

Article

Palaeoecology as a Tool for the Future Management of Forest Ecosystems in Hesse (Central Germany): Beech (*Fagus sylvatica* L.) versus Lime (*Tilia cordata* Mill.)

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Abstract: In the Central German Uplands, *Fagus sylvatica* and *Picea abies* have been particularly affected by climate change. With the establishment of beech forests about 3000 years ago and pure spruce stands 500 years ago, they might be regarded as ‘neophytes’ in the Hessian forests. Palaeoecological investigations at wetland sites in the low mountain ranges and intramontane basins point to an asynchronous vegetation evolution in a comparatively small but heterogenous region. On the other hand, palynological data prove that sustainably managed woodlands with high proportions of *Tilia* have been persisting for several millennia, before the spread of beech took place as a result of a cooler and wetter climate and changes in land management. In view of increasingly warmer and drier conditions, *Tilia cordata* appears especially qualified to be an important silvicultural constituent of the future, not only due to its tolerance towards drought, but also its resistance to browsing, and the ability to reproduce vegetatively. Forest managers should be encouraged to actively promote the return to more stress-tolerant lime-dominated woodlands, similar to those that existed in the Subboreal chronozone.

Keywords: pollen analysis; climate change; forest succession; *Fagus sylvatica*; *Tilia cordata*; Hessian uplands; Central Germany



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1. Introduction

The alarming state of Central European forests against the background of a higher frequency of drought periods has received increasing public attention and is being discussed intensively by experts. With regard to scientific research and the implementation of new concepts, palaeoecology [1] is one important resource that, to date, has not been considered sufficiently. Palaeoecological methods open a window into the past by providing a possibility to study the long-term dynamics of tree populations, which cannot be recorded through experiments or observations due to their long lifespan and reproduction periods. In particular, climatic phases resembling those predicted can be identified and vegetation formations adapted to these conditions, as well as their resource-efficient management over millennia, can be analysed. The preferred method for this is palynology, which, in addition to pollen, also utilises spores and other plant microfossils that are stored in natural archives such as lake sediments, peat bogs, soils or ice as palaeoecological indicators (so-called proxies).

Forests already formed an integral part of the human environment in the Neolithic and have constantly been subject to changes. This is also the case in the Hessian lower mountain ranges, which are nowadays part of the core area of *Fagus sylvatica* (European beech) forests [2,3]. However, together with *Picea abies* (Norway spruce), *Fagus sylvatica* is particularly suffering from the current climatic changes not only at the southern edges and lower elevations of its current distribution range [4,5], but also in the mid-altitude forests of Hesse [6].

Palynological studies show that the predominance of closed *Fagus* forests in the central German uplands is a comparatively young phenomenon. In our study area (Figure 1), the mass expansion of *Fagus* only started 3000–4000 years ago [7–14]. It is closely related to climatic changes, but also to anthropogenic influences. In other regions, however, it occurred much earlier [15–17], but the underlying causes are still a matter of debate [15,17–20]. In the montane zone of Switzerland, for instance, *Fagus* forests existed as early as 7500 calibrated years before present (cal. BP). In the Alpine foothills, *Fagus* spread during the following millennium, and, around 6000 cal. BP, it also became established throughout the southern Vosges and the Lake Constance area [21–23]. By contrast, the Black Forest, northern Vosges and the low mountain ranges to the north were almost devoid of *Fagus* at that time [19,24,25]. In these areas, beech expanded only about 4000 years ago. Due to its late invasion and, most of all, because of the fact that it only spread over larger areas after the introduction of agriculture, Schulze et al. [26] termed it as neo-endemic, and other authors have even referred to *Fagus* as an ‘oversized weed’ [27]. Before its establishment in Central Europe, the majority of *Fagus* habitats were populated by *Tilia* [20,25], which plays an insignificant role in contemporary forests of the Hessian uplands. Owing to its wide ecological tolerance range and its numerous ecosystem services, it may be assumed that *Tilia* has the potential to become a crucial factor in future silviculture [28,29].

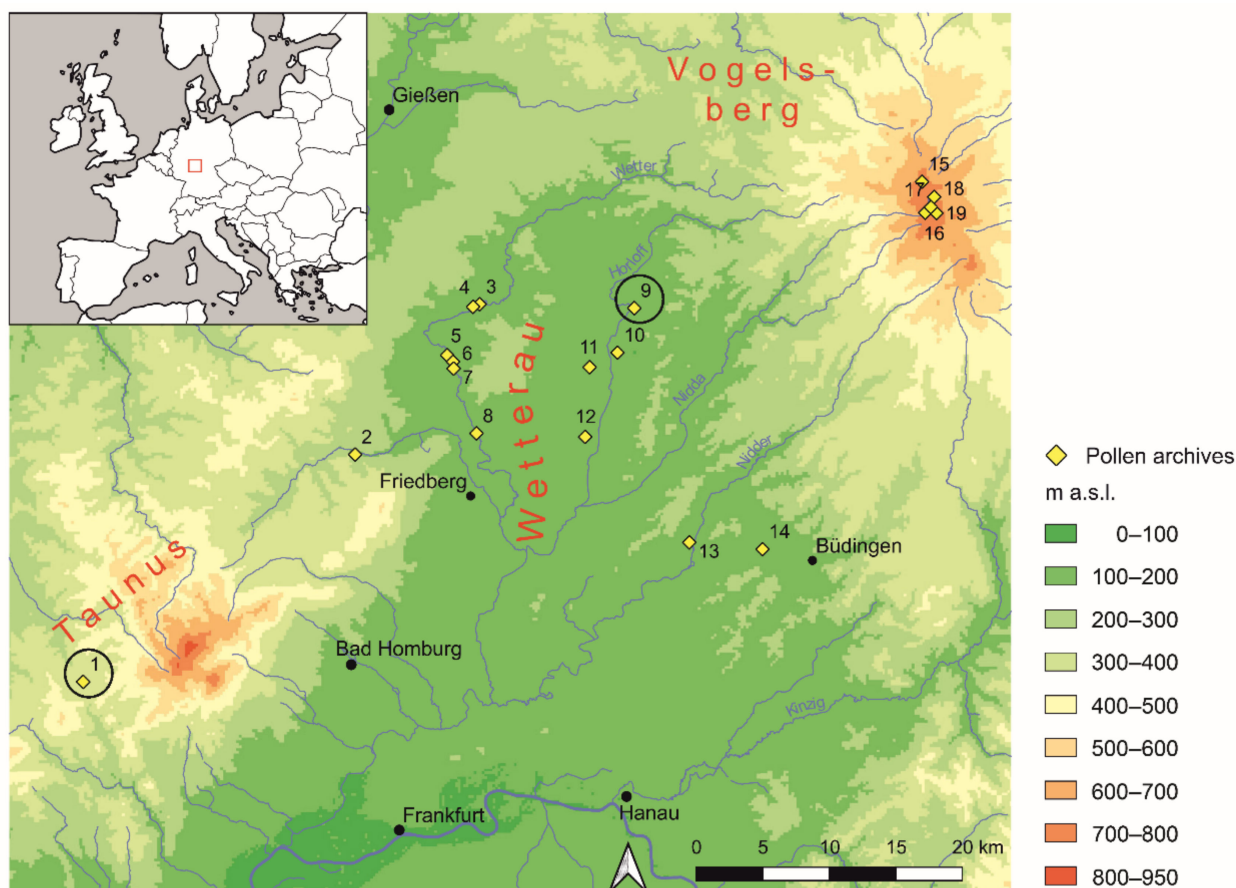


Figure 1. Map of the study region with previously published pollen archives: 1: Heftrich, 2: Usa valley, 3: Salzwiese, 4: Ober-Hörgern 2, 5: Rockenberg, 6: Oppershofen 5, 7: Opershofen 3, 8: Wisselsheim, 9: Moenchborn, 10: Widdersheim/Horloffau, 11: Dorfwiese, 12: Echzell, 13: Heegheim, 14: Büches, 15: Sieben Ahorn, 16: Forellenteiche, 17: Breungeshainer Heide, 18: Goldwiese, 19: Lattenbruch). Black circles mark the two sites in the focus of this study.

