



Estimating past vegetation openness using pollen–vegetation relationships: A modelling approach

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ABSTRACT

We used a modelling approach to assess past landscape openness in mid-Holocene natural vegetation. Two simple landscape scenarios were modelled: a first landscape was based on the “Vera cycle” hypothesis for western Europe, including different phases of herbivore-induced vegetation change and regeneration, while a second landscape was created based on views how a mid-Holocene natural vegetation may have looked like on the Swiss Plateau according to the closed canopy theory. These simulated landscapes were used to produce pollen assemblages by means of a pollen dispersal and deposition model. The resulting modelled pollen assemblages were then compared to a typical mid-Holocene pollen record from the Swiss Plateau. Our results indicated that the mid-Holocene pollen record is likely to be the result of a closed beech forest. However, the vegetation cover on the Swiss Plateau had components from both the closed woodland and the wood pasture landscape designs, with the latter likely at frequently disturbed or naturally open habitats.

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1. Introduction

During the past decades, different management types of near-natural forest ecosystems in Europe have been under debate. Generally, it is assumed that in temperate climates the zonal vegetation succession leads to a climax vegetation consisting of closed canopy forests (e.g., [Ellenberg, 1982](#); [Burga and Perret, 1998](#)) in which regeneration of trees takes place in small gaps. This idea has been generally supported by palynological data from Central and North-western Europe (e.g., [Berglund et al., 1996](#)), suggesting that lowland landscapes on nutrient-rich, humid soils were mainly covered by dense woodland vegetation during the Holocene and previous interglacials. However, [Vera \(2000\)](#) and others interpreted the high abundance of *Quercus* and *Corylus* in European Holocene pollen assemblages as reflecting an open to semi-open park-like landscape rather than closed canopy forests because these trees are not able to regenerate in shady circumstances. Large herbivores are thought to have maintained a park-like open landscape already before the onset of anthropogenic forest clearance. Such open landscapes are thought to be comparable to the European wood pastures of the Middle Ages. [Mitchell \(2005\)](#) summarized the crux of the problem as follows: the traditional view implies that forest structure dictates herbivore density, whereas the Vera hypothesis implies that herbivore density controls forest structure.

[Vera \(2000\)](#) distinguished different phases of vegetation development starting with the development of thorny bush in open grassland.

Here, seedlings of trees can grow sheltered from large herbivores, such as bison and deer. Eventually, the trees grow taller than the bush and by growing together, they are forming a grove. The grove can extend when the bushes expand further into the grasslands. Within the grove, regeneration of trees is not possible because of shady conditions as well as browsing and trampling by large herbivores. Opening up of the grove is possible when herbivores strip the trees, or by natural catastrophes such as droughts, storms, fires, flooding, and diseases. When increasingly large areas turn into open terrain, the grove will turn into grassland again, because of foraging by the large herbivores. Thorny shrubs eventually establish and the process repeats itself. [Kirby \(2004\)](#) attempted to model this cycle by using different landscape structures to mimic land cover change for a 2500 ha area over a 500-year period. If both an open landscape and old trees could maintain over time and space, he assumed that the modelled processes were compatible with a herbivore-driven dynamic system. [Kirby \(2004\)](#) reports that one of the landscapes, a predominantly wooded landscape (with 50% woodland phase, 25% park phase, 15% scrub, and 10% break-up phase) could be herbivore-driven.

Several authors have used palynology to waylay the wood pasture theory that [Vera \(2000\)](#) proposed. [Svenning \(2002\)](#) considered the non-arboreal pollen percentages from the last interglacial and from the pre-agricultural Holocene, when human impact was negligible, to indicate vegetation openness in four different major landscape units. He concluded that closed forest predominated, but that longer-lasting openings could have occurred. In addition, open vegetation would have been frequent on floodplains, nutrient-poor soils, and in dry and

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warm areas, where large herbivores and fire are key forcing factors. Mitchell (2005) compared Holocene pollen assemblages from mainland Europe with Irish pollen assemblages at a time when large herbivores were already extinct in Ireland. Based on the similarity between the datasets he concluded that large herbivores could not have been driving the abundance of *Quercus* and *Corylus*. Moreover, Mitchell (2005) concluded from the comparison of pollen data from small European and North-American sites that an open canopy forest could only maintain when human exploitation of such a forest had started.

