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Aquatic biota and the detection of climate change: are there consistent aquatic ecotones?

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Abstract

In this study, we analyse the cumulative rate of compositional change along an altitudinal gradient in the Swiss Alps for three different groups of aquatic organisms – Cladocera, chironomids, and diatoms. In particular, we are interested in the magnitude of unusually large changes in species composition that allows the detection of critical ecotones for each of these three organism groups. The estimated rate-of-change is the distance in ordination space using principal coordinate analysis based on chord distance and chi-square distance. These analyses highlight the cumulative rate-of-change and the cumulative relative rate-of-change, as the chi-square distance is relative to the total species composition. We found that the major changes in taxonomic composition for the three organism groups and therefore also the major ecotones are just below the modern tree-line (1900–2000 m a.s.l.), which may indirectly be an effect of the tree-line. For diatoms and Cladocera (only chi-square distance) there is also an ecotone at 2055 m a.s.l., which may be a direct or indirect response to climate. Further, the ecotone region below the modern tree-line is much wider for chironomids, with an extension downwards due to a shift in relative abundance patterns. For diatoms there is a stronger rate-of-change above 1650 m a.s.l. when chi-square distance is used. Coupled with the even distribution of diatom richness, this suggests that at higher altitudes the change is more strongly associated with a few species becoming dominant compared to lower elevations. Hence, there are considerable differences among the three organism groups, suggesting that different environmental factors may influence the rates of compositional change within and among groups. This supports the general usefulness of multi-proxy studies, namely the study of several independent groups of organisms to reconstruct past environmental conditions but also points to the importance of careful site selection in such studies.

Introduction

The study of the diversity of nature is a focal point for many contemporary biological investigations (see Huston 1994; Rosenzweig 1995; Gaston and Blackburn 2000). Diversity has classically been categorised as alpha-, beta-, and gamma-diversity (Whittaker 1960, 1972). Alpha- and gamma-diversity are considered as species richness at nested scales (Rosenzweig 1995), whereas beta-diversity has been characterised as the difference in species composition between two geographically or temporally separated observational units (Koleff and Gaston 2002). Beta-diversity has throughout modern ecological theory been a confusing concept as numerous different procedures have been presented for estimating it and various interpretations have been discussed (e.g., May 1973; Cody 1975; Pielou 1975; ter Braak 1983; Wilson and Shmida 1984; Lennon et al. 2001; Koleff et al. 2003; Heegaard 2004). Thus, less effort has been placed on studying the rate-of-change in species composition in comparison to species-richness studies (Gaston and Blackburn 2000), especially in the context of comparative patterns among different groups of organisms. Do different groups of organisms show similarities in their rate-of-change in composition along climatic, environmental, and geographic gradients? Such rates-of-change have been shown to vary considerably, and locations with unusually high species turnover are commonly defined as ecotones (Whittaker 1972; Margalef 1975; van der Maarel 1990). This is a concept traditionally used in vegetation science to delimit climate-related vegetation formations or biomes, but it has also been adopted on a smaller scale for aquatic systems (e.g., Smol et al. 1991; Naiman and Décamps 1997). At a macro-scale, transition zones, i.e. ecotones, are well defined by changes in species assemblage structure and composition as well as in the physiognomy of the vegetation as seen, for example, at the tree-line transition (McCoy et al. 1986; Odland and Birks 1999; Holtmeier 2003; Körner 2003). Both palaeoecologists and global-change ecologists have emphasised the importance of ecotonal boundaries for studying natural dynamics, in particular for using biological evidence to detect past climate changes (e.g., Moser et al. 1996; Seppä and Weckström 1999; Weckström and Korhola 2001; Seppä et al. 2002; Lotter and Birks 2003b), and for detecting species responses to present-day climatic changes (Walker et al. 1993). Fægri and Iversen (1989) pointed out that sites near ecotonal boundaries where numerous species appear and/or disappear are more likely to show responses to climatic change than areas more distant from ecotonal transitions. This is due to the fact that biota are near their range limits and any additional climate change will create physiological stress that reduces their competitive ability or may even be lethal for the organism. Thus, numerous ecologists and palaeoecologists have focused their studies on arctic, sub-arctic, and alpine vegetation transitions to gain knowledge about past, present, and future climate–vegetation relationships and dynamics (e.g., Pienitz and Smol 1993; Kupfer and Cairns 1996; Moser et al. 1996; Arft et al. 1999; Chapin et al. 2000; Lotter and Birks 2003a). Commonly, terrestrial vegetation and especially trees are assumed to show a lagged response to climatic change due to numerous factors, e.g. long generation times, migrational lags, and pedogenesis (Iversen 1964; Birks 1981; Wright 1984; Monserud and Leemans 1992; Kupfer and Cairns 1996). The study of aquatic organisms in sediments is generally regarded as a means of minimising this problem as these organisms migrate faster, have shorter generation times, are independent of pedogenesis, and may thus colonise new habitats faster than trees (Lotter et al. 1995, 2000; Lotter 2003). However, recent studies have shown a close correlation between organism distributions in aquatic habitats and major features of terrestrial habitats (e.g., Weckström and Korhola 2001). Such correlations may influence or even compromise organism-specific climatic reconstruction models including vascular plants (Birks et al. 2000; Kühl et al. 2002), chironomids (e.g., Walker et al. 1997), diatoms (e.g., Pienitz et al. 1995; Wunsam et al. 1995), and Cladocera (e.g., Lotter et al. 1997) which have permitted quantitative temperature reconstructions from fossil assemblages. Such quantitative reconstructions have so far mainly been applied to late-glacial and early Holocene sediments (e.g., Walker et al. 1991; Schmidt et al. 1998; Lotter et al. 1999, 2000; Birks et al. 2000; Heiri and Millet 2005), and few such multi-proxy reconstructions cover the Holocene period or have been carried out at high-elevation or high-latitude sites (e.g., Korhola et al. 2000b; Rosén et al. 2001; Bigler et al. 2002; Lotter and Birks 2003a). Most of these studies concentrate on the location of the former tree-line as a conspicuous transition zone at the landscape scale. This assumes a direct link between species distribution and composition and tree-line (e.g., Walker and MacDonald 1995; Porinchu and Cwynar 2000). Several studies show that the assemblage structure and composition of aquatic organisms exhibit conspicuous changes along climatic gradients (e.g., Smol et al. 1991;

Lotter et al. 1997; Korhola et al. 2000b) so that on a macro-scale, we may consider the presence of regions with high species turnover or, in other words, the concept of ‘aquatic ecotones’ (DeDeckker and Forester 1988). At finer spatial scales such as a single lake, there are, of course, other factors important that may determine local-scale aquatic ecotones in the strict sense of the term (Allen and Hoekstra 1990; Kolasa and Zalweski 1995).

