

# Long-term changes in floristic diversity in southern Sweden: palynological richness, vegetation dynamics and land-use

Björn E. Berglund · Marie-José Gaillard ·  
Leif Björkman · Thomas Persson

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**Abstract** The rarefaction technique is applied to two Holocene pollen sequences (covering the last 12,000 calendar years) from two lakes in southern Sweden. One represents an open agricultural landscape, the other a partly wooded and less cultivated landscape. The inferred palynological richness is interpreted as an approximate measure of floristic diversity at the landscape scale. The overall trend is an increased diversity from the mid-Holocene to the Modern period, which is linked to a parallel rise in human impact. The pattern is similar for the two sites with peaks corresponding to archaeological periods characterised by deforestation and expanding settlement and agriculture. The highest diversity was reached during the Medieval period, about A.D. 1,000–1,400. Declining diversity during the last 200 years characterises the agrarian landscape. These results confirm, for southern Scandinavia, the “intermediate disturbance” hypothesis for biodiversity at the landscape scale and on millennial to century time scales. They have implications for landscape management in modern nature conservation that has the purpose of maintaining and promoting biodiversity.

**Keywords** Southern Sweden · Rarefaction analysis · Disturbance · Human impact · Prehistoric land-use · Landscape management

## Introduction

Both climate change and human impact play an enormous role in the development and sustainability of ecosystems and their biodiversity over different temporal and spatial scales. The relationships between biodiversity, landscape features and ecosystem sustainability are the subject of much ecological research (e.g. Jongman 1995; Cousins and Eriksson 2001, 2002; Cousins et al. 2002). In this respect palaeoecology, in particular palynology, is a powerful tool to help explore the relationships between biodiversity (in our case the floristic diversity of vascular plants) and environmental changes at the landscape scale on various time scales. It is an ideal approach for gaining a better understanding of the possible processes and controls on long-term ecosystem variability and trajectories (Odgaard 1999; Honnay et al. 2004; Antrop 2005; Emanuelsson 2005).

Several hypotheses concerning the factors influencing biodiversity have been presented by ecologists. Connell’s (1978) “intermediate”-disturbance hypothesis argues that diversity is highest at intermediate levels of disturbance (see also Rosenzweig 1997). For plants, this might be explained by the fact that, at a fine spatial scale (plant community/population), disturbance (e.g. fire, grazing, deforestation, etc.) may favour competitively poor species and therefore increase the number of species and plant communities. At a broader spatial scale (e.g. landscape), disturbances may create new

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B. E. Berglund (✉) · L. Björkman · T. Persson  
Department of Geology/Quaternary Sciences,  
GeoBiosphere Centre, Lund University,  
Sölvegatan 12, 223 62 Lund, Sweden  
e-mail: bjorn.berglund@geol.lu.se

M.-J. Gaillard  
Biology and Environmental Science,  
University of Kalmar, 391 82 Kalmar, Sweden

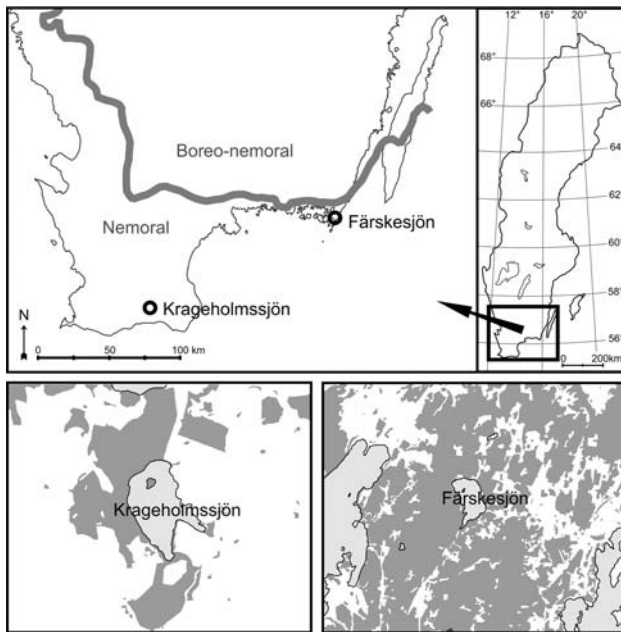
landscape units and therefore increase landscape, plant community and species diversity. This latter is also in accordance with the hypothesis that the larger the area, the larger is the number of species, which is explained by “the larger the area, the higher the number of vegetation units/biota” (Rosenzweig 1997). These hypotheses have to some extent been tested by ecologists at very short time scales (e.g. Rosenzweig 1997), but are very seldom tested at longer timescales, i.e. with the help of palaeoecological studies (e.g. Odgaard 1999). Odgaard (1994) reconstructed Holocene changes in floristic diversity from fossil pollen data and suggested that floristic diversity during the Holocene was highest at an intermediate level of human impact on vegetation, i.e. intermediate landscape/vegetation openness. Similarly, he proposed that floristic diversity was highest at an intermediate frequency of fires, as inferred from changes in the amount of microscopic charcoal fragments (Odgaard 1994).

