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From pollen percentage to vegetation cover: evaluation of the Landscape Reconstruction Algorithm in western Norway

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ABSTRACT: The Landscape Reconstruction Algorithm (LRA) with the two models REVEALS and LOVE is developed to transform pollen percentage data to vegetation cover. This paper presents the first study to evaluate LRA in a region with large topographic variations within a short distances. The REVEALS model estimates regional vegetation abundance based on pollen assemblages from large lakes (100–500 ha). Pollen surface samples from one large and 28 small lakes are used together with a combination of regionally derived pollen productivity estimates and available estimates from other regions of Europe. The results show a good relationship between REVEALS-estimated forest cover and vegetation abundance based on the CORINE land-cover data. The REVEALS results using various sets of pollen assemblages from small lakes were comparable to those using one large lake. Local vegetation abundance using the LOVE model was estimated around 26 lakes. For common taxa, such as *Pinus* and Poaceae, the LOVE-based estimates of plant abundance match well with the distance-weighted plant abundances based on vegetation maps. Our results indicate that the LRA approach is effective for reconstruction of long-term vegetation changes in western Norway and other regions with high topographic relief when no major gradients exist in the pollen data.

KEYWORDS: lakes; Landscape Reconstruction Algorithm; pollen productivity; pollen surface samples; western Norway.

Introduction

Reconstruction of vegetation cover from pollen records has been a major but difficult task for palynologists since the field's inception (von Post, 1918; Firbas, 1934; Davis, 1963, 2000). Several approaches and methods have resulted in an increased understanding of the relationship between pollen production and dispersal, as well as of the effect of type and size of the investigated basin on the pollen record (Andersen, 1970; Janssen, 1973; Parsons and Prentice, 1981; Prentice, 1985; Sugita, 1993, 1994). Among methods aiming to better understand past vegetation changes, the Landscape Reconstruction Algorithm (LRA) – a theory-based mechanistic approach (Sugita, 2007ab) – corrects for different pollen production and dispersal among species. The non-linearity of pollen percentage data, and the different source areas reflected in the basins from which pollen records are obtained, is also corrected for. So far, LRA has been applied to reconstruct subcontinental-scale changes of vegetation and land-cover in Europe (Gaillard *et al.*, 2010; Mazier *et al.*, 2012; Nielsen *et al.*, 2012; Fyfe *et al.*, 2013; Marquer *et al.*, 2014; Trondman *et al.*, 2015), as well as landscape-scale changes of vegetation and land-cover in Sweden and Estonia (Fredh, 2012; Cui *et al.*, 2013; Poska *et al.*, 2014; Hultberg *et al.*, 2015). LRA consists of two models: REVEALS, the Regional Estimate of VEgetation Abundance from Large Sites (Sugita, 2007a); and LOVE, the LOcal Vegetation Estimate (Sugita, 2007b). REVEALS, which is used to reconstruct the vegetation cover within 50–100 km surrounding a site, has so far been evaluated against actual vegetation in Sweden and Switzerland (Hellman et al., 2008a,b; Soepboer *et al.*, 2010). The reconstructions are based on pollen assemblages from large lakes (≥100–500 ha) or, where large lakes are lacking, on several small lakes which give similar results, although with larger error estimates (Sugita, 2007a; Sugita *et al.*, 2010; Fyfe *et al.*, 2013). REVEALS-based estimates of regional vegetation are input parameters in the LOVE model for reconstruction of local vegetation. The LRA approach using both REVEALS and LOVE has been tested through comparisons with historical maps (Nielsen and Odgaard, 2010; Cui *et al.*, 2013; Poska *et al.*, 2014), forest inventory data (Overballe-Petersen *et al.*, 2013) and detailed vegetation survey data (Sugita *et al.*, 2010). All find significantly improved vegetation reconstruction using the LRA approach compared with pollen percentages alone.

Further testing of the LRA approach is, however, necessary under different geographical, climatic and topographical conditions. While the LRA approach has been evaluated in relatively flat areas of Europe and the United States (Hellman *et al.*, 2008a,b; Nielsen and Odgaard, 2010; Soepboer *et al.*, 2010; Sugita *et al.*, 2010), its suitability in regions with complex local topography, i.e. western Norway, remains unclear. One important input parameter for the taxa used in LRA is relative pollen productivity estimates (PPEs), where several different values, even for the same taxon, have been produced (overview in Broström *et al.*, 2008; Mazier *et al.*, 2012). Different vegetation survey methods (Bunting and Hjelle, 2010; Bunting *et al.*, 2013), flowering age and forest structure (Matthias *et al.*, 2012), and differences in climate and human impact (Broström *et al.*, 2008) are among the factors that may influence the estimates. If reliable estimates for a region are lacking, one solution is to combine available values into mean estimates as done by Mazier *et al.* (2012).

By using pollen and vegetation data from a landscape of high topographic relief in western Norway, this paper aims to: (i) evaluate the effects of different relative PPEs on vegetation reconstruction using REVEALS and LOVE, (ii) test and evaluate the REVEALS-based regional vegetation

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estimates using pollen data from various combinations of differently sized lakes and (iii) evaluate the accuracy of the LOVE-based estimates of local vegetation.

Material and methods

Study area

The study area in western Norway is characterized by islands, fjords and mountains with increasing altitudes eastwards; from <400 m by the coast to >1000 m in the inner parts of the fjords (Fig. 1). The natural vegetation varies with climate, soil and topography, where conifers of boreal forests mix with warmth-demanding deciduous trees (Moen, 1999). *Pinus sylvestris*, *Alnus glutinosa*, *A. incana*, *Betula pubescens* and *Sorbus aucuparia* are common tree species. Also, *B. pendula*, *Corylus avellana*, *Fagus sylvatica*, *Populus tremula*, *Prunus padus*, *Quercus robur*, *Tilia cordata*, *Fraxinus excelsior* and *Ulmus glabra* are present in the area. *Picea abies* is now spreading from spruce plantations (planted in the early 20th century) into other plant communities. Pastures, meadows,

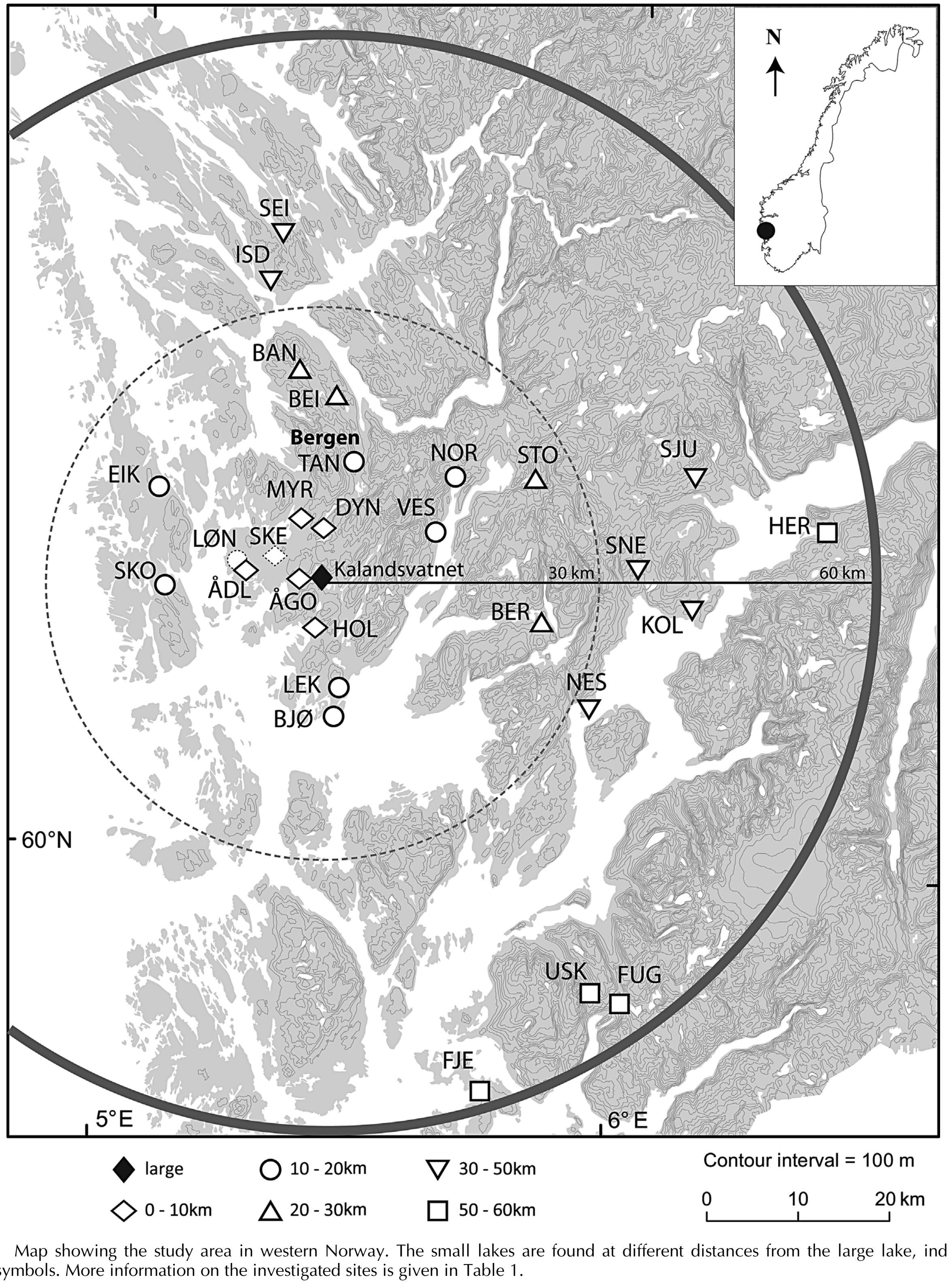

Figure 1. Map showing the study area in western Norway. The small lakes are found at different distances from the large lake, indicated by different symbols. More information on the investigated sites is given in Table 1.

