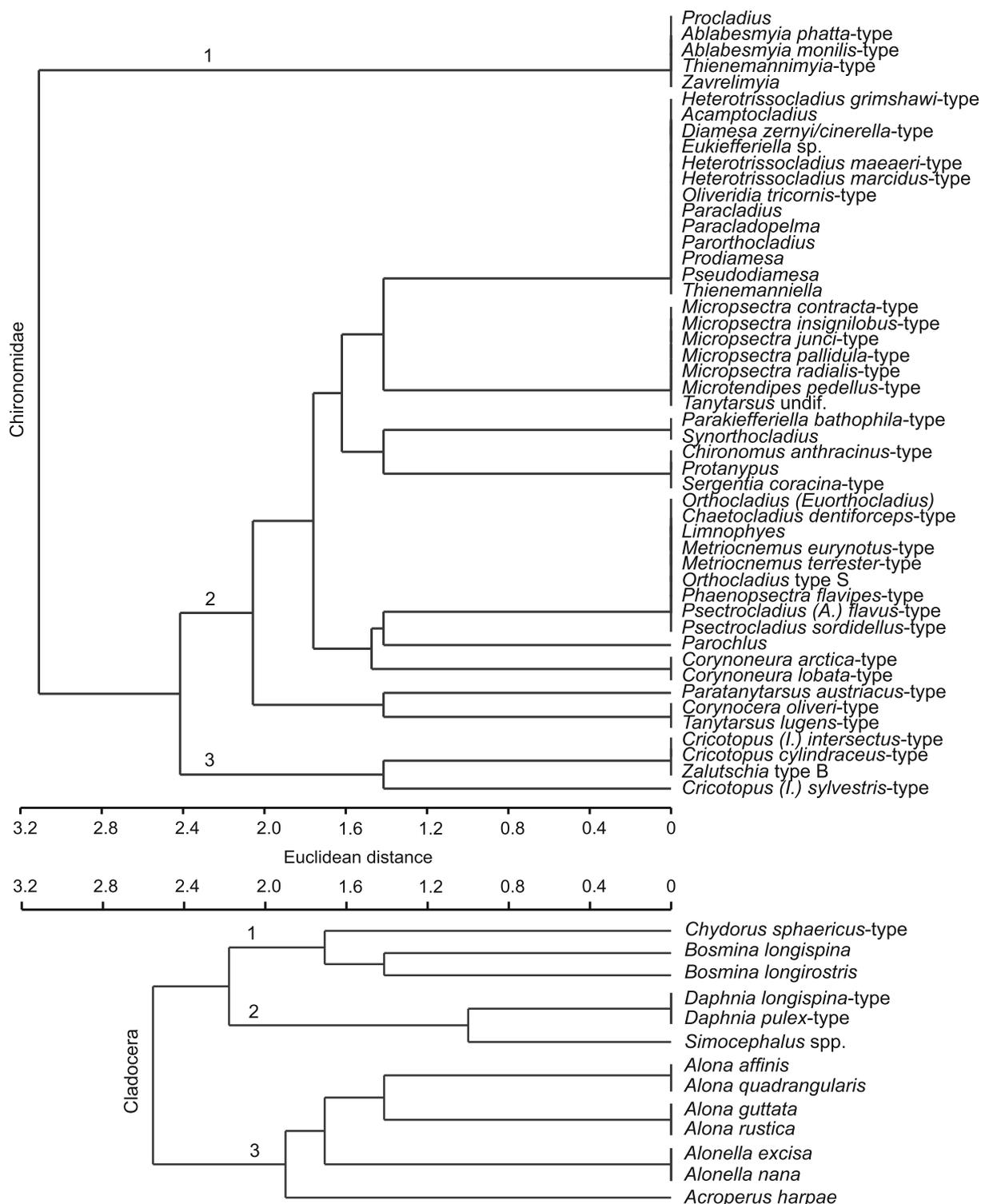


Fig. 1 Functional dendrogram of Chironomidae and Cladocera taxa encountered from the study lakes. Major functional groups are indicated with numbers 1–3, which refer in chironomids to open-water predators (1), vegetation-associated shredders and scrapers (2),

and sediment-associated collector-filterers and collectors-gatherers (3), and in cladocerans to open-water filterers (1–2, separated further based on body size and shape) and sediment- and vegetation-associated scrapers (3)