Bradshaw et al. (2003) argued that the closed forest theory alone is not a perfect model for the early Holocene vegetation structure, because it cannot explain the long-term maintenance of *Quercus* and *Corylus* in the pollen records. They proposed a forest consensus theory (Bradshaw et al., 2003), in which closed canopy forest is indeed the dominant vegetation type during interglacials. Because of diverse disturbances such as floods, fires, or wind-throw, and locally by animals such as beavers and deer, some parts of the landscape may remain open. Fire together with grazing pressure of herbivores may have created appropriate conditions for regeneration of *Quercus*, *Corylus*, and *Pinus* without the development of so-called 'wood pastures'. Soil properties and pedogenesis are also responsible for variations in the vegetation composition. For instance, sandy soils are less fertile and have a lower water retention than loamy soils, thus favouring forests more open in structure. In such open vegetation, *Quercus* and *Corylus* prosper as light-requiring species, and pine as a more fire tolerant tree. These factors created a varied landscape with a high diversity (Bradshaw et al., 2003).

The above-mentioned hypotheses are strongly based on the results of pollen analyses. Non-arboreal pollen (NAP) percentages were traditionally used to estimate vegetation openness. However, this approach is not accurate, neither in practice nor in theory (Broström et al., 1998; Sugita et al., 1999). Model-based reconstructions of regional Holocene vegetation have shown that pollen proportions underestimate landscape openness (Sugita et al., 2007).

The interpretation of pollen data is complex because of differences in pollen production, dispersal, and deposition among plant taxa (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Prentice, 1985; Sugita, 1993; Sugita, 1994). For instance, for some European regions estimates show that *Quercus* and *Corylus* produce more pollen per surface area than *Fagus* (e.g., see the comparison in Soepboer et al., 2007). Also, the pollen grains of these two taxa are dispersing better (Eisenhut, 1961; Gregory, 1973), leading to a higher amount of their pollen in the pollen assemblages and thus to higher pollen percentages relative to other species.

The Extended R-Value (ERV) models (Parsons and Prentice, 1981; Prentice and Webb, 1986; Sugita et al., 1999) are calibration models to link pollen representation at multiple sites to the vegetation surrounding these sites. When the vegetation abundance around small to medium-sized lakes is surveyed and distance-weighted by using the Prentice–Sugita model, i.e. by taking the dispersal characteristics of the pollen into account (Prentice, 1985, 1988; Sugita, 1994), the ERV models provide, amongst others, Pollen Productivity Estimates (PPE) and a measure for the relevant source area of pollen (Sugita, 1994). Recently, such PPE have been established for several regions of Europe and North America (Sugita, 1994; Calcote, 1995; Jackson and Kearsley, 1998; Sugita et al., 1999; Broström et al., 2004; Nielsen, 2004; Bunting et al., 2005; Soepboer et al., 2007). The ERV models and the Prentice–Sugita model are subroutines in POLLSCAPE, a modelling scheme that uses vegetation and landscape maps to generate amongst others modelled pollen assemblages in sedimentary basins (lakes or mires). POLLSCAPE allows testing of the effects of changes in vegetation and species composition on pollen assemblages (Sugita, 1994; Sugita et al., 1999). Recently, the model was used for an evaluation of the PPE derived from modern data from the Swiss Plateau (Soepboer et al., 2008). It can also be used to compare multiple past landscape scenarios to fossil pollen assemblages and thus test theories of vegetation structure and openness in the past.

Table 1
Pollen productivity estimates (PPE) and pollen fall speed

Taxon	PPE	Fall speed (m s ⁻¹)
<i>Betula</i> spp.	2.42	0.026
Cichorioideae	0.17	0.051
<i>Corylus avellana</i>	2.58	0.025
<i>Fagus sylvatica</i>	0.76	0.055
<i>Fraxinus excelsior</i>	1.39	0.022
<i>Plantago lanceolata</i>	0.24	0.029
Poaceae	1	0.035
<i>Quercus</i> spp.	2.56	0.035
<i>Pinus (cembra and sylvestris)</i>	1.35	0.041
<i>Abies alba</i>	9.92	0.120

In this study, we used POLLSCAPE to assess past landscape scenarios. We used data from the Swiss Plateau. Two landscape designs mimicked two scenarios of a mid-Holocene landscape in lowland Switzerland. The first landscape was based on the "Vera cycle", with different vegetation phases as described by Kirby (2004) that are compatible with herbivore-driven processes. The second landscape was based on ideas of how natural mid-Holocene vegetation for the Swiss Plateau may have looked according to the closed canopy theory. The resulting simulated pollen assemblages for small lakes were then compared to a pollen record representative for mid-Holocene pollen assemblages from small lakes on the Swiss Plateau.