Table 1. Investigated sites for validation of the LRA-model in western Norway. Distance from the large lake (in intervals), geographical position, altitude, lake size, radius and sampling year.

Name of lake (code)	Distance (km)	Latitude (°N)	Longitude (°E)	Altitude (m asl)	Area (ha)	Radius (m)	Sampling year
Kalandsvatnet (KAL)	0	60°16′25″	5°23′47″	53	340	1040	2010
Skeievatnet (SKE)*	0–10	60°17′19″	5°18′24″	21	9.11	170	2002
Myravatnet (MYR)	0–10	60°19′57″	5°21′27″	31	5.89	137	2005
Dyngelandsvatnet (DYN)	0–10	60°19′22″	5°23′37″	71	4.43	119	2003
Holevatnet (HOL)	0–10	60°13′45″	5°23′41″	3	3.04	98	2003
Ågottjørna (ÅGO)	0–10	60°16′17″	5°21′20″	53	1.61	72	2002
Ådlandsvatnet (ÅDL)	0–10	60°16′29″	5°14′41″	5	2.33	86	2003
Lekvenvatnet (LEK)	10–20	60°10′70″	5°26′35″	39	1.15	61	2003
Lønnestjørna (LØN)*	10–20	60°17′77″	5°13′44″	6	1.19	62	2002
Eikhammersvatnet (EIK)	10–20	60°19′51″	5°04′32″	5	3.37	104	2002
Tangelandsvatnet (TAN)	10–20	60°23′49″	5°27′16″	116	9.73	176	2003
Nordbøvatnet (NOR)	10–20	60°23′40″	5°39′26″	26	3.93	112	2003
Skogsvatnet (SKO)	10–20	60°16′14″	5°04′58″	24	8.24	162	2002
Veslavatnet (VES)	10–20	60°19′33″	5°37′11″	25	3.76	109	2003
Bjørnenvatnet (BJO)	10–20	60°08′46″	5°26′44″	9	7.59	156	2003
Berhovdatjørna (BER)	20–30	60°14′40″	5°50′49″	85	10.95	187	2004
Banntjørna (BAN)	20–30	60°28′55″	5°20′90″	92	2.34	86	2003
Beitelsvatnet (BEI)	20–30	60°27′00″	5°24′29″	66	4.74	123	2003
Storebotn (STO)	20–30	60°23′80″	5°48′48″	78	1.85	77	2003
Isdalsvatnet (ISD)	30–50	60°34′30″	5°16′30″	32	4.99	126	2003
Sjusetevatnet (SJU)	30–50	60°23′37″	6°08′90″	306	2.07	81	2003
Seimsvatnet (SEI)	30–50	60°36′46″	5°17′17″	39	8.31	163	2003
Sneldevatnet (SNE)	30–50	60°18′11″	6°01′20″	296	1.83	76	2003
Nesvatnet (NES)	30–50	60°10′90″	5°56′27″	31	6.95	149	2003
Kolltveittjørn (KOL)	30–50	60°16′40″	6°07′37″	73	0.56	42	2003
Herandsvatnet (HER)	50–60	60°20′53″	5°23′30″	76	17	233	2005
Fjellandsbøvatnet (USK)	50–60	59°52′43″	5°57′58″	191	13.06	204	2004
Fuglatjørn (FUG)	50–60	59°52′12″	6°01′20″	325	2.56	90	2004
Fjellandsvatnet (FJE)	50–60	59°46′56″	5°45′44″	18	16.02	226	2004

*Not included in LOVE-based estimates.

heathland and orchards dominate the cultural landscape, whereas bogs and alpine vegetation contribute to other open vegetation communities.

Study sites include one large lake (Kalandsvatnet, 340 ha) and 28 small lakes (0.56–17 ha) within a radius of 60 km of the large lake (Table 1; Fig. 1). The lakes are mainly from the lowland, with an altitudinal range from 3 to 325 m a.s.l. All lakes are surrounded by a mixture of open vegetation types and woodland within a radius of 1500 m.

Quantitative reconstructions using REVEALS and LOVE

The LRA is a two-step approach (Fig. 2); the regional vegetation is reconstructed using REVEALS, followed by local vegetation reconstruction using LOVE (Sugita, 2007ab). Pollen counts and taxon-specific PPEs are input parameters. Once the regional vegetation is estimated, a LOVE model program first uses an iteration process (Sugita, 2007b; Sugita *et al.*, 2010) to estimate the relevant source area of pollen (RSAP), beyond which pollen loading coming from the regional source becomes consistent among sites for all the constituent plant taxa. The LOVE model is then used to reconstruct local vegetation composition within the RSAP for all the taxa. RSAP is defined as the area beyond which the relationship between pollen loading and vegetation does not improve (Sugita, 1994). In theory, RSAP is the smallest spatial scale possible to quantitatively estimate the vegetation composition using pollen data from several similarly sized sites in a vegetation type or zone (Sugita, 1994 2013). The software programs REVEALS.v4.5 and LOVE.v4.6.2 (S. Sugita, unpublished) were used. For the LRA calculations, the maximum spatial extent of regional vegetation is set to 60 km, wind speed is set to 3 m s^{-1} and atmospheric conditions are set to be neutral.

Selection of lakes

For estimating the regional vegetation composition with REVEALS, we used pollen data from Kalandsvatnet and 28 small lakes within a radius of 60 km (Fig. 1). Impacts of the selection of PPE values on the results were evaluated using

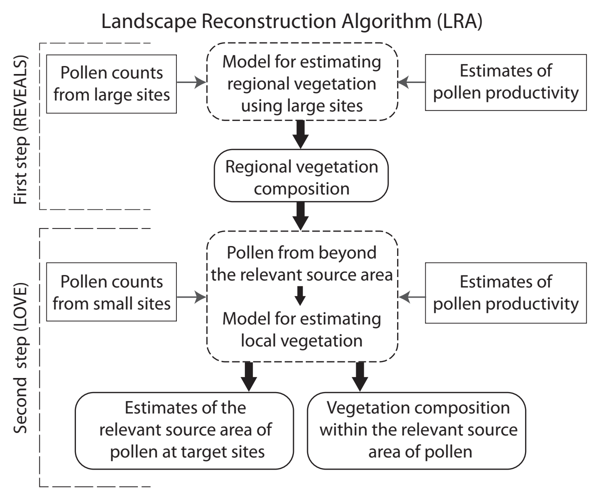

Figure 2. Principle for using the Landscape Reconstruction Algorithm, LRA (after Sugita, 2013).

pollen data from Kalandsvatnet, from 18 lakes within a radius of 30 km and for all the 28 small lakes. For comparisons of the REVEALS-based estimates of regional vegetation based on pollen data from Kalandsvatnet with those based on multiple small lakes, we selected five sets of small lakes: (i) six lakes within a radius of 10 km, (ii) 14 lakes within 20 km, (iii) 18 lakes within 30 km, (iv) 24 lakes within 50 km and (v) 28 lakes within 60 km.

For LOVE-based estimates of local vegetation composition at all small sites, we used the regional vegetation estimates based on the pollen data from Kalandsvatnet. Because vegetation survey data around Skeisvatn and Lønnestjørna were missing (Table 1; Fig. 1), we selected the remaining 26 small lakes and evaluated the LOVE-based estimates against the vegetation survey data around the individual lakes. Impacts of the selected PPEs on the LOVE results were also evaluated using pollen data from those 26 small sites.

Pollen data and pollen productivity estimates

Surface sediments from Kalandsvatnet and the 28 small lakes were sampled using the HTH sediment corer, which is an improvement of the HON-Kajac corer, with 66 mm inner diameter (Renberg and Hansson, 2008). From these, the top sample (0−0.5 cm) was analysed except for two lakes where the top 1 cm was analysed due to low pollen concentration in the sample from 0–0.5 cm. ^{210}Pb dates from two small lakes (Seimsvatnet and Herandsvatnet) indicate that the upper 0.5 cm reflects the sampling year, and it is assumed that the surface samples from all lakes are recent. These were sampled in 2002–2005, whereas Kalandsvatnet was sampled in 2010 (Table 1). The pollen assemblages from two samples from Kalandsvatnet representing 1999 and 2009 (^{210}Pb-dated) were combined to cover the time interval reflected in the top sediments of the small lakes. In the laboratory, subsamples of 1 cm^3 were processed using standard procedures, including acetolysis and HF (Fægri and Iversen, 1989). A minimum of 1000 terrestrial pollen grains were counted except for two samples (with sums 414 and 427) due to low pollen concentration. The keys in Fægri and Iversen (1989), Moore et al. (1991) and Beug (2004) and the reference collection at the University of Bergen were used for pollen identification.