In order to determine the relevance of particular tree species under modified ecological conditions of the future and particularly as a basis for computer modelling, pollen records highlighting past vegetation formations during specific palaeoclimatic phases are especially

suitable [19,30–36]. The parallelisation with past vegetation scenarios is complicated by the fact that anthropogenic influences have been an important driver of European vegetation dynamics since the mid-Holocene [37]. Existing models, however, often use data from the warm and humid Holocene Climate Optimum, before human disturbances started to seriously affect woodland composition [35,36]. Other investigations have targeted historical epochs, which do not go back beyond the Migration period (1700–1400 cal. BP) [38], thus relating to a time when the forests were already completely transformed by human impact and hence do not reflect the climatic trends expected for the future. Considering only the distributions of tree species over the last centuries may also result in the underestimation of the future potential of those taxa that have been persisting in anthropogenically reduced ecological niches for millennia, such as *Tilia* and *Ulmus* [32,35,36,39]. While their relative proportional population growth rates were negatively affected by intensified land use, those of *Quercus*, *Fagus* and *Picea* were positively affected [40], which is why the latter taxa are likely to be overrated in future simulations.

Other than previous vegetation modelling approaches, this paper focuses on palynological analyses of a comparatively small study area between the Taunus and Vogelsberg mountains in Hesse, Central Germany, and the regional vegetation evolution between 9500 and 1500 cal. BP with particular focus on the Subboreal chronozone (approximately 6200–2800 cal. BP). The underlying archives originate from small fens (<10 ha), which have the potential to directly reflect local climatic and/or anthropogenic influences.

So far, woodland development from the Late Neolithic to the Iron Age (5300–2000 cal. BP) has not been considered in modelling even though it can assist in the analysis of current environmental developments in the light of past changes in climate, vegetation and land use, and thus serve as an example for practical forest management due to the following reasons:

1. The Subboreal chronozone has been characterised by a warm and dry climate with air temperatures 1.0–3.5 °C above modern levels. Between 7000 and 4000 cal. BP (Holocene Climate Optimum), the range of *Tilia* advanced 300 km north compared to its modern distribution.
2. At that time, the mixed deciduous forests were already partly cleared and extensively used. The development of increasingly complex economies, new crops, innovations in metallurgy and the secondary use of domestic animals all contributed to the intensification of human impact.
3. *Fagus sylvatica*, which is considered the potentially natural tree species for the Hessian uplands today, was not yet widespread in the forests, and *Picea abies* was completely absent.

From the Hessian uplands and intramontane basins, numerous palynological data are available, on the basis of which the following hypothesis is checked: as aridity increases, the potential natural vegetation will no longer be a *Fagus sylvatica* forest, but a mixed deciduous forest in which *Tilia cordata* may be the dominant species.

2. Material and Methods

2.1. Study Area

The study area lies in the German Central Uplands between the Taunus mountains in the west across the Wetterau basin to the Vogelsberg in the east, all located in the state of Hesse, Germany (Figure 1).

The Taunus is bounded by the Rhine, Main and Lahn valleys and consists of old sedimentary and metamorphic rocks. Its highest peaks lie near the Southern edge and rise to over 800 m (Großer Feldberg: 879 m above sea-level (a.s.l.)), while the farther Taunus gently slopes towards the Lahn Valley in the north. Soils range from shallow nutrient-poor Cambisols to fertile Luvisols in loess areas. Mean annual temperatures reach between 7 and 9 °C, precipitation is highest in the central part (800–1000 mm), while some lee-side areas in the north receive less than 600 mm. As part of the Rhine-Main economic region, the anterior Taunus is densely populated and, similar to the farther Taunus, contains large proportions of arable land. The high Taunus is predominantly forested. The most prominent phytocoenosis is the *Luzulo-Fagetum* with a species-poor herb layer, but mixed

oak woods and commercial spruce forests are widespread as well. Since the Neolithic, the Taunus has been settled—Linear Pottery culture sites are mainly concentrated in loess areas but occur up to an altitude of 400 m. Other well-documented archaeological periods are the Middle Bronze Age (Tumulus culture) as well as the Late Bronze Age and Iron Age when hillforts and oppida were built.

As a northern extension of the Rhine rift valley, the Wetterau is a large (around 800 km²), intensely cultivated loess basin (below 250 m a.s.l.) that is bordered by the Taunus and the Vogelsberg. Soils comprise Luvisols and degraded Chernozems. The climate is warm and mild (annual means of 8–9 °C and 536–650 mm), and, together with the fertile soils, offers ideal conditions for farming, which is why the Wetterau is known as the most productive agricultural region in Hesse. Today, forests cover only 15% of the region that, according to Bohn et al. [2], lies in the centre of the European beech zone. In some drier parts, thermophilous woodlands dominated by *Quercus petraea* would prevail; in the valleys, the potential natural vegetation is believed to have included communities such as the *Stellario-Carpinetum*, *Pruno-Fraxinetum* and *Querco-Ulmetum*. The Wetterau is a famous 'Altsiedelland' that underwent a very early Neolithic colonisation with the earliest Linear Pottery. Since then, almost all archaeological periods have been documented. A high settlement density is also known from the Middle and Late Bronze Age and the following Iron Age.

The Vogelsberg is an eroded volcanic cone with a diameter of 60 km and constitutes the largest basalt area in continental Europe (2260 km²). The central part reaches an elevation of 450–773 m a.s.l. Cambisols are the predominant soils. The climate is comparatively rough with mean annual temperatures of 6–7 °C and rainfall up to 1400 mm. In the volcanic core area, beech forests are considered the potential natural vegetation (with the higher montane beech zone above 650 m a.s.l. and the lower montane beech zone below 650 m a.s.l.). Below 500 m a.s.l., in the beech—mixed beech forest zone, agriculture is widespread nowadays. Linear Pottery finds are also known from the Vogelsberg (at 310 m a.s.l.), together with an increased number of Middle Bronze Age finds, while Late Bronze Age sites are less frequent. Different from the Taunus, only a few Iron Age finds are documented up to elevations of 500 m a.s.l.