It is often assumed that similar physical/climatic factors affecting the distribution of terrestrial organisms also determine the distribution of aquatic organisms on a broad spatial scale. The forcing of environmental factors such as climate would then intuitively limit the distributions of aquatic organisms to lakes in certain climatic zones or altitudes corresponding to changes in terrestrial organisms or terrestrial ecotones (Smol et al. 1991). Nevertheless, whether or not climatic threshold factors, such as, for example, summer temperature or growing-degree days that may influence the position of the terrestrial ecotones also limit the distribution of aquatic organisms remains unclear (Blom et al. 1998, 2000; Korhola et al. 2000a, c; Seppä et al. 2002; Lotter and Birks 2003a).

If there are different spatial scales involved in determining the location of conspicuous transitions in species composition in terrestrial and aquatic organisms, this has major implications for palaeoecological and palaeoclimatological multi-proxy studies at past and present ecotonal locations. Further, if different aquatic organisms provide different information and variable quality of information at different parts of climatic gradients, this will undoubtedly have consequences for the value and reliability of climatic reconstructions based on biological data.

We use here a modern calibration set of sediment–surface samples collected along an altitudinal gradient in the Alps formerly used to develop a series of quantitative inference models for different groups of aquatic organisms (Lotter et al. 1997, 1998) to address these issues. As the assemblage compositions of the investigated organisms show a strong relationship to altitude (Lotter et al. 1997) we use them in the present study to consider the following questions; (1) are transitions in species composition different between different groups of aquatic organisms, and (2) are the transitions for different aquatic organisms comparable to the tree-line ecotone? Based on the answers to these questions, we evaluate the consequences for palaeoclimate studies using aquatic organisms in multi-proxy reconstructions.

Methods

Data sets

The diatom, chironomid, and chydorid (benthic Cladocera) data used in this study were collected from surface–sediment samples at the deepest part of 68 small lakes along an altitudinal transect in the Alps, ranging from 409 to 2339 m a.s.l. The present-day tree-line in the investigated area of the Alps is situated between 1900 and 2000 m a.s.l. Five sites located on the southern side of the Alps were excluded here because they are located in a different climatic regime. Details about the taxonomic composition of the assemblages and sample preparation, as well as site-specific information are given in Lotter et al. (1997, 1998) and Müller et al. (1998).

For numerical analyses the sites were ordered according to their elevation. Only taxa with an abundance of at least 0.5% and an occurrence in at least 3 lakes were used in the diatom data-set (63 lakes, 120 taxa). In the chironomid data-set, a minimum of 48 head capsules (53 lakes, 54 taxa) and in the chydorid data-set at least 30 remains were required (52 lakes, 25 taxa). Further, to enhance comparability of the results we only used lakes that were analysed for all three groups of taxa, leaving 44 lakes for the analysis of altitudinal trends in beta-diversity.

Rate of compositional change

A major concern in the application of beta-diversity estimates in ecology has been species richness (see Gaston and Blackburn 2000 and references within), and the inherent differences in richness among taxonomic groups. To minimise these problems we define beta-diversity as the distance between two points in species space (ter Braak 1983; Heegaard 2004). By ordination of the species data an inter-taxonomical comparable estimate of the difference between neighbouring sites can be derived by using the same number of axes for all comparisons. This reduction of species space to a small number of major axes reduces the problem of local species richness (Heegaard 2004). However, the inherent difference in richness between species groups will influence the covariance of the distances, and therefore we need to scale the estimated beta-diversity to unit variance. This will permit comparison of beta-diversity among the different taxonomic groups.

In this study, we used a principal coordinate analysis (PCoA; Gower 1966; Legendre and Legendre 1998; ter Braak and Šmilauer 2002) as the basis for estimating species turnover. We applied two distance metrics; (1) chord distance, and (2) chi-square distance (see Prentice 1980; Legendre and Gallagher 2001). Of these distance metrics the chi-square distance is a relative distance to the total abundance within each data-set. Hence, the turnover is relative to the total distribution of species abundance.

From the PCoA we use the site scores along the first 4 axes, where x_{ij} is the ordination score for the i th observation on the j th axis. The distance in ordination space between neighbouring observations, in our case lakes, gives the species turnover along the altitudinal gradient, e.g., between observations i and k:

$$\beta = \sqrt{\sum_{j=1}^{4} (x_{ji} - x_{jk})^2} \tag{1}$$

where i and $k = 1 \ldots n$ observations, and $j = 1 \ldots 4$ ordination axes. The cumulative rate-of-change along the altitudinal transect is the response variable. This variable approximates, on investigation, a cumulative Normal distribution.

Ecotone detection

The numerical analysis to detect possible ecotones is based on a Generalised Linear Model (GLM; McCullagh and Nelder 1989), with the cumulative rate-of-change as a response variable and altitude as a predictor variable. To allow for the potential effects of uneven distance and altitudinal trends in species richness, we conditioned the estimate of β-diversity on distance and on species richness.

In a cumulative rate-of-change an ecotone is identified by an abrupt break (a jump in cumulative beta-diversity) or by a region with an unusually steep slope (Figure 1). To select ecotones, we made a backward elimination of all possible ecotone positions. First, all breaks in cumulative turnover were identified. Within each of the intervals defined by the breaks a linear regression was applied as a piecewise regression (Hastie et al. 2001). This creates a full model where each interval can have a different intercept and a different cumulative rate-of-change, i.e. slope (Figure 2). From the full model, each break was removed in turn and the increase in deviance was observed. The breaks with a non-significant change in deviance, assessed by F-statistics, were left out of the final model. These were the potential ecotones separating adjacent regions for which two separate regression lines were not

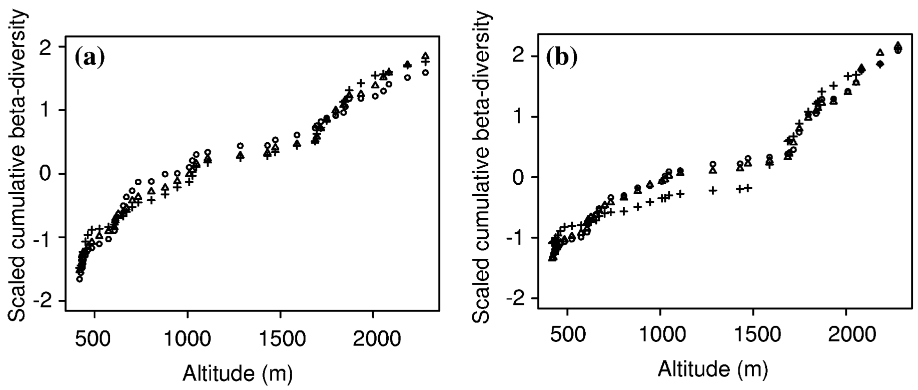

Figure 1. The scaled cumulative beta-diversity estimated by (a) chord-distance, and (b) chi-square distance, with circles = diatoms, triangles = chydorids, and crosses = chironomids. The scaling of cumulative beta-diversity is done for graphical comparison, and here we scaled the cumulative beta-diversity to zero mean and unit variance.