In this paper, we explore fossil pollen data from two Holocene sequences in southern Sweden with the aim of understanding the influence of human land-use on floristic diversity in the past, and of testing the intermediate-disturbance hypothesis on a range of time scales, i.e. the effect of human disturbance, such as deforestation, fire, and agricultural activities (cultivation, grazing), on flowering plants, biota and landscape diversity.

The rarefaction technique applied to sequences of fossil pollen spectra has been developed as a tool to better understand vegetation dynamics in ancient agrarian landscapes (Birks et al. 1988; Birks and Line 1992). Odgaard (1994, 1999) confirmed the broad but complex relationship between floristic and palynological richness. Odgaard (2001) also discussed the possible errors and problems related to the interpretation of pollen data in terms of floristic diversity, and showed that the effect of changes in the composition and evenness of pollen assemblages (“pollen populations”) through time should be considered when inferring changes (increases or decreases) in floristic diversity from changes in “palynological richness”. Weng et al. (2006) touch on similar and additional problems. They emphasise that the over-representation of some taxa suppresses the detection probability of rare taxa and that low total pollen abundance in a sample enhances the detection probability of rare taxa and long-distance transported pollen grains. They propose that palynological richness in a pollen count proportional to its pollen influx may be one proxy for reconstructing diversity trends through time that overcomes most problems encountered in rarefaction analysis. However, it is constrained by inaccuracy in

estimating pollen influx because of the imprecise time control of sediment cores in many cases. Weng et al. (2006) also discuss estimates of palynological richness by mathematical methods, and suggest that by associating one site from a large basin with a series of sites from very small basins (e.g. forest-hollows), information about both regional and local diversity might be obtained. Nevertheless, the use of the suggested methods and approaches does not solve all the problems mentioned.

So far only a few Late Holocene pollen records have been used to infer changes in past floristic richness/diversity, and to explore their relationship with past land-use changes in northern Europe (Birks et al. 1988; Birks and Line 1992; Berglund et al. 1991b; Bennett et al. 1992; Peglar 1993; Odgaard 1994; Björkman 1996; Lindbladh and Bradshaw 1998; Lindbladh 1999; Poska et al. 2004; Veski et al. 2005). These studies did not attempt to infer species richness from palynological richness (Odgaard 1994), nor did they try to correct for the biases due to variations in “palynological evenness” through time (Odgaard 1999). They simply used changes in “palynological richness” as a relative measure of changes in floristic diversity through time. Similarly, we are using in this study the estimated number of pollen taxa obtained by rarefaction analysis without any corrections, i.e. raw “palynological richness”, as a measure of plant community/vegetation type/landscape diversity rather than strict species/taxon diversity. We have selected two pollen sequences from southern Sweden that meet reasonably well high quality demands of high pollen sums and detailed pollen identifications. These are from Krageholmssjön, a lake in the open agricultural landscape of southernmost Sweden (Gaillard 1984) and from Färskesjön, a lake in the wooded and less cultivated landscape of south-eastern Sweden (Berglund 1966a, b) (Fig. 1). These sites represent two contrasting landscapes and biotic regions in southern Sweden (Naturgeografisk regionindelning av Norden 1984) that are also reflected in today’s cultural landscape (Helmfrid 1994). The two lakes are “large lakes” sensu Sugita (Sugita 1994, 2007) and therefore represent vegetation at the broad regional spatial scale (ca. 100 km<sup>2</sup>) or more (Hellman et al. 2007). This implies that any reconstruction of “floristic diversity” will represent diversity at the broad landscape scale rather than at the fine vegetation spatial scale or strict species scale (“species richness”). Therefore the reconstruction will detect the influence of human impact on floristic diversity in terms of richness in landscape units and vegetation types, and the degree/density of the past landscape/vegetation mosaic.



**Fig. 1** Map of southern Sweden showing the location of the two sites studied in relation to the nemoral/boreo-nemoral forest border (Sjörs 1963). *Small maps*: dark grey represents forested areas, and white represents non-wooded areas such as cultivated fields and grazed land. Light grey areas are lakes

### The sites

*Krageholmssjön* (55°30'N, 13°45'E) is situated near the coast in the southernmost part of the province of Skåne, in southern Sweden, at an elevation of 43 m (Fig. 1). The surrounding landscape is a fertile agriculture area, although woodlands (mainly *Fagus sylvatica* and other broadleaved trees) occur to the west and south of the lake. The lake size is 220 ha. It has been a eutrophic lake throughout the Holocene. The pollen data used in this paper are from a 5 m core taken in the south-western bay of the lake, at 178 m from the shore (BP XVII, Gaillard 1984). It covers the time span from 12,200 cal B.P. until the present (Fig. 2), and is comprised of 96 pollen spectra with 500–1,300 pollen grains and fern spores of terrestrial plants in each count. The total number of terrestrial taxa is 93.

