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ORIGINAL ARTICLE

The role of landscape structure in determining palynological and floristic richness

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Abstract The associations between floristic and palynological richness and landscape structure were studied based on modern pollen–vegetation data from a patchy cultural landscape in southern Estonia (northern temperate vegetation zone). Nine study sites (small lakes and their surrounding vegetation) represent land cover gradient from closed forest to semi-open vegetation. Floristic richness (number of species) and floristic richness of pollen types (number of pollen-equivalent taxa) were used to describe the vegetation within the radius of 250 m from the pollen sampling sites. Palynological richness was calculated to describe the modern pollen samples diversity. Landscape structure was estimated on the basis of landscape openness and three landscape diversity measures: richness of community patches, Simpson evenness of community patches and Simpson diversity of community patches. To study the effect of the spatial scale of landscapes on the vegetation–landscape and pollen–landscape associations, landscape structure was estimated within eight radii (250–2,000 m) around each lake. The results showed that landscape openness was the most important determinant of both floristic richness and palynological richness in southern Estonia and that landscape diversity estimated by Simpson diversity index was also significantly associated with the richness estimates. Floristic and palynological richness were significantly positively correlated with landscape structure within the radii greater than 1,000 m from the pollen sampling sites, which is similar to the estimated Relevant Source Area of Pollen in southern Estonia. We conclude that within one floristic or climatic region, palynological richness gives reliable estimates about the variation in floristic richness and landscape structure; however, caution must be taken when comparing pollen-inferred vegetation diversities from different regions or when interpreting fossil pollen records from times with highly different vegetation associations.

Keywords Palynological richness · Floristic richness · Landscape diversity. Landscape openness · Landscape patchiness · Estonia

Introduction

Preservation of biodiversity is one of the major global concerns today. Human-induced changes in landscape structure due to intensification of forestry and agriculture, urbanization and over-use of natural areas are considered among the main threats to biodiversity (Vitousek et al. 1997; Foley et al. 2005). Studies of past biodiversity and its change through time and space are valuable for understanding the present-day patterns of biodiversity and for predicting the response of

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diversity to future changing environmental conditions and anthropogenic land-use. Knowledge of the long term history of biodiversity is difficult to obtain, as written sources are scarce and rarely extend back more than a few centuries. Fossil pollen is one of most widely used sources of information for investigating past vegetation assemblages. In order to interpret the historical pollen data, it is necessary to study the present-day relationships of palynological diversity (based on sedimentary pollen data) with surrounding vegetation diversity and landscape diversity.

During the last two decades, several quantitative pollen-based vegetation reconstruction models have been developed (Sugita 1994, 2007a, b) leading to a number of pollen-based quantitative vegetation composition reconstructions and a few spatial land-cover reconstructions (Nielsen and Odgaard 2005; Veski et al. 2005; Poska et al. 2008). One of central concepts of these models is the Relevant Source Area of Pollen (RSAP) in order to define the spatial scale of vegetation represented by pollen assemblages (Sugita 1994). Several model-based and empirical investigations have detected a significant relationship between the size of RSAP and the spatial structure of the landscape (Sugita et al. 1999; Broström et al. 2005; Nielsen and Sugita 2005; Hellman et al. 2009; Poska et al. 2011).

Although quantitative vegetation reconstructions based on vegetation reconstruction models have been shown to reflect relatively well the abundances of the dominant taxa in the surrounding vegetation (e.g. Hellman et al. 2008; Soepboer et al. 2010), reconstructions of past vegetation diversity based on pollen data remain rare because the drivers of the relationship between vegetation diversity and palynological diversity are still unclear (Odgaard 2001). It is generally accepted that palynological richness (number of pollen types in pollen samples) reflects the floristic richness (number of species) of the surrounding landscape (e.g. MacDonald et al. 2008), but this assumption has rarely been tested with modern pollen and vegetation data (but see Meltsov et al. 2011). One of the possible reasons behind the discrepancy between palynological richness and floristic richness is caused by the fact that pollen types that can potentially be identified in the sedimentary pollen record do not necessarily correspond to plant species. The reduction in richness during transformation from floristic species to pollen equivalent taxa is considerable (about 60 % in southern Estonia—Meltsov et al. 2011). Furthermore, many of these pollen types are rarely, if ever, found in sediments, which in turn, reduces significantly the palynological richness (Meltsov et al. 2011). Despite this drastic decrease in species number, Meltsov et al. (2011) found significant positive relationships between palynological richness, floristic richness of pollen types (based on pollen equivalent taxa in the actual vegetation) and floristic richness. They also showed that although the total floristic richness of pollen types in the 250 m radius around the study lakes was correlated with the total palynological richness, the correlation was not found if only wind-pollinated taxa were considered.