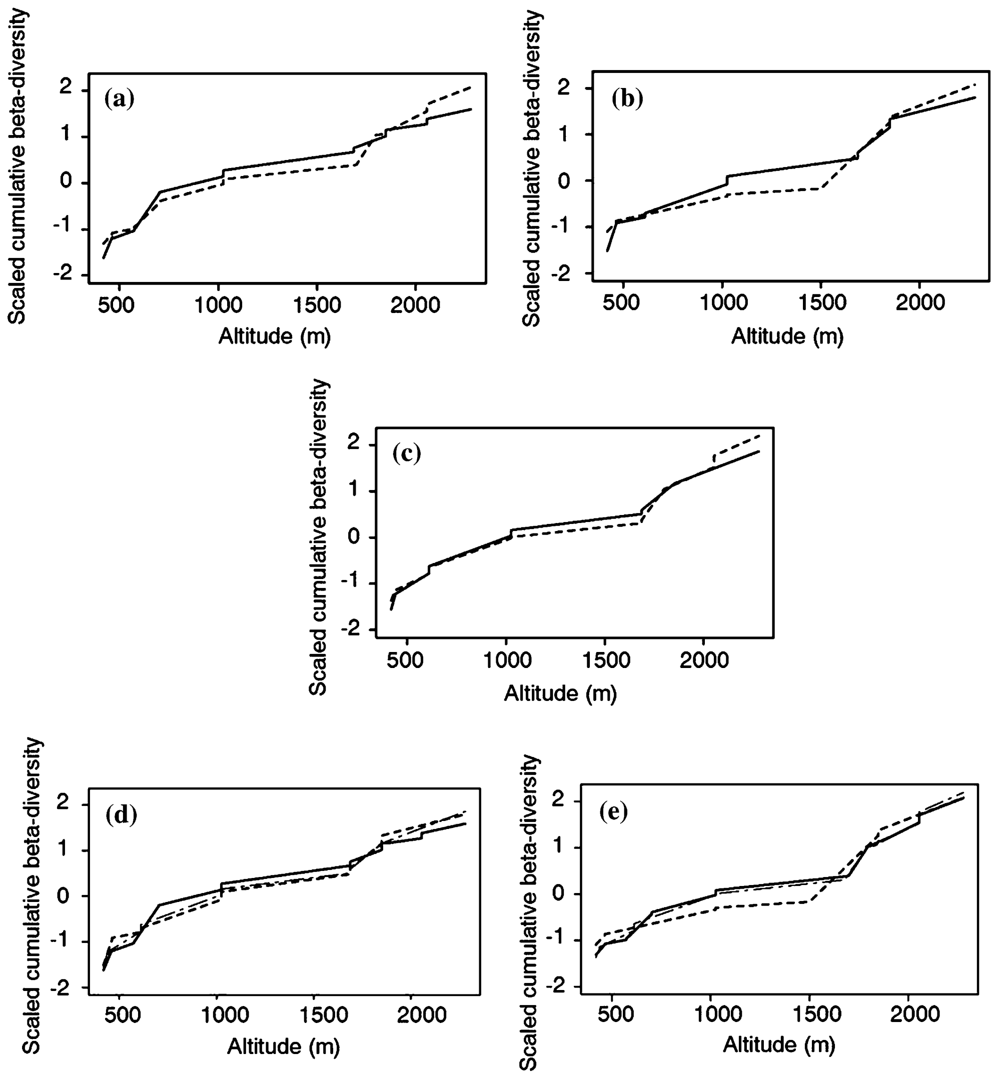

Figure 2. The cumulative rate of change for the species groups (a) diatoms, (b) chironomids, and (c) chydorids estimated by the chord (bold), and chi-square (dotted) distances. The cumulative rate of change following the distances (d) chord, and (e) chi-square with the species groups diatoms (bold), chironomids (dotted), and chydorids (broken). The scaling of cumulative beta-diversity is done for graphical comparison, and here we scaled the cumulative beta-diversity to zero mean and unit variance.

forming a significant contribution in comparison to defining it as one inter-ecotone region. As a final check of an ecotone the sites across it should not be progressively more similar than the sites defining the transition.

Results

The eigenvalues of the PCoA indicate that chord-distance extracts a high portion of the variability in the species composition (Table 1). In particular for the chydorids as much as 78.2% of the total variance was captured by the first 4 axes. There is, however, not a strong correlation between the average number of species per lake and the percentage explained. The chironomids have the lowest percentage of captured variance but an intermediate number of species per lake (Table 1), whereas the diatoms capture 57.4% of the variance and show the highest number of species per lake. This indicates a difference between the taxonomic groups in the overall structure of species composition along the altitudinal gradient.

Table 1. Summary of Principal Coordinate Analyses for the three species groups showing a different structuring of the species composition along the first four axes for each group. Cum.percent = Cumulative percentage explained by the axes, Sum = sum of eigenvalues, and Species = within-lake average number of species.

	Distance		1	2	3	4	Sum	Species
Chydorids	Chord	Eigenvalue	0.144	0.114	0.071	0.047	0.481	10.9
		Cum.percent	29.9	53.6	68.4	78.2		
	Chi-square	Eigenvalue	0.392	0.311	0.255	0.239	1.957	
		Cum.percent	20.0	35.9	49.0	61.2		
Chironomids	Chord	Eigenvalue	0.134	0.089	0.068	0.048	0.677	17.2
		Cum.percent	19.8	32.9	43.0	50.1		
	Chi-square	Eigenvalue	0.774	0.702	0.537	0.343	4.956	
		Cum.percent	15.6	29.8	40.6	47.5		
Diatoms	Chord	Eigenvalue	0.156	0.132	0.107	0.063	0.798	37.5
		Cum.percent	19.5	36.1	49.5	57.4		
	Chi-square	Eigenvalue	0.702	0.629	0.57	0.525	7.212	
		Cum.percent	9.7	18.5	26.4	33.6		

The results of the piecewise regression analysis for ecotone detection are summarised in Table 2. The general rate-of-change is similar among the taxonomic groups according to the chord-distance (Figure 2d). There is a high rate-of-change at the lowest elevations, and there is a high turnover in

Table 2. Analysis of deviance for the model influence of the removal of subsequent ecotones. The analysis was performed conditioned on both distance between lakes and average richness of neighbouring lakes being included in the model.