2. Material and methods

2.1. Software and settings

POLLSCAPE (Sugita, 2006) is a modelling scheme that uses vegetation and landscape maps to generate pollen assemblages in sedimentary basins (lakes or mires). It uses the Prentice–Sugita model to simulate pollen dispersal and deposition. The Prentice–Sugita model includes parameters such as fall speed of pollen, wind speed, pollen productivity estimates, and basin size. The software POLSIM v. 3.3 (Sugita, unpublished) was used to apply POLLSCAPE. Some assumptions in the Prentice–Sugita model might hamper its application in topographically more complex areas such as the rolling to hilly Swiss Plateau. Also, the model does not take height differences between plants into account. However, Soepboer et al. (2008) showed that POLSIM is able to simulate modern pollen assemblages on the Swiss Plateau within reasonable accuracy.

In this study we also used MOSAIC (Middleton and Bunting, 2004) a software that allows landscape design and OPENLAND (Eklöf et al., 2004) that classifies vegetation in stepwise increasing distances from the sampling sites. POLSIM estimates the pollen input on the surface of a basin (pollen loading). Pollen fall speed (i.e., velocity of deposition, m s⁻¹), PPE for individual taxa, as well as vegetation maps and the location and size of the depositional basins are needed as input parameters for the models. The PPE and pollen fall speeds used here (Table 1) were taken from Soepboer et al. (2007). These PPE were derived from modern pollen and vegetation data on the Swiss Plateau, using ERV sub-model 3 (Sugita, 1994). As a first approximation we assume PPE to be constant through time (Sugita, 2007b). Wind speed in the simulations was set to 3 m s⁻¹.

2.2. Landscape design

The artificial landscape used for modelling was inspired by the wood pasture as described by Kirby (2004). It was designed in such a way that it allows a herbivore-driven dynamic process (i.e. the forest cycle as proposed by Vera, 2000) to have occurred across western Europe (including lowland Switzerland). In this landscape open conditions as well as old groves occur simultaneously (Kirby, 2004). A quarter of the landscape is in a park-like state (park phase, i.e. open with some scattered trees). Half of the landscape is forested (woodland) and the

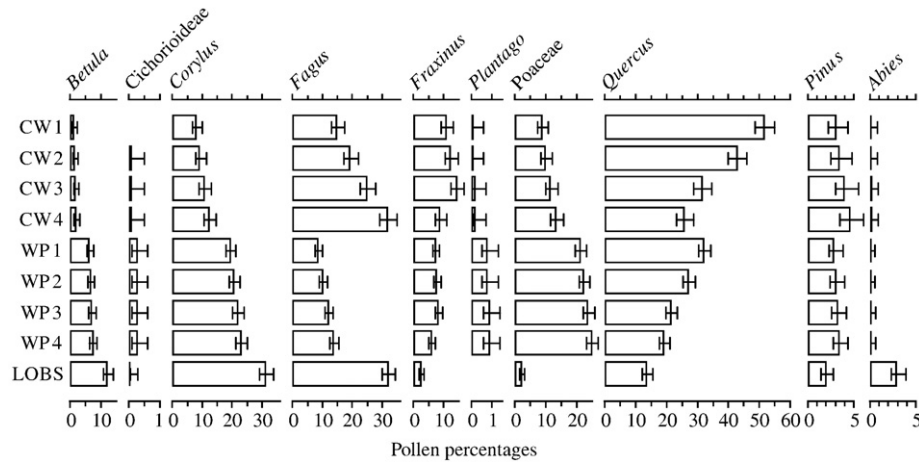


Fig. 2. Simulated pollen assemblages for closed wood (CW) and wood pasture (WP) scenarios as well as the observed pollen assemblage of Lobsigensee at 6000 cal. years BP (LOBS). The error bars depict the 95% confidence intervals of the pollen percentages.