Floristic richness is typically positively associated with environmental heterogeneity and landscape diversity within the studied area (Burnett et al. 1998, 2003; Nichols et al. 1998; Weibull et al. 2003; Statzner and Moss 2004; Lundholm 2009). The relationship between floristic richness and landscape diversity can be viewed in terms of the habitat diversity hypothesis (sensu Shmida and Wilson 1985), by which more diverse landscapes contain more available habitats and can, therefore, accommodate more species. Similarly, the “mosaic concept” developed by Duelli (1997) assumes that floristic richness in mosaic landscapes depends on the number of habitat patches. In addition, high landscape diversity in the surroundings of the study area increases the pool of species (Pärtel et al. 1996) that can colonize the local habitats (Öster et al. 2007; Reitalu et al. 2009, 2011). In addition to landscape diversity, openness in the landscape (the amount of the non-forested area) is considered to be an important factor influencing floristic richness in the northern temperate zone (Billeter et al. 2008; Meltsov et al. 2011). Semi-open landscape exhibits greater floristic richness than completely open or completely forested landscapes (Billeter et al. 2008).

Although several studies have shown significant relationships between floristic richness and landscape structure and diversity (Duelli 1997; Honnay et al. 2003; Statzner and Moss 2004; Billeter et al. 2008; Reitalu et al. 2011), it remains unclear how well floristic richness based on pollen taxonomy and palynological richness are suitable for representing floristic richness and reflecting landscape diversity.

In this study, we explore the relationship between palynological richness, floristic richness, floristic richness of pollen types and landscape diversity using a modern pollen–vegetation calibration dataset from small lakes in southern Estonia. Our objectives were:

(a) To test whether floristic richness, floristic richness of pollen types and palynological richness are similarly associated with landscape structure and diversity.
(b) To explore the influence of spatial scale of the studied landscape on the association between floristic/palynological richness and landscape diversity.

Materials and methods

Study area

The study was carried out in southern Estonia (Fig. 1), which is situated in the northern temperate forest zone. The land-cover of the study area is patchy, consisting of a mixture of forests, mires, cultivated fields, grasslands and settlements. Forests cover about 58 % of the total area (Pärt et al. 2008). The main tree species that comprise most of the forests are *Alnus incana*, *Betula pendula*, *Picea abies* and *Pinus sylvestris*. Temperate broad-leaved deciduous trees, such as *Acer platanoides*, *Fraxinus excelsiour*, *Quercus robur*, *Tilia cordata* and *Ulmus glabra* appear occasionally. The main crops grown in the fields are cereals (*Avena sativa*, *Hordeum vulgare*, *Secale cereale*, and *Triticum aestivum*), rape (*Brassica napus*) and potatoes (*Solanum tuberosum*). The most abundant species on the grasslands are graminoids, such as *Agrostis capillaris*, *Alopecurus pratensis*, *Dactylis glomerata*, *Elymus repens*, *Festuca rubra*, *F. pratensis*, *Phleum pratense* and *Poa trivialis* (Kukk and Kull 2005).

Nine small lakes with a median diameter of 200 m (area 1–14 ha) were selected for study (Fig. 2; Table 1). The greatest distance between two lakes is about 100 km (Fig. 1). The lakes were selected along a gradient of different land-cover patterns, and landscape openness within a radius of 2 km from the lake varied from 1 to 51 % (Fig. 2; Table 1).

Vegetation mapping

Vegetation mapping was implemented within a 2 km radius of each lake in accordance with the simulation-based estimate of RSAP (sensu Sugita 1994) of the lakes (Gaillard et al. 2008). Detailed vegetation surveys were carried out within 250 m around the lakes. The vegetation maps were digitalised using MapInfo Professional 7.5 (MapInfo Corporation, Troy, NY, USA).

Vegetation mapping within 2 km

The vegetation maps were compiled within a 2 km radius around each lake. The state forestry database was used to compile the forest maps (“Environmental Information”—http://www.keskkonnainfo.ee/). In non-forested areas or in forested areas with no forest data available, vegetation field-surveys were performed using aerial photographs (scale 1:10,000) as base-maps. During the field-survey, the communities were identified (according to Paal’s 1997 vegetation classification scheme). In every mapped community patch, the percentage cover of the major wind-pollinated pollen taxa (*Alnus*, *Betula*, *Corylus*, *Fraxinus*, *Picea*, *Pinus*, *Quercus*, *Salix*, *Ulmus*, *Tilia*, *Artemisia*, Cerealia, Chenopodiaceae, Cyperaceae, *Plantago lanceolata*, *P. major/media*, Poaceae, *Rumex acetosa* and *Urtica*) was determined visually at three random points. The average of the three determinations was used as an estimate of pollen taxon abundance within each community patch.

Vegetation mapping within 250 m

An inscribed circle was fitted to aerial photographs of each lake such that it touched the nearest edge of the lake. Vegetation surveys were made within a 250 m wide buffer area from the edge of the inscribed circle around each lake.