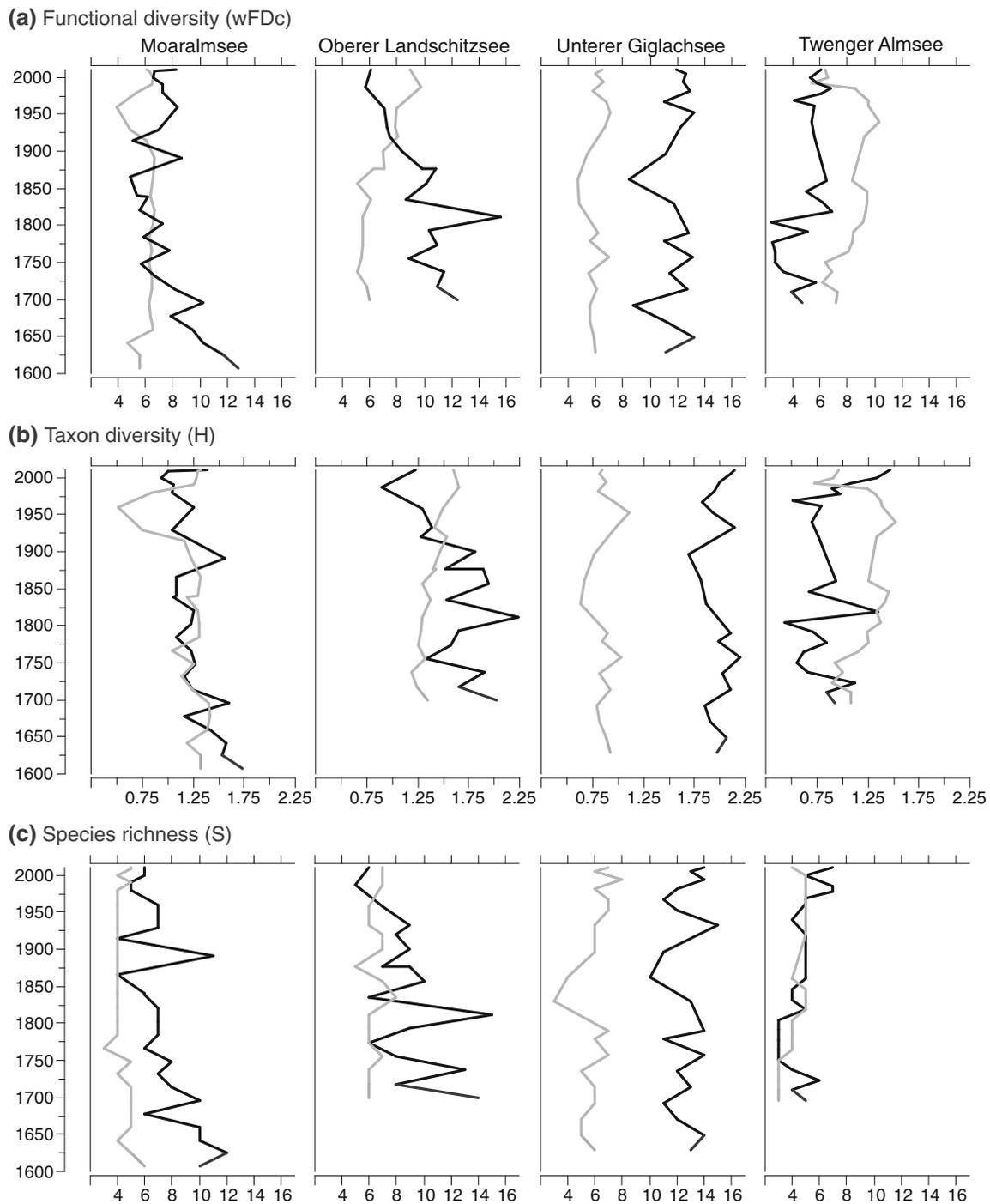
