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The glade effect: Vegetation openness and structure and their influences on arboreal pollen production and the reconstruction of anthropogenic forest opening

Ingo Feeser *, Walter Dörfler

Institute of Pre- and Protohistoric Archaeology, Kiel University, Germany

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ABSTRACT

This study highlights the importance of landscape openness and structure as an environmental factor influencing the total arboreal pollen production of a landscape. This influence poses an unconsidered bias that potentially affects the results of landscape reconstructions. The so-called "glade effect" is an increase in arboreal pollen production as a result of landscape opening. This increase is based on the assumption that an opening up of the woodland canopy results in increased availability of light, and hence flowering activity in the crown areas of trees. A simple simulation of the glade effect suggests that: (a) the relationship of landscape openness and the arboreal/non-arboreal pollen ratio is non-linear and (b) the spatial pattern of the landscape opening process (e.g. uniform or patchy) is important for the degree of such underrepresentation. The simulation results reveal similar patterns found in empirical pollen data from two laminated lakes in Northern Germany. An increase in arboreal and non-arboreal pollen influx at the transition from hunter–gatherer to farming communities is regarded to result from increasing openness of the woodland canopy, reflecting the proposed glade effect. A subsequent decrease of arboreal pollen influx likely corresponds with an anthropogenic change in landscape structure, i.e. the creation of larger permanent open field systems. Therefore the interpretation of pollen influx data under consideration of the glade effect helps for interpretation of pollen diagrams and facilitates conclusions regarding the spatial pattern of early forest opening.

Introduction

One of the main aspects of studying human influence on the environment in naturally wooded areas is reconstructing the openness of landscapes. Hereby quantitative estimates become increasingly important. Most available applied approaches are based on palynological data (Gaillard et al., 2008; Bunting and Middleton, 2009; Nielsen et al., 2012; Theuerkauf et al., 2013). This kind of data generally includes the relative abundance values of different pollen taxa within a fossil pollen spectrum. In order to reconstruct the quantitative importance of different taxa in the catchment of the pollen archive, relative pollen productivity estimates (PPE) and dispersal functions are available (cf. Sugita, 2007; Broström et al., 2008). At present, applied models use taxa specific PPE based on modern pollen data and the spatial coverage of the related plant species in relevant catchment areas. To allow for regional variation of pollen productivity, the applied PPE should ideally derive from the same study area or wider region. Matthias et al. (2012), however, showed that factors within a study region, such as the forest structure, also have a strong influence on the pollen productivity of certain plant species. Although considerations on regional variations in pollen productivity have been attempted (Broström et al., 2008), the quantification approaches, so far, do not consider the possibility of species-related variation of pollen productivity within a study area due to changes in the forest structure or vegetation composition, i.e. the used PPE are constant through time. Nevertheless, in his classical work on trees as anthropogenic indicators in pollen diagrams, Aaby (1986) already described that arboreal pollen influx seems to increase distinctly together with evidence for human interference with the natural woodland. This pattern suggests that pollen productivity should not be regarded as constant throughout time. The phenomenon described by Aaby, in the remainder of this contribution referred to

Abbreviations: AP, arboreal pollen; NAP, non-arboreal pollen; PPE, pollen productivity estimates.

* Corresponding author at: Institute of Pre- and Protohistoric Archaeology, Kiel University, D-24098 Kiel, Germany. Tel.: +49 431 880 3374.
E-mail address: ifeeser@ufg.uni-kiel.de (I. Feeser).

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as the "glade effect", can be explained by differences in the pollen production of solitary trees compared to trees in close stands (cf. also Borse, 1939; Andersen, 1974). Hereby, the pollen production of a tree increases with increasing light availability in the crown area, e.g. due to an opening of the forest canopy structure. According to Aaby (1986), a positive relationship between human activity and arboreal pollen influx in sediment archives can be assumed as long as the landscape can be considered to be mainly forested. A further opening of the landscape, in which woodland only plays a minor role, would subsequently result in a reduction of arboreal pollen influx in pollen diagrams.

In terms of the interpretation of fossil pollen records, this means that although low values of indicators for open landscape suggest woodland clearance, the corresponding increase in the arboreal pollen production leads to an underestimation of landscape openness. Therefore, a better understanding of the glade effect and the factors involved is important for improving the quality of pollen based palaeoecological reconstructions.