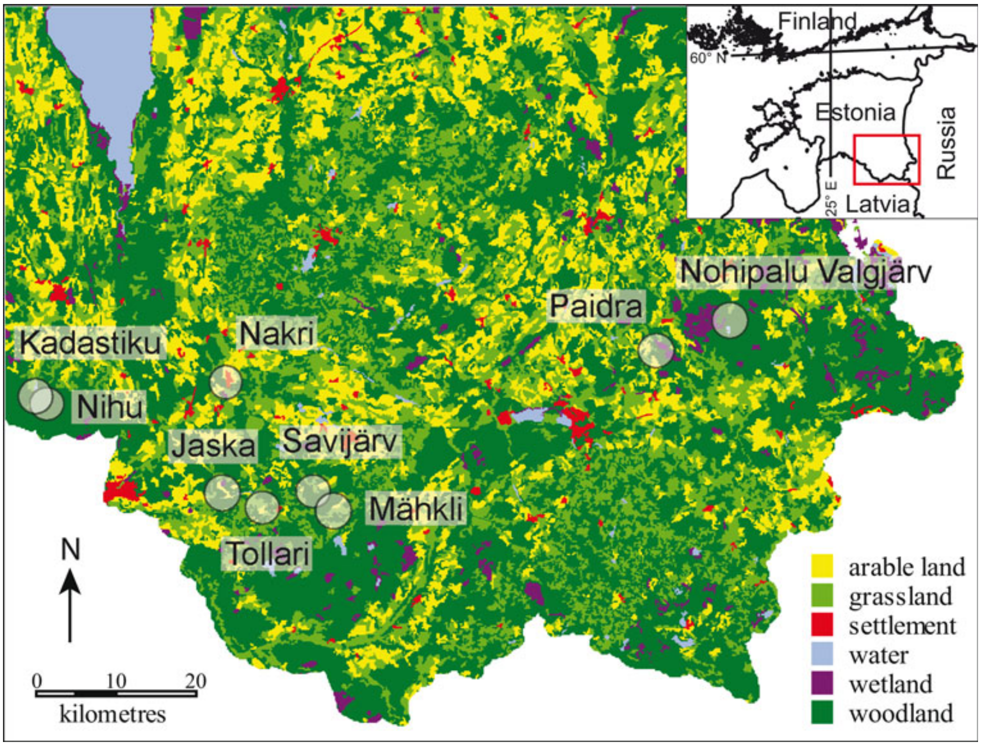

Fig. 1 The study area in southern Estonia. The sites for pollen and vegetation data collection are marked with *circles*