To identify potential gradients in the pollen data that may affect the LRA results, we used principal components analysis (PCA) with square root transformation of pollen percentage data to down-weight high pollen producers and up-weight taxa with low pollen production, as well as centring/standardization by species (canoco for Windows 4.5; ter Braak and Šmilauer, 2002). A preliminary analysis using detrended correspondence analysis (DCA) gave a gradient length of 1.6, supporting the use of PCA.

Regional abundances of 19 wind-pollinated taxa were estimated using REVEALS and classified to three groups: (i) conifers (*Picea* and *Pinus*); (ii) deciduous trees and shrubs (*Alnus*, *Betula*, *Corylus*, *Fagus*, *Fraxinus*, *Quercus*, *Salix*, *Tilia* and *Ulmus*); and (iii) open-land plants (*Juniperus* (shrub), *Calluna* (dwarf-shrub), and Cerealia, Cyperaceae, *Filipendula*, *Plantago lanceolata*, Poaceae and *Rumex acetosa* type (graminoids and herbs)). For local vegetation reconstruction using both REVEALS and LOVE and its evaluation against the vegetation survey data, we excluded *Ulmus*, *Tilia*, *Fagus*, Cerealia and *Plantago lanceolata* because they were absent or rarely recorded in the vegetation surveys around individual sites.

For evaluating the impacts of PPEs on REVEALS and LOVE results, two different sets of PPEs relative to Poaceae were used (Table 2): (i) PPE2, which are values from the standard 2 set in Mazier *et al.* (2012), and (ii) PPE2N, which is a combination of values for *Alnus*, *Calluna*, Cyperaceae, *Fagus*, *Juniperus*, *Picea*, *Pinus*, *Quercus*, *Rumex acetosa* type and *Salix* in Norway (Hjelle and Sugita, 2012), for Cerealia in Denmark (Nielsen, 2004) and the rest from the PPE2 set (Mazier *et al.*, 2012). In PPE2, estimated values are obtained from previous studies on PPEs in Europe as follows: for a given taxon, the highest and lowest PPE values were excluded for calculation of the mean when five or more estimates of pollen productivity were available; when four estimates were available, the most extreme was excluded, and when three or fewer estimates were available, all values were included (Mazier *et al.*, 2012). PPEs from Norway (Hjelle, 1998) were included in the calculations for *Calluna*, *Filipendula* and *Plantago lanceolata* in PPE2.

Table 2. Pollen productivity estimates (PPE) and fall speed of pollen (FSP) for each taxon. PPE2 refers to standard 2 from Mazier *et al.* (2012), and PPE2N to Hjelle and Sugita (2012), Mazier *et al.* (2012) and Nielsen (2004).

Pollen taxa	FSP (m s^{-1})	PPE2 (SE)	PPE2N (SE)
Alnus	0.021	9.07 (0.10)	3.22 (0.22)
Betula	0.024	3.09 (0.27)	3.09 (0.27)
Calluna	0.038	0.82 (0.02)	0.87 (0.05)
Cerealia type*	0.060	1.85 (0.38)	0.75 (0.04)
Corylus	0.025	1.99 (0.20)	1.99 (0.20)
Cyperaceae	0.035	0.87 (0.06)	1.37 (0.21)
*Fagus**	0.057	2.35 (0.11)	0.80 (0.09)
Filipendula	0.006	2.81 (0.43)	2.81 (0.43)
Fraxinus	0.022	1.03 (0.11)	1.03 (0.11)
Juniperus	0.016	2.07 (0.04)	0.79 (0.21)
Picea	0.056	2.62 (0.12)	1.20 (0.04)
Pinus	0.031	6.38 (0.45)	5.73 (0.07)
Poaceae	0.035	1.00	1.00
Quercus	0.035	5.83 (0.15)	1.30 (0.10)
*Plantago lanceolata**	0.029	1.04 (0.09)	1.04 (0.09)
Rumex acetosa type	0.018	2.14 (0.28)	0.39 (0.10)
Salix	0.022	1.22 (0.11)	0.62 (0.11)
*Tilia**	0.032	0.80 (0.03)	0.80 (0.03)
*Ulmus**	0.032	1.27 (0.05)	1.27 (0.05)

*Not included in LOVE-based estimates.

We evaluate the extent to which the differences between PPE2 and PPE2N affect the REVEALS and LOVE results, by visual inspection of the results against vegetation composition, as described in the next subsection.

Vegetation data

CORINE (Coordination of Information on the Environment) land-cover 2006 data (Aune-Lundberg and Strand, 2010) are compared with regional vegetation reconstructions using REVEALS. Within the 60-km radius, the CORINE data include 24 land-cover classes. These were reclassified into eight classes (Fig. 3). For each vegetated class a cover estimate of open vegetation, conifers and deciduous trees/shrubs was given based on visual inspection of some sites within the different classes. The eight classes are: (i) bare ground, which includes artificial surfaces, bare rocks, sparsely vegetated areas and glaciers; (ii) sea and inland water; (iii) pasture and meadows, which includes non-irrigated arable land, pastures and complex cultivation patterns (100% open); (iv) bogs and heathland, which includes agriculture with significant natural vegetation, heathland and peat bogs (100% open); (v) deciduous forest (20% open, 80% deciduous trees); (vi) coniferous

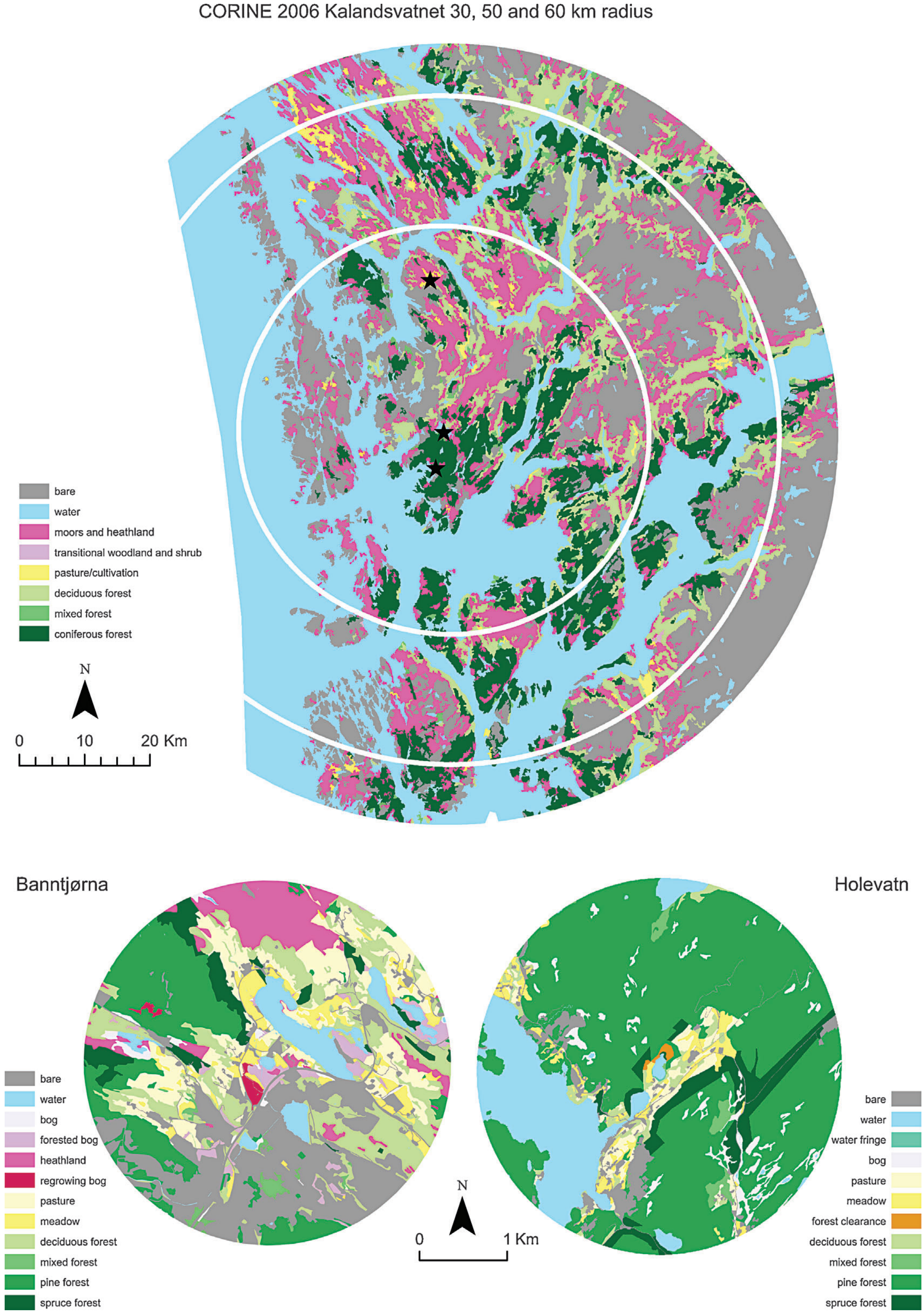

Figure 3. Vegetation maps used in comparisons between estimated vegetation cover using LRA and observed vegetation: upper, land cover classes based on CORINE 2006 within a radius of 60 km surrounding the large lake; lower, example of vegetation maps surrounding two small lakes.

forest (30% open, 35% pine, 35% spruce); (vii) mixed forest (20% open, 40% deciduous trees, 40% pine); and (viii) transitional woodland shrub (50% open, 50% deciduous trees). The final estimates of vegetation cover (i.e. percentage of the total vegetated area, see Fig. 6a below) is calculated based on the area covered by the different classes on the CORINE map, combined with the abundance of open vegetation, conifers/*Pinus* and deciduous trees/shrubs within each of these classes.

