ORIGINAL ARTICLE

Vegetation and disturbance history of the Bavarian Forest National Park, Germany

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Abstract

National parks are supposed to protect large-scale ecological processes, along with species and ecosystems. Detailed knowledge about past vegetation and disturbance regimes therefore forms an important basis for appropriate management. In the Bavarian Forest National Park in SE Germany, we therefore studied fossil pollen, spores and macrofossils from lake Rachelsee, a nearby mire, and Stangenfilz mire, all lying at higher elevations. Results indicate that deciduous forest on lower slopes (ca. 500–1,000 m a.s.l.) were first affected by humans in Neolithic times ca. 4500 BC with marked declines of *Tilia*, *Ulmus* and *Fraxinus*. High-montane mixed forests (1,000–1,450 m a.s.l.) were in a near-natural state consisting of *Picea*, *Abies* and *Fagus* in comparable proportions up to ca. 500 BC (a natural baseline condition), after which they were impacted by forest grazing and/or logging, starting between early-Roman times to early-Medieval times depending on location. *Abies* especially declined markedly. Forest partially recovered during the migration period fifth-eighth century AD, especially *Carpinus*, but not *Abies*. Subsequently, deforestation increased at lower elevation for food production, and forest grazing and wood extraction at higher elevation led to a further strong decline of *Abies* around AD 1000 near Rachelsee. After that, nutrient levels increased continually at all elevations, and a forest fire occurred in the 13th century near Stangenfilz. During the 19th century, forests around Rachelsee recovered partially whereas overgrazing of Stangenfilz resulted in a hiatus. Forests declined further in the 20th century around the study sites, but after ca. AD 1960 less so around Rachelsee thanks to local conservation measures. Historically recorded large-scale bark-beetle infestations following heavy storms, such as in the AD 1870s and 1980s, hardly left traces in the pollen data. From a palaeoecological perspective the Park's no-intervention management strategy is well-suited to facilitate recovery of original forest functioning and diversity, as it is slowly leading to renewal of natural mixed forest of *Abies*, *Picea* and *Fagus*. This development may have considerable influence on the future disturbance regime, and the insights obtained will be important for the park management.

Keywords Bavarian Forest · Spruce bark beetle · Natural vegetation · Forest disturbance · Palaeoecology · Holocene · Forest management

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Introduction

Bark-beetle infestations of spruce (*Picea*) are more or less frequent in spruce-dominated forests all over the world (Bentz et al. 2010; Seidl et al. 2011). In the Bavarian Forest in Germany and the adjacent Šumava in the Czech Republic, recurrent outbreaks of the European spruce bark beetle (*Ips typographus* L. Col. Scol.) during at least the last 250 years killed Norway spruce trees (*Picea abies* (L.) Karst.) over tens of thousands of hectares (e.g. Heurich and Englmaier 2010; see ESM, A for more information).

Here we assess human impact during the past centuries to millennia and we address the question whether or not

large-scale bark-beetle infestations also occurred at intervals prior to the historical record. We also reconstruct how the mountain belt forests might have looked before human action started to influence their composition. Palaeoecological methods have been used to shed light on such questions (e.g. Stähli et al. 2006; Willis and Birks 2006; Valsecchi et al. 2010; Morris and Brunelle 2012), but so far no bark-beetle related study existed for the Bavarian Forest National Park. Assessing natural baselines and consequences of climate change and land use on vegetation may contribute to anticipating future vegetation dynamics under global change conditions and by this to an improved management of the Bavarian Forest National Park.

Landscape and history of the Bavarian Forest National Park

The Bavarian Forest National Park (NP) along the border between Germany and the Czech Republic (Fig. 1) is part of an approximately 2,000 km², densely wooded, middle-high mountain range in Central Europe. The altitudes range from 650 to 1,453 m a.s.l. This landscape belongs to the so called "Bohemian Masse", a very old mountainous region built of crystalline rocks such as gneiss and granite. Climatic conditions are cool and humid, with a mean annual temperature varying from 6.5 °C in the low mountain ranges to 3–4 °C at high elevation and an annual precipitation varying from approximately 1,000 mm in the valleys to 2,500 mm at high altitude. Long and cold winters with a lot of snow are typical for this region. Poor, acid and stony soils predominate. Wet

Fig. 1 Map of Bavarian Forest National Park in Germany, showing the study sites. *DE* Germany, *CZ* Czech Republic, *AT* Austria

and swampy soils play an important role, resulting in the development of peat bogs. 97% of the Bavarian Forest NP is covered by forests. The most important forest communities are montane beech (*Fagus sylvatica* L.) forest with silver fir (or fir; *Abies alba* Mill.) and spruce (52%), subalpine spruce forest (19%), spruce-fir forest on wet mineral soils in the valleys (8%), and spruce forest on wet organic soils (6%) (Heurich et al. 2010).

The Bavarian Forest NP was established in 1970 along the border between Germany and the Czech Republic as the first national park in Germany. The original area was 130 km² and was enlarged in 1997 to 240 km². Adjacent to this strictly protected area the Šumava NP was founded in 1991 on the Czech side with a total area of 680 km². Both NPs together form the largest protected densely forested area in Central Europe.

The general vegetation history can be glimpsed from pollen analysis carried out by Stalling (1987). After 4,500 year BP (years before present, i.e. before AD 1950), *Abies alba*, which grew in almost any location with the exception of particularly wet and extremely poor soils, was able to occupy the entire range of altitudes. Below 950 m a.s.l., beech-fir forests developed, in which *Picea abies* only played a subordinate role, being restricted to extreme locations, such as talus (or scree) fields and organic soils. At the time, spruce-fir-beech forests existed up to the highest altitudes. Heurich and Englmaier (2010) provide a detailed summary of the forest history and composition in the Bavarian Forest NP; see ESM B for more information. In summary, the almost undisturbed forest wilderness that existed until the early Middle-Ages became impacted by glassworks peaking in the 16th century and continuing to the early 19th century. This favoured spruce at the cost of fir and deciduous trees. Forest management intensified during the 20th century, which resulted in a striking collapse of fir especially after the 1930s. The Bavarian Forest NP declared a no-intervention strategy in 1983, resulting in a gradual decline of spruce and increase of fir, beech and other deciduous trees. Near our study sites, spruce is dominant at Stangenfilz, whereas spruce, beech and fir are important at Rachelsee and Alter Rachelsee.
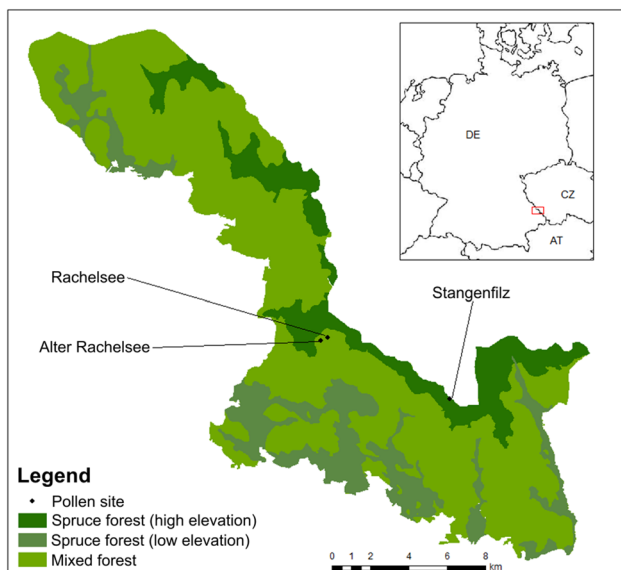
Sites and field work

For site and coring details see ESM, Tables 1–5.

Stangenfilz

The mire Stangenfilz lies in the Rachel–Lusen region of the Bavarian Forest National Park just west of Lusen Mountain, 7.5 km south-east of Rachelsee. The vegetation of Stangenfilz is reminiscent of raised bog, with species like *Sphagnum*

magellanicum, *Oxycoccus palustris*, *Carex pauciflora* and *Andromeda polifolia*. It lies in the spruce-dominated, uppermost vegetation zone of the Bavarian Forest. Most spruce trees adjacent to the mire died in the bark-beetle infestation of 1995 and 1996, resulting in dead trees on a large scale, but rapid regrowth of spruce took place in the following years (Zeppenfeld et al. 2015).