2.2. Pollen Sampling

The investigations focus on the small (<10 ha) mires 'Heftrich' (Figure 1, no. 1) from the farther Taunus and 'Moenchborn' (Figure 1, no. 9) from the eastern edge of the Wetterau. Both archives originate from rich fens and contain a rather undisturbed peat sequence in the relevant chronozones, thus allowing the comparison between upland and basin landscapes. The site Moenchborn is one of many palynological archives from the Wetterau and lies at 130 m a.s.l. [10–12,41,42]. Coring took place with the help of an open gauge auger, collecting cores of 6 cm Ø and 1 m length in overlapping segments, resulting in a 3 m long peat sequence covered by 1.50 m of colluvium (Figure 2). In the previous century, the fen has been drained and converted to cultivated pastures. In the course of renaturation projects, the location became waterlogged again and now comprises a large reed area. The 190 cm long core from the Heftrich mire, a 9 ha protected area in the Idstein basin at 320 m a.s.l. [8,14], was retrieved from the central part. Between 170 and 40 cm, peats are found on top of organic silts (Figure 3). This is not particularly featured in this work but is used as background information pertaining to the profiles Heegheim (12,13,41,43), Dorfwiese [10] and Salzwiese [11,12,41–43], together with the Breungeshainer Heide profile from the high Vogelsberg (65 ha, 720 m a.s.l.) [7] and the Usa valley profile from the Taunus [8].

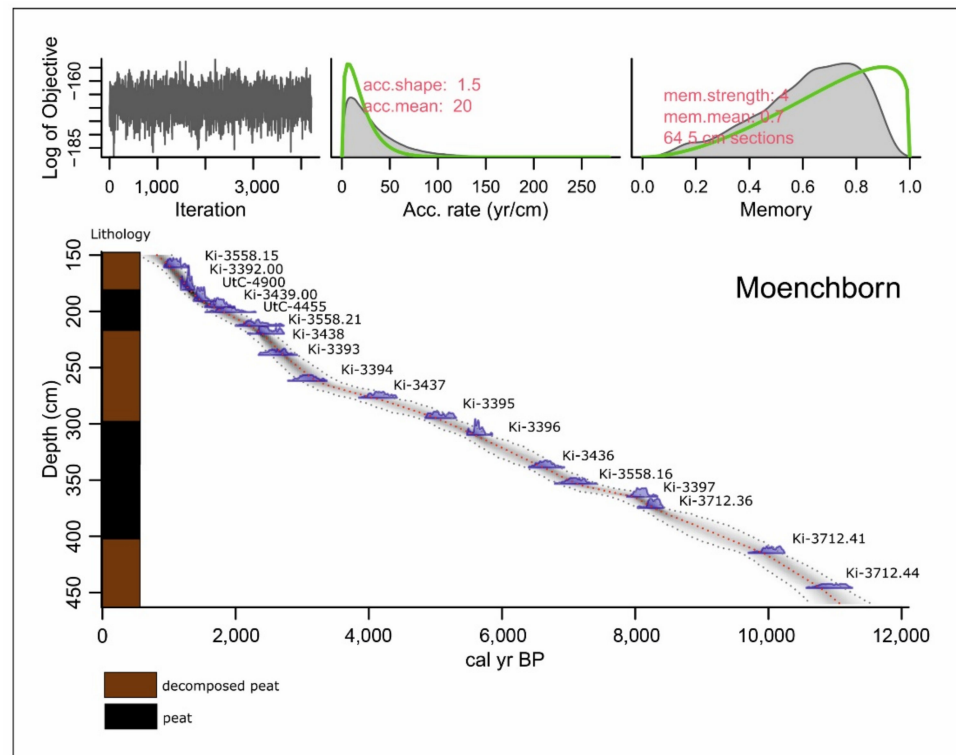


Figure 2. Age-depth model of profile Moenchborn.

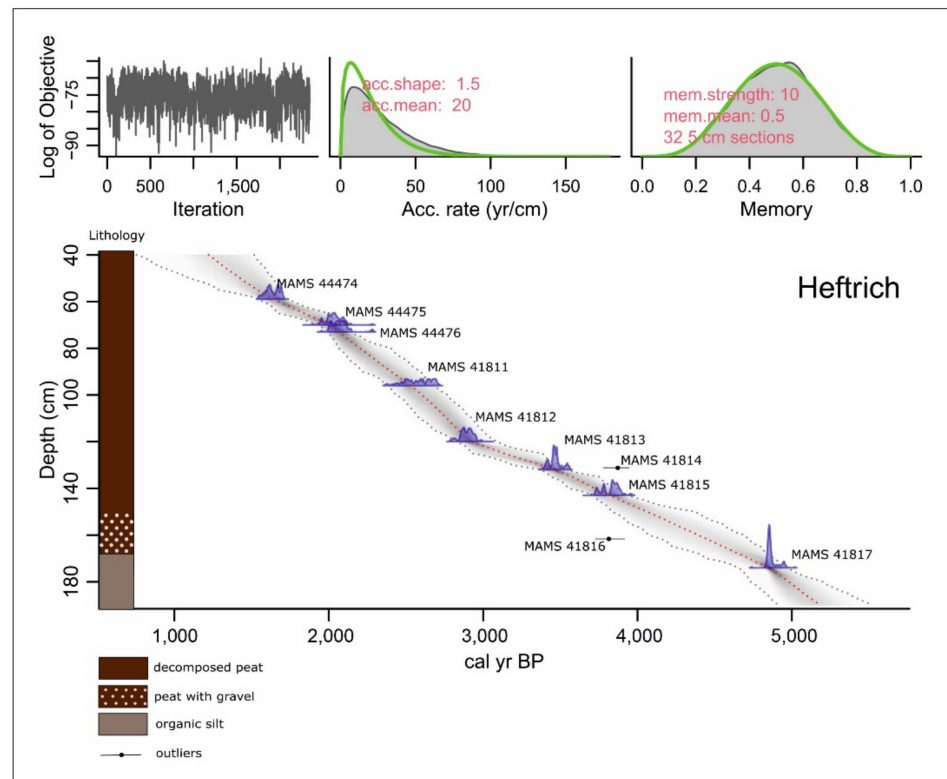


Figure 3. Age-depth model of profile Heftrich.

2.3. Dating and Pollen Analysis

The absolute chronology of the profiles is based upon 18 ¹⁴C dates from Moenchborn (Table 1, Figure 2), and 10 ¹⁴C dates from Heftrich (Table 1, Figure 3). Age-depth modeling

was performed with the R package Bacon 2.3.9.1 [44]. In the general discussion, the published data from other sites (Wetterau and Vogelsberg) were considered as well.

Table 1. Radiocarbon dates from the profiles Moenchborn and Heftrich.