*Färskesjön* (56°10'N, 15°52'E) is situated on the Torhamn Peninsula of the province of Blekinge, in south-east Sweden, at an elevation of 15 m (Fig. 1). The surrounding landscape is rocky with thin soils and therefore cultivation is of low intensity. The lake size is 50 ha. It was isolated from the Baltic Sea at ca. 11,500 cal B.P.. It has been an oligotrophic lake throughout the Holocene. A sediment sequence was obtained from the lake centre, at ca. 250 m from the

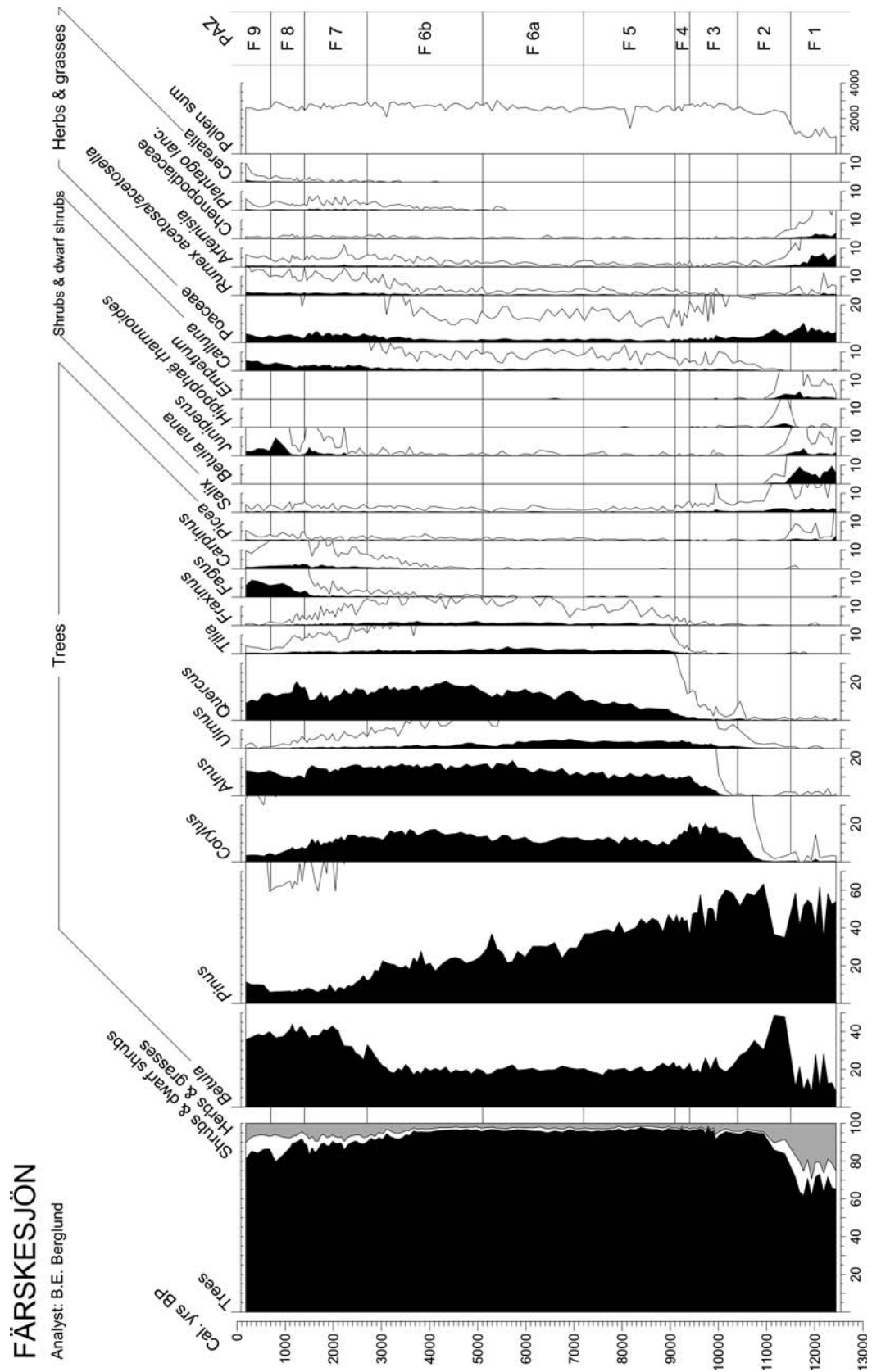
nearest shore. At that location the Holocene was represented by 5 m of gyttja sediments (Berglund 1966a, b). The pollen diagram covers the time span from 12,400 cal B.P. to the 18th century, i.e. part of the Late-glacial and the entire Holocene except the 19th and 20th centuries. The coring techniques at the time did not permit the retrieval of the upper, more recent sediments (Fig. 3). The pollen data comprise 128 pollen assemblages with 2–3,000 pollen grains and fern spores of terrestrial plants in each count, except for the lowermost 11 samples where 900–1,100 grains were counted. The total number of terrestrial taxa is 142.