Two peat sections were collected from Stangenfilz (ESM, Tables 3 and 4). The short section (SFC2; 85 cm deep) was dug out in one piece. It was collected with the aim of retrieving as much as possible of the recent peat growth (last few centuries). The location was therefore selected where the well-preserved, still-growing upper peat layer was thickest (26 cm compared to 10 cm in the long core DFG) and also the directly underlying decomposed peat layer was thickest (10 cm compared to 7 cm in DFG). We failed to find a spot where the transition between the two layers was gradual, which implies that a hiatus between the two (missing peat layers) is more than likely (Sjögren et al. 2007). The long core (DFG) was extracted in 1 m core sections with a Streif–Livingstone piston corer by the coring team of the University of Bern, at the location where we could core deepest without obstruction by impenetrable wood. The coring was repeated in six different boreholes (B–G) lying very close together because many of the 1 m corings resulted in incomplete recovery. We used cores D, F and G, parallelized using clear litho-stratigraphic markers.

Alter Rachelsee

The mire Alter Rachelsee is a filled-in former lake; the name means 'Old Rachel-Lake', Rachel being the name of the nearby highest mountain top. The forests directly around the mire are dominated by *Picea abies*, with small proportions of *Abies alba* and *Fagus sylvatica*. The mire lies ca. 200 m south of the shore of the lake Rachelsee. Most of the unforested part of Alter Rachelsee is minerotrophic fen dominated by *Carex rostrata*. The peat section was collected in a large patch of vegetation similar to raised bog. Coring with a piston-corer failed because of too much wood below 30 cm, 50 cm and 65 cm, so that the study section was dug out in one piece by the first author. The coring location was where we could penetrate deepest with a gouge. All other tested places had impenetrable wood at 30 to 50 cm peat depth. Hauner (1980) showed an overview pollen diagram of Alter Rachelsee.

Rachelsee

Rachelsee is a glacial cirque lake, bordering partly on fen, partly on dense forest undergrowth, except for an artificial sandy-pebbly beach a few tens of metres long on the SSE side. The forests directly around Rachelsee are dominated by *P. abies*, with a large proportion of *A. alba* and less *F. sylvatica*. The lake water depth at the coring location is estimated at 13 m. 1,180 cm of sediment was recovered for the long core (RAA). Coring stopped in impenetrable gravelly sand. The short cores (RAS and RA0) were taken with the intention of recovering also the upper, unconsolidated sediments that are always lost with the coring technique used for the long core. RAS was taken just prior to the coring of RAA at the same location, whereas RA0 was taken at a different location closer to the beach.

Laboratory methods and data analysis

The collected peat cores and lake sediments were subsampled and prepared in the laboratory for the analysis of micro- and macrofossils, micro-charcoal, and radiocarbon; see ESM, C for details. Exotic markers (*Lycopodium* tablets) were added for the determination of pollen concentrations (Stockmarr 1971). Industrial soot (spherical carbonaceous particles) was counted on the pollen slides, microscopic charcoal particles were counted in cores SFC2 and RA0. Pollen was identified with help of the usual pollen floras and atlases. In Rachelsee RAA, 20 *Tilia* pollen grains in 13 samples between 204 and 276 cm depth were identified to species level (*T. cordata*, *T. platyphyllos*) following Christensen and Blackmore (1988). The identification of conifer stomata follows Trautmann (1953).

The pollen sum on the basis of which all percentages were calculated includes terrestrial pollen, whereas aquatic and wetland pollen was excluded. The sediment accumulation rates were calculated on the basis of the age-depth models. Numerical zonation of the pollen data was carried out by optimal sum of squares partition and the number of statistically-significant splits was determined with the broken-stick model (MacArthur 1957), following the recommendations of Bennett (1996). The datasets used for zonation included all terrestrial pollen, excluding aquatic and wetland pollen. For Rachelsee datasets (RAA, RA0 and RAS) Monolete fern spores were also included, as this taxon may play an important role in the reconstructed forest dynamics. *Melampyrum* was excluded for Stangenfilz, since here this is a wetland plant of strictly local occurrence. The zonation of the long core of Rachelsee was transferred to the short cores from the same lake (RA0 and RAS) on the basis of pollen stratigraphy. The numerical zonation is useful for the interpretation of forest dynamics but appeared to be too coarse, so we distinguished a number of additional zones.

The interpretation of the data takes account of taphonomy and of the production and dispersal properties of the micro- and macrofossils of the involved plant taxa. In ESM, D we discuss how this works out for our data and for the region of study.

Results and interpretation

Lithology

At Stangenfilz many of the core sections of the long core suffered selective loss of peat during coring, especially those containing layers of tough fibres consisting of *Eriophorum vaginatum* leaf bases alternating with layers of less fibrous, decomposed peat and gyttja layers, probably reflecting higher water tables (ESM Tables 3, 4). The mechanism of peat loss is in all likelihood that the cutting edge of the corer tends to push a fibrous layer down for some vertical distance before cutting through it, at the same time pushing sideward the underlying less fibrous decomposed peat. This problem was solved by connecting the parallel cores of three boreholes (D, F and G) to gain a near-complete stratigraphy.

At Alter Rachelsee the sediment consists of peat and wood. The collected peat section was compact and rather dry, and little or no water came in the hole during digging (ESM Table 5). Finally, the sediments of Rachelsee consist of black organic gyttja without visible traces of sand except for a rounded, oval stone embedded in core RAA stretching from 70 to 73.5 cm sediment depth, which must have been thrown into the lake, presumably from the small beach being the only part of the lake shore that has any gravel at the surface.

Chronology

A total of 30 radiocarbon dates was obtained from Stangenfilz, Alter Rachelsee and Rachelsee using plant material (Table 1). Radiocarbon dates were calibrated to calendar years AD and BC with use of the IntCal13 calibration curve (Reimer et al. 2013). The age-depth models are shown in Fig. 2, the model for the Stangenfilz DFG (Fig. 2a) was constructed by linear interpolation between calibrated radiocarbon dates, the top, and two pollen dates derived from Lake Rachelsee RAA (Fig. 2b). All radiocarbon dates were accepted for building the age-depth model. The two pollen dates from RAA are the ages of the start and end of the marked *Carpinus* maximum in zone 6b. The transfer of dates in this direction is justified by the more constant sediment-accumulation rates in RAA whereas in DFG they are likely variable due to selective loss of sediments during coring (see above), and in addition, the ages of this event in RAA are highly plausible when compared to other diagrams in the region (Stalling 1987) and can be assigned to the Migration Period. The dating of events (marked by pollen zones) seems thus in RAA more robust than in DFG. In Stangenfilz SFC2, the radiocarbon date at 36.4 cm falls out of sequence, so it was not used (Fig. 2c).

A joint age–depth model of the mire Alter Rachelsee (AR) and the upper section of the lake Rachelsee (including RAA < 153 cm and RAS) was established at the Laboratory for the Analysis of Radiocarbon with AMS (LARA) in Bern (Szidat et al. 2014) using Bacon 2.2 (Blaauw and Christen 2011). Recently, Rey et al. (2019) showed for high-resolution chronologies of laminated sediments from two Swiss lakes that Bacon is suitable for most sedimentary investigations at centennial time scales. The three sequences were merged as follows: First, RAS and the upper part of RAA were synchronized based on the increase and decrease of Monolete fern spores (zone 9), indicating similar deposition rates of both sediments. The top of this combined sequence was adjusted to the top of RAS, because the upper part of RAA is missing. The combined RAS/RAA sequence was then compared to AR using these anchor points: onset and decline of Industrial soot (zones 11b and 11c), sudden decrease of *Blechnum spicant* and *Juniperus communis* (zone 8b) and the contemporaneous increase of Cyperaceae. This comparison revealed a very good correlation between RAS/RAA and AR ($r^2 = 0.99$), with a slope of 0.768 indicating the difference of deposition rates between the lake sediments (RAS/RAA) and the mire (AR). The factor of 0.768 was then applied to establish a joint sequence of AR, RAA < 153 cm and RAS, of which the top of AR represents the coring year 2011. Pollen influx data have been applied in order to refine radiocarbon-based chronologies using different approaches. For example, Goslar et al. (2009) employed pollen concentrations to quantify relative changes of sedimentation ranges in a free-shape statistical model. We applied a simplified procedure and performed a correction of the sediment density using the sum of the volume-related pollen concentrations (all upland taxa except *Picea*) of RAS/RAA to establish an exponential fit of the average density increase. This fit was then used to determine density-corrected depths of the joint sequence of AR, RAA < 153 cm and RAS, with which Bacon age–depth modelling was performed. Figure 2d shows the results of this approach based on the density-corrected depths, whereas the chronologies of Figs. 8–15 refer to the original depths of the individual cores.