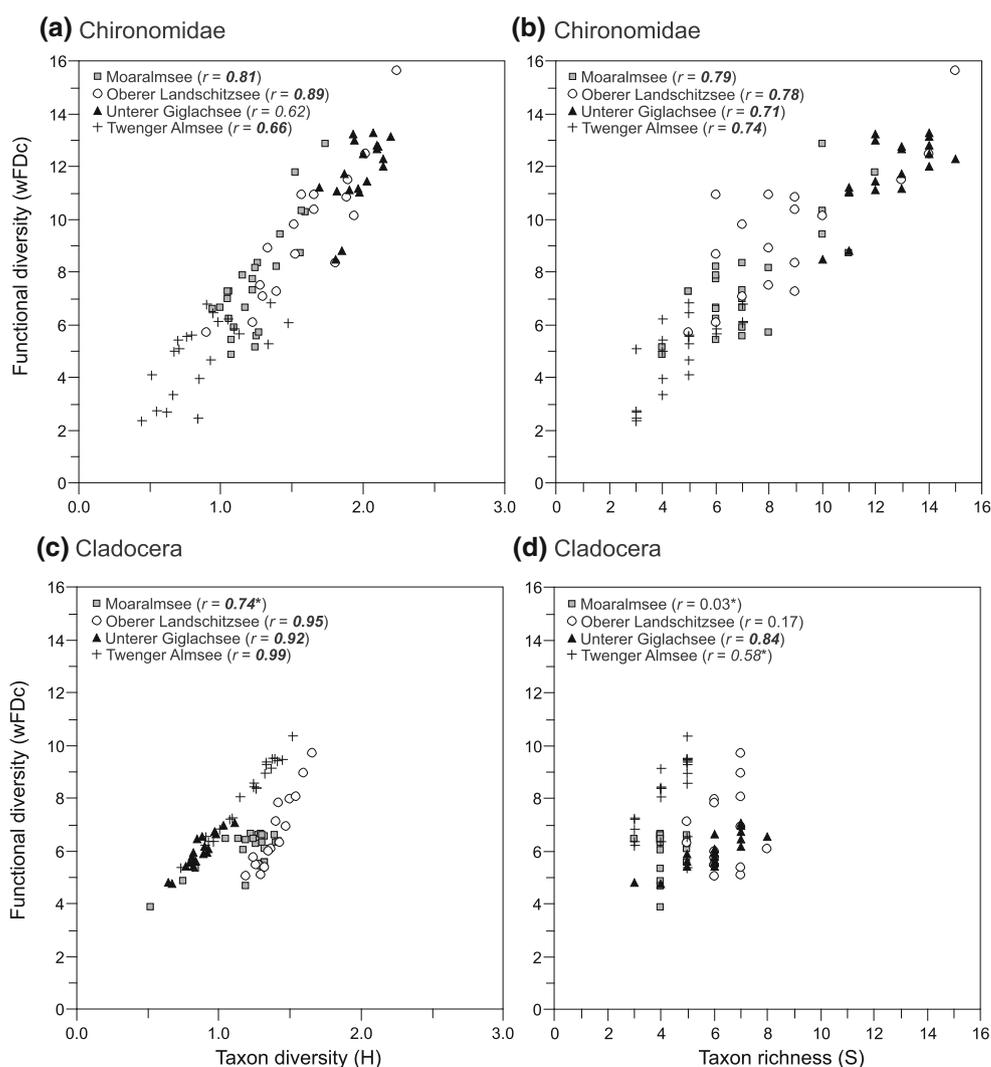