Location	Sample Depth (cm)	Laboratory Code-Number	¹⁴ C date BP	Age (cal. BP) (2σ 95.4%)	Delta 13	Dated Material
Moenchborn	160–162	Ki-3558.15	1160 ± 60	1249–934	−28.2	peat
Moenchborn	179–184	Ki-3392.00	1370 ± 50	1360–1176	−29	peat
Moenchborn	190–193	UtC-4900	1612 ± 41	1570–1389	−31.3	peat
Moenchborn	195–198	Ki-3439.00	1840 ± 65	1923–1585	−28.4	peat
Moenchborn	200–202	UtC-4455	1950 ± 100	2146–1620	−26	peat
Moenchborn	212–215	Ki-3558.21	2300 ± 90	2700–2061	−28.4	peat
Moenchborn	218–222	Ki-3438	2400 ± 60	2705–2338	−28.4	peat
Moenchborn	237–242	Ki-3393	2560 ± 90	2845–2360	−29.5	peat
Moenchborn	260–265	Ki-3394	2930 ± 75	3332–2873	−27.9	peat
Moenchborn	276–279	Ki-3437	3780 ± 75	4408–3934	−30.3	peat
Moenchborn	293–298	Ki-3395	4430 ± 55	5285–4867	−28.6	peat
Moenchborn	308–313	Ki-3396	4890 ± 55	5745–5478	−28.3	peat
Moenchborn	338–341	Ki-3436	5840 ± 80	6850–6445	−29.8	peat
Moenchborn	351–355	Ki-3558.16	6210 ± 90	7319–6884	−27.1	peat
Moenchborn	363–368	Ki-3397	7270 ± 75	8298–7938	−27	peat
Moenchborn	373–377	Ki-3712.36	7480 ± 70	8413–8058	−27.4	peat
Moenchborn	413–417	Ki-3712.41	8940 ± 65	10,235–9798	−28.1	peat
Moenchborn	444–448	Ki-3712.44	9620 ± 100	11,226–10,688	−29.2	peat
Heftrich	58–60	MAMS 44474	1741 ± 21	1705–1567	−24.2	peat
Heftrich	70–71	MAMS 44475	2073 ± 26	2118–1944	−29	peat
Heftrich	73–74	MAMS 44476	2106 ± 22	2143–1997	−26.6	peat
Heftrich	96–97	MAMS 41811	2471 ± 20	2710–2429	−26.1	peat
Heftrich	120–121	MAMS 41812	2793 ± 21	2960–2801	−24.2	peat
Heftrich	132–133	MAMS 41813	3256 ± 21	3557–3400	−22.7	peat
Heftrich	137–138	MAMS 41814	3611 ± 22	3980–3845	−26.6	peat
Heftrich	143–144	MAMS 41815	3547 ± 20	3900–3724	−24.1	peat
Heftrich	162–163	MAMS 41816	3560 ± 20	3959–3728	−26.7	peat
Heftrich	174–175	MAMS 41817	4300 ± 21	4952–4833	−25.9	organic silt

The preparation of pollen samples in the archaeobotanical laboratory followed standard procedures [45]. Taxa were identified with the aid of the departmental reference collection and respective literature [46–49]. The pollen types were divided into local (wetland and aquatic plants including carr forest genera *Alnus*, *Salix* and *Populus*, Cyperaceae and spores) and regional taxa (including unspecified Poaceae). The results were processed with the TILIA software (version 2.6.1, Grimm, 1993–2015). The pollen assemblage zones (PAZ) were designated according to visual interpretations of the depth distributions of major terrestrial taxa (Tables 2 and 3, Figures 4 and 5).

Table 2. Pollen assemblage zones (PAZ) of profile Moenchborn.

Depth (cm)	PAZ	Approximate Age (cal. BP)	Palynological Characterisation
390–366	<i>Pinus–Corylus–Poaceae</i>	9100–8100	<i>Pinus</i> and <i>Poaceae</i> dominant, <i>Corylus</i> ca. 20%, <i>Ulmus</i> 5–10%, <i>Tilia</i> and <i>Quercus</i> < 5%
366–355	<i>Poaceae–Pinus</i>	8100–7250	<i>Poaceae</i> dominant, <i>Pinus</i> subdominant, <i>Corylus</i> ca. 10%, <i>Ulmus</i> , <i>Tilia</i> , <i>Quercus</i> 5–10%
355–335	<i>Corylus–Ulmus–Quercus</i>	7250–6550	<i>Corylus</i> , <i>Ulmus</i> , <i>Quercus</i> , <i>Pinus</i> , <i>Poaceae</i> dominant; <i>Cerealia</i> type, <i>Plantago lanceolata</i>
335–320	<i>Poaceae–Quercus</i>	6550–6000	<i>Poaceae</i> dominant (40%), <i>Corylus</i> and <i>Quercus</i> subdominant; <i>Ulmus</i> and <i>Tilia</i> < 5%
320–300	<i>Corylus–Quercus–Tilia</i> subzone a	6000–5200	<i>Corylus</i> dominant (max. 50%), <i>Quercus</i> subdominant, <i>Cerealia</i> and <i>Plantago lanceolata</i>
300–278	subzone b	5200–4200	<i>Corylus</i> dominant (30–40%), <i>Quercus</i> and <i>Tilia</i> subdominant (<i>Tilia</i> maximum 20%)
278–263	<i>Poaceae–Quercus–Corylus</i>	4200–3250	<i>Poaceae</i> dominant (ca.40%), <i>Corylus</i> and <i>Quercus</i> subdominant, closed <i>Fagus</i> curve, increase in NAP
263–237	<i>Fagus–Quercus</i>	3250–2750	<i>Fagus</i> dominant (ca. 25%), <i>Quercus</i> and <i>Poaceae</i> subdominant, increase in <i>Betula</i>
237–219	<i>Fagus–Quercus–NAP</i>	2750–2400	<i>Poaceae</i> dominant, <i>Pinus</i> , <i>Quercus</i> , and <i>Fagus</i> subdominant, increase in NAP/anthropogenic indicators
219–203	<i>NAP–Quercus</i>	2400–2000	<i>Poaceae</i> dominant, <i>Quercus</i> and <i>Pinus</i> subdominant, <i>Fagus</i> <5%

Table 3. Pollen assemblage zones (PAZ) of profile Heftrich.

Depth (cm)	PAZ	Approximate Age (cal. BP)	Palynological Characterisation
192–176	<i>Corylus–Quercus–Tilia</i> subzone a	6100–5100	<i>Corylus</i> dominant (max. > 70%), <i>Tilia</i> subdominant (ca. 20%), <i>Quercus</i> , <i>Fraxinus</i> ca. 10 %
176–163	subzone b	5100–4500	Decrease in <i>Corylus</i> , increase in <i>Tilia</i> , <i>Quercus</i> and <i>Poaceae</i>
163–134	<i>Tilia–Quercus–Corylus</i>	4500–3600	<i>Tilia</i> dominant (max. > 45%), <i>Corylus</i> decreases to 20%, <i>Fraxinus</i> < 5%.
134–110	<i>Tilia–Fagus</i>	3600–2800	<i>Tilia</i> (ca. 25%) and <i>Fagus</i> (ca. 25%) dominant; NAP ca. 20%, increase in <i>Plantago lanceolata</i> and <i>Cerealia</i> type, increase in <i>Kretzschmaria deusta</i>
110–103	<i>Corylus–Quercus–Tilia</i> subzone a	2800–2600	<i>Tilia</i> (ca. 20%) and <i>Fagus</i> (ca. 15%) dominant, increase in NAP
103–97	subzone b	2600–2450	<i>Fagus</i> (>25%) dominant, <i>Tilia</i> decreases to 5%, NAP increase to 20%
97–72	<i>NAP–Quercus</i>	2450–2000	<i>Poaceae</i> (ca. 30%) dominant, <i>Pinus</i> 20%, <i>Quercus</i> 15%, increase in <i>Plantago lanceolata</i> , dung spores and charcoal

2.4. R Values and Rank Correlation

Due to the different pollen production of plant taxa, the fact that some pollen types are more easily dispersed than others and because records include pollen both from nearby and far away sources that usually differ in vegetation cover, pollen percentages do not directly reflect the actual species abundances in the regional and local plant communities. To interpret palynological data in terms of the past vegetation composition, they have to be corrected for these biases. There are many new and promising approaches to determine pollen productivity estimates (PPE) such as REVEALS [50], LOVE [51] and MARCO POLO [52]. They are partly based on earlier calibration attempts such as the development of so-called representation factors (R values) by Andersen in 1970, in order to be able to approximate the actual frequency of tree species in the vegetation formations around the pollen profiles. R values as simple factors or divisors only give a rough overview of the composition of forests, as they cannot easily be compared spatially or temporally [53]. For the aim of this study, however, where the focus is set on the woodland succession in the surroundings of the pollen archives, R values after Andersen [54] are adequate, while additional external drivers of pollen productivity such as the ‘glade effect’ are also considered in the discussion [55]. R values were calculated for all tree taxa (e.g., *Tilia* times 2, *Corylus* divided by 4, *Quercus* divided by 4 and the original values in case of *Fagus*). The R values in relation to the (equally corrected) arboreal pollen totals are shown in Figures 6 and 7, serving as a main basis for our discussion, as they allow maximum visibility of the existing differences. Since the taxa are not normally distributed, the Spearman correlation coefficient was used instead of Pearson’s to describe the strength and direction of relationship of the species.