The model of the lower section of Rachelsee (i.e. RAA > 153 cm) follows the age scale of Carter et al. (2018) (see Fig. 2b).

Zones 1–11 and subdivisions were designed to reflect similar biostratigraphic features in the regional microfossil assemblages in all pollen diagrams, so that they represent synchronous periods. The microfossils used for synchronisation within the last 2.5 millennia include primarily Industrial soot (*SCP* Spheroidal Carbonaceous Particles), Monolete fern spores (within Rachelsee), *Cannabis sativa*, and *Carpinus betulus* (for the Migration Period). Two diagrams go back to the early Holocene, others start later.

Table 1 Radiocarbon dates

Depth (cm)	Thickness (cm)	Material dated	Radiocarbon age (BP)	Lab.code
Stangenfilz DFG				
58	1	*Sphagnum* stems	870 ± 30	Poz-54090
138	1	*Sphagnum* stems	2,935 ± 35	Poz-54091
194	2	*Sphagnum* stems	3,660 ± 35	Poz-34041
291	2	*Sphagnum* stems	4,620 ± 35	Poz-34042
337	1	*Sphagnum* stems	6,880 ± 50	Poz-54092
424	2	*Carex* seeds	8,630 ± 50	Poz-34043
Stangenfilz SFC2				
10.5	1.0	*Sphagnum* stems	− 773 ± 36	Poz-34035
20.5	1.0	*Sphagnum* stems	− 3,943 ± 40	Poz-34036
25.8	0.4	*Sphagnum, Drepanocladus*	225 ± 30	Poz-29921
30.05	0.3	*Sphagnum* stems	325 ± 30	Poz-34131
36.4	0.4	*Sphagnum* cf. *fuscum*	905 ± 30	Poz-29922
48.5	1.0	*Sphagnum* stems	805 ± 35	Poz-34132
51.5	1.0	*Sphagnum* stems	750 ± 80	Poz-34040
59.5	0.4	*Sphagnum* cf. *fuscum*	1,095 ± 30	Poz-29923
Rachelsee RAA				
89		*Picea, Abies, Fagus*[a]	56 ± 22	BE-3034
117		*Picea, Fagus*[a]	693 ± 30	BE-3035
128		*Picea*[a]	1,170 ± 29	BE-3036
143		*Picea*[a]	1,861 ± 22	BE-3037
216		Plant material	4,910 ± 35	Poz-85119
276		Plant material	9,120 ± 50	Poz-85121
308		Plant material	9,980 ± 60	Poz-85122
Rachelsee RAS				
32.0	1.0	*Picea* needles	133 ± 21	BE-3033
Alter Rachelsee AR				
11.8	0.6	*Sphagnum*	− 920 ± 22	BE-3027
19.8	0.6	*Sphagnum* stems	− 2,800 ± 21	BE-3028
23.0	1.0	*Sphagnum*	− 2,445 ± 35	BE-4620
25.8	0.6	*Sphagnum* stems	45 ± 21	BE-3029
33.3	0.4	*Sphagnum* stems	26 ± 28	BE-3030
48.8	0.6	*Sphagnum*	100 ± 20	BE-4621
51.8	0.6	*Sphagnum* stems	122 ± 22	BE-3031
57.8	0.6	*Sphagnum* stems	84 ± 22	BE-3032

[a]Dated material includes fragments of needles, leaves, and/or twigs

Palynology and macrofossil inferred vegetation history

An average pollen sum of 627 ± 330 grains was counted in the pollen samples. The results of pollen and spores and of macrofossils are shown in Figs. 3–15. Pollen percentage diagrams are the main basis for the interpretation in terms of past vegetation, whereas pollen influx diagrams yielded support in three sites. Macrofossil diagrams of two sites provide information on local past vegetation. Charcoal and soot records are used to reconstruct the fire and pollution history.

Early Holocene shift from boreal to temperate forests, 9500–8500 BC

The pollen record from Rachelsee (zone 1, Fig. 3) suggests that *Betula* and *Pinus* dominated boreal or nemo-boreal forests (few pollen grains and partly continuous curves of *Quercus, Corylus avellana, Ulmus, Fraxinus excelsior, Acer, Tilia*). The forests were rather closed (90% arboreal pollen, AP; Lang 1994; Lotter 1999). Open land was restricted to natural opening e.g. by lightning or windthrow (Poaceae < 10%); if corrected for underrepresentation of herbaceous species in pollen diagrams open land may have
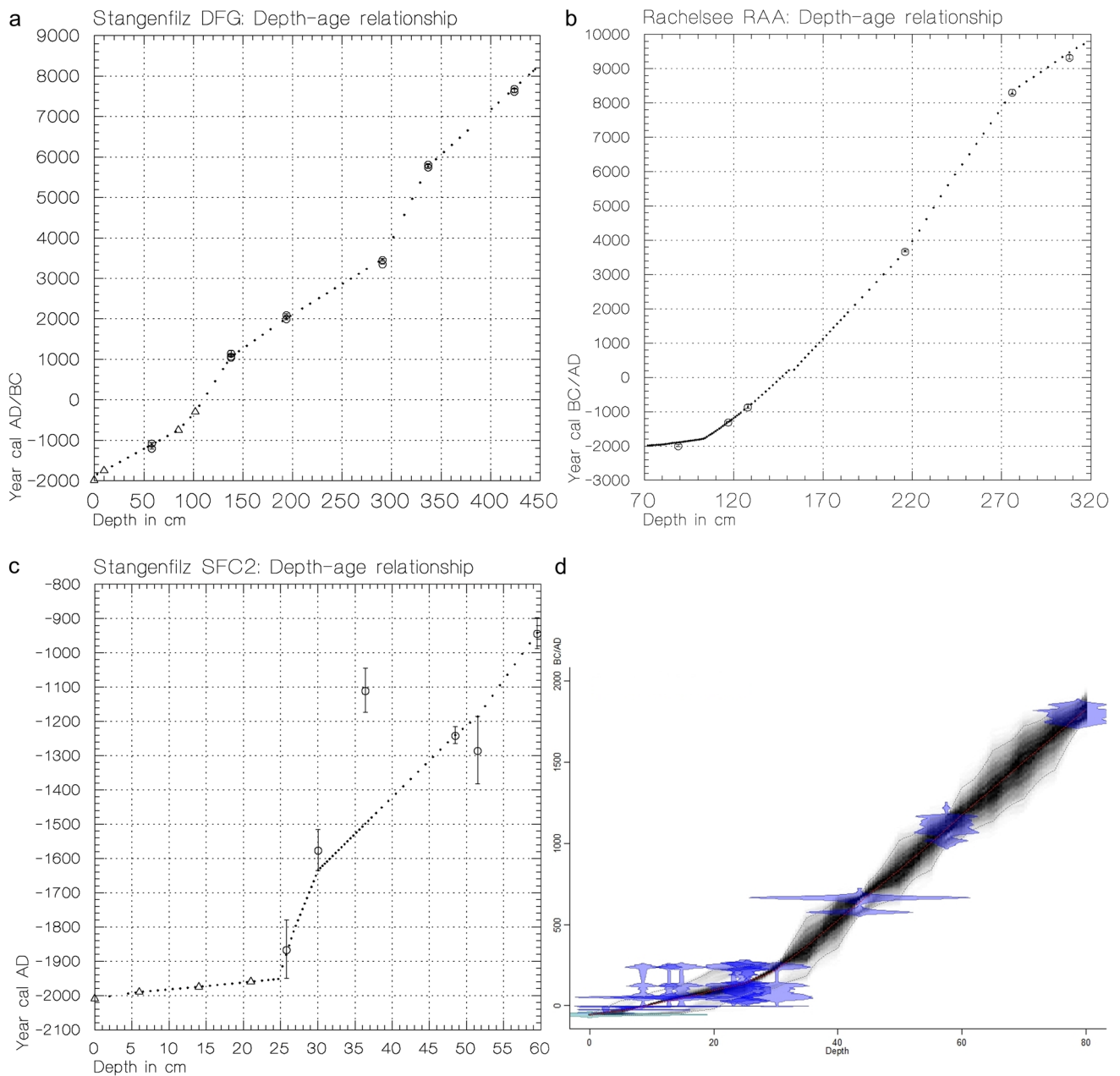
Fig. 2 Age–depth relationships—triangles are pollen-stratigraphic dates, circles are calibrated radiocarbon dates (with 1σ error bars); **a** Stangenfilz DFG, **b** Rachelsee RAA, **c** Stangenfilz SFC2, **d** age–depth relationship of the combined sequence of AR, RAA < 153 cm and RAS based on Bacon modelling using the density-corrected depths of the synchronized cores