Species	Distance	Ecotones (altitude; metres)	R.df	R.dev	Dev	*F*	Pr(> *F*)
Diatoms	Chord	463;574;702;1026;1687;1849	27	4.7			
		463;574;702;1026;1687;1849;2055	25	3.6	1.1	3.9	0.033
		463;574;702;1026;1430;1687;1849;2055	23	3.2	0.4	1.3	0.296
	Chi-square	463;574;702;1026;1687;1798;1870	25	14.4			
		463;574;702;1026;1687;1798;1870;2055	23	9.3	5.1	6.2	0.007
		463;574;702;1026;1430;1687;1798;1870;2055	21	9.0	0.3	0.4	0.701
Chironomid	Chord	463;1026;1687;1849	31	2.3			
		463;611;1026;1687;1849	29	1.7	0.6	4.9	0.015
		463;611;1026;1430;1687;1849	27	1.5	0.2	2.2	0.132
		463;611;1026;1430;1687;1849;2055	25	1.3	0.2	2.2	0.128
		463;611;702;1026;1430;1687;1849;2055	23	1.1	0.1	1.5	0.252
	Chi-square	1026;1472;1849	33	14.7			
		463;1026;1472;1849	31	5.0	9.7	30.1	< 0.001
		463;611;1026;1472;1849	29	4.3	0.7	2.3	0.123
		463;611;702;1026;1472;1849	27	3.5	0.8	3.0	0.065
		463;611;702;1026;1472;1849;2055	25	3.4	0.2	0.6	0.574
		463;611;702;1026;1472;1687;1849;2055	23	3.3	0.1	0.4	0.663
Cladocera	Chord	611;1026;1687;1849	31	8.2			
		436;611;1026;1687;1849	29	3.6	4.7	19.0	< 0.001
		436;611;702;1026;1687;1849	27	3.0	0.6	2.6	0.096
		436;611;702;1026;1687;1849;2011	25	2.7	0.3	1.4	0.264
		436;485;611;702;1026;1687;1849;2011	23	2.6	0.1	0.5	0.588
		436;485;611;702;1026;1430;1687;1849;2011	21	2.5	0.1	0.4	0.688
	Chi-square	611;1026;1687;1798;2055	29	14.4			
		436;611;1026;1687;1798;2055	27	8.2	6.2	10.3	0.000
		436;611;702;1026;1687;1798;2055	25	6.8	1.4	2.5	0.104
		436;611;702;1026;1430;1687;1798;2055	23	6.6	0.3	0.5	0.633
		436;485;611;702;1026;1430;1687;1798;2055	21	6.4	0.2	0.3	0.711
		436;485;611;702;1026;1430;1687;1798;1849;2055	19	6.3	0.1	0.1	0.890

the interval 1650–1850 m a.s.l., i.e., below the modern tree-line at 1900–2000 m in this region of the Alps. An interesting feature is the clear ecotone detected for diatoms at approximately 2055 m (Figure 2a). This was not detected for chironomids (Figure 2b), and only apparent for chydorids by the chi-square distance, i.e. the relative distance in species composition (Figure 2c). The major differences between the taxonomic groups were found using the chi-square distance (Figure 2e). In comparison with the chord distance, the chi-square distance shows in general a lower turnover at low altitudes but a stronger taxonomic cumulative difference above 1650 m (Figure 2a, b and c). According to the chi-square distance the region of highest species turnover for chironomids spans 1475–1850 m, whereas for both the diatoms and the chydorids the highest rate of change occurs between 1650 and 1850 m a.s.l. Hence, there is a stronger dynamic in the relative species composition for chironomids than for the other two taxonomic groups (Figure 2e). These differences in species turnover between taxonomic groups are not related to the trends in species richness, because for both chironomids and chydorids there is a steady but weak decline in species richness with altitude, whereas for the diatoms there are minimal changes along the altitudinal gradient (Figure 3). The major ecotone is found for all groups just below the tree-line, and it is a region spanning ca. 200 m of altitude with unusually high rate-of-changes. Further, there are detectable ecotones for diatoms and chydorids at 2055 m a.s.l. At lower elevations, i.e. below 1000 m a.s.l., there is a high turnover below 460 m a.s.l. for all groups. Between 460 and 1000 m a.s.l. an ecotone is only observed for diatoms and chydorids (Figure 2a and b), and a minor ecotone for chironomids by chord distance at ca. 600 m a.s.l. (Figrue 2b). The ecotone for chydorids is abrupt at 600 m a.s.l. corresponding to one of the chironomid ecotones (Figure 2c), whereas the diatoms show a region of high beta-diversity in the interval 575–700 m a.s.l. (Figure 2a). The numbers of ecotones as either 'jumps' or regions of high turnover are; (1) for diatoms 6 and 5, (2) chironomids 4 and 3, and (3) chydorids 4 and 5, using chord- and chi-square distance, respectively. Only for chydorids did the relative distance, i.e., chi-square distance, detect more ecotones than are detected by the chord-distance.

Discussion

In ecology and palaeoecology, an important concept is that organisms respond to environmental conditions, and as a result of differentiated

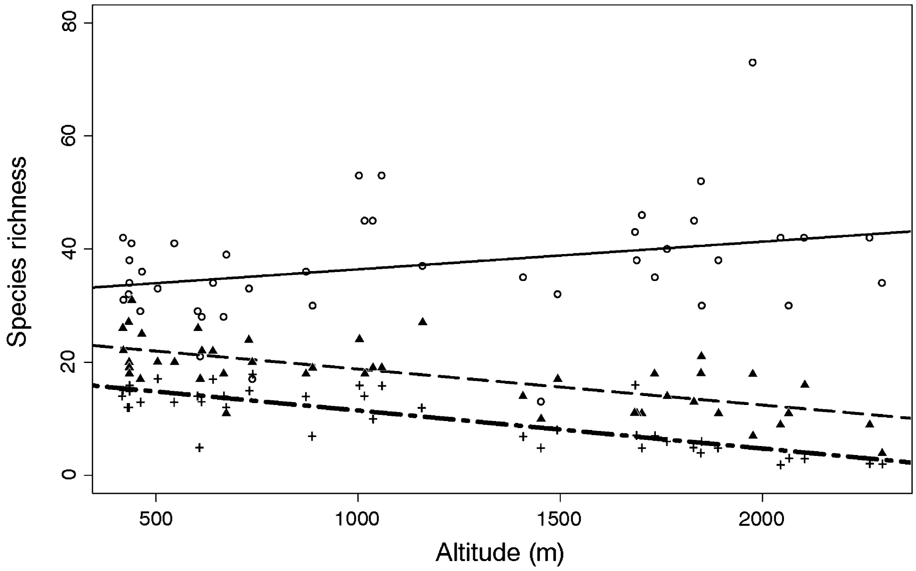

Figure 3. The species richness of the three organism groups along the altitude gradient: (1) diatoms (circle, solid line), (2) chironomids (triangles, broken line), and (3) chydorids (crosses, dashed and dotted line).