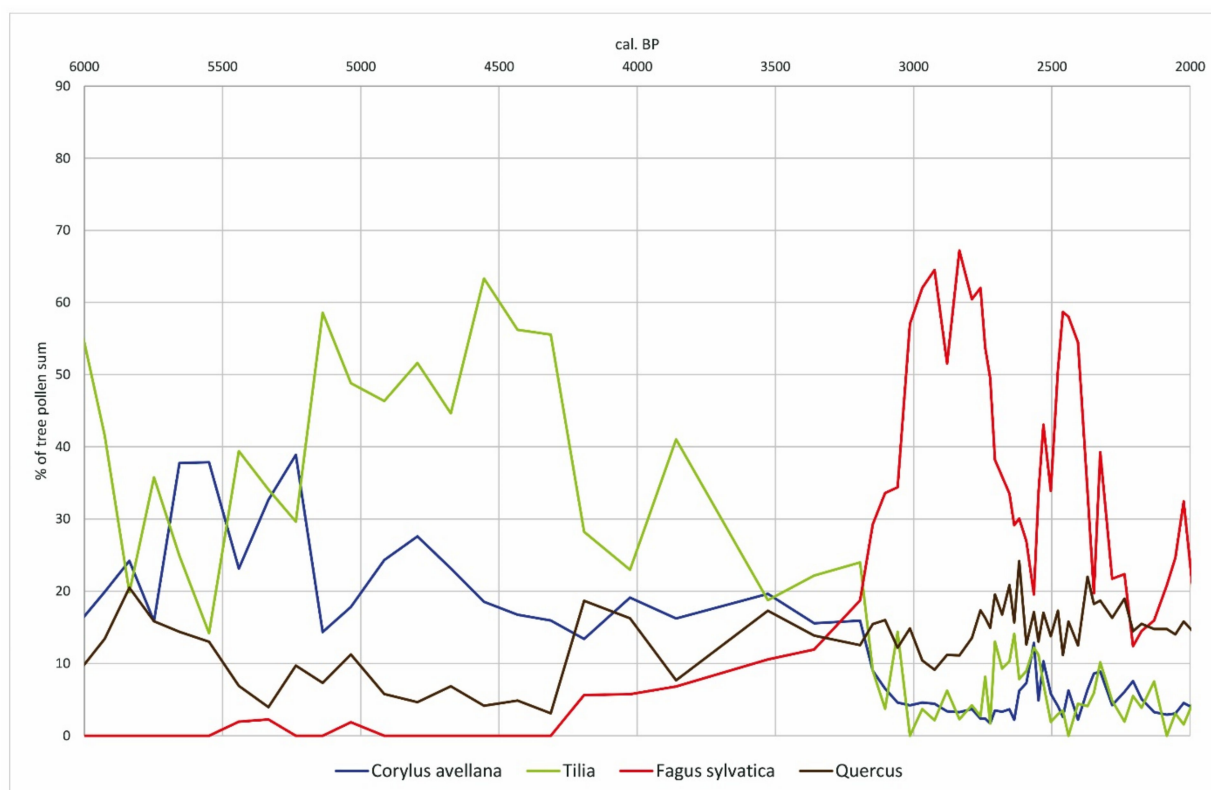


Figure 6. Pollen percentages transformed by R values of selected tree taxa at profile Moenchborn.

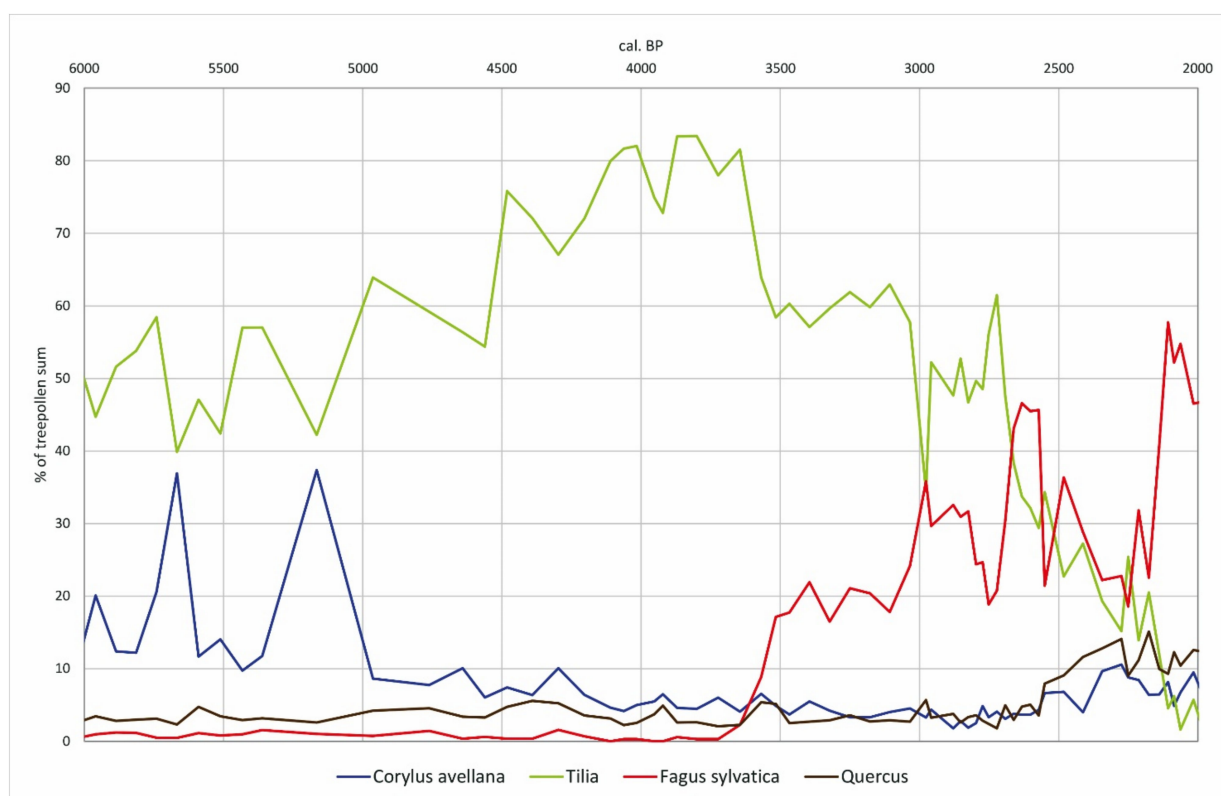


Figure 7. Pollen percentages transformed by R values of selected tree taxa at profile Heftrich.