### Materials and methods

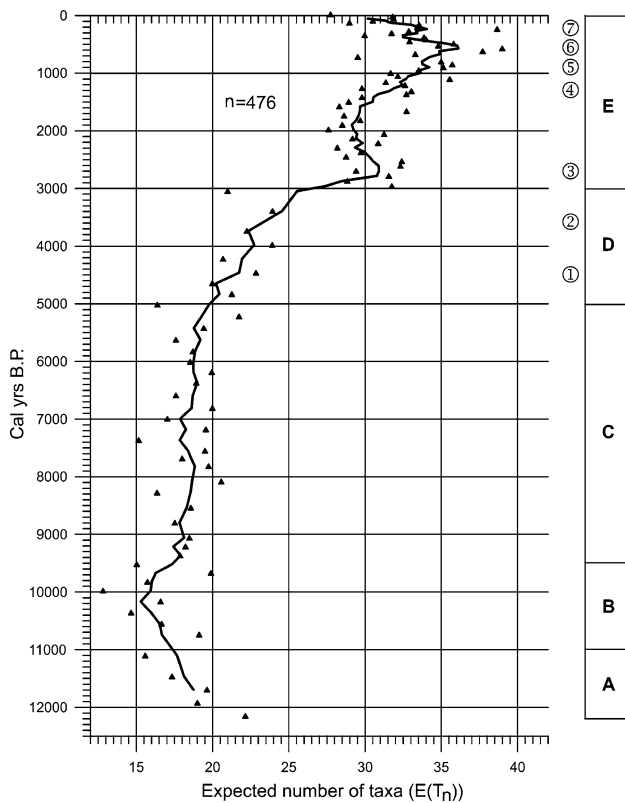
The two sediment sequences were dated by pollen-analytical correlation with other radiocarbon-dated pollen profiles from the same region (Birks and Berglund 1979; Gaillard et al. 1991). The pollen diagram from Krageholmssjön was correlated with a peat profile from Ageröds Mosse (Nilsson 1964), while the pollen diagram from Färskesjön was correlated with peat profiles from Hallarums Mosse and Store Mosse (Berglund 1966b). These tentative  $^{14}\text{C}$ -chronologies were calibrated as calendar-year chronologies using INTCAL98 in the OxCal program version 3.9 (Stuiver et al. 1998). Hence all dates below are given in calibrated  $^{14}\text{C}$  years B.P.. The corresponding B.C./A.D. age is given in the text in cases where archaeological periods are discussed. The pollen assemblage zones were identified using numerical zonation techniques (Gordon and Birks 1972).

Palynological richness analysis was applied to both sequences using the rarefaction technique (Birks and Line 1992). The latter provides estimates of the expected number of terrestrial pollen taxa ( $E(T_n)$ ) (i.e. palynological richness), given that all pollen counts were of the same size. All terrestrial spermatophytes and pteridophytes were included in the analysis. The rarefaction analysis of the pollen data used a base pollen sum of 476 for Krageholmssjön (Fig. 4) and 892 for Färskesjön (Fig. 5). In the case of Färskesjön, a base pollen sum of 2,099 (excluding, for example, the Late-glacial samples with low pollen counts) was also used for rarefaction analysis. The curves in Figs. 4 and 5 are based on running means for five samples. Figure 6 compares the two sites for the last 5,000 years. Increases and peaks in palynological richness are numbered in Figs. 4, 5, and 6 for use in the interpretation and discussion of the results.





**Fig. 3** Simplified percentage pollen diagram from Färskesjön, SE Sweden (Berglund 1966a, b)



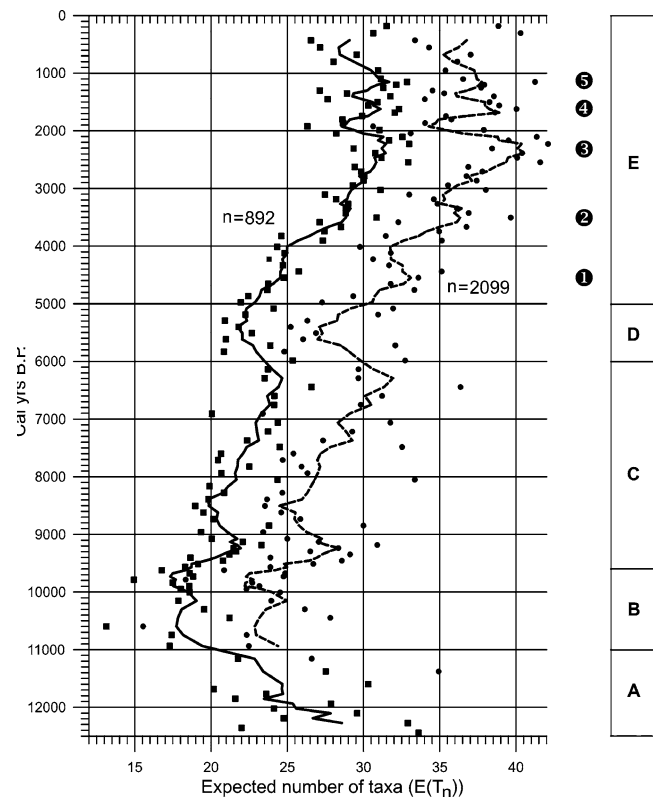
**Fig. 4** Palynological richness [estimated number of pollen taxa  $E(T_n)$ ] based on rarefaction analysis of pollen data from Krageholmssjön, core BP XVII. The curve is based on running means for five samples. A to E refer to different periods of palynological richness as described in the text. The numbers 1–7 refer to diversity “events” (increases and maxima of palynological richness) (see text for more explanations)

## Results

Based on the rarefaction analysis, five time periods are distinguished in terms of palynological richness (expected number of taxa  $E(T_n)$ ) at both sites. The chronozones are according to Mangerud et al. (1974), while the archaeological chronology mainly follows Burenhult (1999). See Fig. 7.