The composition of the shore vegetation was derived from the average shore vegetation that was surveyed around 20 small lakes on the Swiss Plateau in 2003 (Soepboer et al., 2007). For the park vegetation, we set a high Poaceae content, with some scattered trees still present. As bushes develop (shrub phase) trees can grow in places that are sheltered from browsing and grazing herbivores. Then, woodland develops with a more or less closed canopy. Here, no herbs are present. For woodland, we used four different vegetation compositions that mostly differ in the amount of *Fagus* and *Quercus*. After the woodland begins to break up, the amount of open landscape increases, represented by increasing Poaceae cover.

Soepboer et al. (2008) showed that the use of detailed regional vegetation data improved POLSIM simulations, thus demonstrating the importance of acquiring an accurate regional vegetation estimate. Also, we have to keep in mind that the amount of pollen originating from regional vegetation in modern lake surface sediment samples on the Swiss Plateau is up to 50% (Soepboer et al., 2007). Even though an estimation of regional vegetation composition in the past may be difficult and uncertain, it is essential to incorporate such regional characteristics. In this way, the influence of a larger landscape surrounding the 10 × 10 km plots is considered. In modern studies, the regional vegetation area is found to be 200 km around the Swiss Plateau, thereby also including the Alps (Soepboer et al., 2008). The regional vegetation composition used here was based on an expert judgement of the composition of dominant vegetation types in different altitudinal belts in the whole of Switzerland and the proportion of area covered by these elevation classes. Only the taxa that were present at 6000 cal. BP were considered. We used the same regional vegetation for the wood pasture simulations.

The vegetation composition of all classes is shown in Table 2. The resulting pollen assemblages are named after the different woodland composition designs: CW1 to 4 (closed wood) and WP1 to 4 (wood pasture).

3. Results

3.1. Pollen assemblages

Fig. 2 shows the simulated pollen assemblages for all eight scenarios. In general, the relative amounts of herbaceous and shrub taxa were higher in the wood pasture (WP) assemblages, whereas the tree taxa were more abundant in the closed wood (CW) assemblages.

With the differences in the woodland compositions (1 to 4, see Table 2), we mainly see effects on the taxa whose cover increased in woodland composition 1 to 4 (*Fagus*) or decreased (*Quercus* and in woodland 4 also *Fraxinus*). In CW1 to 4, *Fagus* proportions increased

from 15 to 31%, while *Quercus* proportions decreased from 52 to 26%. In WP1 to 4, *Fagus* proportions increased from 9 to 14% and *Quercus* proportions decreased from 32 to 19%. However, we also see that *Corylus*, Poaceae, *Pinus* as well as *Fraxinus* increased from CW1 to 3. *Fraxinus* decreased in the scenarios CW4 and WP4 compared to CW3 and WP3, respectively.

The pollen assemblages of CW2 and WP2 look roughly as the averaged results of four scenarios, except for the taxa *Fagus* and *Quercus*. Therefore, we shall summarise the differences between the two contrasting designs by describing the pollen assemblages of WP2 and CW2. The differences between CW2 and WP2 were not pronounced for the taxa Cichorioideae (0.1–0.3%), *Plantago* (0.2–0.8%), *Pinus* (3.5–3.1%), and *Abies* (0.2%). For *Betula* and *Fraxinus* the differences were moderate, in the order of 4–5%. Larger differences occur for *Corylus* and Poaceae. Their proportions in CW2 were about 10%, whereas in WP2 they were 21–22%.

In Fig. 2, the simulated results are compared to the observed mean pollen assemblage from Lobsigensee. The observed *Fagus* content was rather high (34%). Such a high *Fagus* pollen percentage resulted only from the CW4 scenario (31%). The best matching *Quercus* percentage resulted from scenario WP4 (19% versus 23% observed). For *Betula* and *Corylus* the WP4 results were closest to the observed proportions (12 and 32%, respectively). The observed *Fraxinus* proportion (3%) was closest to WP4 (6%). The observed proportion of all NAP was 2.4%. The simulated proportions of herbaceous taxa were higher, ranging between 9 and 14% for CW1 to 4 and between 22 to 26% for WP1 to 4. Thus, considering the sum of herbaceous taxa, the CW1 to 4 matched the observed pollen data better than WP1 to 4.