For testing of LOVE, vegetation data from a radius of 2000 m surrounding the centre of each of the 26 lakes were obtained based on digital land resource maps (DMK ver.3.4, available through Geovekst www.statkart.no) with 14 classes of relevant vegetation information (Bjørdal *et al.*, 2004). Field surveys were carried out at all sites to produce site-specific data and used in combination with aerial photos (www.norgeibilder.no) to update/supplement vegetation type and extent. Percentage cover was given for trees in the woodlands and for herbaceous taxa, dwarf-shrubs, shrubs and trees in open and semi-open communities. Species composition in vegetation types not surveyed in the field was estimated, based on the cover from comparable communities. In some cases field surveys and aerial photos were insufficient for accurately updating the two classes 'other earth covered ground' and 'shallow ground', and they were reclassified according to the surface cover of neighbouring areas. After updating the maps, the number of pollen-producing vegetation classes at each site varied between five and 16. Non-pollen-producing areas are water-bodies, roads and built-up areas, screes, gravel pits and rock surfaces. Maps were made at 3×3-m resolution. Plant abundance was calculated in concentric rings of 10 m width within a 2-km radius of each lake, using the HUMPOL (HUll Method of POLlen simulation) software (Bunting and Middleton, 2005). Distance-weighted plant abundance was obtained for comparisons with the LOVE-estimated vegetation cover using the program ERV. Analysis v.1.2.3 (S. Sugita, unpublished); parameter setting was the same as for the LOVE program runs. To get distance-weighted estimates for all the vegetation data, the mean radius option, including plant abundance data within the average radius for all lakes was used (cf. Hjelle and Sugita, 2012). All GIS editing and analyses were done in ESRI® ArcGIS.

Results and interpretation

Surface pollen samples

In the pollen diagram (Fig. 4) the sample from Kalandsvatnet is shown at the top, followed by the small lakes grouped according to their distances to the large lake (Fig. 1). Within each of the distances there are variations in pollen composition, indicating the high heterogeneity of the vegetation within small distances in the region. *Pinus* is the dominant tree taxon in several samples, followed by *Betula* and *Alnus*. *Corylus*, *Quercus* and *Picea* are present in pollen assemblages from all lakes, with up to about 10, 5 and 3%, respectively. *Fraxinus*, *Salix* and *Ulmus* are also commonly present at low percentages. Poaceae is the dominant open-land taxon in all samples, except for one where *Calluna* predominates. *Calluna*, Cyperaceae and *Juniperus* are present in all samples and often at >2%. *Rumex acetosa* type reaches >1% in several samples, whereas the proportion of *Plantago lanceolata* is mainly <0.5%. Only a few pollen grains of Cerealia type are recorded.

Pollen counts of the 19 taxa used in REVEALS represent 88.8–99.8% (mean 94.4%) of the total terrestrial pollen counted, whereas the 14 taxa used in LOVE represent 87.1–99.8% (mean 93.4%).

Nearly 50% of the variation in the dataset is reflected along the first PCA axis (Fig. 5), separating pine-dominated sites from sites with deciduous trees, such as *Corylus*, *Betula* and *Alnus*. Poaceae and numerous herb species are found on the negative side of both axes (lower left corner). The PCA plot shows that Kalandsvatnet is quite centrally located along axes 1 and 2, and that small lakes are spread over the entire plot regardless of their geographical locations, such as the two closely located lakes LEK and BJØ (Figs. 1 and 5). This indicates that although heathlands dominate along the coast and more forest is found along the fjords (Fig. 3), the heterogeneity of the landscape results in the absence of a main geographical gradient in the pollen assemblages. Furthermore, this indicates that the pollen assemblage from the large lake can be representative for the region.

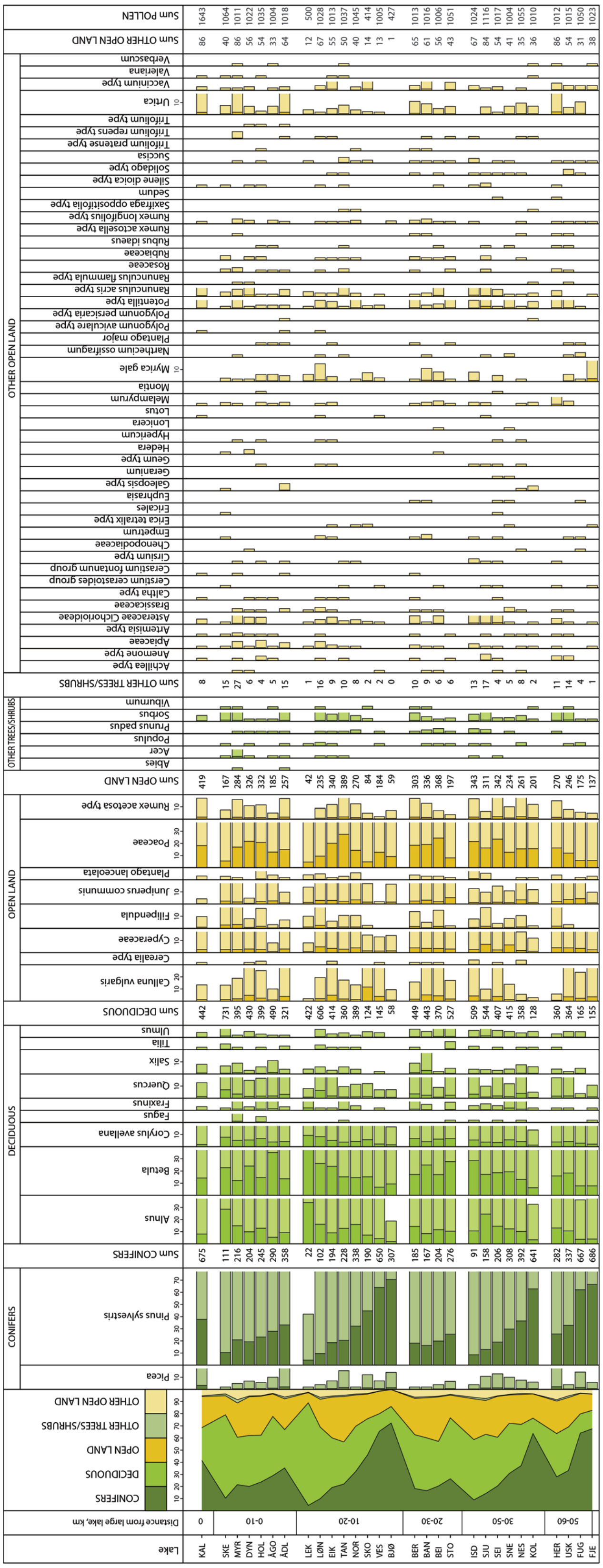

Figure 4. The pollen data (percentages (calculated on the basis of the pollen sum) and 10× exaggerations) from Kalandsvatnet and 28 small lakes grouped according to distance from the large lake. Within each distance, the lakes are ordered according to the first PCA axis. The three groups, conifers, deciduous and open land, represent the 19 taxa included in REVEALS. Thirty-three taxa present in only one sample are not shown in the diagram. For information on lakes and abbreviations, see Table 1.

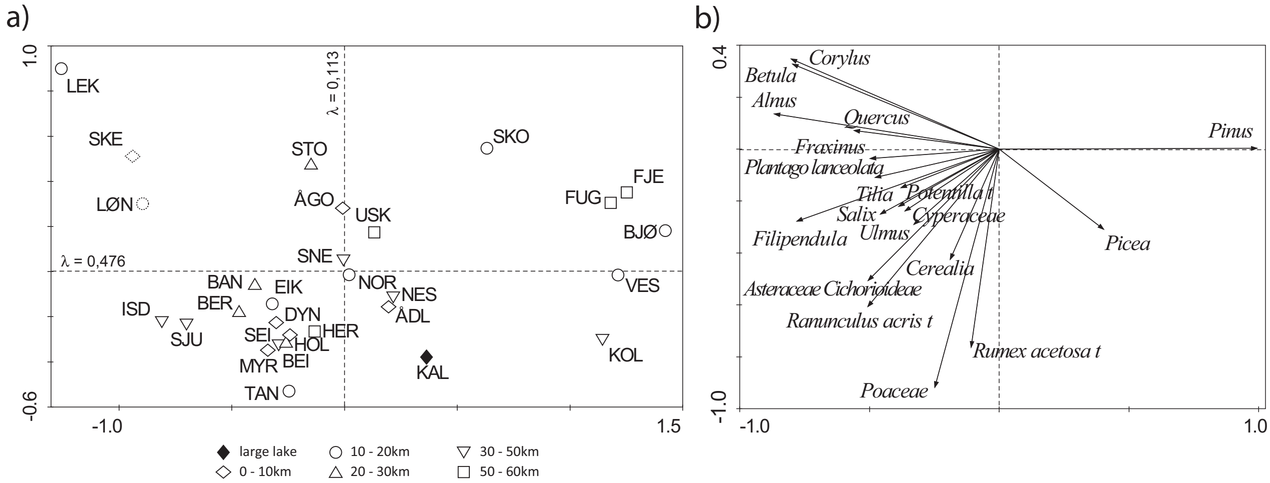

Figure 5. PCA scatter plots showing the main gradients in the dataset: (a) Kalandsvatnet and 28 small lakes where symbols for the small lakes indicate distance to the large lake (Fig. 1; Table 1); and (b) pollen taxa.