comprised ca. 10–30% of total vegetation (Carter et al. 2018).

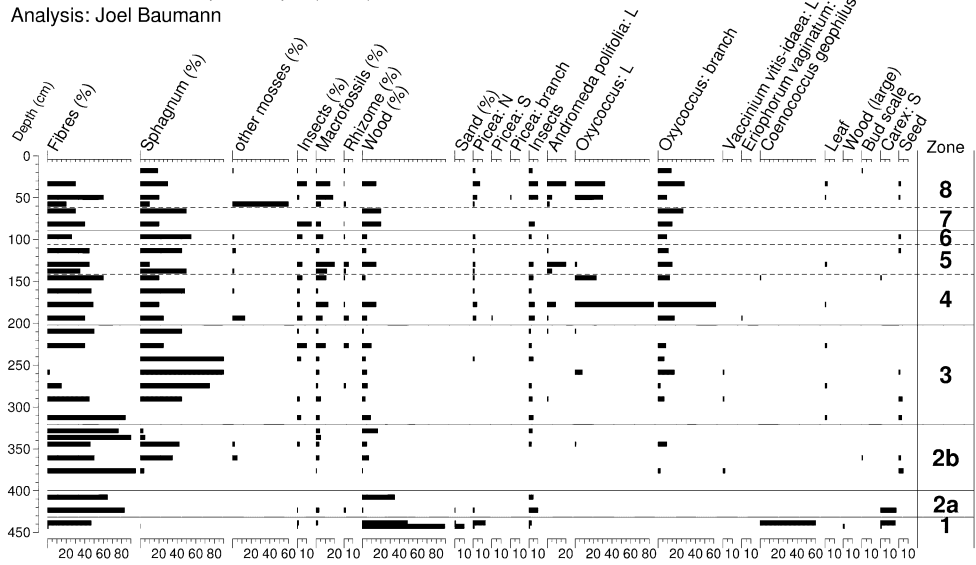## Early and mid Holocene continental temperate forests, 8500–5000 BC

The pollen record from Rachelsee and the pollen and macrofossil records from Stangenfilz (zone 2, Figs. 3, 4, 5) suggest that *Corylus avellana* with *Picea abies*, *Ulmus*,

Fraxinus excelsior, *Quercus*, *Alnus glutinosa/incana* and *Tilia* expanded in the pine and birch forests. Locally at the highest altitudes (Stangenfilz) *P. abies* was probably the most important species, as documented by the macrofossil record. Around 6500–6000 BC the *F. sylvatica* pollen record becomes continuous, suggesting that first small stands of the species had established in the NP area. *Isoëtes* established in Rachelsee. Towards the end of the zone around 5500 BC *Fagus* expanded massively, suggesting that the tree

Fig. 3 Rachelsee RAA Holocene: pollen percentages; selected types. Solid zone lines are statistically significant. AP (arboreal pollen) = Trees + Shrubs; NAP (non-arboreal pollen) = Upland herbs

Fig. 4 Stangenfilz DFG Holocene: pollen percentages; selected types. Solid zone lines are statistically significant. AP (arboreal pollen) = Trees + Shrubs; NAP (non-arboreal pollen) = Upland herbs. Sample at 401 cm is at top of core section; *Abies alba* and *Fagus sylvatica* pollen suggests that it is contaminated with younger material – the sample would smoothly fit in at ca. 330 cm depth

Stangenfilz DFG Holocene: macrofossils

Volume % and counts per sample (50 ml)
Analysis: Joel Baumann

Stangenfilz SFC2

pollen %

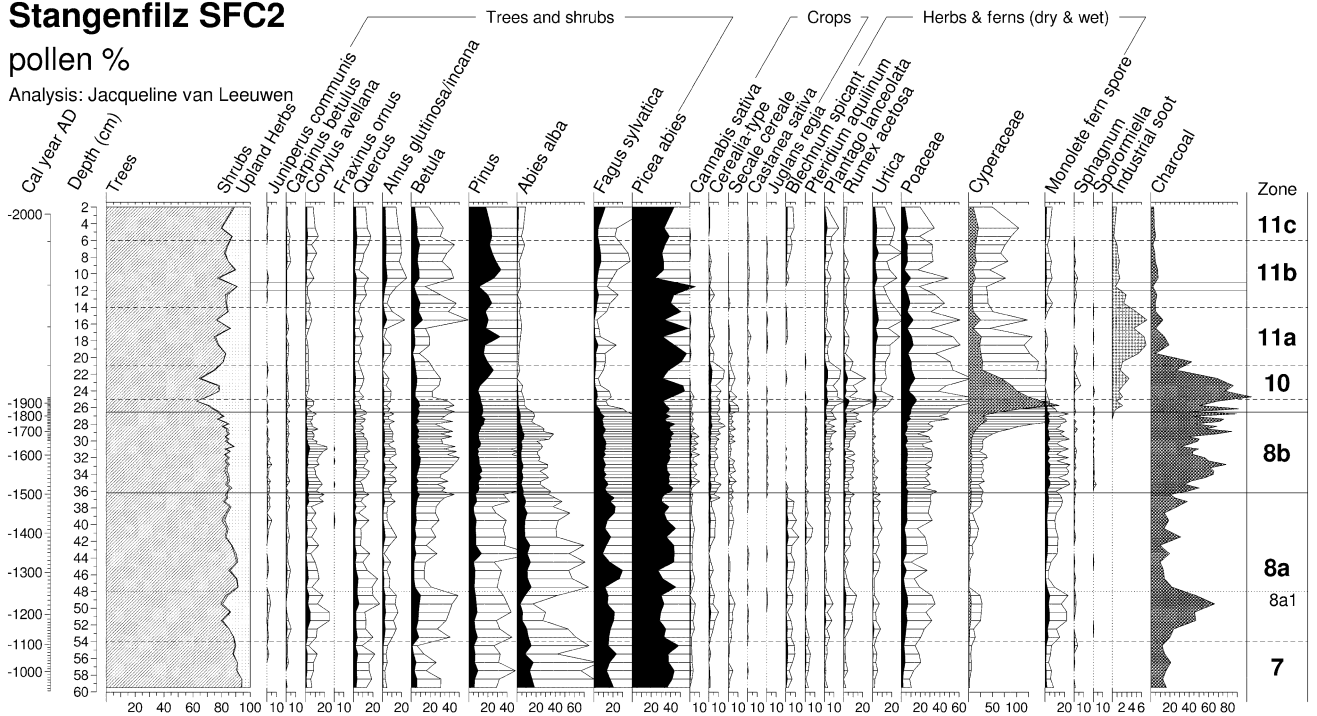Analysis: Jacqueline van Leeuwen

Fig. 6 Stangenfilz SFC2 (short core): pollen percentages; selected types. Solid zone lines are statistically significant; zone lines at 11 and 12 cm depth are not used

became competitive, partly replacing other taxa, specifically the light-demanding *Pinus* (Stangenfilz) and/or *Corylus* (Rachelsee). Finally, *A. alba* reached its empirical limit (i.e. a continuous curve) around 5000 BC. Forests were very dense and the proportion of open land was reduced to less than ca. 5% (AP vs. NAP, see also Carter et al. 2018).