*Krageholmssjön* (Figs. 2, 4, 6)

- (A) 12,200–11,300 B.P. (PAZ K 1, Younger Dryas and early Preboreal chronozones): moderate  $E(T_n)$  values, 22–17.
- (B) 11,300–9,500 B.P. (PAZ K 2–3, mainly Preboreal and early Boreal chronozones): low  $E(T_n)$  values of 18–14, i.e. the lowest values of the Holocene.
- (C) 9,500–5,000 B.P. (PAZ 4–6, late Boreal, Atlantic and early Subboreal chronozones), with slightly increasing  $E(T_n)$  values, 18–20.
- (D) 5,000–3,000 B.P. (PAZ K 7, mainly Subboreal chronozone), with distinctly increasing  $E(T_n)$



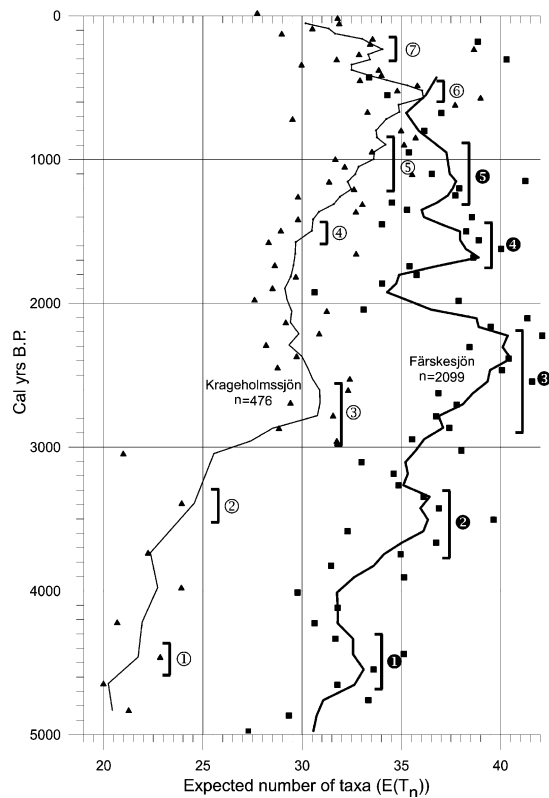
**Fig. 5** Palynological richness [estimated number of pollen taxa  $E(T_n)$ ] based on rarefaction analysis of pollen data from Färskesjön. Two rarefaction curves are compared, (1) based on a pollen sum of 892 (including late-glacial samples), and (2) based on a pollen sum of 2,099 (Holocene samples only). The curves are based on running means for five samples. A to E refer to different periods of palynological richness as described in the text. The numbers 1–5 refer to diversity “events” (increases and maxima of palynological richness) (see text for further explanation)

values, 20–27, particularly 4,600–4,400 and 3,600–3,300 cal B.P..

- (E) 3,000 B.P. to present (PAZ K 8–11, late Subboreal and Subatlantic chronozones), with  $E(T_n)$  values increasing from 27 to a maximum of 38, although the curve is fluctuating and exhibits increases with peaks at 3,000–2,500, 1,600–1,400, 1,200–900, 600–500 and 300–200 cal B.P..

*Färskesjön* (Figs. 3, 5, 6)

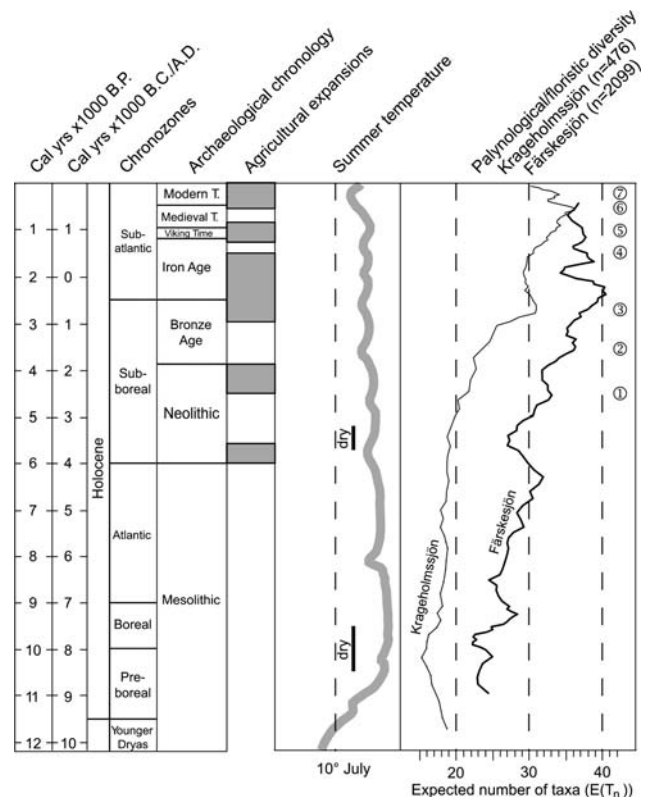
The two curves of palynological richness based on pollen sums of 892 and 2,099 exhibit the same patterns of changes. However, the  $E(T_n)$  values are higher and the peaks/troughs are more pronounced when the larger pollen sum is used. For a more relevant comparison with Krageholmssjön, the  $E(T_n)$  values are given for a base pollen sum of 892  $E(T_n)$  in the following description. Values obtained with a pollen sum of 2,099 are presented in brackets.