3. Results and Discussion

Here, we present the regional pollen percentage diagrams with selected pollen types from the locations Moenchborn (reduced to the relevant section from 9500 to 2000 cal. BP) and Heftrich (Figures 4 and 5). The bivariate scatter plots and rank coefficients (Figure 8) show moderate negative correlations for *Corylus-Fagus* and *Tilia-Fagus*, but the diagrams also reveal that especially *Tilia* and *Fagus* tend to mutually exclude each other in many samples, demonstrating their general competition.

3.1. Forests in the Hessian Uplands during the Warm and Moist Atlantic

The Atlantic chronozone (approximately 8200–6200 cal. BP) was characterised by mean annual temperatures up to 3.5 °C higher than the present ones and also a greater amount of precipitation, but the mild winters were comparable to today [56–58]. The vegetation consisted of mixed deciduous forests with a different composition of tree species, largely depending on the soil types and local precipitation patterns [10,59]. *Pinus* was able to persist in the drier loess basins such as the Wetterau, where the present-day precipitation lies below 550 mm (Figure 4). Here, high values of wild grasses still account for open woodlands and floodplain areas in places with less rainfall. In the areas with more rainfall and at higher altitudes, deciduous trees prevailed. Waterlogged soils were colonised by *Quercus*, and mixed, species-rich oak woodlands became established on moist, nutrient-rich sites, with a *Querco-Ulmetum* (with small percentages of *Fraxinus*) in the alluvial plains. *Quercus*, *Ulmus* and *Tilia* continued to spread and, in the late Atlantic, mainly replaced the heliophilous *Corylus*. The altitudes from 150 to 500 m were dominated by extensive *Tilia* forests. In areas between 500 and 700 m with less fertile soils, forests rich in *Tilia*, *Ulmus* and *Fraxinus* could be found. On sites below 700 m with higher precipitation, *Tilia* predominated in the late Atlantic, while at higher elevations, *Ulmus* and *Corylus* were widespread [10,59,60].

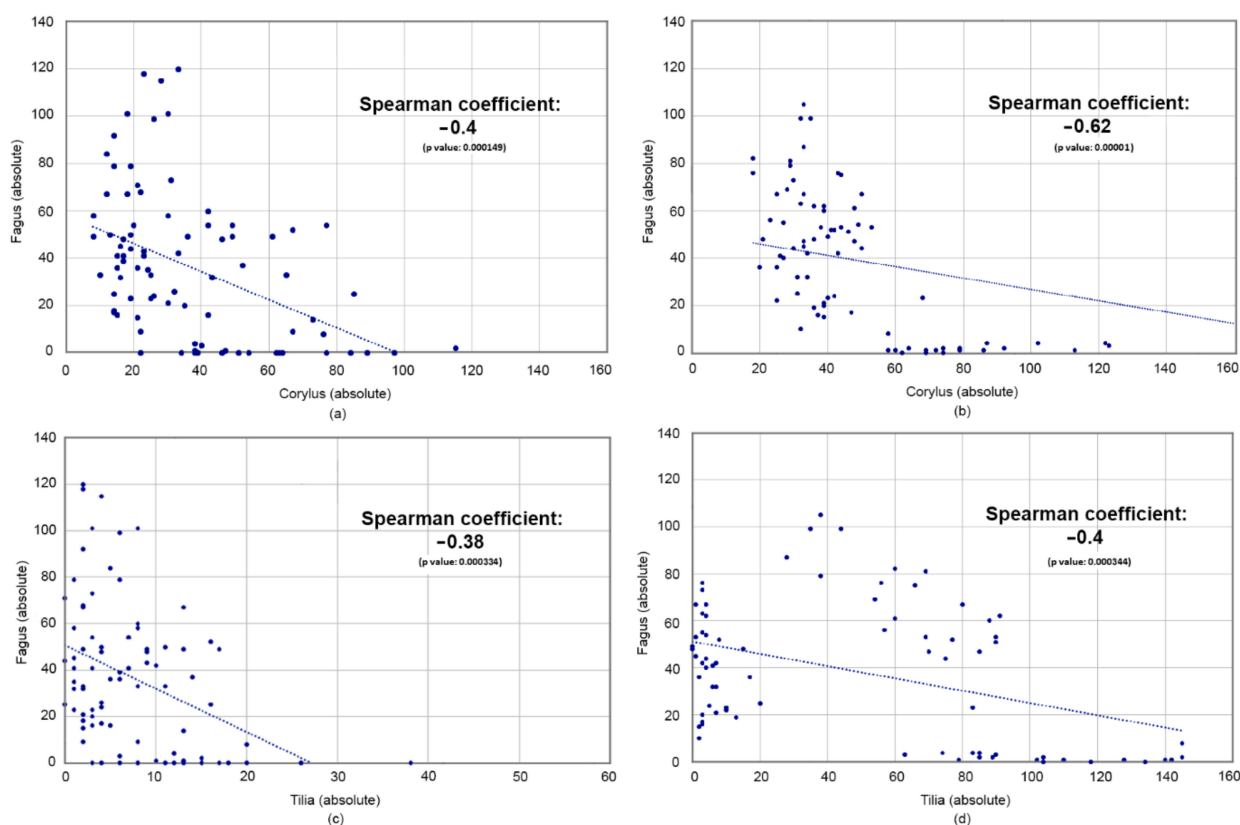


Figure 8. Scatterplots of selected tree taxa with linear trendlines (a) *Fagus*–*Corylus* at Moenchborn; (b) *Fagus*–*Corylus* at Heftrich, (c) *Fagus*–*Tilia* at Moenchborn (modified x-axis), (d) *Fagus*–*Corylus* at Heftrich.

The Hessian uplands are one of the core areas of the first farming communities of the Linear Pottery culture, which preferably populated the fertile loess lowlands. In these basin areas, vegetation changes indicating land use, such as the first forest clearings and anthropogenic indicators (*Cerealia* type and *Plantago lanceolata*), can be observed. Occasionally, there was a rise of *Fraxinus*, due to pollarding, and also of *Quercus* [10,59]. *Fagus* pollen is detected in the central Wetterau for the first time [59]. However, there was no obvious change in forest composition owing to human activities in the Early and Middle Neolithic. Therefore, in spite of the woodland clearances, Early Neolithic life seems to have remained strongly confined to the forest ecosystem [61].

3.2. More Than 2000 Years of Stable Deciduous Forests under Warm and Dry Climatic Conditions

Marked vegetation changes can be seen around 6200/6000 cal. BP. A stronger anthropogenic influence through the Michelsberg culture (6300 to 5500 cal. BP) of the Young Neolithic promoted the development of hazel-rich mixed deciduous woodlands, in which *Tilia* dominated the canopy, especially in the Taunus. Indicators for pastoralism and spores of coprophilous fungi attest anthropo-zoogenic activities. In the pollen diagrams from southern Germany, large-scale woodland clearance is evident, indicating substantial changes in land use from this time onward. The records from northern Germany show the adoption of agriculture by Mesolithic people. All data reflect the new forms of land use by Neolithic farmers [61]. During this phase, increased microcharcoal contents in many pollen diagrams attest ‘forest cultivation with burning’ [62–66]. The regular fires quickly led to the spread of heliophilous herbs and shrubs, such as *Corylus*, and hence landscape openness in the Young Neolithic.