Selection of PPEs for REVEALS and LOVE application

PPE2 and PPE2N give similar REVEALS-based estimates for *Pinus* when using the two datasets of small lakes (Fig. 6a). The same is true for deciduous trees when using the pollen assemblage from the large lake. When the taxa are classified into forest and open land, PPE2N gives closer to a one-to-one relationship between REVEALS-based estimates of vegetation cover and CORINE land-cover, than does PPE2.

Using 26 small lakes, the RSAP is estimated to 918 and 998 m using PPE2 and PPE2N, respectively. The distance-weighted plant abundances within 900 and 1000 m are quite similar, and 900 m (Table 3) is used for comparisons with pollen percentages and LOVE estimates. When estimated local vegetation cover using LOVE is classified into forest and open land and compared with distance-weighted plant abundance within RSAP (Fig. 6b), there is a tendency for both higher over-estimation and higher under-estimation of forest cover using PPE2 compared with PPE2N. We therefore use the PPE2N dataset in the following analyses.

Reconstructed vegetation cover using REVEALS from several small lakes compared with one large lake

Figure 6(a) shows that the estimated forest cover/open land using REVEALS is quite similar when pollen data from one

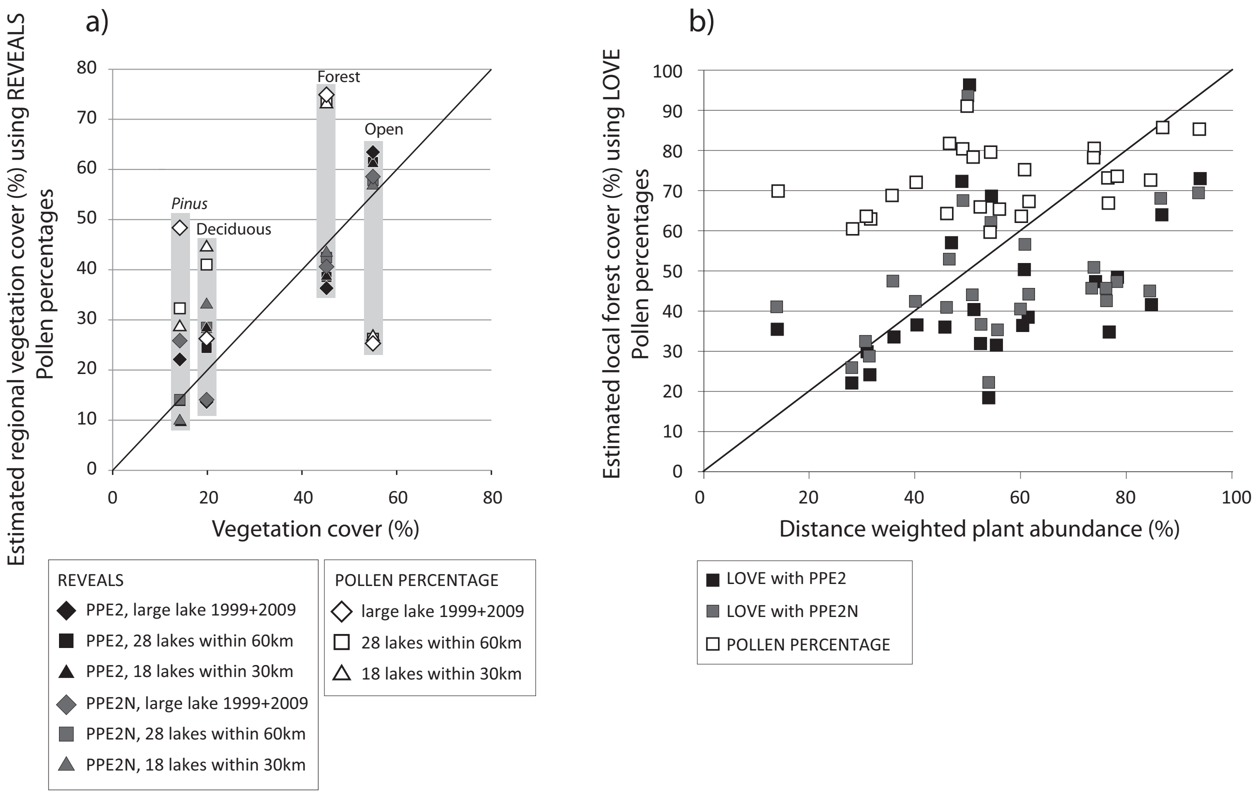

Figure 6. Comparisons of LRA estimates and vegetation cover using two different pollen productivity estimates: PPE2 from Mazier *et al.* (2012) and PPE2N from Hjelle and Sugita (2012), Mazier *et al.* (2012) and Nielsen (2004) (cf. Table 2. (a) Estimated regional vegetation cover and pollen percentages compared with observed vegetation percentage based on CORINE 2006 land cover; (b) LOVE-estimated forest cover within RSAP for 26 lakes compared with distance-weighted plant abundance from vegetation maps. RSAP is estimated to be 918 m using PPE2 and 998 m using PPE2N. The results are shown in relation to distance-weighted plant abundance within 900 m.

Table 3. Distance-weighted plant abundance (%) within a radius of 900 m from the lake shore for the 14 taxa used in LOVE (Figs 8 and 9). The sum of eight tree/shrub taxa makes the forest cover used in Fig. 6(b). Lake code refers to Table 1.

Lake code	*Picea*	*Pinus*	Alnu	Betu	Cory	Frax	Quer	Sali	Forest	Call	Cyp	Fili	Poac	Jun	Rum
MYR	1.5	0.2	27.1	1.4	0.0	25.5	20.2	0.7	76.6	0.0	0.0	0.0	18.1	0.0	5.3
DYN	0.6	6.6	0.6	41.8	0.9	3.5	0.3	1.4	55.8	0.5	10.4	0.5	30.2	0.5	2.1
HOL	1.7	32.8	1.1	10.1	0.9	4.8	0.0	1.3	52.7	3.8	0.4	0.0	34.2	5.2	3.7
ÅGO	5.3	16.1	2.8	13.1	3.4	4.1	0.0	4.3	49.1	4.2	0.3	0.7	30.4	15.2	0.2
ÅDL	0.4	2.0	3.3	3.6	16.2	0.3	8.4	6.1	40.3	0.3	0.1	0.5	57.9	0.1	0.8
LEK	1.2	4.1	7.2	7.2	6.7	17.9	2.3	3.4	50.0	0.2	0.0	0.0	45.5	0.1	4.1
EIK	2.7	10.2	0.0	11.5	3.7	0.2	0.0	2.6	30.9	5.9	8.1	0.2	47.3	6.8	0.8
TAN	5.6	5.6	2.2	18.9	6.4	9.3	0.0	6.1	54.1	0.5	0.0	0.2	36.1	0.1	8.9
NOR	0.0	35.4	14.4	30.9	0.0	0.0	0.0	3.6	84.4	0.0	0.0	0.0	11.9	0.1	3.5
SKO	12.1	9.8	2.6	14.0	6.2	3.8	0.0	2.5	51.0	16.6	2.5	0.0	25.7	4.2	0.0
VES	2.6	33.0	3.0	33.4	0.0	1.2	0.6	0.3	74.0	2.8	0.2	0.0	17.9	2.9	2.2
BJØ	0.1	86.4	1.7	2.7	1.0	1.0	0.3	0.5	93.7	0.0	0.0	0.0	1.3	0.0	5.0
BER	0.2	15.8	7.3	22.7	0.0	1.0	14.6	0.2	61.7	0.2	0.5	0.6	33.1	0.0	3.9
BAN	2.8	2.6	2.3	16.5	6.9	9.9	0.0	5.0	46.0	2.1	3.0	0.0	38.6	0.6	9.6
BEI	1.4	6.3	3.3	14.5	0.2	1.3	0.0	1.2	28.2	1.0	0.3	0.5	62.1	3.6	4.3
STO	2.8	16.8	9.6	22.2	0.4	2.5	0.0	0.0	54.5	1.6	13.5	0.0	29.3	0.7	0.5
ISD	2.7	25.4	0.5	15.9	13.0	2.5	0.0	0.2	60.2	0.0	7.2	0.0	30.3	0.2	2.0
SJU	4.9	2.1	1.3	27.0	0.3	0.3	0.0	0.0	35.9	0.3	2.7	0.0	60.0	0.4	0.8
SEI	2.8	2.7	0.8	2.2	0.0	22.9	0.0	0.0	31.4	0.0	0.0	0.0	62.9	0.0	5.8
SNE	12.6	17.7	0.0	27.5	1.8	0.2	0.9	0.0	60.8	0.0	1.4	0.0	30.9	0.0	6.9
NES	7.9	41.5	0.0	4.1	18.1	1.9	4.8	0.0	78.3	0.1	0.4	0.0	19.6	0.0	1.6
KOL	0.4	70.2	0.2	0.1	1.7	1.2	0.1	0.0	73.8	0.0	0.6	0.8	24.6	0.0	0.2
HER	0.9	1.9	0.2	4.1	1.1	5.1	0.1	0.6	13.9	0.1	0.0	0.3	83.6	0.1	2.1
USK	0.7	1.9	1.6	70.8	0.0	0.0	0.0	1.6	76.5	3.6	1.2	0.0	14.8	3.7	0.2
FUG	0.0	40.3	0.0	5.4	0.0	0.0	0.0	0.8	46.5	26.8	0.3	0.0	23.6	2.7	0.0
FJE	1.3	79.0	0.0	4.7	0.0	0.4	1.1	0.0	86.6	0.8	0.5	0.0	11.6	0.0	0.5