Elm and linden decline in the mixed spruce-beech forests, 4500–2100 BC

The pollen records from Rachelsee and Stangenfilz (zone 3, Figs. 3, 4, 5) indicate that on lower slopes or foothills elm (*Ulmus*) and linden (*Tilia*) declined around 4500 BC.

Stangenfilz SFC2: macrofossils

Volume percent (%) or counts standardized to 10 cm³
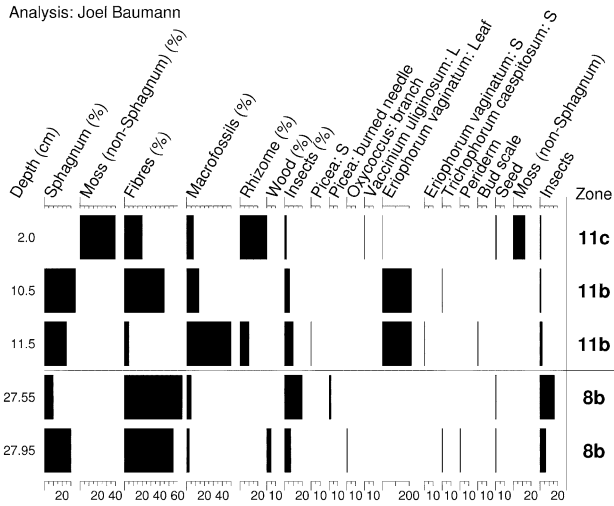Analysis: Joel Baumann

Fig. 7 Stangenfilz SFC2 (short core): macrofossils

This is a wide-spread response to Neolithisation in Europe around this time (e.g. Welten 1982; Lang 1994; Tinner et al. 1999; Birks and Tinner 2016), but since other indications for human impact on the forested landscape are very minor we must conclude that Neolithic activity did not affect the forests at higher altitudes in the surroundings of the study sites. These were stable with dominance of *Fagus*

around the more sheltered Rachelsee and *Picea* around the more exposed, higher-lying Stangenfilz, which *Abies* gradually invaded as the third major forest constituent. Indications of the quasi-natural character of most of the forest are the gradual decline (or low values) of trees with a pioneer character (*Corylus*, *Betula*, *Pinus*), the presence of *Taxus*, and the low values of grass pollen (Poaceae). Other trees grew admixed or in specialized habitats and mostly at lower elevations: *Alnus glutinosa/incana*, *Fraxinus excelsior*, *Acer*, *Populus*, *Sorbus*, *Quercus*, and *Carpinus betulus* (first occurrence).

Intensified human impact on lowland forests in the late Holocene, 2100-500 BC

The records from Rachelsee and Stangenfilz (zone 4, Figs. 3–5) indicate that land use increased after ca. 2100 BC (Bronze Age), mainly through the creation of grasslands (*Plantago lanceolata* as main indicator) and, very rarely, arable fields (first Cerealia-type pollen at Rachelsee ca. 1500 BC). This intensification of land use must have affected mainly valley-bottom forests (e.g. further reductions of *Tilia*), as the steady population expansion of *Abies* shows that the mixed spruce–fir–beech forests around the study sites were still rather closed at regional to local scales (high AP, low NAP; Carter et al. 2018).

Rachelsee RAA-top: pollen %
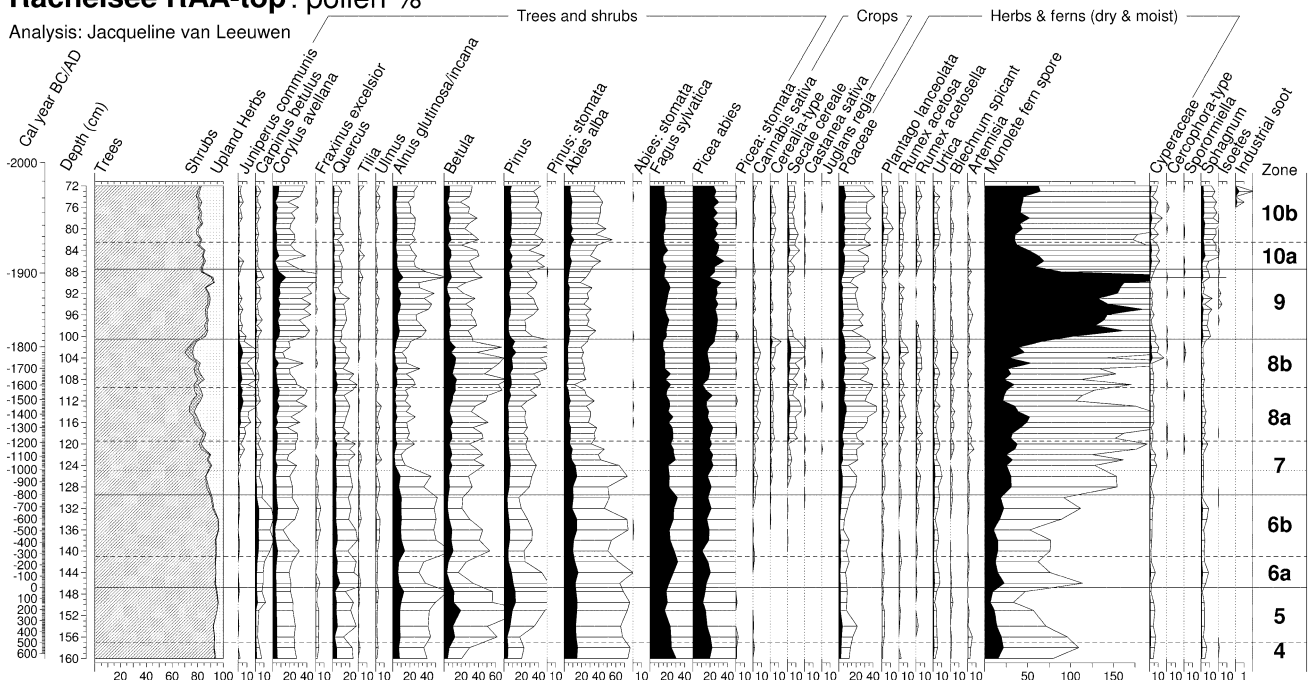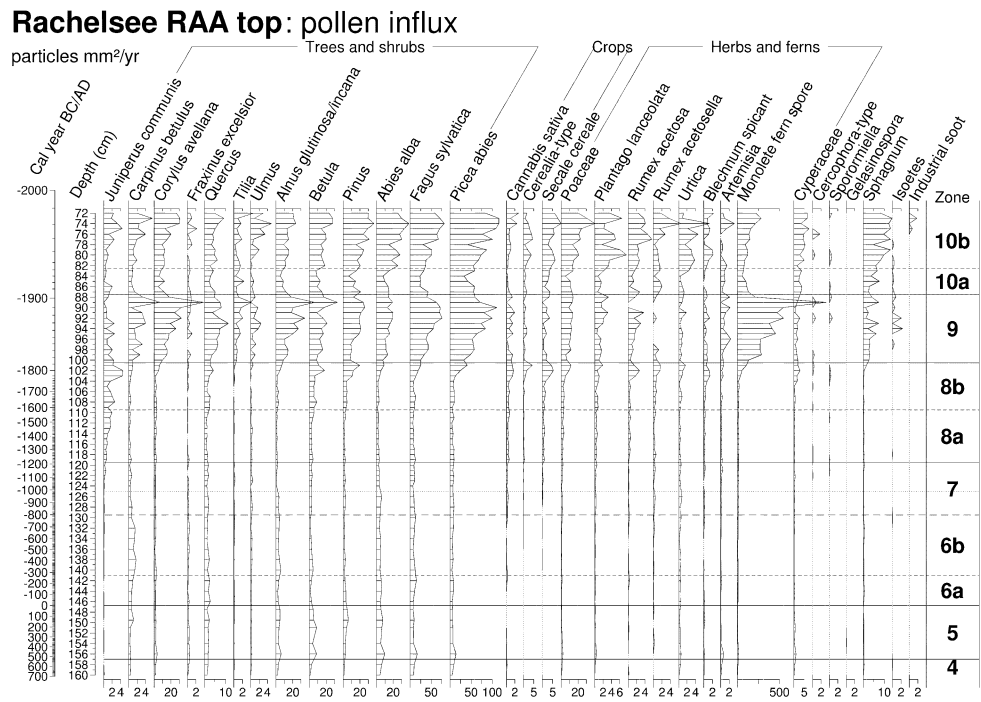
Analysis: Jacqueline van Leeuwen