environmental relationships of organisms, alterations in species composition appear along spatial and temporal gradients provided there is an environmental change of sufficient magnitude (Austin and Smith 1989; Oksanen and Minchin 2002). Changes in species composition form continua, and hence an important question in ecology, palaeoecology, and biogeography is what causes rapid changes in species composition in space and time? Is it increased environmental change, is it a similar ecological threshold among taxa, is it due to species-richness patterns, or is it due to different spatial distances among observations? Although different theories exist, none of these four factors is mutually exclusive in relation to species turnover.

In our study, we show that three groups of aquatic organisms (diatoms, chironomids, chydorids) differ in rate-of-change compositionally along the same altitudinal gradient, and both the position and strength at the ecotone differ considerably among the organisms when comparing the rate-of-change (chord distance) and the relative rate-of-change (chi-square distance). The differences between the two distance metrics indicate that a primary structure of the successive compositional difference is due to differences relative to the total compositional abundance structure. For diatoms, this is above 1650 m a.s.l. where the chi-square distance indicates a stronger change than the chord distance. Hence, above 1650 m a.s.l. some species become more dominant than at lower elevations. Similarly, for chironomids the first part of the ecotone between 1475 and 1850 m a.s.l. is only recognised by the chi-square distance. This indicates that there is a strong change in the relative abundance structure followed by a general turnover between 1650 and 1850 m a.s.l. For chydorids such a difference between the two distance metrics is only apparent at the 2055 m a.s.l. ecotone. Across this ecotone, there is a shift in the relative abundance that is stronger than the general trend in rate-of-change as indicated by the chord distance. Thus, the difference in compositional rate-of-change and ecotone position between the two distance metrics indicates that the groups of taxa may respond differently to the environmental conditions of their surroundings, creating a different assemblage structure along the altitudinal gradient although the species co-occur in the same lakes and all are exposed to similar environmental conditions. However, the altitudinal gradient is an indirect variable (*sensu* Austin and Smith 1989), i.e. it correlates with several physiologically important variables, such as temperature, duration of ice-cover, water-chemistry, oxygen availability, etc. (Engstrom 1987; Pienitz and Smol 1993; Weckström and Korhola 2001; Birks et al. 2004; Schmidt et al. 2004; Antoniades et al. 2005). Therefore, the species groups either respond to environmental heterogeneity along different direct gradients, where the heterogeneity is expressed at various points along the indirect altitudinal gradient, or the species groups show differential thresholds to the same environmental gradient. It is difficult to separate these two alternatives using observational studies of indirect gradients only. However, to what degree do the ecotones of the different groups correspond to known abrupt changes in the abiotic and biotic environment?

Along the altitudinal gradient one of the strongest abrupt landscape changes recognised is the tree-line (Körner 2003; Körner and Paulsen 2004). Several studies have analysed the correlation of the alpine and arctic tree-line with both the environment (climate in particular, e.g., Körner and Paulsen 2004) and species composition of various organisms, e.g., vascular plants (McCoy et al. 1986; Odland and Birks 1999) and aquatic organisms, such as diatoms (Weckström and Korhola 2001) and chironomids (Seppä et al. 2002). Obvious patterns are found in related terrestrial organisms such as tree-nesting birds, epiphytes, etc., but the strong correlation recorded for diatom assemblages and tree-line is more surprising (Weckström and Korhola 2001). Weckström and Korhola (2001) argue that the great change in diatom composition at the arctic tree-line is due to the indirect environmental influences of climate, catchment erosion, ice and snow cover, etc. (e.g., Pienitz et al. 1995; Vyverman and Sabbe 1995; Patrick and Reimer 1966; Lotter et al. 1997; Rouse et al. 1997). However, our analysis only partly supports the observations of Weckström and Korhola (2001), as the obvious region of high compositional rate-of-change is found just below the alpine tree-line (1900–2000 m a.s.l.), but for diatoms and chydorids also above the tree-line at 2055 m a.s.l. Moreover, in our study, the estimated beta-diversity is conditioned on species richness, whereas the index used by Weckström and Korhola (2001) is strongly influenced by species richness. Thus, their observed change in diatom composition at the arctic tree-line is most likely due to patterns in species richness. This interpretation is confirmed by the correlation between species richness and the index reported in their Figure 5 (Weckström and Korhola 2001, p. 37). On the other hand, previous studies have shown a strong correlation between chironomids and climate in subarctic Fennoscandia (Seppä et al. 2002), but they found that chironomids did not correlate in particular with the arctic tree-line. In our study, chironomids show a major ecotone region just below the modern altitudinal tree-line. Thus, there may be some relationship with the tree-line, directly or indirectly, as the chironomids have an imago life-stage outside the water. The distribution of chironomids can, therefore, be strongly linked to the distribution of forest as wind regimes change dramatically across the tree-line ecotone. However, this ecotone is also observed for diatoms and chydorids, which do not have an imago stage. This suggests that there are some changes to the limnological characteristics just below the tree-line. This pattern can be related to the effect of trees with increasing downhill influence, as the indirect influence of water chemistry will follow the downhill runoff. Further, the effect of forest on lake characteristics can be assumed to increase downhill as the density of trees increases, i.e. the tree-line is the top of the interval with increasing influence of forest downwards. Hence, the ecotones found just below the tree-line are interpreted here as most likely due to an indirect effect of forest on lake characteristics such as chemistry and snow and ice-cover (Pienitz et al. 1995; Vyverman and Sabbe 1995; Patrick and Reimer 1966; Lotter et al. 1997; Rouse et al. 1997; Catalan et al. 2002). Thus, the tree-line may influence the compositional transition of these organism groups, but the ecotone detected above the tree-line for both diatoms and chydorids is more likely to be some effect of climate. Livingstone et al. (2005) showed a change in thermal regime for Alpine lakes above 2000 m a.s.l. The decoupling between water temperature and altitude in summer as described by them, may explain the ecotone above the modern tree-line.