Abbreviations: Alnu, *Alnus*; Betu, *Betula*; Cory, *Corylus*; Frax, *Fraxinus*; Quer, *Quercus*; Sali, *Salix*; Call, *Calluna*; Cyp, Cyperaceae; Fili, *Filipendula*; Poac, Poaceae; Jun, *Juniperus*; Rum, *Rumex acetosa* type.

large lake, 18 small lakes within 30 km of the large lake, and 28 lakes within 60 km are used. Those REVEALS results correspond well to the vegetation data based on CORINE. Also, the pollen percentages from these three lake datasets are similar. The results using only *Pinus* show a larger variation, with pollen percentages varying from ca. 50% in the large lake to around 30% in the combinations of small lakes. The lowest percentage is found in the 18 lakes dataset. In the REVEALS estimated cover, the 28 lakes dataset gives the best estimates compared with the actual vegetation, whereas pine cover is overestimated using the large lake and underestimated using 18 lakes. For deciduous trees, both the pollen percentages and the estimated vegetation cover using REVEALS differ between the datasets. The large lake and the 28 small lakes show the best correspondence with the CORINE land-cover.

Compared with the CORINE land-cover, forest cover is moderately underestimated in REVEALS, whereas openness is moderately overestimated. Overall, the REVEALS estimates of open and forested areas are reasonable within the 60-km radius, which is a major improvement over the pollen percentage values alone.

For most plant taxa, REVEALS gives similar results of regional plant cover among the six different scenarios (Fig. 7): when pollen data from (i) six lakes within 10 km of the large lake, (ii) 14 lakes within 20 km, (iii) 18 lakes within 30 km, (iv) 24 lakes within 50 km, (v) 28 lakes within 60 km and (vi) the large lake are used. Exceptions are for *Corylus* and *Juniperus*, which have smaller estimates of cover based on the pollen data from the large lake than those from the small lakes, and for *Picea*, which has higher estimates using the large lake than those using the small lakes. When using six lakes within 10 km of the large lake, the REVEALS estimate for *Pinus* differs significantly from those using the large lake. The standard errors are considerably larger using small lakes than using one large lake, as expected (Sugita, 2007a; Fyfe *et al.*, 2013). The pollen sum included in the analysis increases with increasing number of lakes (six lakes, 5741; 14 lakes, 11 893; 18 lakes, 15 718; 24 lakes, 21 567; 28 lakes, 25 411; cf. Fig. 4), whereas there are small differences in the error estimates for individual taxa in the different datasets.

Some taxa, such as Poaceae and *Pinus*, increase in estimated cover when an increased number of lakes at longer distances to the large lake are included, whereas the opposite trend appears for *Alnus*, *Betula*, *Corylus*, *Fagus*, *Filipendula*, *Plantago lanceolata*, *Quercus* and *Tilia*. In most cases, the REVEALS-based estimates using pollen records from 28 lakes are the closest to those using pollen records from the large lake.

Reconstructed local vegetation cover compared with pollen percentages and observed local vegetation

With the regional vegetation estimates based on the pollen data from the large lake (cf. Fig. 2), LOVE-based vegetation reconstruction has been carried out at 26 lakes using 14 taxa (Fig. 6b). Tree pollen percentages range from ca. 60% to ca. 90%, whereas estimated forest cover is mainly in the range 20–70%. Although differences between lakes are observed, there is a general improvement in the relationship between the LOVE-based estimates of forest cover and distance-weighted plant abundance within the RSAP, compared with the relationship between forest pollen percentages and distance-weighted plant abundance.

In general, the LOVE-based estimates of plant cover are closer to the distance-weighted plant abundance based on vegetation maps than to pollen percentages, particularly for

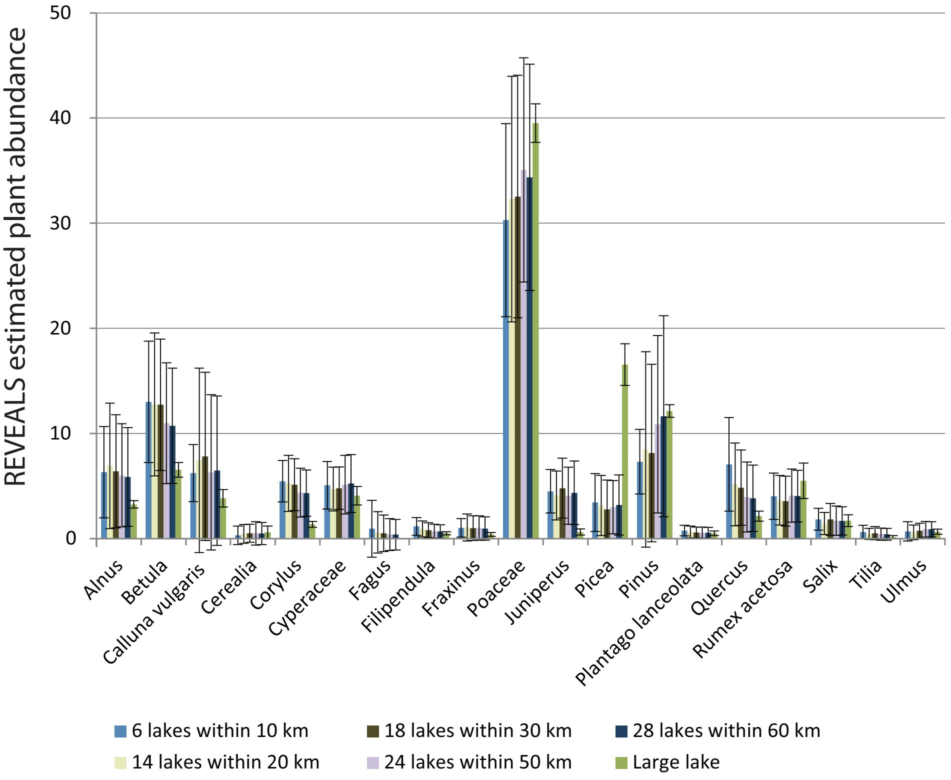

Figure 7. REVEALS estimates of vegetation cover based on different datasets of small lakes: (1) six lakes within 10 km, (2) 14 lakes within 20 km, (3) 18 lakes within 30 km, (4) 24 lakes within 50 km and (5) 28 lakes within 60 km of the large lake, and REVEALS estimates on the combined 1999 and 2009 year samples from the large lake. Vegetation is estimated to a radius of 60 km.

common and abundant taxa such as *Pinus* and Poaceae (Fig. 8). Also for *Alnus* and *Betula*, the relationship between the LOVE estimates and distance-weighted plant abundance is reasonable, although with large variations in the LOVE estimates. LOVE-based estimates of *Corylus*, *Quercus* and *Salix* show improvements over the pollen percentages, whereas both *Fraxinus* and *Picea* are underestimated by LOVE. The LOVE model tends to overestimate the local abundances of *Juniperus* and *Calluna* against the vegetation data, whereas the LOVE estimates for *Rumex acetosa* type have large standard errors.

For several taxa, the LOVE results show positive vegetation cover at individual sites, where those taxa are not recorded, or very rare, in the vegetation survey data. This is especially the case for tree taxa such as *Alnus*, *Corylus* and *Quercus*, and for open-land taxa such as *Calluna*, Cyperaceae, *Filipendula* and *Juniperus*. We suspect that more detailed vegetation surveys around sites are necessary for those taxa. The opposite is seen for *Picea*, which is planted but not flowering and thereby present in the vegetation at several sites without being estimated to be present locally using the LOVE model.

The 26 lakes are found at different distance to the large lake. There are no indications that the lakes found at short distance to the large lake perform better in the LOVE estimates than the lakes found 50–60 km from the large lake (Fig. 8a).

Comparison of pollen percentages and LOVE-based estimates of vegetation cover for the individual sites gives an indication of the variation in estimated cover when the pollen percentages are quite similar (Fig. 9). The over-estimation of *Pinus*, *Alnus* and *Betula* in pollen percentages is clear, and *Pinus* may contribute up to 20% in the pollen assemblages without being present within the RSAP. The underestimation of *Calluna*, *Fraxinus*, *Juniperus*, Poaceae and *Quercus* is also distinct, as well as the high values and great variation in the vegetation cover that may occur even with low pollen percentages of these taxa.