Fig. 8 Rachelsee RAA (long core) top: pollen percentages; selected types

Fig. 9 Rachelsee RAA (long core) top: pollen influx (particles/mm²/year)

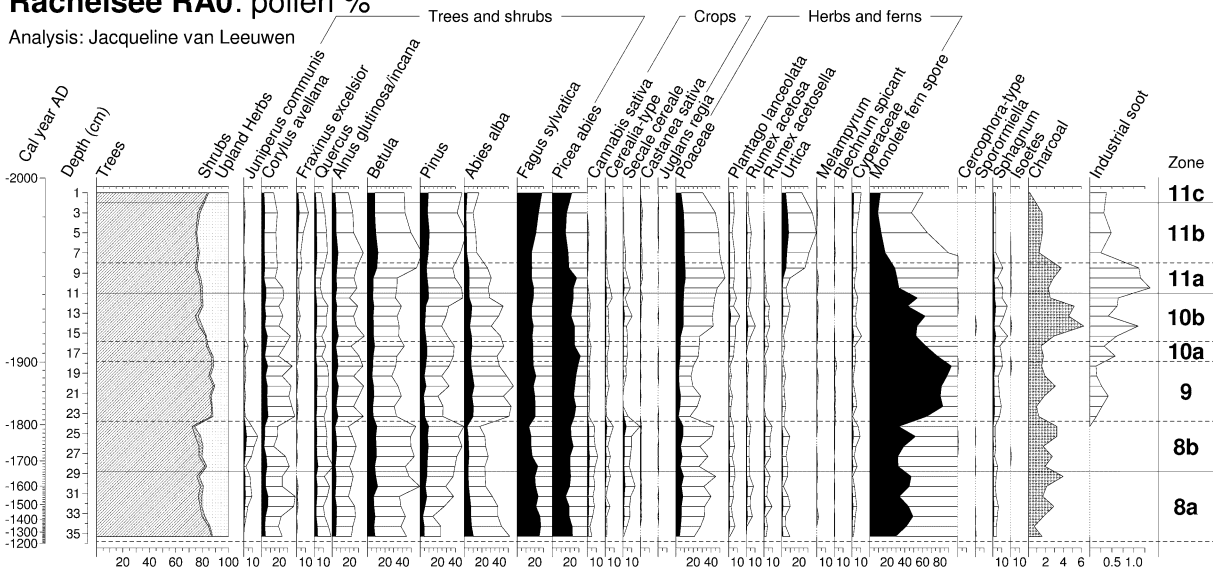**Rachelsee RAA top**: pollen influx

Fig. 10 Rachelsee RA0 (short core): pollen percentages; selected types. Solid zone lines are statistically significant

First important human forest opening both at lower and higher elevations, 500-1 BC

In the Iron Age, maxima in first *Betula* and then *Pinus* pollen are likely related to human action; in a forested area on poor soils as here, these two trees are pioneers on forest edges and abandoned fields. Kozáková et al. (2015) found a similar development in the central Bohemian Forest in the Czech Republic (in Hůrecká Bog). In Stangenfilz

(Figs. 4, 5) a shift to more nutrient-rich conditions locally is indicated by increased ferns (Monolete spores) and grasses (Poaceae) and by a shift in peat composition from well-preserved to decomposed (ESM Table 3). This may have resulted from livestock grazing, and was soon followed by a clear decline of *Abies alba* and *Ulmus*, trees that are sensitive to livestock grazing and fire disturbance (Tinner et al. 2000).

Rachelsee RA0: macrofossils
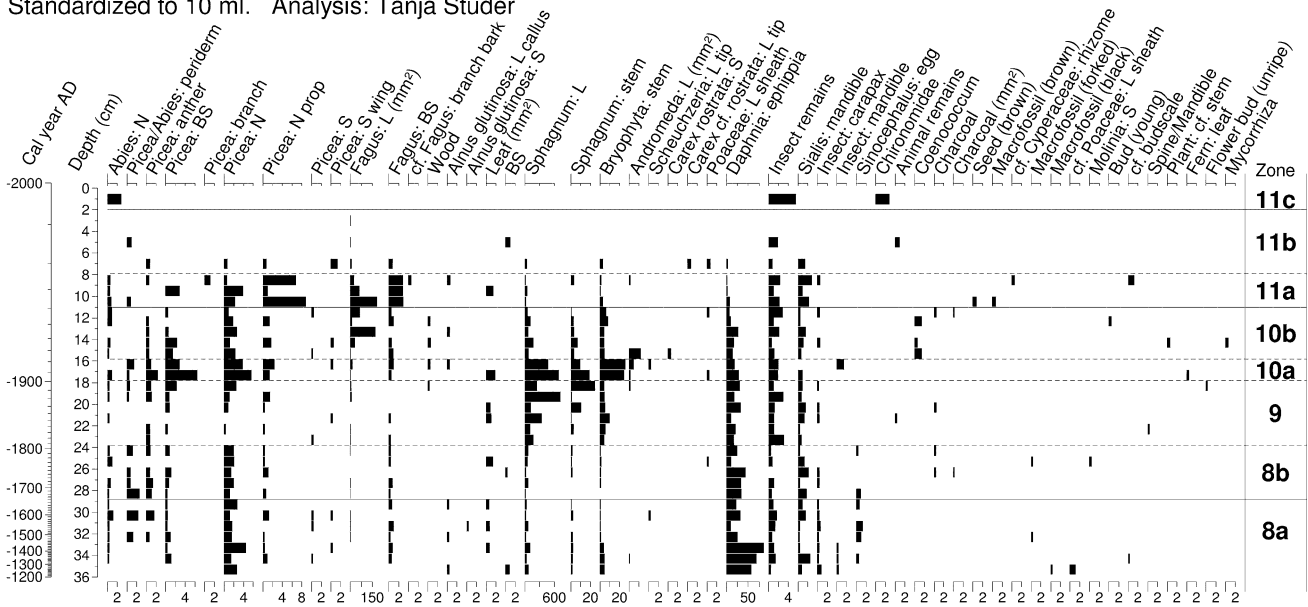
Standardized to 10 ml.   Analysis: Tanja Studer