A particularly important aspect of palaeoclimatology is whether aquatic organisms depend on the tree-line, as has lately been proposed for diatoms and chironomids (Walker and MacDonald 1995; Olander et al. 1999; Weckström and Korhola 2001). Commonly, it has been thought that aquatic organisms respond more rapidly to climatic changes than terrestrial organisms (e.g., Iversen 1964; Fægri and Iversen 1989). Our study presents a more complex picture, as for all three organism groups there are species that seem to respond positively to trees within the catchments, and at the same time other taxa do not respond to the presence of the tree-line. This is corroborated by studies of individual species that show individual responses to the tree-line (Walker and MacDonald 1995), responses to climate correlative with determinants of the tree-line (Larocque et al. 2001; Seppä et al. 2002), or species that do not respond across the tree-line (Seppä et al. 2002). This lends support to the ideas of establishing sequential or Bayesian transfer-functions that take into account information about individual taxa to gradients other than the particular environmental gradient being reconstructed. This is important as otherwise the reconstruction may be biased by the lag in the geographical movement of the tree-line. In cases where aquatic organisms would in general respond quickly to climatic change independent of the tree-line, we would anticipate that the ecotone would be at a higher altitude than the tree-line as the temperature in the last decade has increased and the tree-line has been observed to move upwards in this region of the Alps (Gottfried et al. 1999). Such a lag is indicated in this study as today's tree-line is located at a lower altitude than the ecotone at 2055 m (diatoms and chydorids), which climatically is most likely related to the tree-line. Hence, this study supports the use of aquatic organisms as a useful tool for tracking historical tree-line distributions (Walker and MacDonald 1995; Porinchu and Cwynar 2000; Weckström and Korhola 2001), but with some caution about the potential lag between the response of various aquatic and non-aquatic organisms. Thus, it is clear that aquatic organisms may respond to the climatic changes indirectly through numerous environmental factors, but at the same time there is a strong correlation of tree-line, either directly or indirectly, with changes in species diversity and in particular with the species richness for the three aquatic groups of organisms.

The patterns found in this study have implications for the multi-proxy approach to reconstructing past environment and climate (Lotter

2003). They show that by applying a multi-proxy approach for climatic reconstructions (e.g., Birks et al. 2000; Korhola et al. 2000b; Lotter et al. 2000), careful interpretation of the results is needed as different biota may have different responses to the same environmental variable. In addition, the different ecotones for the various organisms suggest that cores taken at different geographical localities may maximise the environmental sensitivity and hence the reconstruction ability of particular organisms. When combined, this may lead to a better understanding of the dynamics of the organisms through time and in particular to more reliable reconstructions of past climate. However, none of the organism groups studied here shows a high rate-of-change at the centre of the gradient. Thus, in this particular study area it would be unwise to employ such a record as a considerable environmental change must occur there before it would be detected in the palaeoecological record (see Fægri and Iversen 1989, Figure 7.1).

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References

Allen T.F.H. and Hoekstra T.W. 1990. The confusion between scale-defined levels and conventional levels of organization in ecology. J. Veg. Sci. 1: 5–12.

Arft A.M. 1999. Responses of tundra plants to experimental warming: meta-analysis of the International Tundra Experiment. Ecol. Monogr. 69: 491–511.

Antoniades D., Douglas M.S.V. and Smol J.P. 2005. Quantitative estimates of recent environmental changes in the Canadian High Arctic inferred from diatoms in lake and pond sediments. J. Paleolimnol. 33: 349–360.

Austin M.P. and Smith T.M. 1989. A new model for the continuum concept. Vegetatio 83: 35–47.

Bigler C., Larocque I., Peglar S.M., Birks H.J.B. and Hall R.I. 2002. Quantitative multiproxy assessment of long-term patterns of Holocene environmental change from a small lake near Abisko, northern Sweden. The Holocene 12: 481–496.

Birks H.J.B. 1981. The use of pollen analysis in the reconstruction of past climates: a review. In: Wigley T.M. (ed.), Climate and History. Cambridge University Press, Cambridge, pp. 111–138.

Birks H.H., Battarbee R.W. and Birks H.J.B. 2000. The development of the aquatic ecosystem at Kråkenes lake, western Norway, during the late glacial and early Holocene – a synthesis. J. Paleolimnol. 23: 91–114.

Birks H.J.B., Jones V.J. and Rose N.L. 2004. Recent environmental change and atmospheric contamination on Svalbard as recorded in lake sediments – synthesis and general conclusions. J. Paleolimnol. 31: 531–546.

Blom T., Korhola A. and Weckström J. 1998. Physical and chemical characterisation of small subarctic lakes in Finnish Lapland with special reference to climate change scenarios. In: Lemmelä R. and Helenius R. (eds), Proceedings of the Second International Conference on Climate and Water, Espoo, Finland, 17–20 August 1998 Espoo, Finland. EditaLtd, Helsinki, pp. 576–587.

Blom T., Korhola A., Weckström J., Laing T., Snyder J., MacDonald G.M. and Smol J.P. 2000. Physical and chemical characterisation of small subarctic headwater lakes in Finnish Lapland and the Kola Peninsula. Verh. Int. Verein. Limnol. 27: 316–320.

Catalan J., Vetura M., Brancelj A., Granados I., Thies H., Nikus U., Korhola A., Lotter A.F., Barbieri A., Stuchlik E., Lien L., Bitusik P., Buchaca T., Camarero L., Goudsmit G.H., Kopacek J., Lemcke G., Livingstone D.M., Müller B., Rautio M., Sisko M., Sorvari S., Sporka F., Strunecky O. and Toro M. 2002. Seasonal ecosystem variability in remote mountain lakes: implications for detecting climatic signals in sediment records. J. Paleolimnol. 28: 25–46.

Chapin F.S.III, McGuire A.D., Randerson J., Pielke R.Sr., Baldocchi D., Hobbie S.E., Roulet N., Eugster W., Kasischke E., Rastetter E.B., Zimov S.A. and Running S.W. 2000. Arctic and boreal ecosystems of western North America as components of climate system. Glob. Change. Biol. 6: 211–223.

Cody M.L. 1975. Towards a theory of continental species diversity: bird distributions over Mediterranean habitat gradients. In: Cody M.L. and Diamond J.M. (eds), Ecology and Evolution of Communities. Harvard University Press, Cambridge, Massachusetts, pp. 214–257.

DeDeckker P. and Forester R.M. 1988. The use of ostracods to reconstruct continental palaeoenvironmental records. In: DeDeckker P., Colin J.-P. and Peypouquet J.-P. (eds), Ostracoda in the Earth Sciences. Ostracoda in the Earth Sciences, Elsevier, Amsterdam, pp. 175–199.