Fig. 2 **a** Functional diversity (wFDc), **b** taxon diversity (H), and **c** taxon richness (S) of Chironomidae (*black line*) and Cladocera (*gray line*) throughout the sediment cores of the study lakes

normal bivariate distributions, a strong correlation was observed only between FD and H (Fig. 3). Diversity indices in chironomids and cladocerans exhibited opposite trends in Oberer Landschitzsee, where chironomid wFDc, H, and S decreased toward present while cladoceran wFDc and H increased (Fig. 2). In the topmost samples of Oberer

Landschitzsee, chironomid H increased (Fig. 2b) and FD had a strong positive correlation with H and S for chironomids, but in cladocerans a highly significant positive correlation was observed only between wFDc and H (Fig. 3). Chironomid and cladoceran diversity indices showed similar trends in Unterer Giglachsee, where all

Fig. 3 Relationships between functional diversity (wFDc) and taxon diversity (H) and richness (S) of Chironomidae (**a, b**) and Cladocera (**c, d**) in the sediment cores of the study lakes. Pearson's correlations (r) are shown in brackets, where significance at $p \leq 0.001$ is indicated by *bold* and *italics* and at $p \leq 0.01$ in *italics*, and non-normal bivariate data distributions by *asterisk*



indices were lowest at ca. 1,850–1,900 AD and increased during the twentieth century (Fig. 2). FD of both invertebrate groups correlated strongly and positively with the taxonomic diversity indices in Unterer Giglachsee (Fig. 3). In Twenger Almsee, chironomid diversity increased toward core top; FD was more stable, whereas H and S increased in the topmost section (Fig. 2). In cladocerans, all diversity indices showed similar trends increasing from ca. 1,750 AD onward and decreasing in the core top (Fig. 2). FD correlated strongly with H and S in the Twenger Almsee core in both invertebrate groups (Fig. 3), but bivariate normal distribution was not observed between cladoceran FD and S. T-test showed that chironomid and cladoceran FD were significantly different in each lake, and that largest differences between the invertebrate groups were observed in Unterer Giglachsee ($t = 16.70$) and Twenger Almsee ($t = -7.56$). FD scores also varied significantly among lakes for Chironomidae ($F = 49.06$) and Cladocera ($F = 19.60$), as indicated by one-way ANOVA (Table 2).

Discussion

Functional dendrogram and functional diversity in the alpine lakes

Taxonomic characterization has been traditionally used to evaluate biodiversity, but functional (or operational, sensu Moss et al. 2009) grouping and the use of FD indices have been used more recently to examine biodiversity in relation to ecosystem functioning (Petchey and Gaston 2002; Heino 2008). For example, changes in biodiversity after species invasions may be regarded as functional trait-mediated rather than taxonomic-based interactions between invasive and indigenous taxa (Ricciardi and Mottiar 2006; Visconti and Manca 2010). As observed from the dendrogram of the fossil assemblages (Fig. 1), taxon richness was higher in chironomids (49 identified taxa) than in cladocerans (13). Taxon richness in the current sites is generally comparable to previous studies in lakes around tree-line from the Swiss

Table 2 Comparison of functional diversity (wFDc index) between chironomid and cladoceran communities in each lake according to mean FD and t-test ($p \leq 0.001$), and among the lakes according to one-way ANOVA ($p \leq 0.001$)

	Moaralmsee	Oberer Landschitzsee	Unterer Giglachsee	Twenger Almsee	All lakes
Chironomidae mean (SD)	7.63 (2.04)	9.52 (2.51)	11.76 (1.36)	4.91 (1.44)	
Cladocera mean (SD)	6.06 (0.71)	6.62 (1.43)	5.96 (0.66)	8.13 (1.39)	
T-test	3.63	4.16	16.70	-7.56	
Chironomidae ANOVA					F = 49.06
Cladocera ANOVA					F = 18.60

Alps (Lotter et al. 1997; Bigler et al. 2006) and in Austria (Kamenik et al. 2007).

The trait-based classification of chironomids and cladocerans from their regional species pool in the four alpine lakes provided a very general classification of the major functional groups (Fig. 1) and can therefore be considered as an example of a regional functional dendrogram of the taxa. In chironomids, the dendrogram separated taxa primarily according to habitats, feeding type and trophic position into three separate functional groups; in cladocerans habitat and feeding also were principal functional traits separating taxa (Fig. 1). These traits appeared to be most important in the clustering, likely because they are closely related with each other, for example, habitat defines feeding type and feeding type defines the trophic position being highly ecologically relevant characteristics.

Previous paleolimnological biodiversity evaluations have focused on species diversity responses to environmental changes and gradients (e.g. Nevalainen 2010; Velghe et al. 2012; Richard Albert et al. 2010), while FD *per se* has not been used in examining the relationship between biodiversity and ecosystem functioning. Overall, FD evaluations of aquatic communities are still quite rare (Weithoff 2003; Barnett et al. 2007; Heino 2008; Vogt et al. 2010). Chironomid FD was highest in Unterer Giglachsee and lowest in Twenger Almsee, where FD also showed lowest variation (Table 2). Cladoceran FD showed the opposite, being lowest in Unterer Giglachsee and highest in Twenger Almsee.