Discussion

Evaluation of pollen productivity estimates

When classifying plant taxa into forest and open land types, the LRA performs well both at regional and at local scales. This indicates that the LRA approach is effective even in landscapes with high topographic relief. However, as in other studies testing LRA (Hellman *et al.*, 2008a,b; Nielsen and Odgaard, 2010; Overballe-Petersen *et al.*, 2013), the relationships between distance-weighted plant abundance and LOVE-based estimates of plant abundance regarding individual taxa sometimes become less clear. Possible reasons include uncertainties in the PPEs, vegetation survey and CORINE data (Abraham *et al.*, 2014; Woodbridge *et al.*, 2014).

The PPE2N values performed better than using the standardized values of Mazier *et al.* (2012) alone. The largest differences in these datasets are for *Alnus* (9.07 PPE2–3.22 PPE2N) and *Quercus* (5.83 PPE2–1.3 PPE2N) (cf. Table 2), which may explain the larger under-estimation of forest cover and over-estimation of openness (Fig. 6) using PPE2 compared with PPE2N. Under-estimation of *Quercus* in REVEALS-based reconstructions in southern Sweden indicates that the Swedish estimate of 7.53 (Sugita *et al.*, 1999; Broström *et al.*, 2004) is probably too high (Hellman *et al.*, 2008a). The results of the present study indicate that the Norwegian PPE for *Quercus* is not too low. *Alnus* gives a more complex pattern; it shows a good relationship between LOVE-based estimates and distance-weighted plant abundance in some cases, in some it is overestimated, indicating that the Norwegian estimate may be too low, but there is also some under-estimation of vegetation cover. It therefore seems reasonable to apply the Norwegian estimate for *Alnus* in our region.

Fraxinus cover seems to be underestimated using LOVE, which may indicate that the mean value used is too high. PPEs from Sweden (Sugita *et al.*, 1999; Broström *et al.*, 2004) and England (Bunting *et al.*, 2005) gave values lower than 1.03 (Mazier *et al.*, 2012), supporting this possibility. In

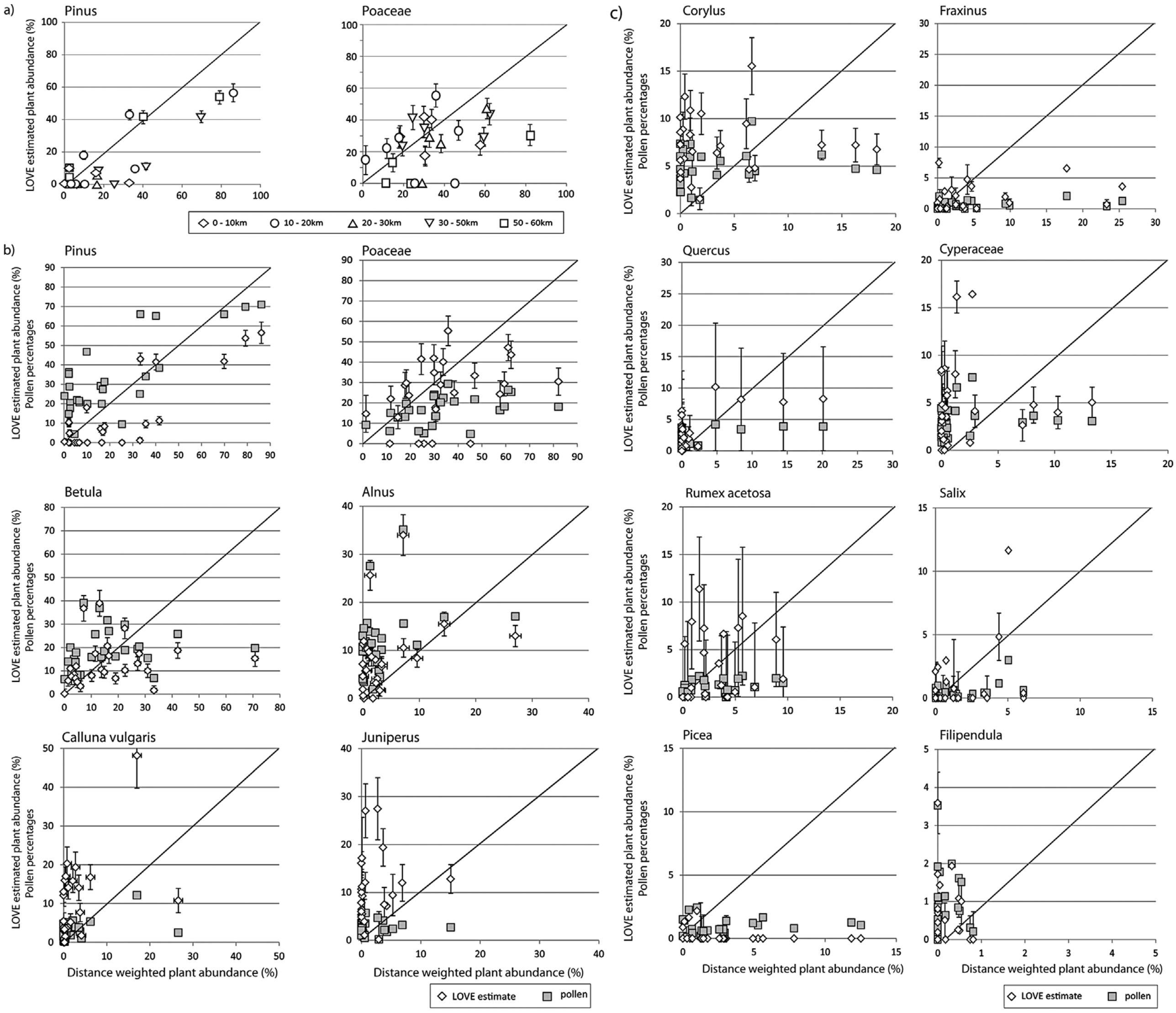

Figure 8. LOVE-based plant abundance estimates and pollen percentages plotted against distance-weighted plant abundance for the 26 small lakes. Both pollen percentages and plant abundances are calculated based on the 14 taxa used in the analysis: (a) LOVE-estimated plant abundance for *Pinus* and Poaceae plotted against distance-weighted plant abundance at individual lakes with symbols referring to Fig. 1; (b,c) pollen percentages and LOVE-based plant abundance estimates plotted against distance-weighted plant abundances. Note the different scales.

contrast, *Juniperus* seems to be overestimated, indicating that a higher PPE should have been used for this taxon.

The planted *Picea* is a challenging taxon in modern samples from western Norway because it has not matured to flowering in many of the plantations (cf. Matthias *et al.*, 2012). This can explain the lack of correspondence between LOVE-based estimates and vegetation maps (Fig. 8). In our region, without natural occurrence of *Picea*, this problem may be solved by excluding the taxon from long-term reconstructions. *Rumex acetosa* type, *Filipendula*, *Fraxinus*, *Salix* and *Picea* have pollen percentages <1% in several samples, and *Filipendula*, in particular, is also rare in the vegetation. Taxa with pollen percentages <1% are generally not recommended used in land cover reconstructions due to high error estimates (Poska *et al.*, 2014), which is especially seen for *Rumex acetosa* in our study. Although low abundances make it difficult to evaluate the PPEs used for *Filipendula* and *Rumex acetosa*, including these species may have contributed to the overall good relationship between LRA-based and map-based estimates of open vegetation.

Of the tested PPEs in the present study, PPE2N performed best using modern pollen assemblages and modern vegetation. Pollen productivity may, however, have differed in the past, which means that PPEs from different regions and climate should be considered for reconstructions of past situations.

Importance of vegetation data in the evaluation of LRA

Different land-cover types may be difficult to identify using CORINE data, but the method is found to work well at a large scale (Woodbridge *et al.*, 2014). This is supported by our investigation, which indicates a good correlation between CORINE and REVEALS-based forest cover, while the correlations for deciduous trees and conifers were poorer. Following this, we used land resource maps and not CORINE data on the site-specific scale. In our study, no terrain model was added to the distance-weighted plant abundance, an effect that could be evaluated in further studies. The grouping of communities into neighbouring communities (see Methods) may also have affected the resulting distance-weighted plant abundance. The method used in the vegetation survey is critical for estimation of PPEs (Bunting and Hjelle, 2010; Bunting *et al.*, 2013), and may also be critical in evaluation of LRA (Woodbridge *et al.*, 2014). In the present study, most