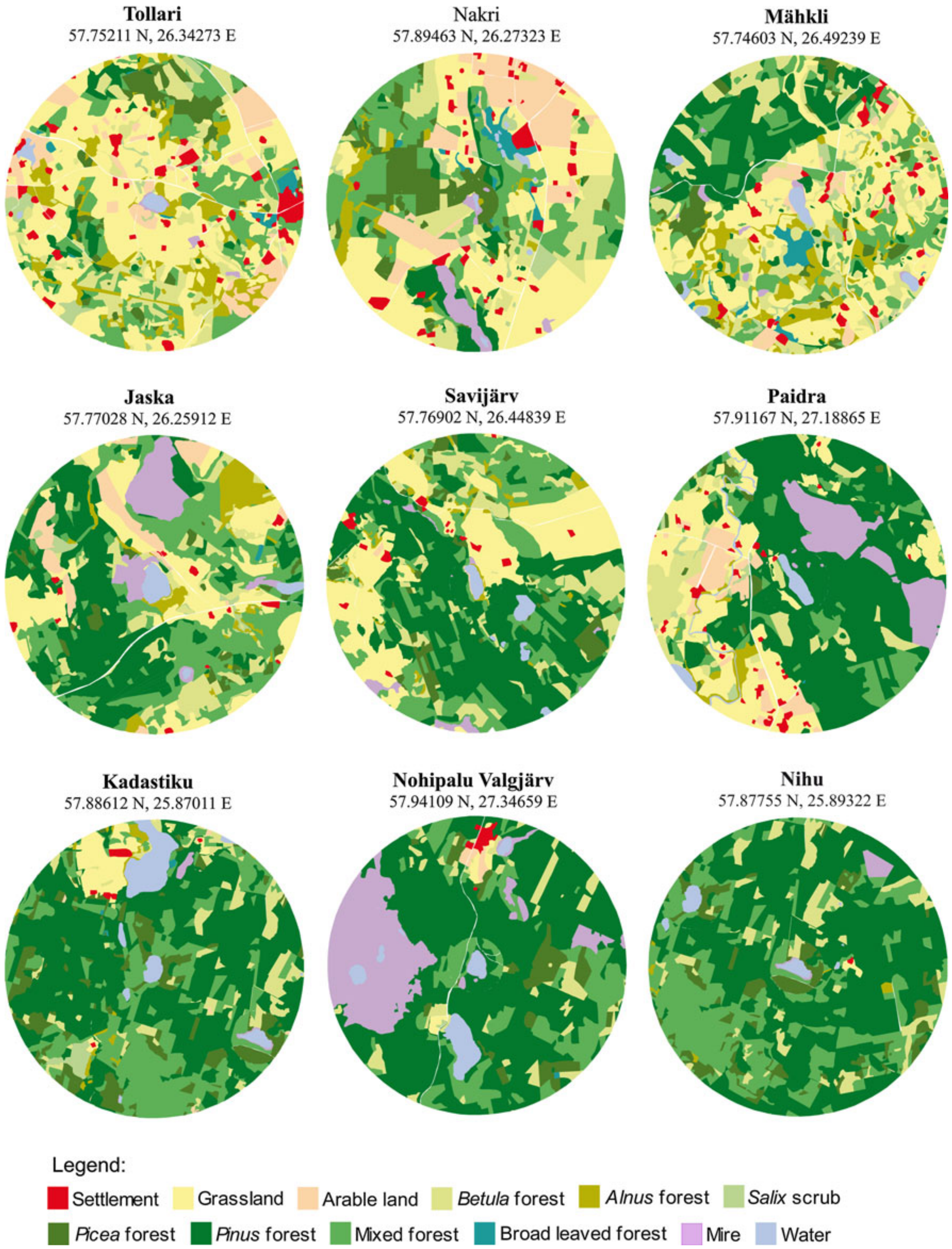

Fig. 2 Vegetation maps of nine study sites (within a 2 km radius from the lake basin)

Two different methods were used during the vegetation survey:

(1) *Plot method*. On aerial photographs (scale 1:10,000) the 250 m wide band was divided into four equal sectors and ten vegetation survey points were placed in each sector as evenly as possible considering the landscape patchiness. The percentage cover of all vascular plant species was recorded within a 1 m × 1 m plot in each of the 40 survey points.

Table 1 Characteristics of study sites

Study site	Openness (%)	Lake area (ha)	Lake diameter (m)	Water depth (m)	Fr	Frp	Pr
Jaska	29	14.3	340	3.2	147	74	32
Kadastiku	6	7.2	208	6.4	101	53	28
Mähkli	39	8.3	170	4.6	153	71	31
Nakri	48	1.0	43	2.5	118	71	33
Nihu	1	5.5	185	4.0	80	46	26
Nohipalu Valgejärv	2	6.6	230	6.2	83	54	30
Paidra	25	11.0	210	6.2	99	58	30
Savijärv	26	6.7	162	8.6	110	55	28
Tollari	51	5.8	210	3.0	163	78	34

(2) *Community species list method*. Inside the 250 m wide band, vegetation communities (according to Paal 1997) were identified and mapped in the field and a full species list, including abundance estimates using the Braun-Blanquet cover-abundance scale (rare—1, uncommon—2, moderately common—3, frequent—4, dominant—5) was recorded for each community patch.

A pollen-type equivalent taxon according to Fægri and Iversen (1989) and Beug (2004) was assigned to each recorded species.

Pollen-based vegetation classification scheme

The vegetation classification scheme used for vegetation mapping (according to Paal 1997) does not always reflect the landscape structure from the pollen "point of view". For example Paal's (1997) communities "poor paludified forest" and "dry boreal forest" can both be pine forests with *Vaccinium* shrub and occurring next to each other, they would form one community patch from the pollen "point of view" instead of two community patches.

Cluster analysis was used to create a vegetation classification scheme that would reflect the pollen "point of view". The community species lists ("Vegetation mapping within 250 m" section, method 2) with abundance estimates of the major wind-pollinated pollen taxa within each 250 m mapping area were used to determine the pollen-based vegetation classification scheme. Program Past 2.10 (Hammer et al. 2001) and Ward's method were used to carry out the cluster analysis. According to the cluster analysis the vegetation was classified to the following pollen-based community types: mire, grassland, arable land for open areas; and *Salix*, *Alnus*, *Betula*, *Picea*, *Pinus* and mixed forest for forested areas. "Settlement", "temperate broad leaved forest" and "water body" were added to the community type list, as these communities were not identified using cluster analysis due to a lack of vegetation data or poor representativity. All communities mapped in the field according to Paal's (1997) vegetation classification scheme within 2 km were renamed according to the above described pollen-based classification scheme.

Pollen sampling and pollen analysis

A sediment sample (upper 1 cm) was taken from the centre of each lake using a Willner-type gravity corer (produced in Uppsala University e.g. Nilsson 2004), which operates similarly to Kajak-type corers (Glew et al. 2001). Two cm^3 of sediment were taken from each well-mixed sample for pollen analysis. Pollen samples were prepared with the standard KOH, acetolysis method (Erdtman 1969) and mounted in silicone oil (Andersen 1960). A total of 1,500 arboreal pollen grains was counted in each sample. Pollen identification was carried out according to Fægri and Iversen (1989) and Beug (2004) and using the modern pollen reference collection of the Department of Botany at the Estonian University of Life Sciences.