The current long-term records of the examined invertebrate groups showed no common trends in FD in all of the four studied lake (Fig. 2a), and chironomid ($F = 49.06$, $p \leq 0.001$) and cladoceran ($F = 19.60$, $p \leq 0.001$) FD varied significantly among lakes (Table 2). However, some similar trends in chironomid FD were observed; it decreased from the bottom of the cores in lakes Moaralmsee and Oberer Landschitzsee, although the changes in diversity were smoother and stabilized earlier in Moaralmsee. In addition, chironomid FD increased during the twentieth century in lakes Unterer Giglachsee and Twenger Almsee. In cladocerans, there was a common increasing trend in FD in lakes Oberer Landschitzsee and Twenger Almsee since the eighteenth and nineteenth century (Fig. 2a).

Lake-specific responses in functionality

All of the studied lakes are ecotonal tree-line lakes and therefore they can be considered to be climatically sensitive sites in a regional context (Thompson et al. 2005). There are, however, individual historical changes that may have impacted lake-specific trends in FD over time. Moaralmsee is previously described to be a regionally anomalous lake due to its extremely low summer water temperatures (Thompson et al. 2005). It stands out from the rest of the lakes also with its FD trends over time, since FD of both invertebrate groups was mostly stable during the LIA and after (Fig. 2a). This stability was most likely caused by the thermal stability of the lake water as it has remained cold due to ground water input and topographic features reducing sunlight and slowing snowmelt (Luoto and Nevalainen 2013c). The chironomid FD clearly showed highest values in the bottom of the core (Fig. 2a) in samples that were estimated to date back to the seventeenth century. The high FD (and TD, Fig. 2b, c) during this time period was driven by the presence of several taxa from different functional groups; *Micropsectra contracta*-type (group 2 in Fig. 1), *Psectrocladius sordidellus*-type (group 2), *Cricotopus cylindraceus*-type (group 3), and *Procladius* (group 1). The sudden and clear decrease in FD (driven apparently by an increase and dominance of *Paracladius*, group 2) may be related to the onset of LIA altering aquatic habitats through changes in lake level (Luoto and Nevalainen 2013d). In common with this, a regional and temporal comparison of midge feeding traits from boreal-subarctic lakes showed that cold climate decreases feeding diversity (Luoto and Nevalainen 2014).

Chironomid and cladoceran FD exhibited opposite trends in Oberer Landschitzsee (Fig. 2a), where post LIA environmental changes lead to increased water temperature, altered deep-water oxygen and thermal stratification regimes, and increased aquatic vegetation (Nevalainen and Luoto 2012). The chironomid communities of the nineteenth and twentieth century were dominated by *S. coracina*-type and more recently by *M. contracta*-type, which are detritivorous collector-gatherers (group 2 in Fig. 1; Nevalainen and Luoto 2012). This community change, associated likely with altered stratification and

oxygen regimes, reduced the evenness of the different functional groups that were present in the older sediments, and resulted in decreased FD. On the other hand, cladoceran FD was likely enriched by more even distribution of vegetation-associated taxa such as *A. excisa* and *A. harpae* (group 3) and by the increase of semi-planktonic *C. sphaericus*-type and immigration of planktonic *Bosmina longirostris* (group 1; Nevalainen and Luoto 2012) that were apparently driven by warmer water temperatures, altered phytoplankton communities, and more abundant aquatic vegetation during the late twentieth century.

Functionality of the aquatic communities seemed to have been most stable in Unterer Gliglachsee during the past centuries and, additionally, chironomid and cladoceran FD showed high similarity in their subtle trends (Fig. 2a) although FD means differed between them (Table 2). The previous microfossil study from the lake (Luoto and Nevalainen 2013a) did not identify any specific climate-driven limnological shifts occurring in the lake. However, a common faunal breakpoint was evident in the assemblages ~1,900 AD associated with regional climate warming, and this was also reflected in invertebrate FD values as a slight increase. In chironomids, *Procladius* (group 1 in Fig. 1), *Microrotendipes pedellus*-type (group 2), and *Cricotopus* (group 3) increased and in cladocerans planktonic *Daphnia* (group 2) and *Bosmina* (group 1) and vegetation-associated *A. excisa* increased (group 3) (Luoto and Nevalainen 2013a). Chironomid FD was clearly highest in Unterer Gliglachsee, which is the largest of the four lakes (Tables 1, 2). This is in agreement with macroinvertebrate functional richness in boreal lakes where larger lake area enhanced diversity (Heino 2008). In general, higher habitat variability in larger lakes provides more niches for taxa. Cladocerans, on the other hand, exhibited lowest FD in Unterer Gliglachsee, which is likely due to the dominance of *Bosmina longispina* with 60–80 % relative share of the community (Table 2; Luoto and Nevalainen 2013a).