**Fig. 6** Comparison of the palynological richness [estimated number of pollen taxa  $E(T_n)$ ] at the two sites Krageholmssjön and Färskesjön for the period 5,000 B.P. to the present. The curves are based on running means for five samples. Diversity “events” 1–7 (Fig. 4) and 1–5 (Fig. 5), respectively, are indicated for comparison (see text for further explanation)

- (A) 12,500–11,000 B.P. (PAZ F 1 and F 2 lower part, Younger Dryas and early Preboreal chronozones), with high  $E(T_n)$  values, 35–25.
- (B) The period 11,000–9,600 B.P. (PAZ F 2 upper part and F 3, late Preboreal and early Boreal chronozones), with the lowest  $E(T_n)$  values of the Holocene, 20–17 (25–22).
- (C) 9,600–6,000 B.P. (PAZ F 4, 5 and 6a lower part, late Boreal and Atlantic chronozones), with  $E(T_n)$  values increasing from 17 (25) to 25 (33).
- (D) 6,000–5,000 B.P. (PAZ F 6a upper part, early Subboreal chronozone), with slightly lower  $E(T_n)$  values, 22–24 (27–30).
- (E) 5,000–ca. 200 B.P. (PAZ F 6b, 7, 8 and 9, late Subboreal and Subatlantic chronozones), with distinctly increasing  $E(T_n)$  values from (23) 30 to a maximum of ca. 33 (42), although the curves are fluctuating and exhibit peaks at 4,700–4,300, 3,800–3,300, 2,800–2,200, 1,800–1,500 and 1,300–900 B.P..

A comparison of the rarefaction curves for the two sites (Figs. 6, 7) shows a congruent pattern with high



**Fig. 7** Synthesis of Holocene vegetation/landscape diversity in southern Sweden based on pollen data from Krageholmssjön and Färskesjön, plotted against chronozones (Mangerud et al. 1974), archaeological chronology (after Burenhult 1999), agricultural expansion phases (according to Berglund et al. 1991a, 2002) and estimated summer temperatures (from Digerfeldt 1988; Snowball et al. 2004). Diversity “events” 1–7 are indicated for comparison (see text and caption to Fig. 6 for further explanation)

values in the Late Weichselian, a minimum in the early Holocene and after that, steadily increasing values throughout the Holocene, with several peaks and troughs during the late Holocene. “Diversity events”, i.e. periods of expansions and peak values of  $E(T_n)$  were identified (Figs. 4, 5, 6). A tentative between-site correlation of these “diversity events” is suggested, bearing in mind that firstly the quality of the chronologies is not optimal as they are based on an indirect relative dating by pollen-stratigraphical cross-correlation with other  $^{14}\text{C}$ -dated sites (see “Materials and methods”), secondly the precision of the  $E(T_n)$  values is lower for Krageholmssjön than for Färskesjön because of a lower base sum for rarefaction and thirdly the Krageholmssjön curve is continuous to the present time and characterised by a higher time resolution than the Färskesjön curve for the last 1,000 years; the “diversity events” 6 and 7 are therefore identified only in the Krageholmssjön sequence. The approximate age of the identified “diversity events” and their correlation with archaeological periods are as follows:

1. 4,700–4,300 B.P. (2,750–2,350 B.C.), Middle to Late Neolithic
2. 3,800–3,300 B.P. (1,850–1,350 B.C.), early Bronze Age
3. 2,900–2,200 B.P. (950–250 B.C.), Late Bronze Age and Pre-Roman Iron Age
4. 1,800–1,500 B.P. (A.D. 150–450), Roman Iron Age
5. 1,300–850 B.P. (A.D. 650–1,100), Viking period to early Medieval period
6. 600–400 B.P. (A.D. 1,350–1,550), Late Medieval period
7. 300–150 B.P. (A.D. 1,650–1,800), Modern period

## Discussion

The two pollen sequences discussed in this paper are of regional character (*sensu* Jacobson and Bradshaw 1981; Sugita 1994, 2007), i.e. they represent very large areas of ca. 100 km<sup>2</sup> or more (Hellman et al. 2007). As stated in the introduction, palynological richness can be used as a rough measure of floristic diversity at the landscape level, as long as one is aware of the influence of changes in taxa composition and “palynological evenness” on palynological richness (Odgaard 1999, 2001; Weng et al. 2006). In other words, “palynological richness” from large lakes is not a direct measure of species richness and cannot be converted into “floristic richness” following the approach of Odgaard (1994) because of the regional scale of the pollen assemblages and their implied bias in terms of species richness (Odgaard 2001). Therefore changes in palynological richness at Krageholmssjön and Färskesjön are interpreted in terms of landscape diversity, i.e. richness in vegetation/landscape units around the lakes, or diversity within the landscape mosaic. The assumption is that the more vegetation/landscape units there are, the higher the species number, and hence the higher the palynological richness.