Vegetation and pollen variables (Table 2)

Floristic richness (Fr) indicates the number of species recorded per sampling site (Magurran 2004; Van Dyke 2008), estimated as the total number of species identified in the 40 vegetation plots around each lake within a 250 m radius. Since the vegetation plots contained only herb taxa, the number of tree species recorded in the community species lists ("Vegetation mapping within 250 m" section, method 2) were added to the herb Fr.

Floristic richness of pollen types (Frp) is the corresponding term for Fr when all species were reduced to pollen type equivalents.

Palynological richness (Pr) reflects the number of pollen types in the pollen sample for a specific counting sum (Birks and Line 1992; Odgaard 1999). Pr was estimated for a constant counting sum (1,612) using rarefaction analysis (Birks and Line 1992). The result of rarefaction analysis represents the estimated number of taxa reduced to the lowest pollen

Table 2 Explanations and abbreviations of diversity measures

Type of diversity	Diversity measure and explanation	Abbreviation
Palynological diversity	Palynological richness—number of pollen types found in the pollen sample (rarefaction to 1,612 pollen grains)	Pr
Vegetation diversity	Floristic richness—number of species within 250 m radius around the pollen sampling site	Fr
	Floristic richness of pollen types—number of pollen-equivalent taxa within 250 m radius around the pollen sampling site	Frp
Landscape diversity	Patch richness—number of community patches in the landscape within eight radii (250–2,000 m) according to pollen-based vegetation classification scheme	PatchR
	Patch evenness—Simpson evenness of community patches in the landscape within eight radii (250–2,000 m) according to pollen-based vegetation classification scheme	PatchE
	Patch diversity—Simpson diversity of community patches in the landscape within eight radii (250–2,000 m) according to pollen-based vegetation classification scheme	PatchS

sum for a set of samples. The estimated number of taxa $[E(T_n)]$ is calculated according to the formula:

$$E(T_n) = \sum_{i=1}^{T} 1 - \left[\frac{(N - N_i)!(N - n)!}{(N - N_i - n)!N!}\right] \tag{1}$$

where $E(T_n)$ is the expected palynological richness in standardized pollen count N_i, T is the total number of pollen types in the original pollen assemblage, N is the overall pollen sum, and n is the number of grains selected for standardization in the rarefied sample (Birks and Line 1992).

Landscape variables (Table 2)

Diversity can be divided into two main components: richness and evenness.

The richness of community patches (PatchR) was estimated as the number of community patches around each lake.

The evenness of community patches (PatchE) was calculated according to Simpson's evenness (E) formula (Magurran 2004):

$$E = \frac{1/\sum_{i=1}^{S} p_i^2}{S} \tag{2}$$

where p_i is the proportion of area covered by patch i and S is the number of patches.

Diversity indices that integrate both richness and evenness are also often used to describe landscape structure (McGarigal 2002). The Simpson's diversity index (D) (Magurran 2004) was used to calculate diversity of community patches (PatchS):

$$D = 1 - \sum_{i=1}^{S} p_i^2 \tag{3}$$

The E and D range from zero to one. Simpson's diversity index and Simpson's evenness index were chosen as both give more weight to the more abundant taxa and Simpson's evenness index is independent of the number of taxa (Smith and Wilson 1996; Magurran 2004).

In addition to the landscape diversity measures, the proportion of unforested area around each lake was used as a measure of landscape openness.

All the above listed measures of landscape structure were calculated separately within eight radii around each lake (250, 500, 750, 1,000, 1,250, 1,500, 1,750 and 2,000 m radius from the inscribed circle within the lake) using the pollen based vegetation classification scheme.

Numerical analysis

To test whether the vegetation structure was spatially autocorrelated (geographically close locations being also more similar in their vegetation composition), we used Mantel tests of spatial distance (Euclidean distance) between the lakes with vegetation dissimilarity (Fd), vegetation dissimilarity of pollen types (Fdp) and palynological dissimilarity (Pd). The Bray-Curtis dissimilarity coefficient (Bray and Curtis 1957) was used to calculate the vegetation and pollen dissimilarities. Correlation analyses using the Pearson product-moment correlation coefficient were carried out to find relationships between Fr/Frp/Pr and PatchR/PatchE/PatchS/Openness within eight radii around the lakes (250, 500, 750, 1,000, 1,250, 1,500, 1,750 and 2,000 m).

In the present study we did 96 correlation tests, which may lead to false significances (Type I error). To correct for the high number of significance tests, the Benjamini and Hochberg (1995) correction was used to adjust the p values.

The software package R (version 2.10.1) was used for statistical analysis (R Development Core Team 2009).