The present study, however, does not aim to provide a quantitative approach to improve reconstructions based on empirical pollen data. The intention was rather to investigate the potential bias of the proposed glade effect on pollen data. This is done using a simple simulation approach, which allowed testing of different intensities of increased arboreal flowering as well as different landscape opening scenarios, i.e. the spatial distribution of open habitat. These tests illustrate the range and direction of possible biases of the glade effect on pollen data. The results are subsequently used to discuss empirical influx data spanning the Mesolithic–Neolithic transition from two laminated lake profiles of Northern Germany.

Material and methods

Simulating the glade effect

The simulation (written in VisualBasic as implemented in Microsoft Office 2007) is based on a 100×100 grid, each cell representing a single landscape unit (Fig. 1). Each landscape unit can be denoted as either wooded or open and therefore producing either arboreal (AP) or non-arboreal pollen (NAP), respectively. The pollen production of both units was initially set to 1. In order to simulate the glade effect, a quarter of the pollen productivity of a wooded unit was increased by a given factor (glade effect factor) for each adjacent horizontal or vertical cleared unit (e.g. in case two of the four adjacent units are cleared and given a glade effect factor of 15 the pollen production would be $2/4 \times 1 + 2/4 \times 15 = 8$). The pollen production of a woodland unit therefore can range between 1 – in case that all four bordering units are woodland – and the given glade effect factor as maximum – in case that all four bordering units are open habitat. The model simulates the pollen production of a landscape which is regarded to be most comparable to the regional pollen component in lake archives (see also section "Pollen influx data from two lakes of Northern Germany"). The patchiness of the spatial distribution of open habitat can be quantified by the calculation of dispersion indices. Generally, the calculation of different indices revealed similar results. We decided to show the Green's Index (Green, 1966; calculated using continuous subsamples of the landscape scenario map of 10×10 units). This index ranges from 0 to 1 indicating a random or maximal clumped distribution, respectively.

For a landscape scenario map the following parameters are calculated:

- absolute numbers and relative proportion of cleared and woodland units,
- absolute numbers and relative proportion of AP and NAP production of the landscape,
- Green's index (GI).

In a next step, different landscape opening scenarios were created and subsequently simulated. A landscape opening scenario consists of a series of landscape scenario maps (cf. Fig. 2) characterised by an increasing proportion of open habitat (0–50% cleared units). Different intensities of increased arboreal flowering activity due to the glade effect (represented by the glade effect factor), as well as different landscape opening scenarios, have been used. This allowed to investigate the range and direction of influences of the proposed glade effect on the simulated pollen production. The authors are aware, that the simulation does neither consider any pollen dispersal models, nor the pollen influx into a sediment archive. It is rather simulating the pollen production of a region, which, with respect to empirical pollen data, is regarded to be comparable to the regional pollen component in lake archives.

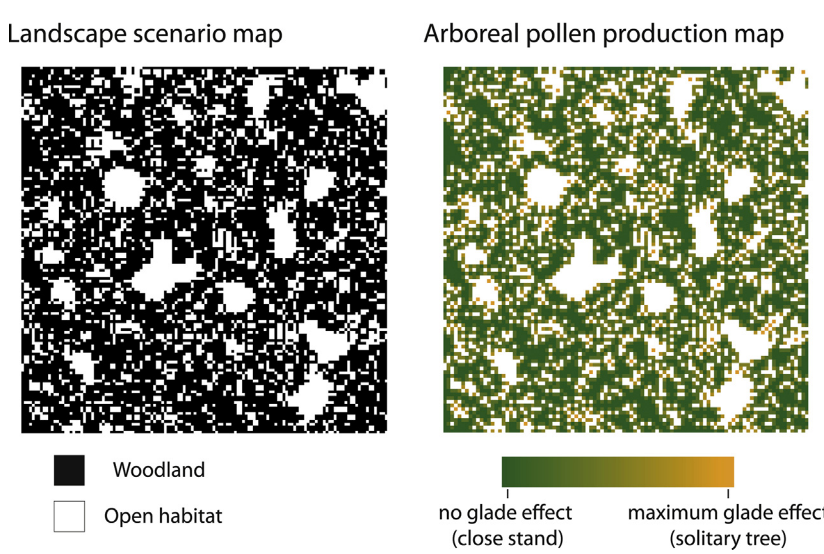

Fig. 1. Examples of 100×100 raster maps used in the presented simulation of the glade effect. Left: landscape scenario map showing distribution of woodland and open habitat cells. Right: Map indicating the degree of simulated arboreal pollen productivity using the landscape scenario in the map presented to the left. Woodland cells bordering open habitat cells have increased pollen production, which simulates the glade effect.