The high diversity values in the late-glacial Younger Dryas zone are interpreted as a consequence of a mosaic landscape with species-rich steppe and tundra ecosystems (Iversen 1954; Berglund 1966a). In the early Holocene, before 9,500 B.P., most of the late-glacial elements disappeared and the vegetation was characterised by a species-poor flora of boreal character (Hultén 1971). Nevertheless, it should be stressed that the early Holocene, from 11,500 to ca. 11,000 B.P., is still characterised by relatively high values of palynological richness and therefore still had some remnants of late-glacial vegetation. The trough in the curve can also partly be explained by the reduced evenness of pollen assemblages, since three tree pollen taxa

(*Betula*, *Pinus* and *Corylus*) are very dominant. This minimum is followed by a steady rise in palynological richness until 6,000 B.P. (Färskesjön) and 5,000 B.P. (Krageholmssjön) which we correlate with the gradual immigration of a nemoral flora. This development can be compared—in a space-for-time analogy—to the well-established modern gradient in floristic richness from boreal to nemoral vegetation zones in Fennoscandia (Hultén 1971; Grytnes et al. 1999).

From 6,000 B.P. onwards, the expansions and peaks in palynological richness may be correlated with disturbance phases caused by deforestation and expansion of the open landscape (Figs. 2, 3; Berglund 1966b, 1969; Berglund et al. 1991b; Gaillard 1984; Gaillard and Göransson 1991; Regnéll 1989, 1991). The period 6,000–5,000 B.P. in the Färskesjön sequence shows a minimum of palynological richness around 5,500 B.P.. This was unexpected for this period of Neolithic landnam with small-scale clearances that might have caused some fragmentation of the forests (Berglund 1966b). However, the small human impact in that area may have been strong enough to favour increased tree pollen production and under-representation of herb pollen. The strong increase in the amount of *Pinus* pollen at the same time may also contribute to a reduced evenness of the “pollen population” and therefore to a minimum of palynological richness.

During the Late Holocene (ca. 5,000 B.P. to present), the two sequences demonstrate distinctly increasing diversity with amazingly congruent patterns from 5,000 to ca. 2,000 B.P.. After that, more pronounced between-site differences occur. From ca. 3,000 B.P. both regions were strongly influenced by the steady expansion of farming, which caused disturbance and fragmentation of the forests by clearance, grazing, small-scale farming, etc. The mosaic character of the landscape increased strongly and many ecotonal boundaries would have been created. Open or half-open communities expanded, which led to an enrichment of the flora with new species, apophytes as well as anthropochores. A comparable development was described in an area of marginal farmlands in the province of Småland, northwest of the region of Färskesjön, where infield/outland land-use is still preserved (Lindbladh and Bradshaw 1998; Lindbladh 1999). Local pollen diagrams from infields with small-scale farming in a half-open landscape were compared with diagrams from “outfield” (or outland, see definition in Crozier 1991) grazed forests. According to Lindbladh and Bradshaw (1998) and Lindbladh (1999), vegetation diversity was moderate in both the infields and “outfields” from 2,000 until 1,000 B.P. when clearings and cultivation started in the area. From that time, the infields developed into a



mosaic, half-open landscape with small fields, dry meadows and wet meadows that was maintained until the present day, whereas the “outfield” area remained wooded with low diversity.

Another observation is of interest, namely the distinct diversity minima in the Färskesjön curve during the Iron Age. The first minimum is also correlated with lower values of palynological richness at Krageholmssjön between ca. 2,250 B.P. and 1,650 B.P. (300 B.C. and A.D. 300). Tentatively, we correlate the two minima at Färskesjön with agrarian and settlement crises during the period 1,950–1,750 B.P. and 1,450–1,250 B.P. (A.D. 1–200 and 500–700) (Berglund et al. 2002). At Färskesjön, there is also a diversity decrease after 1,050 B.P. (A.D. 900) with a trend towards a minimum around (650–450 B.P.) A.D. 1,300–1,500. This is possibly caused by a decrease in settlement and farming in the mid-Medieval period. The situation seems to have been the opposite at Krageholmssjön where maximum diversity is recorded at that time. It is also known from historical sources that the Medieval agrarian crisis only affected the area around that lake to a minor extent (Skansjö 1991).