In Twenger Almsee, which has exhibited increases in water temperature and deeper thermal stratification during the twentieth century (Luoto and Nevalainen 2013b), there was an increasing trend in chironomid and cladoceran FD (Fig. 2a). The chironomid community became dominated by *M. radialis*-type (group 2 in Fig. 1) during the late nineteenth century while predacious taxa such as *Procladius* and *Zavrelimyia* decreased (group 1; Luoto and Nevalainen 2013b). However, several taxa, e.g. *Paracladius* and *Heterotrissocladius marcidus*-type from the detritivore sub-clusters (group 2) simultaneously increased, thereby adding different functional characteristics to the community and increased FD. The cladoceran FD, which increased until the mid 20th century, was the result of new species with different functions (*B. longispina* from group 1 and *A. harpae* from group 3) with their first occurrence in

the stratigraphy around 1,800 AD (Luoto and Nevalainen 2013b). The changes in aquatic invertebrates and FD were likely caused by the recent increase in water temperatures, deepening of the thermocline, and higher benthic oxygen availability (Luoto and Nevalainen 2013b). The strong decrease of FD in the top sediment section (Fig. 2) was driven first by the sudden dominance of semi-planktonic *C. sphaericus*-type (group 1; Luoto and Nevalainen 2013b) and later planktonic *B. longispina*, reducing the functional characteristics of the community. This shift apparently occurred as a response to commercial fish stockings, taking place in the mid 1990s and, together with changes in thermal structure, created short-term conditions where *Daphnia* was extirpated and *Chydorus* (and later *Bosmina*) increased (Nevalainen et al. 2014). This was most likely due to their differences in vulnerability to fish predation (i.e. body size and shape). The two dominant semi-planktonic/planktonic taxa with similar functions (group 1) reduced FD (Figs. 1, 2a).

Taxonomic versus functional diversity

In terrestrial plant communities, FD tends to correlate with species richness, if niche space coverage increases with increasing number of species (Díaz and Cabido 2001). In general, increasing FD alongside increasing species richness would be expected in aquatic communities too because functional characteristics of coexisting taxa should differ to some extent. However, FD is not always a surrogate for taxonomic diversity because it depends on species' tendencies to occupy niche space (cf. Díaz and Cabido 2001). FD does not necessarily have a clear relationship with taxon richness. The comparison of FD with TD indices throughout the sediment cores showed that there exists a strong correlation between functional and taxonomic diversity in Chironomidae (Fig. 3a, b). In Cladocera, the correlation between FD and H was obvious for all lakes (Fig. 3c), while FD and S were significantly correlated in only two of the study lakes (Unterer Gliglachsee and Twenger Almsee in Fig. 3d). Accordingly, our data suggest that there may be group-specific differences in the relation of functional and species diversity indices.

The general correlation between invertebrate TD and FD (Fig. 3) suggests that taxonomic diversity mostly corresponds to FD and that FD may be used alongside taxonomic diversity indices or independently in evaluating biodiversity patterns. However, in Moaralmsee and Oberer Landschitzsee, taxon cladoceran richness did not correlate with FD (Fig. 3d) and, therefore, FD may be a more reliable estimate of community biodiversity in these sites. The lack of a significant relationship between FD and taxon richness in cladocerans at the two sites may be due to uneven distribution of taxa with different functions (e.g.

clear dominance of *C. sphaericus*-type in Moaralmsee during the 1950s) or by the fact that the niche space of extirpated or less common taxa with similar functions in the ecosystem is filled by taxa exhibiting different functions (e.g. increase of several littoral-benthic taxa and emergence of *B. longirostris* in Oberer Landschitzsee during the 1900s).