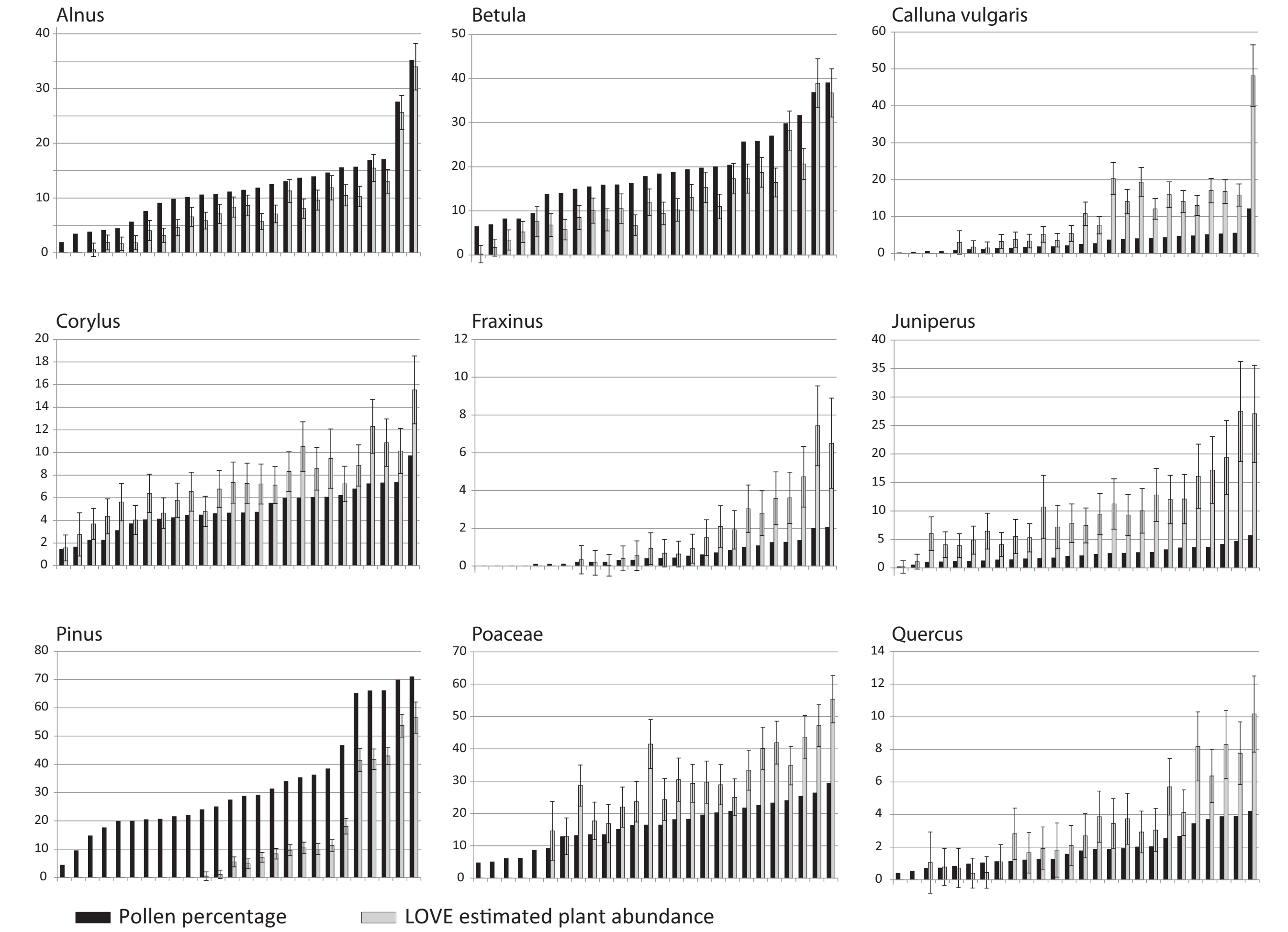

Figure 9. Pollen percentages and estimated plant abundance using LOVE for the 26 small lakes. The sites are ordered according to the pollen percentages for each individual taxon.

vegetation communities were visited and surveyed, but not all patches around individual lakes were checked. Species often found as solitary trees within farming communities, i.e. *Fraxinus* and *Quercus*, may also have been overlooked during vegetation surveys. Forest inventory data (Matthias *et al.*, 2012; Overballe-Petersen *et al.*, 2013) probably produce a better estimate of taxa abundance, but are not always available. Standardization of collection strategies for vegetation data for estimation of PPEs has been suggested (Bunting *et al.*, 2013) and should also be considered for validation of the LRA.

The RSAP for the region has been estimated to a radius of 900–1100 m, based on the ERV (Extended *r*-Value) model using pollen data from 34 sites (Hjelle and Sugita, 2012). Thus, the LOVE-based estimates of the RSAP of 918 and 998 m in the present study are reasonable. Previous studies in Sweden and Estonia suggest that the reconstructed RSAP radii in the past would be two to three times larger than those estimated in the present-day landscapes in the same regions using the ERV model (Broström *et al.*, 2005; Poska *et al.*, 2011, 2014; Fredh, 2012; Cui *et al.*, 2013). There are various possible reasons for these results; previous studies estimated the regional vegetation with REVEALS using pollen records from one or two relatively small lakes that are sometimes far from the target sites for the LOVE application. Thus, the reliability of the regional vegetation estimates can be limited. In addition, the number of small sites from which pollen data are obtained and used for LOVE was limited (sometimes only one small site was used). Reliable estimates of RSAP require a relatively large number of sites in theory and practice (Sugita, 2007b; Sugita *et al.*, 2010). The inverse modelling approach implemented in the LOVE model programs for the past RSAP estimate also has its own limitation. In particular, the RSAP estimate tends to be sensitive to rare plant taxa in the pollen data; the greater the number of rare taxa, the larger the RSAP estimates (S. Sugita, personal observation). The version of LOVE used here (LOVE.v4.6.2) down-weights the effects of rare taxa on the RSAP estimates and hence has contributed to the improved correspondence between the ERV- and LOVE-based estimates in this study. It is clear, however, that further studies and improvements are required for the RSAP reconstruction in the past.

The LRA approach in landscapes of high topographic relief

Although pollen data from several large lakes or from several points within one large lake are preferable to improve the REVEALS-based estimates (Hellman *et al.*, 2008a), we used one large lake with one sampling point. By contrast, the use of two samples (AD 1999 and 2009) reduces the effect of annual variability in pollen production (Andersen, 1974; Hicks, 1985; Autio and Hicks, 2004), and the relatively high pollen sum (1536) results in a low error estimate (Sugita, 2007a).

The pollen sum is higher in the different combinations of small lakes than in the large lake, but the between-site variation in pollen composition results in overall higher error estimates than from the large lake (Sugita, 2007a). In most cases, the samples from the small lakes are from the top 0.5 cm of sediment, which according to ^{210}Pb dates from two lakes reflect 1 year of pollen deposition (Appleby and Piliposyan, 2009, 2013), but the lakes were sampled during a 4-year period, reducing the annual variation also in these data. The results support earlier studies (Sugita *et al.*, 2010; Fyfe *et al.*, 2013) and demonstrate that several small lakes may be used for regional vegetation reconstructions using REVEALS also in landscapes with high topographic relief.

A trend in the differences between the large lake and the combinations of small lakes is that *Picea* and Poaceae are better represented in the large lake, whereas the different deciduous trees are better represented in the small lakes. This may reflect local vegetation near the small lakes. Also, *Pinus* tends to be better represented in the large lake, but by increasing the number and size of the area of small lakes included in the REVEALS-based estimates, the results become similar. When the highest number of small lakes is used, the regional vegetation is probably well represented and the results are most similar to those from the large lake. In a flat landscape, a lake of size 100–500 ha is considered to reflect an area of radius 100–400 km from the lake (Sugita, 1994 2007a, 2013). It seems unrealistic that a large lake (340 ha) represents an area of radius 60 km when the landscape is diverse with mountains >1000 m a.s.l. as in the present case. The high correspondence between the REVEALS-based estimates from the large lake and the 28 small lakes is probably caused by the mosaic of vegetation types producing an overall similarity in vegetation in different geographical areas, again resulting in large similarities in pollen deposition as indicated in the gradient analysis. REVEALS-based estimates based exclusively on lakes from the heathland region may, by contrast, give results different from Kalandsvatn (cf. Nielsen and Odgaard, 2010). As absence of a geographical gradient in the pollen data is an assumption for the LRA approach (Sugita, 1994 2007a,b), this needs to be studied in the future.

Conclusions

The LRA approach performs well in a region with high topographic variation when a mosaic of vegetation types results in similar overall vegetation composition without a strong geographical gradient in the resulting pollen data. Also in such a landscape, several small lakes can be used for regional vegetation reconstructions using LRA when pollen data from large lakes are lacking.

Two datasets of PPEs have been applied. The dataset based on a combination of regionally derived estimates and mean values of available European estimates performs better than a dataset based on mean values from Europe only. This indicates that different PPEs should be tested when applying LRA and that more research on PPEs from different geographical regions is needed.

On a regional scale, REVEALS-based estimates of forest cover correspond well with CORINE land cover. In relation to distance-weighted plant abundance, LOVE-based estimates of forest cover and cover of common taxa such as *Pinus* and Poaceae, also show improvements compared with pollen percentages. The pattern is, however, less clear for several individual taxa. Producing good vegetation data is probably a critical step for testing and validating LRA on a site-specific and taxon-specific scale.

In the present study, recent vegetation has been reconstructed using LRA and compared with modern vegetation. With the awareness that pollen productivity may have changed through time, the resulting good relationships between REVEALS-based and LOVE-based forest cover, and land-cover data, opens up for quantitative reconstructions on different spatial and temporal scales.

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Abbreviations. CORINE, Coordination of Information on the Environment; ERV, Extended r-Value; HUMPOL, HUll Method of POLlen simulation; LOVE, LOcal Vegetation Estimate; LRA, Landscape Reconstruction Algorithm; PCA, principal components analysis; PPE, pollen productivity estimate; REVEALS, Regional Estimate of VEgetation Abundance; RSAP, relevant source area of pollen.

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