Fig. 11 Rachelsee RA0 (short core): macrofossils

Rachelsee RAS: pollen %

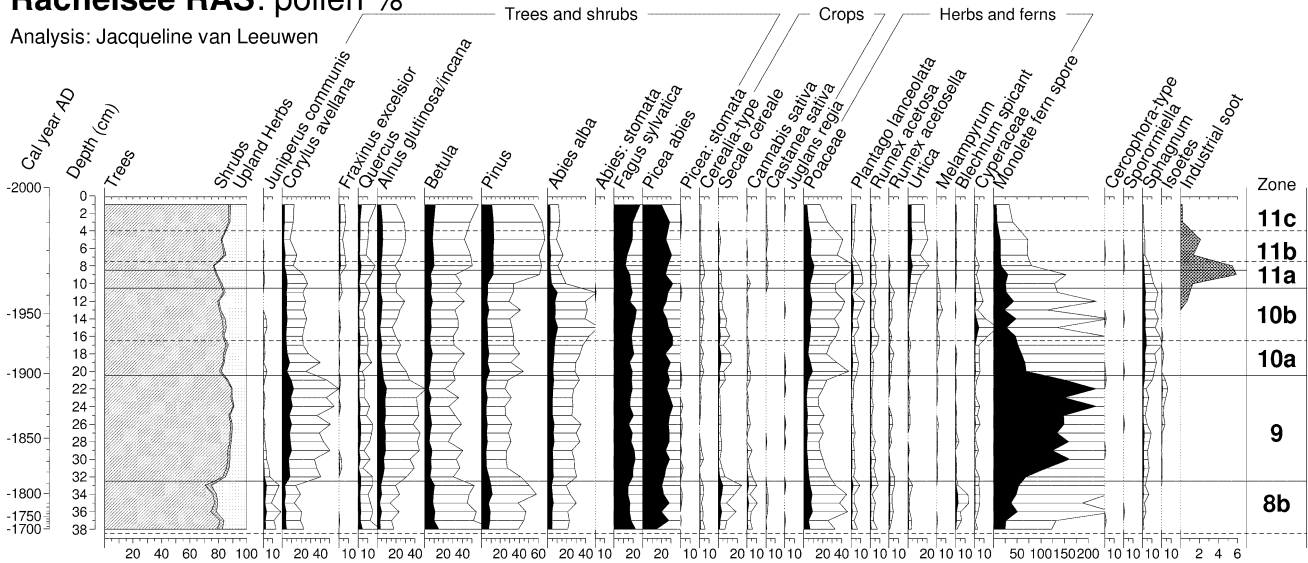Analysis: Jacqueline van Leeuwen

Fig. 12 Rachelsee RAS (short core): pollen percentages; selected types. Solid zone lines are statistically significant; zone line at 8.5 cm is not used

The Carpinus expansion and forest recovery, AD 1-800

In zone 6a (DFG and RAA, Figs. 3–5, 8, 9), falling into Roman Times, a minimum of *Alnus glutinosa/incana* and *Betula* pollen may indicate a temporary opening of forested fen, probably due to a rise in ground-water level.

Other trees (growing on drier ground) seem unaffected and there is no increase of human impact. In zone 6b, the pollen maximum of *Carpinus betulus*, a lowland tree, falls into the Migration Period, during which forest encroached abandoned cleared areas in valley bottoms. There are no indications of human impact close to the sites.
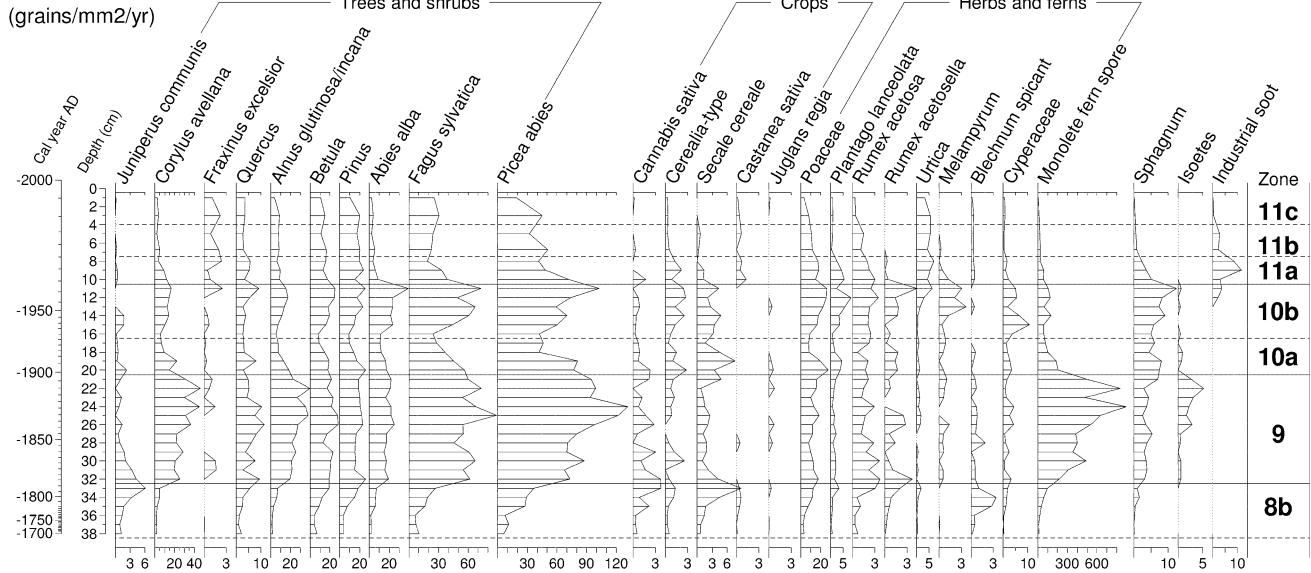
Fig. 13 Rachelsee RAS (short core): pollen influx (particles/mm^2/year)
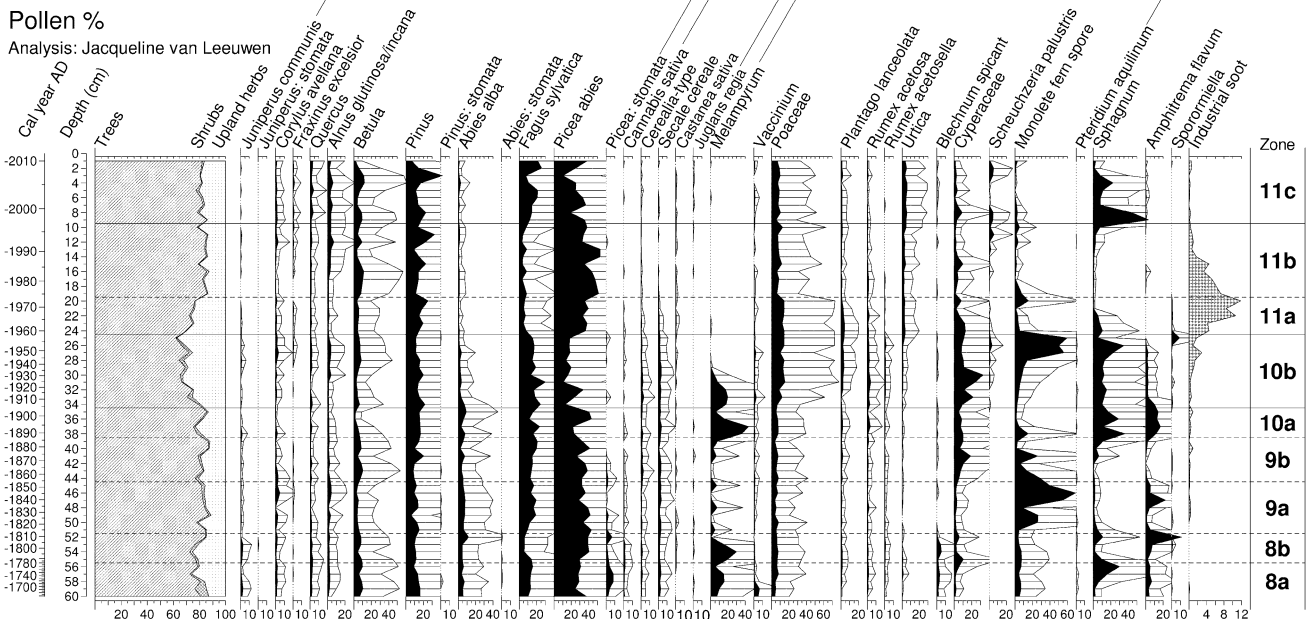

Fig. 14 Alter Rachelsee AR: pollen percentages; selected types. Solid zone lines are statistically significant