The decreasing trend in diversity values at Krageholmssjön during the last 200 years is significant. It is also characteristic of pollen diagrams from nearby lakes, such as the small lake Bussjösjön (Regnéll 1989; Berglund et al. 1991b). This recent, declining trend in palynological richness correlates with the documented restructuring of the agriculture and landscape of the region that started in the nineteenth century (Bengtsson-Lindsjö et al. 1991; Berglund et al. 1991a; Lewan 1991; Olsson 1991). The agrarian development with expanding cultivation implied the abandonment of the infield/“outfield” system, accompanied by a dramatic reduction in the area of hay-meadows, open pastures, wood pastures, and woodlands. Efficient, high-productive agriculture also involved drainage of fields and creation of larger field units which meant a further reduction in semi-natural vegetation units such as ditch banks, hedges, etc. This development led to a major decrease in the landscape/vegetation diversity of the entire farming regions of the southern and western parts of the Skåne province, and particularly in central agrarian areas such as that of Krageholmssjön. Similar trends of decreased diversity in connection with agricultural expansion and deforestation during the recent centuries have been reported from other areas in Europe, e.g. south-east England (Peglar 1993). If the sequence from Färskesjön covered the last centuries, the trend in palynological richness might have been different in that case, since the modern landscape is still characterised by a mosaic of fragmented wood-

and heathland vegetation with some small-scale farming. However, formerly grazed open “outfields” (heath areas) have been abandoned and converted into poor woodlands with low floristic diversity (cf. Berglund 1963; Emanuelsson 1997, 2005).

## Conclusions

1. The rarefaction technique applied to detailed pollen sequences is a useful tool to detect past changes in palynological richness that can be interpreted in terms of vegetation and landscape diversity and mosaic, given that the pollen data are of high quality, i.e. pollen counts are large and pollen identification is as detailed as possible. The technique should preferably be applied to sediment cores with a high and consistent time resolution.
2. During the mid-Holocene, 9,000–6,000 B.P., the two lake sequences studied here demonstrate a gradual rise in floristic diversity related to the forest development from boreal to nemoral ecosystems. This is comparable to the known modern gradient in floristic diversity from boreal to nemoral forests in Fennoscandia.
3. During the Late Holocene, 5,000 B.P. to the present, the lake sequences show distinctly higher values of floristic diversity than earlier. This trend is associated with increased human impact on the landscape, i.e. the start and expansion of agrarian land-use since the Neolithic time. During this period the forests became more fragmented and open vegetation communities became more frequent. This resulted in the expansion of plants from various niches in the landscape. At the same time the flora was enriched by new, introduced taxa.
4. From 5,000 B.P. there is a congruent pattern of floristic diversity at the two sites. Seven “diversity events” were identified. These increases and maxima in floristic/landscape diversity are ascribed to changes in human activity/land use.
5. At Färskesjön, situated in the marginal agrarian landscape of south-east Sweden, distinct diversity fluctuations are recorded during the Iron Age. The minima are correlated with agrarian and societal crises during the periods 1,950–1,750 B.P. (A.D. 1–200) (also registered at Krageholmssjön) and 1,450–1,250 B.P. (A.D. 500–700). The mid-Medieval agrarian crisis 650–450 B.P. (A.D. 1,300–1,500) is also reflected at the same site.
6. The falling trend in floristic/landscape diversity since 150 B.P. (A.D. 1,800) at Krageholmssjön is

correlated with the expanding, restructuring agriculture that caused abandonment of the ancient infield/“outfield” system and a considerable reduction in the area of meadows, pastures, and woodlands, i.e. development towards the modern, monotonous agricultural “steppe”.

7. The results presented in this paper suggest that:
  - (a) disturbances by human activities (e.g. fire, grazing, deforestation, etc.) since the Neolithic time led to an increase in the number of species and plant communities at the local, fine spatial scale. New landscape units were created and therefore landscape, biota and species diversity increased at the broad spatial, landscape scale. This implies that the hypothesis “the higher the number of vegetation units/biota, the larger the number of species” (Rosenzweig 1997) is confirmed for the Holocene of southern Sweden on the time-scales of centuries and millennia.
  - (b) human impact from the Late Bronze Age to 150 B.P. (A.D. 1,800) probably represented an “intermediate” level of disturbance that resulted in the highest values of “palynological richness” of the Holocene. Before 3,000 B.P. (1,050 B.C.), the level of disturbance was probably still too low to produce diversity maxima, and from 150 B.P. (A.D. 1,800) the level of disturbance exceeded the ideal “intermediate” state and had a negative effect on floristic diversity, i.e. the latter decreased. Connell’s intermediate-disturbance hypothesis (1978) is therefore supported for the Holocene period in southern Sweden on the time scales of centuries and millennia. Our results are comparable to those of Odgaard (1994) for Holocene landscapes in Denmark, which confirms the intermediate-disturbance hypothesis in southern Scandinavia.
8. These results imply that high biodiversity levels could be achieved today if landscape management involved disturbance regimes analogous to those of the agrarian landscapes of the Bronze Age, Late Iron Age and Medieval period up to ca. 150 B.P. (A.D. 1,800). Moreover, global warming might lead to a northward shift of the nemoral/boreo-nemoral vegetation boundary in Scandinavia, which would imply an increase in floristic diversity at latitudes north of the present location of that boundary. Sætersdal et al. (1998) suggested that such changes may occur in the southern boreal vegetation zone.

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