Despite the strong correlations (Fig. 3a, b), TD of chironomids tended to increase more pronouncedly than FD in the top core sections of all the lakes, especially in Twenger Almsee (Fig. 2), suggesting that taxonomic diversity does not always enhance FD. This may result from a situation where species' niches overlap. In the case of alpine lakes, this may even be an indication of taxa immigration that are functional generalists and that increase from recent environmental changes related to climate warming. On the other hand, this may also be a reflection of communities that are dominated by one or a few taxa. The situation where species' niches are overlapping should, in fact, provide ecological redundancy and buffer against the loss of specific functions in these aquatic communities that is important in the response of individual lakes to environmental change (cf. Gallagher et al. 2013 for plant communities).

The relationship between taxonomic and functional diversity in the current data set is dependent on the selected functional diversity index (wFDc). The structure of the functional dendrogram presented here (Fig. 1), and the resulting wFDc index for evaluating FD in the sediment cores, depend on the number of traits and their qualitative, i.e. binary, nature and does not consider any autocorrelation between the variables. In general, the selection of functional traits and their number to be included in FD analyses will affect the resulting functional characterization of the community and, consequently, FD index values (Barnett et al. 2007). Accordingly, the inclusion of numerically more traits and more specific qualitative traits (e.g. microhabitats, micromorphology) and measured quantitative traits (e.g. detailed body size, food particle size) should give valuable supplementary information to evaluate FD among aquatic invertebrates. Additionally, functional diversity may easily be underestimated due to our restricted knowledge on invertebrate ecology, especially that of littoral-benthic taxa, whereas fossil assemblages may give an adequate picture on taxonomic diversity through good preservation of the remains (Neväläinen 2010).

Concluding remarks

The current long-term FD evaluation in the four alpine lakes is based on what is currently known about chironomid and cladoceran ecology. As knowledge about the

habitat and feeding ecology of these taxonomic groups grows, especially that of littoral-benthic taxa, it will be possible to refine information on FD and thus improve its use in ecology and paleolimnology. The current study showed a classification that is based on a limited amount of basic functional traits (Fig. 1). The inclusion of more detailed functional characteristics of the invertebrates will enhance the reliability of future FD estimates. Since reference data for regional FD in the aquatic invertebrate groups are currently lacking, it is challenging to evaluate which type and magnitude of change in FD can be considered ecologically relevant. Evaluation of FD from future spatial surface sediment data sets along major environmental trajectories may contribute significantly in refining the paleolimnological FD interpretations.

The results show that FD had a positive long-term relationship with taxonomic diversity in the chironomid and cladoceran communities of the studied alpine lakes (Fig. 3). Even though this relationship exists, FD can be a useful index in paleolimnological biodiversity evaluations since it relates strongly to ecosystem properties and responses to environmental change. However, FD does not always act as a surrogate for TD (Fig. 3d) and therefore its use can help to improve the understanding of lake ecosystem functioning and its response to environmental change. FD varied between the two invertebrate groups in each lake and among lakes (Table 2), showing individual magnitude and trends (Fig. 2). Apparently, twentieth century climate warming has not resulted in a general and regional decrease of FD in aquatic invertebrates but rather FD trends in the examined alpine lakes followed climate-regulated limnological shifts (e.g. altered thermal and oxygen regimes). Accordingly, FD may detect ecosystem tipping points and describe irreversible changes in baseline conditions such as the ones related to climate change impacts in the current data set. The results suggest that a paleolimnological approach has great potential in biodiversity evaluations because the variation in temporal and spatial diversity of aquatic communities can be assessed efficiently through fossil assemblages and their functional traits.

Acknowledgments This study is a contribution to the projects DETECTIVE (Decadal detection of biodiversity in alpine lakes, Nationalkomitee Alpenforschung of the Austrian Academy of Sciences), ILMAVEIVI (#250343, Academy of Finland), EGGER (Kone Foundation), and VIOLET (#265507, Academy of Finland). We thank Prof. Roland Psenner, Dr. Karin Koinig and Dr. Rainer Kurmayer for valuable remarks and two anonymous reviewers for constructive comments that helped improve the manuscript.

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