4. Discussion and conclusion

In this study, we created two landscape designs that are based on the closed canopy and the wood pasture hypotheses. The level of landscape openness that we designed in our simulations cannot directly provide a causal explanation for the observed openness. We can only indicate whether the simulated pollen assemblages reflect the trends found in an observed pollen assemblage in a lake of similar size.

Some aspects of the simulated pollen assemblages were similar to the observed Lobsigensee assemblage. Firstly, the low NAP values at Lobsigensee being closest to CW1 are in favour of the closed wood design; all herbaceous taxa had significantly higher relative abundances in the wood pasture simulations. Secondly, *Fagus* as the dominant taxon in the Lobsigensee pollen record was better approximated by the closed wood landscape designs and the observed value was comparable to that in CW4. However, there are also some points in favour of the wood pasture designs: the pollen percentages of *Betula*, *Corylus*, *Fraxinus*, and *Quercus* were closer to the results of the

wood pasture scenario. The proportions of *Pinus* and *Abies* were not simulated in the woodland, shrub, park or break-up phase, and therefore not very indicative to any design.

The high *Fagus* content in the Lobsigensee pollen assemblage and the observed low NAP abundance point to an extended vegetation cover of woodland dominated by beech (e.g., CW4). In addition, we can deduct that *Quercus* vegetation cover was not very abundant within such a woodland (less than 5%, see Table 2). On the other hand, the *Corylus* proportion at Lobsigensee was quite high. Assuming the PPE of *Corylus* to be correct (Soepboer et al., 2008) and knowing that the *Corylus* vegetation proportion we used for the shrub-phase was, in fact, overestimated (to compensate for the lack of thorny bush taxa), the reason for this underestimation of *Corylus* in the pollen assemblage could be caused by an underestimation of the shrub-phase cover in the landscape designs (both the wood pasture and the closed wood designs). Moreover, the regional *Corylus* component may have been higher.

In this study, we used simple and limited approach (in number of designs and compositions) to test vegetation theories. An alternative approach would be to quantitatively reconstruct past vegetation using the “Landscape Reconstruction Algorithm” (Sugita, 2007a,b). This approach enables estimating vegetation proportions at regional and local scale in regions where PPE and pollen data from multiple lakes of various sizes are available. The reconstruction of regional vegetation in Sweden has shown that the landscape openness around 6000 cal. BP was not larger than 10–20% (Sugita et al., 2007). Yet, openness might be better indicated at a local scale (Fyfe, 2007). Although the LRA approach will give vegetation cover estimates, the exact distribution of the taxa in the landscape remains to be assessed.

It is also possible to spatially define vegetation structures based on, for instance, elevation, slope, and soil moisture to create a ‘real-world’ past landscape design (e.g., Fyfe, 2006). A similar approach (Vervoort, 2006) in which past vegetation on the Swiss Plateau was simulated with a land-use change model (Verburg et al., 2002) suggested that sufficiently detailed biophysical information (spatial resolution < 100 m) is necessary to estimate pollen assemblages in an adequate way. Bunting et al. (2007, 2008) used the Multiple Scenario Approach which develops multiple past scenarios based on simple ecological rules such as elevation ranges combined with appropriate GIS data. By using this method, the construction of a large number of landscapes becomes relatively easy.

Different landscape designs and vegetation compositions might produce similar results as shown in our study, or even results that are more similar to the Lobsigensee values. Based on the results of our simple simulation experiment we conclude that the mid-Holocene pollen assemblages observed at Lobsigensee, and at many other Swiss Plateau sites, are likely the result of vegetation cover that consisted of rather closed beech forests. The high *Corylus* proportion in the observed pollen assemblage shows that the disturbance area must have been larger than can be expected from the closed forest theory alone. On the other hand, our results indicate that the extent of landscape openness as suggested by Vera (2000) and Kirby (2004) is too high. Natural (e.g. river plains, wetlands, poor soils) and disturbance-induced (floods, wind-throw, fire) small openings in closed beech forests may have produced the observed pollen assemblage at Lobsigensee 6000 years ago. The debate about the amount of vegetation openness in the past will benefit from further research using more sophisticated pollen-vegetation models, such as the LRA and MSA.

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