About 1000 years later, from 5000 to 4000 cal. BP, *Tilia* reached its greatest extent at altitudes below 700 m between the Taunus and Vogelsberg mountains, while *Corylus* values decreased. *Tilia* flowers are entomophilous, and, even when pollen is produced in

large quantities, pollination by insects and the large and heavy pollen grains cause poor pollen dispersal. *Tilia* is therefore usually underrepresented in pollen diagrams [54]. When values rise over 10%, the existence of *Tilia* forests can be assumed [25]. These percentages are exceeded at the sites Moenchborn and Heftrich (Figures 4 and 5). By using R values (Figures 6 and 7), the dominance of *Tilia* becomes even more apparent. After the respective corrections, *Tilia* accounts for 60% of all tree pollen at the Wetterau margins and even 80% in the Taunus. The proportions of *Quercus*, however, are generally less than 10% and rarely rise above 20% between 6000 and 1000 cal. BP. We believe that this cannot be ascribed to the glade effect, since the growth of light-requiring species such as *Corylus* was inhibited. It rather appears that dense stands of *Tilia* prevailed, where large quantities of pollen were produced in the crown areas [67]. *Tilia* has the distinctive ability to develop sprouts and reproduce vegetatively. It can therefore regenerate quickly, especially after destructive influences such as browsing and bark damage, periods of drought and parasitic infections [68]. It thus easily gains ground at the expense of other taxa. Accordingly, the use of the woodlands for forest pasture, possibly also the use of linden bast and coppicing may have favoured the spread of *Tilia* and secured its dominance over other tree species. *Fagus* was not competitive in these forests, possibly also due to burning in woodland management [15]. Fires of low magnitude but with increasing frequency may have supported the competitiveness of *Tilia* and *Corylus avellana* [69].

3.3. Beech Takes Advantage of the Moment

Around 4200 cal. BP, the vegetation in some upland areas changed noticeably, even though this is not evident in all pollen diagrams. The central loess basins were still used extensively. On the eastern edge of the Wetterau, on the other hand, intensified land use led to a decline in *Tilia* pollen. Instead, *Quercus* values and especially non-arboreal pollen increased markedly (Figures 4 and 6). A novelty in this period are wet meadows, which developed in the alluvial areas previously overgrown with *Alnus* [10]. In the Taunus and Vogelsberg mountains, forest pasture was still in effect. However, also in the Taunus (Usa valley profile), a decline in *Corylus* and *Tilia* as well as an increase in *Quercus* and non-arboreal pollen can be observed. In the Vogelsberg, pollen analyses of soils show an increase in non-arboreal pollen around 4150 cal. BP [70]. In the fertile Idstein basin of the farther Taunus, on the other hand, the lime values reach their maximum. It is only around 500 years later, from 3700/3600 cal. BP (Middle Bronze Age) onwards (Figures 5 and 7), that land use intensifies. This can equally be observed at the higher elevations of the Vogelsberg [7].

The period around 4200 cal. BP is considered to be a phase of abrupt worldwide climate change, also known as the '4.2 ka BP event' [71–73], encompassing 200–300 years of mega-droughts, cold temperatures and strong winds that affected large areas [74]. The event is often linked to social collapses such as in Mesopotamia [75–77]. North of the Alps, on the other hand, little convincing evidence has been found so far, and it is assumed that this event had more visible consequences in the Mediterranean and the Middle East than in northwestern Europe [78]. In the area of investigation, it was probably due to cool and wet conditions that people abandoned marginal sites at higher elevations and returned to the climatically favoured basins. Therefore, such 'boom and bust' phases [79,80] cannot necessarily be paralleled in neighbouring landscapes with different ecological settings.

Although the beech has been documented in pollen diagrams from the Hessian low mountain ranges as early as the Atlantic chronozone, it only began to spread gradually since the Bronze Age. It took around 1000 years (Moenchborn profile), during which the region was under intensive cultivation and the forests were heavily thinned, until the beech finally became predominant. It experienced its last boost between 3500 and 3200 cal. BP, roughly at the occurrence of the '3.2 ka BP event', which is linked to a clear climate signal in the Mediterranean that terminated the Bronze Age in that region [81]. Subsistence crises are also suspected for northwestern Europe at this time, triggered by a volcanic eruption (Hekla on Iceland). This had a strong influence on the settlement

patterns in the Late Bronze Age (Urnfield culture, 3200–2800 cal. BP) [82], accompanied by a reorganisation of economic zones, changes in resource use and food diversification. In the Hessian low mountain ranges, settlements at middle and higher elevations were abandoned [83], and the population started to retreat once more to the favourable basins. In the formerly cultivated uplands, *Fagus* expanded and formed dense largely untouched forests throughout the Late Bronze Age. The final dominance of *Fagus* occurred abruptly in some places (Figures 4 and 6). Within 200 years, shady forests developed [84], in which the regeneration of other species, especially heliophilous species such as *Corylus*, but also *Tilia*, was hardly possible. In the Taunus, on the other hand, *Tilia* and *Fagus* struggled for supremacy for almost 1000 years. It was not until around 2600 cal. BP that the values of *Fagus* finally surpassed those of *Tilia* (Figure 5). In the fertile lowlands, on the other hand, the anthropogenic influence was so great during the entire Bronze Age that neither *Fagus* nor *Tilia*, but *Quercus* predominated in the remaining open woodlands.

Various reasons need to be discussed for the mass expansion of *Fagus* [19] and the decline of *Tilia* [85,86] in the Hessian low mountain ranges:

1. An advancement of *Fagus*, triggered by a cooler and more humid climate at the Subboreal/Subatlantic chronozone transition at the expense of *Tilia*, is obvious. A climate-related hypothesis for the reduction of *Tilia* stands had already been postulated by Godwin [87] and Firbas [88] and is also proposed by Pigott [89], who attributes the decline of *Tilia cordata* in England to the inhibited seed production at lower temperatures. This facilitated the spread of *Fagus sylvatica*. Such a scenario seems plausible for the margins of the Wetterau, but not so much for the Taunus, where, despite cooler and wetter conditions and an evident *Fagus* expansion, *Tilia* values remain distinctly high for around 1000 years. Nevertheless, a cooler climate likely had a negative influence on *Tilia* and gave an advantage to *Fagus*. This fact, however, is difficult to deduce from palynological records, since *Tilia* is known to produce pollen but no longer forms any fertile seeds under critical climatic conditions. Due to its ability to reproduce vegetatively and, above all, its high life expectancy of up to 1000 years [90], *Tilia* could have survived several hundred years and still produce pollen [91] before it finally had to give way to the shade-tolerant *Fagus*.
2. Pathogens contributed to a weakening of *Tilia*. Since the Middle Bronze Age, when *Fagus* values do not exceed 1% in the pollen diagrams, but *Tilia* values reach their peak, for example, in the Taunus, spores of the parasitic fungus *Kretzschmaria deusta* have increasingly been detected. In northern Poland, a connection was found between a dry phase of the mire and the high incidence of *Kretzschmaria deusta* in the surrounding forest [92]. In the Taunus, on the other hand, the increase in fungal spores can be paralleled with cooler and more humid climatic conditions, as was equally observed in the Western Carpathians [69]. It is thus possible that both dry and cooler conditions make *Tilia* susceptible to this fungus. However, the infestation probably does not cause the trees to die, but rather stimulates vegetative reproduction [92]. This possibly also contributed to the long dominance of *Tilia* in the Taunus.
3. There is no doubt that anthropogenic activities also had a significant influence on the spread of *Fagus* and the decline of *Tilia* [69,85,86]. At the edges of the Wetterau, the first expansion of *Fagus* around 4200 cal. BP occurred almost simultaneously with a sharp increase in non-arboreal pollen. At the same time, *Tilia* values are dropping, indicating forest clearings. In the Taunus, too, the first increase in *Fagus* at 5800 cal. BP correlates with a rise of non-arboreal pollen, albeit not until a few centuries later (Figures 5 and 7). All subsequent *Fagus* peaks in the Taunus are associated with initial increases in non-arboreal pollen, except for the period between 3000 and 2800 cal. BP. This final *Fagus* maximum is probably the result of changes in forest management and settlement behaviour. In many places, disadvantageous climatic conditions made people retreat from higher altitudes and caused a concentration of settlements in the climatically favoured basins. *Fagus* forests were able to develop in the low mountain ranges with minimal human impact, especially since *Tilia* was no longer competitive.