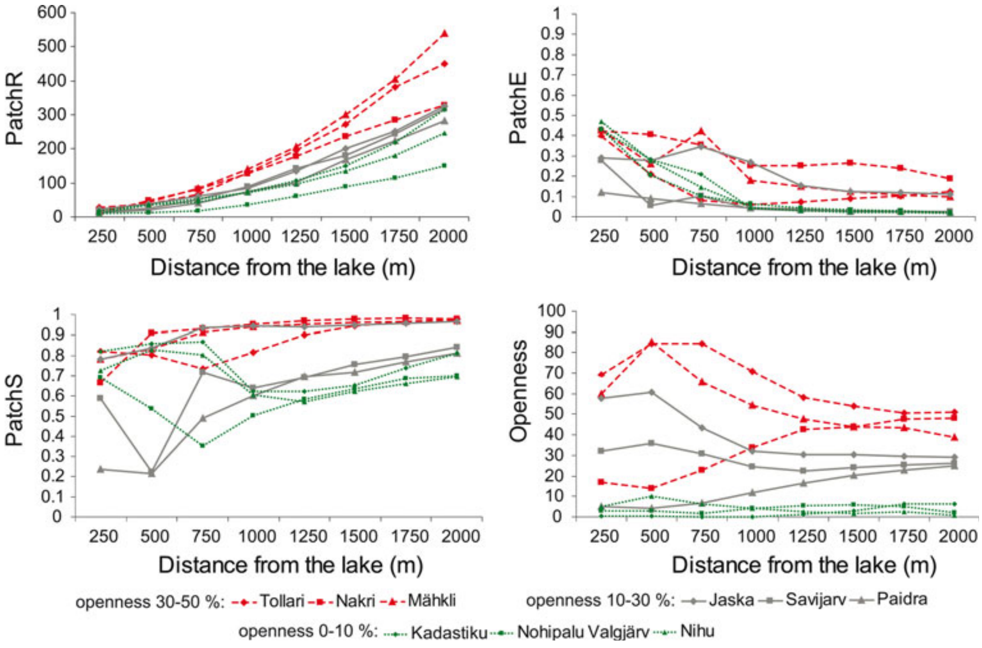

Fig. 3 Variation of measures of landscape diversity (PatchR, PatchE, PatchS and Openness) at different distances from the lakes. Variables are explained in Table 2

Results

Mantel's test between Fd/Fdp/Pd and geographical distance did not show any significant associations (for Fd $r = 0.12$, $p = 0.2$; for Fdp $r = 0.27$, $p = 0.07$; for Pd $r = -10$, $p = 0.67$) indicating that geographically close sites were not more similar in vegetation nor in pollen composition.

Vegetation and pollen variables and landscape variables

A total of 307 plant species corresponding to 127 pollen/spore types were identified in the vegetation of the sampling sites within the radius of 250 m (see the list with pollen-equivalent taxa in Meltsov et al. 2011). Floristic richness (Fr) varied between 80 and 163 (average = 117) and floristic richness of pollen types (Frp) varied between 46 and 78 (average = 62) (Table 1). Fr was strongly positively correlated with Frp ($r = 0.92$, $p < 0.001$) (see also the results of Meltsov et al. 2011).

A total of 52 pollen/spore types were recorded from the nine sediment samples. Palynological richness (Pr) varied between 26 and 34 (average = 30) (Table 1). There were statistically significant positive relationships between total Pr and Fr ($r = 0.76$, $p = 0.018$) and between total Pr and Frp ($r = 0.94$, $p < 0.01$) (see also the results of Meltsov et al. 2011).

Landscape diversity measures richness of community patches (PatchR) and diversity of community patches (PatchS) increased with distance from the lake, whereas evenness of community patches (PatchE) decreased (Fig. 3). Openness showed no clear trend in relation to distance from the lake (Fig. 3).

Relationships between floristic and palynological richness and landscape variables

Fr, Frp and Pr all showed statistically significant ($p < 0.05$) positive relationships with PatchR, PatchS, PatchE and Openness (Fig. 4; ESM Table 1), indicating that landscape openness and patchiness are important predictors of Fr, Frp and Pr.

Landscape openness was the most significant measure to account for both floristic and palynological richness. Openness was positively correlated with both Fr and Frp within all radii from the lake. Pr was also strongly positively ($r > 0.7$) associated with openness but only within the radii > 750 m from the lake. The association of PatchR with Fr and Frp was fairly strong ($r \geq 0.69$) at the shortest distance (250 m), became weaker and insignificant at intermediate distances (500–750 m), and increased again beyond 1,000 m. In contrast to Fr and Frp, Pr was not associated with PatchR at any distance. The importance of PatchS in accounting for the vegetation and pollen variables showed an increasing trend with distance; the correlations became significant within the radii of at least 1,000 m (for Fr and Frp) and at least 1,250 m (for Pr). Although Fr was not significantly associated with PatchE within any radii, both Frp and Pr were significantly correlated with PatchE at 1,750 and 2,000 m.