Engstrom D.R. 1987. Influence of vegetation and hydrology on the humus budgets of Labrador Lakes. Can. J. Fish. Aqu. Sci. 44: 1306–1314.

Fægri K. and Iversen J. 1989. Textbook of Pollen Analysis. In: Fægri K., Kaland PE and Krzywinski K. (eds). John Wiley and Sons, Chichester UK, pp. 328.

Gaston K.J. and Blackburn T.M. 2000. Pattern and Process in Macroecology. Blackwell Science, Oxford, pp. 377.

Gottfried M., Pauli H., Reiter K. and Grabherr G. 1999. A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. Diversity Distr. 5: 241–251.

Gower J.C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. Biometrika 53: 325–338.

Hastie T.J., Tibshirani R. and Friedman J. 2001. The Elements of Statistical Learning. Springer, New York, pp. 533.

Heegaard E. 2004. Trends in aquatic macrophyte species turnover in Northern Ireland – which factors determine the spatial distribution of local species turnover? Glo. Ecol. Biogeogr. 13: 397–408.

Heiri O. and Millet L. 2005. Reconstruction of Late Glacial summer temperatures from chironomid assemblages in Lac Lautrey (Jura, France). J. Quat. Sci. 20: 33–44.

Holtmeier F.-K. 2003. Mountain timberlines – Ecology, Patchiness, and Dynamics. Kluwer Academic Publishers, Dordrecht, pp. 384.

Huston M.A. 1994. Biological Diversity. Cambridge University Press, Cambridge, pp. 679.

Iversen J. 1964. Plant indicators of climate, soil and other factors during the Quaternary. Report VI International Quaternary Association (INQUA) Congress 2: 421–426.

Körner C. 2003. Alpine Plant Life. 2nd ed. Springer, Berlin, pp. 337.

Körner C. and Paulsen J. 2004. A world-wide study of high altitude treeline temperatures. J. Biogeogr. 31: 713–732.

Kolasa J. and Zalewski M. 1995. Notes on ecotone attributes and functions. Hydrobiologia 303: 1–7.

Koleff P. and Gaston K.J. 2002. The relationship between the local and regional species richness and spatial turnover. Glo. Ecol. Biogeogr. 11: 363–375.

Koleff P., Gaston K.J. and Lennon J.L. 2003. Measuring beta diversity for presence–absence data. J. Anim. Ecol. 72: 367–382.

Korhola A., Olander H. and Blom T. 2000c. Cladoceran and chironomid assemblages as quantitative indicators of water depth in subarctic Fennoscandian lakes. J. Paleolimnol. 24: 43–54.

Korhola A., Lotter A.F., Birks H.J.B. and Cameron N.G. 2000a. Climate history as recorded by ecologically sensitive arctic and alpine lakes in Europe during the last 10,000 years: a multi-proxy approach (CHILL-10,000). Proceedings of the European Climate Science Conference CD-ROM, article 132, Vienna, City Hall, 19–23 October, 1998.

Korhola A., Weckström J., Holmström L. and Erästö P. 2000b. A quantitative Holocene climatic record from diatoms in northern Fennoscandia. Quat. Res. 54: 284–294.

Kühl N., Gebhardt C., Litt T. and Hense A. 2002. Probability density functions asbotanical–climatological transfer functions for climate reconstruction. Quat. Res. 58: 381–392.

Kupfer J.A. and Cairns D.M. 1996. The suitability of montane ecotones as botanical indicators of global climatic change. Prog. Phys. Geog. 20: 253–272.

Larocque I., Hall R.I. and Grahn E. 2001. Chironomids as indicators of climate change: a 1000-lake training set from a subarctic region of northern Sweden (Lapland). J. Paleolimnol 26: 307–322.

Legendre P. and Legendre L. 1998. Numerical Ecology. 2nd ed. Elsevier, Amsterdam.

Legendre P. and Gallagher E.D. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129: 271–280.

Lennon J.J., Koleff P.P., Greenwood J.J.D. and Gaston K.J. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. J. Anim. Ecol. 70: 966–979.

Livingstone D.M., Lotter A.F. and Kettle H. 2005. Altitude-dependent differences in the primary physical response of mountain lakes to climatic forcing. Limnol. Oceanogr. 50: 1313–1325.

Lotter A.F. 2003. Multi-proxy climatic reconstructions. In: Mackay A.W., Battarbee R.W., Birks H.J.B. and Oldfield F. (eds), In: Global Change in the Holocene. E. Arnold, London, pp. 373–383.

Lotter A.F. and Birks H.J.B. 2003a. The Holocene palaeolimnology of Sägistalsee (1935 m a.s.l.) and its environmental history – a synthesis. J. Paleolimnol. 30: 333–342.

Lotter A.F. and Birks H.J.B. 2003b. The Holocene palaeolimnology of Sägistalsee and its environmental history. J. Paleolimnol. 30: 253–342.

Lotter A.F., Birks H.J.B. and Zolitschka B. 1995. Late-glacial pollen and diatom changes in responses to two different environmental perturbations: volcanic eruption and the Younger Dryas cooling. J. Paleolimnol. 14: 23–47.

Lotter A.F., Birks H.J.B., Hofmann W. and Marchetto A. 1997. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. J. Paleolimnol. 18: 395–420.

Lotter A.F., Birks H.J.B., Hofmann W. and Marchetto A. 1998. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II. Nutrients. J. Paleolimnol. 19: 443–463.

Lotter A.F., Walker I.R., Brooks S.J. and Hofmann W. 1999. An intercontinental comparison of chironomid palaeotemperature inference models: Europe vs North America. Quat. Sci. Rev. 18: 717–735.

Lotter A.F., Birks H.J.B., Eicher U., Hofman W., Schwander J. and Wick L. 2000. Younger Dryas and Alleröd summer temperatures at Gerzensee (Switzerland) inferred from fossil pollen and cladoceran assemblages. Palaeogeog. Palaeoclimatol. Palaeoecol. 159: 349–361.

Margalef R. 1975. External factors and ecosystem stability. Schweizerische Zeitschrift für Hydrologie 37: 102–117.

May R.M. 1973. Stability and Complexity of Model Ecosystems. Princeton University Press, Princeton, New Jersey, pp. 247.

McCoy E.D., Bell S.S. and Walters K. 1986. Identifying biotic boundaries along environmental gradients. Ecology 67: 749–759.

McCullagh P. and Nelder J.A. 1989. Generalized Linear Models. 2nd ed. Chapman and Hall, London, pp. 510.

Monserud R.A. and Leemans R. 1992. Comparing global vegetation maps with the Kappa Statistic. Ecol. Mod. 62: 275–293.