The reforestation of the hilly areas started only 200 years later, and *Fagus* percentages tend to vary during that time. With the beginning of the Iron Age, the formerly wooded areas of the Taunus and lower Vogelsberg were cultivated again and the arboreal vegetation was absent for around 200 years. The open spaces in the basins had also increased, and the pollen diagrams show intensive agriculture and pastoralism [11,12,41,42]. From around 2600 cal. BP, *Fagus* prevailed again for approximately 200 years in the low mountain ranges, but, already at approximately 2400 cal. BP, anthropogenic influences become conspicuous in all pollen diagrams, together with a decline of *Fagus* pollen. Since then, *Fagus* values show many fluctuations that can be correlated with land use on the low mountain ranges. A large-scale expansion of *Fagus* did not take place again until the Migration period. The forests during that phase are often seen as models for today's natural beech forests, even though they were cleared in many places as early as the 8th century AD. None of the *Fagus* populations proved to be stable over centuries. In the Taunus, closed *Fagus* forests only existed between 3200/3000 and 2800 cal. BP, 2600 and 2400 cal. BP, 1400 and 1200 cal. BP and (more or less) in the last 150 years. In the remaining (approximately) 4600 years, when the species was already established in Hesse, there were no extensive, dense *Fagus*-dominated forests.

A very similar development can also be observed in northern Germany [15]. This clearly distinguishes the region from southern Germany, where the mass spread of *Fagus* at the beginning of the Subboreal chronozone is considered a supraregional signal, and *Fagus* has been an integral part of the south German forests since then [22,23,93]. In the study area, as well as in the Jülich loess belt [94], however, the same habitats were occupied by almost pure *Tilia* stands in the Subboreal chronozone.

3.4. The Forests of the Future as Reflected by the Past

The palynological data show that, during past climatic conditions resembling the forecasted warmer and drier climate of the future, *Tilia* used to be the predominant tree species, while *Fagus* was largely a product of cooler and wetter phases. In regions with precipitation below 600 mm, such as the Wetterau and the lower Main plain, *Tilia* was not able to compete against *Pinus* and *Quercus* [10,59], but *Fagus* never achieved dominance either.

In view of the impending climate change and the fact that, in the uplands, *Fagus* only became dominant during the previous 3000–4000 cool and humid years, the term, potential natural vegetation, in the Hessian mountain regions has to be reconsidered. In the latest recommendations of the Northwest German Forest Research Institute for Hesse, *Fagus* already plays a less important role in many places [6]. Nevertheless, there is great uncertainty with regard to alternative taxa, which prevents forest owners from planting different tree species [95], even if model-based future simulations sometimes show considerable shifts in arboreal species and vegetation zones [30,31,33]. *Tilia cordata* has the potential to be the tree of the future after having been predominant in so many areas throughout the past millennia, especially under drier and warmer conditions and mostly in association with *Quercus* and *Corylus*. *Tilia cordata* was also widespread in continental Central Europe during phase B of the warmer and drier Eem Interglacial, and the distribution of *Tilia platyphyllos* reached much farther north than today [96]. By contrast, the occurrence of *Fagus* was rather insignificant, and its ecological range dominated by *Carpinus betulus*. For future forests, *Carpinus betulus* may be considered as well, which is also supported by palaeoecological records from Central Eastern Europe in the Subboreal chronozone [97–99] but not from our area of investigation where the species was not relevant until the Middle Ages [10]. Such a mixture could prove to be ideal in future plantations in many parts of the Hessian uplands and should thus be targeted in forthcoming forest development plans, with a particular focus on *Tilia*.

Even though this tree is very present in the common vocabulary, especially in the form of numerous traditional place names (villages, court and dance linden), and is one of the most planted trees in urban areas [100], *Tilia* has so far neither been considered in silviculture nor in modelling [101], irrespective of its large ecological amplitude. It is not,

or only slightly, affected by dry spells, tolerates a broad spectrum of soil fertility and grows on acidic (pH 4 and higher) as well as on neutral to alkaline soils. The strong root system protects older trees from storm damage, and, even an infestation with the fungal pathogen *Kretzschmaria*, poses no lethal danger to *Tilia* stands [28,29,92]. Presumably, *Tilia* will need human support for its expansion, especially because of its limited dispersal capacity [28], which is also evident in palynological records, as it hardly recovers after anthropogenically induced declines [69]. After having been an important economic tree in prehistory due to its suitability for coppicing and by supplying bast, *Tilia* is not seen as a profitable tree for the timber industry; however, in view of the increasing environmental stress in today's forests, its high ecological value and climate resilience makes it one of the most promising options for future forest management. To date, *Quercus* has been the preferential tree in terms of future forest stability, but palaeoecological research shows that it only played a minor role in the Subboreal chronozone woodlands. We therefore advocate that the re-establishment of *Tilia cordata* should become one of the key priorities in the formation of future forests, in which *Fagus sylvatica* will no longer be a dominant constituent. Such dynamic change is a normal phenomenon in the development of natural forests and should be actively supported in order to prevent disastrous ecological failures.

The palynological data show that, in the Taunus, Wetterau and Vogelsberg, the vegetation evolution was not synchronous, sometimes with temporal offsets of up to 1000 years, and that the predominance of beech has been restricted to the submontane areas and relatively short periods in time. However, beech forests are presently regarded as the potential natural vegetation of the whole region. Local peculiarities are usually not covered by supraregional computer models, which therefore have limited capabilities when small-scale causalities are important in determining the ecological potential for the development of distinct plant communities. A more realistic approach has to be based on a sound knowledge of the local physical environment; however, palynological data can already give crucial clues about the site-specific potential natural vegetation.

4. Conclusions

In the low mountain ranges and intramontane basins in Hesse (Germany), *Tilia* was an essential part of forests from 9000 to 2500 cal. BP, especially in the period between 6000 and 3000 cal. BP, for which a comparatively warmer and drier climate is postulated. *Fagus sylvatica*, which is considered a potential natural species today, only became dominant about 3000 years ago, when land use patterns changed, and, particularly, the climate became cooler and wetter. The palaeoecological investigations indicate that, in view of global warming, *Tilia* may be predestined to play a central role in forest development in deciduous forests in the Hessen mountains. In association with *Quercus* and *Corylus* and possibly *Carpinus*, it is strongly recommended for experimental mixed plantations in the future.

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