Discussion

Although several studies have used palynological richness to estimate patterns of past vegetation diversity (e.g. Seppä

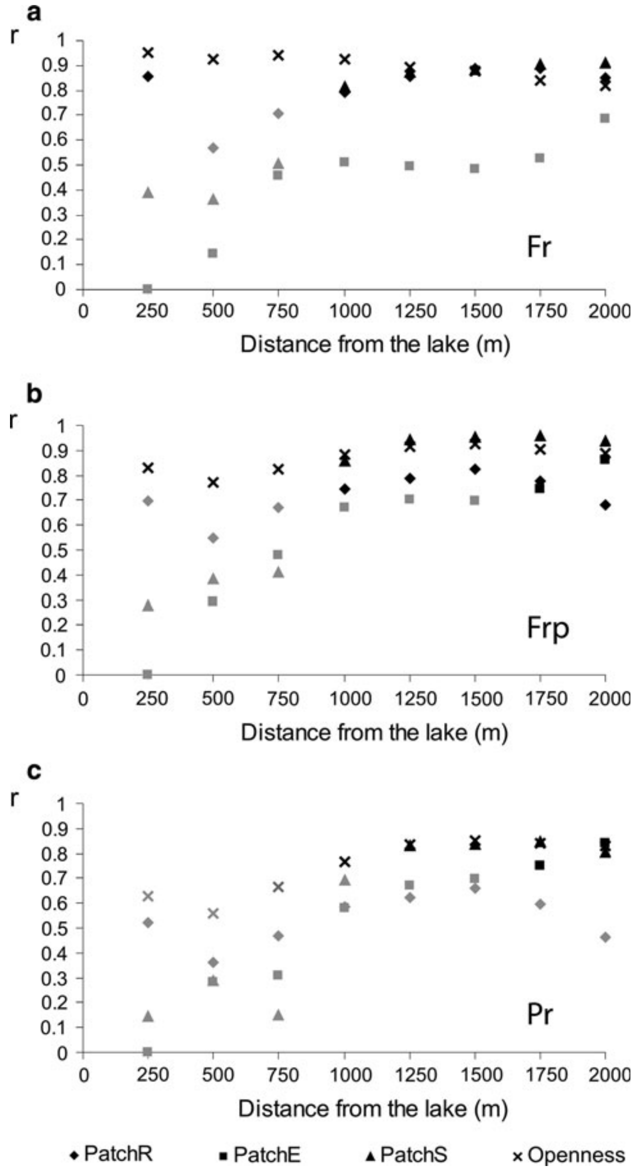

Fig. 4 Correlation coefficients (r) for relationships between measures of landscape structure (PatchR, PatchE, PatchS and Openness) and richness estimates (**a** Fr, **b** Frp and **c** Pr) within the radii of 250–2,000 m from the lakes. *Values in black* are statistically significant at p-value < 0.05. Variables are explained in Table 2

1998; Veski et al. 2005; Berglund et al. 2008; Overland and Hjelle 2009), this study is the first attempt to determine the relationships between landscape structure, floristic richness and palynological richness using modern pollen–vegetation data.

Pollen types do not always correspond to plant species because of the limitations in pollen identification, which allows pollen identification mostly to the genera, and in some cases to the family level (Fægri and Iversen 1989; Moore et al. 1991; Beug 2004). Therefore the transformation of floristic richness (Fr) into floristic richness of pollen types (Frp) results in considerable reduction in richness values. Nonetheless, Fr and Frp are strongly correlated as the floristic species richness corresponds to genera richness and family richness (Mazaris et al. 2010).

Our results show that landscape openness is the most important determinant of both Fr (and Frp) and Pr (Fig. 4) in southern Estonia. Several other studies have shown that both vegetation diversity (Pärtel et al. 2007; Billeter et al. 2008; Reitalu et al. 2010) and palynological diversity (Berglund et al. 2008) are greatest at intermediate levels of landscape openness. Openness in our study sites varies from 1 to 51 %, which reflects largely the human-induced landscape deforestation in Estonia over the last 5,000 years (Poska 2001). In the present study, the relationships between Fr/Frp/Pr values and landscape openness are linear (Fig. 4), probably because the observed openness gradient ranges from completely forested to half-open (Table 1; Fig. 2). However, we speculate that the associations between Fr/Frp/Pr and landscape openness are likely to be unimodal if our study included completely open areas.

Landscape patchiness is also an important measure of landscape structure in accounting for diversity in the vegetation and pollen records (Fig. 4). When comparing the landscape diversity measures (PatchS, PatchR and PatchE), both Fr (and Frp) and Pr were best related to PatchS (Simpson's diversity index; Fig. 4), indicating that a Simpson's diversity index provides more information on the distribution of landscape patches than richness or evenness alone and is therefore suitable to establish relationships with Fr, Frp and Pr.