Moser K.A., MacDonald G.M. and Smol J.P. 1996. Applications of freshwater diatoms to geographical research. Prog. Phys. Geog. 20: 21–52.

Müller B., Lotter A.F., Sturm M. and Ammann B. 1998. The influence of catchment quality and altitude on the water and sediment composition of 68 small lakes in Central Europe. Aqua. Sci. 60: 316–337.

Naiman R.J. and Décamps H. 1997. The ecology of interfaces: riparian zones. Ann. Rev. Ecol. Syst. 28: 621–658.

Odland A. and Birks H.J.B. 1999. The altitudinal gradient of vascular plant species richness in Aurland, western Norway. Ecography 22: 548–566.

Oksanen J. and Minchin P.R. 2002. Continuum theory revisited: what shape are species responses along ecological gradients? Ecol. Mod. 157: 119–129.

Olander H., Birks H.J.B., Korhola A. and Blom T. 1999. An expanded calibration model for inferring lakewater and air temperatures from fossil chironomid assemblages in northern Fennoscandia. The Holocene 9: 279–294.

Patrick R. and Reimer C. 1966. The Diatoms of the United States, Vol. 1: Fragilariaceae, Eunotiaceae, Achnanthaceae, Naviculaceae. The Acadamy of Natural Sciences of Philadelphia, Philadelphia, pp. 688.

Pielou E.C. 1975. Ecological Diversity. John Wiley and Sons, New York, pp. 176.

Pienitz R., Smol J.P. and Birks H.J.B. 1995. Assessment of freshwater diatoms as quantitative indicators of past climate change in the Yukon and Northwest Territories, Canada. J. Paleolimnol. 13: 21–49.

Pienitz R. and Smol J.P. 1993. Diatom assemblages and their relationship to environmental variables in lakes from the boreal forest-tundra ecotone near Yellowknife, Northwest Territories, Canada. Hydrobiologia 269(270): 391–404.

Porinchu D.F. and Cwynar L.C. 2000. The distribution of freshwater Chironomidae (Insecta: Diptera) across tree-line near the lower Lena River, northeast Siberia, Russia. Arct. Antarct. Alp. Res. 32: 429–437.

Prentice I.C. 1980. Multidimensional scaling as a research tool in Quaternary palynology: a review of theory and methods. Rev. Palaeobot. Palynol. 31: 71–104.

Rosén P., Segerström U., Eriksson L., Renberg I. and Birks H.J.B. 2001. Holocene climatic change reconstructed from diatoms, chironomids, pollen and near-infrared spectroscopy at an alpine lake (Sjuodjijaure) in northern Sweden. The Holocene 11: 551–562.

Rosenzweig M.L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, pp. 436.

Rouse W.R., Douglas M.S.V., Hecky R.E., Hersher A.E., Kling G.W., Lesack L., Marsh P., McDonald M., Nicholson B.J., Roulet N.T. and Smol J.P. 1997. In: Cushing C.E. (ed.), Effects of Climate Change on the Freshwater of Arctic and Subarctic North America. Freshwater Ecosystems and Climate Change in North America. John Wiley and Sons, Chichester, pp. 55–84.

Schmidt R., Wunsam S., Brosch O., Fott J., Lami A., Loffler H., Marchetto A., Muller H.W., Prazakova M. and Schwaighofer B. 1998. Late and post-glacial history of meromictic Längsee (Austria), in respect to climate change and anthropogenic impact. Aqua. Sci. 60.56–88.

Schmidt R., Kamenik C., Kaiblinger C. and Hetzel M. 2004. Tracking Holocene environmental changes in an alpine lake sediment core: application of regional diatom calibration, geochemistry, and pollen. J. Paleolimnol. 32: 177–196.

Seppä H. and Weckström J. 1999. Holocene vegetational and limnological changes in the Fennoscandian tree-line area as documented by pollen and diatom records from lake Tsuolbmajavri, Finland. Écoscience 6: 621–635.

Seppä H., Nyman M., Korhola A. and Weckström J. 2002. Changes of tree-lines and alpine vegetation in relation to post-glacial climate dynamics in northern Fennoscandia based on pollen and chironomid records. J. Quat. Sci. 17: 287–301.

Smol J.P., Walker I.R. and Leavitt P.R. 1991. Paleolimnology and hindcasting climatic trends. Verh. Int. Verein. Limnol. 24: 1240–1246.

ter Braak C.J.F. 1983. Principal components biplots and alpha and beta diversity. Ecology 64: 454–462.

ter Braak C.J.F. and Šmilauer P. 2002. CANOCO Reference Manual and User's Guide to Canoco for Windows. User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, NY. 500.

van der Maarel E. 1990. Ecotones and ecoclines are different. J. Veg. Sci. 1: 135–138.

Vyverman W. and Sabbe K. 1995. Diaton-temperature transfer functions based on the altitudinal zonation of diatom assemblages in Papua New Guinea: a possible tool in the reconstruction of regional palaeoclimatic changes. J. Paleolimnol. 13: 65–77.

Walker D.A., Halfpenny J.C., Walker M.D. and Wesman C.A. 1993. Long-term studies of snow–vegetation interactions. Bioscience 43: 287–301.

Walker I.R., Levesque A.J., Cwynar L.C. and Lotter A.F. 1997. An expanded surface–water palaeotemperature inference model for use with fossil midges from eastern Canada. J. Paleolimnol. 18: 165–178.

Walker I.R. and MacDonald G.M. 1995. Distributions of Chironomidae (Insecta: Diptera) and other freshwater midges with respect to treeline, Northwest Territories, Canada. Arct. Alp. Res. 27: 258–263.

Walker I.R., Mott R.J. and Smol J.P. 1991. Alleröd-Younger Dryas lake temperatures from midge fossils in Atlantic Canada. Science 253: 1010–1012.

Weckström J. and Korhola A. 2001. Patterns in the distribution, composition and diversity of diatom assemblages in relation to ecoclimatic factors in Arctic Lapland. J. Biogeogr. 28: 31–45.

Wilson M.V. and Shmida A. 1984. Measuring beta diversity with presence–absence data. J. Ecol. 72: 1055–1064.

Whittaker R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30: 279–338.

Whittaker R.H. 1972. Evolution and measurement of species diversity. Taxon 21: 213–251.

Wright H.E. 1984. Sensitivity and response time of natural systems to climatic change in the late Quaternary. Quat. Sci. Rev. 3: 91–131.

Wunsam S., Schmidt R. and Klee R. 1995. Cyclotella-taxa (Bacillariophyceae) in lakes of the Alpine region and their relationship to environmental variables. Aqua. Sci. 57: 360–386.