Floristic richness (Fr and Frp) in comparison with landscape variables

The highly significant relationship between openness and Fr and Frp (Fig. 4) clearly indicates that increasing openness provides habitats for more species than completely forested landscape (Söderström et al. 2001; Honnay et al. 2003). The landscape at greater distances always includes the landscape at closer distances leading to an inter-correlation of openness at different distances, which accounts for the relatively constant correlation of openness with Fr and Frp at all distances (Fig. 4).

PachR and PatchS exhibit higher and more significant correlations with Fr and Frp at the distances >750 m (Fig. 4). The high diversity of the surrounding landscape is expected to increase the number of species that can colonize local community patches i.e. the local species pool sensu Pärtel et al. 1996 (Öster et al. 2007; Reitalu et al. 2009, 2011; Costanza et al. 2011), which may explain why Fr is related to landscape diversity at the greatest distances. Alternatively, 250 m may be overly close and the vegetation classification scheme too coarse to capture the variation in patch richness at the shortest distances. Increasing the radius allows differentiation of the landscapes according to patch richness, leading to significant associations with Fr and Frp at greater distances.

Palynological richness (Pr) in comparison with landscape variables

Pr has a highly significant correlation with Fr and therefore the landscape diversity and openness are expected to increase Pr as they increase Fr and Frp. Several studies have shown that the boreo-nemoral zone has experienced an increase in Pr with an increase in human-induced landscape openness during the Holocene (Seppä 1997, 1998; Berglund et al. 2008; Overland and Hjelle 2009). However, intensive agricultural management and urbanisation during recent centuries has led to a decrease in Pr (Seppä 1997; Berglund et al. 2008) and Fr (Vitousek et al. 1997; Foley et al. 2005) in over-exploited areas.

Like Fr and Frp, correlations between Pr and landscape diversity (PatchS) and openness are significant at distances of 1,000–2,000 m for lakes with a median diameter of 200 m (Fig. 4). The RSAP for small lakes in southern Estonia is about 1,400–1,600 m (Poska et al. 2011) and our study indicates that the Pr reflects the landscape structure at distances similar to the estimated RSAP.

Our results indicate that Pr estimates within one region and climatic zone give reliable estimates of the variation in Fr and Frp and landscape diversity. However, differences in pollen production and dispersal of major species and land-cover composition in different regions can cause considerable discrepancies in observed Pr and Fr/Frp values and their relationship to landscape diversity. Seppä (1998) compared the Pr of four sites in the northern Fennoscandian tree-line area and found that an open tundra site with low vegetation diversity exhibited higher Pr than areas with more diverse vegetation incorporating birch and pine woods. He also discussed the importance of considering pollen catchment area and concluded that comparisons between sites from different regions are unreliable. These conclusions are also supported by other studies (Weng et al. 2006; Peros and Gajewski 2008), which show that regions where sediment samples have low pollen concentrations, exhibit relatively high Pr and that a high number of rare taxa is detected because more pollen grains of the total population of pollen grains are counted to achieve the desired pollen sum.

Gaillard et al. (1998) found a significant positive correlation between non-arboreal pollen percentages and percentage cover of open herb vegetation in southernmost Sweden. The dataset was later enlarged with additional sites over a larger region of southern Sweden and the relationship became less clear (Broström et al. 1998; Hellman et al. 2009), suggesting, similarly to Seppä (1998), that significant associations between pollen composition and landscape openness are region-specific and enlarging the study area may affect the relationships.

There were highly significant relationships found between floristic richness, floristic richness of pollen types, palynological richness, landscape diversity and landscape openness in southern Estonia. However, caution must be taken when extending our results to compare pollen inferred vegetation/landscape diversities from different regions or when interpreting historical pollen records from times with highly different vegetation associations. Additional studies are needed to understand the wider context of the impact that floristic diversity and landscape structure has on palynological diversity in different regions and under different climatic conditions.

Conclusions

- Although plant species do not entirely correspond to pollen types, the number of species (floristic richness) was closely associated with the number of pollen types (floristic richness of pollen types) in the vegetation, indicating that pollen types are suitable for estimating vegetation diversity.
- Landscape openness was the most important determinant of both floristic richness (Fr and Frp) and palynological richness (Pr) in southern Estonia.
- Landscape patchiness estimated by Simpson diversity index (PatchS) was significantly associated with richness estimates.
- Floristic and palynological richness were significantly positively correlated with landscape structure within the radii larger than 1,000 m from the pollen sampling sites.
- Palynological richness gives reliable estimates about the variation in floristic richness and landscape structure within one floristic or climatic region. However, caution must be taken when comparing pollen-inferred vegetation diversities from different regions or when interpreting pre-historical pollen records from times with highly different vegetation associations.

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