Intensifying land use and forest re-opening AD 800–1200

In Early Medieval times human activity increased in the Rachelsee area (RAA, Figs. 3, 8, zone 7), probably at lower elevations, with both grassland expansion (*Plantago lanceolata* and *Rumex acetosella*) and crop cultivation (*Cannabis*, Cerealia-type and *Secale*). Closer to the lake, increasing Poaceae and ferns suggest some forest grazing, and the marked decline of *Abies* and still modest increase in *Juniperus* indicate selective wood extraction and forest grazing. These features are not so clear in Stangenfilz DFG (Figs. 4, 6), but this may be because of the lower temporal resolution at this site. The expansion of spruce forests (*Picea* pollen) at around AD 1000 was associated with a marked increase
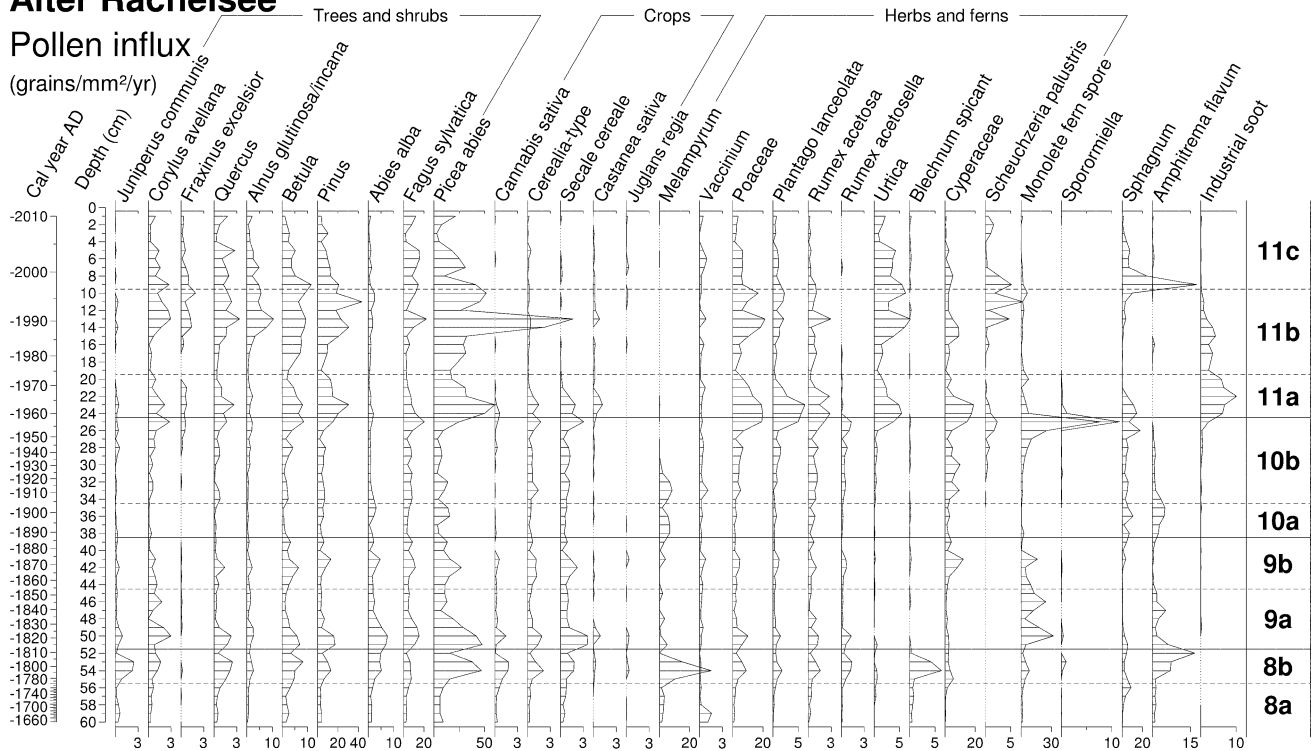
Alter Rachelsee

Pollen influx

(grains/mm²/yr)

Fig. 15 Alter Rachelsee AR: pollen influx (particles/mm²/year)

of open land habitats (Fig. 8, dotted line in zone 7, AP vs. NAP). If corrected for pollen productivity and dispersal biases, the proportion of open land increased locally to regionally from about 2–10% at the beginning of the period to 10–20% at the end. The *Picea* increase may be due to the competitional advantage that *Picea* has over *Abies* in grazed forest, and the decline of *Alnus* and a weaker decline of *Betula* and *Fagus* may be due to soil acidification caused by the expansion of *Picea*.

Land use climax and first regional Abies collapse AD 1200–1800

In late Medieval times (all sites, Figs. 2–15, zone 8a), further forest opening is indicated by increasing crops (*Cannabis*, Cerealia-type and *Secale*) and moderately increasing grassland indicators *Plantago lanceolata*, *Rumex acetosa*, Poaceae and *Juniperus communis*. Especially the latter two taxa and also the ferns (Monolete fern spores) indicate that forest grazing was probably reaching the elevations of the study sites. Stangenfilz SFC2 (Fig. 6) records a short period of burning close to the site (elevated micro-charcoal, *Betula*, Cyperaceae and Monolete fern spores, suppressed *Abies* and *Picea*) at the beginning of the zone (zone 8a1). No such phase of dramatic forest destruction is recorded at Rachelsee RAA (Fig. 8). After about AD 1200 (zone 8a), shifts in major

trees took place. In all pollen percentage diagrams *Fagus* decreased, in a large part of them *Abies* decreased and *Pinus* and *Betula* increased. These shifts were likely man-made, related to forest disturbance e.g. for charcoal production. A large windthrow event is historically recorded in the Rachelsee area in 1786 (within zone 8b), but this is not reflected in the pollen diagrams.

Sediment gap as indirect evidence of grazing on Stangenfilz mire, ca. AD 1800–1950

Zone 9 (AD 1810–1895) is not represented in Stangenfilz, and in diagram SFC2 zone 10 is so thin compared to zones 8 and 11 that we strongly suspect that also a large basal part of this zone is missing (Figs. 5–7). Roughly estimated, the hiatus covers AD < 1800–1950. Sjögren et al. (2007) found that this type of hiatus is more the rule than exception in mires in and around the Alps: highly compacted, relatively dry peat ('Trockenhorizont') overlain by wet, rather loose peat that continues up to the surface, with an abrupt boundary and a jump in the chronology (hiatus) between the two types of peat. Such a stratigraphical gap can be explained by livestock grazing in the past. The trampling by livestock damaged the living, peat-forming moss layer, resulting in increased runoff, so that the peat at the surface becomes compacted and partly erodes. The previously ombrotrophic

mire becomes dominated by *Eriophorum vaginatum* (macro-fossils and Cyperaceae pollen) during the period of grazing. When grazing stops, peat formation resumes and the surface becomes wet again, and *Eriophorum vaginatum* is gradually suppressed.

Forest composition shifts around Rachelsee AD 1810–1895

The Rachelsee percentage diagrams indicate for most of the 19th century (ca. AD 1810–1895) a general shift in forest composition (decline of *Betula* and *Pinus*, increase of *Alnus* and *Corylus*), also nearby the lake (increase of *Abies*, *Fagus* and *Picea*), and a general decline of agropastoral activity (declining pollen of crops, grassland plants and other herbs). This indicates partial forest recovery, at lower elevation but also higher in the mountains where forest-grazing was reduced (declining *Juniperus* and Poaceae pollen). The macrofossil record from Rachelsee (Fig. 10) supports a recovery of the locally growing trees *Abies*, *Picea* and to a lesser degree *Fagus*. An enormous expansion of ferns (Monolete fern spores) and recovery of nutrient-poor fen (*Sphagnum*) took place, probably as a response to the release of grazing pressure in the forest. At Alter Rachelsee (Figs. 14 and 15) vegetation remained more or less stable with rather closed forests and co-dominance of predominantly *Picea*, *Fagus* and less *Abies*.

In agreement, historical sources show that towards the end of the glass manufacturing period in the early nineteenth century, the high-altitude ranges and the more inaccessible locations on slopes and in valleys between Mt Rachel (1,452 m a.s.l.) and Mt Lusen (1,373 m a.s.l.) still retained remnants of practically undisturbed, primeval forest with trees 3–4 centuries old (Heurich and Englmaier 2010). The historically recorded major bark-beetle infestation of the AD 1870s (within zone 9b) does not show up in any of the percentage diagrams, but pollen influx seems to give small hints: the influx has a short-lived maximum in Alter Rachelsee (Fig. 15), and increases in Rachelsee (Figs. 9 and 13).

Open land expansion and industrial air pollution after AD 1900

Pollen indicators of human activity in Rachelsee (Figs. 8, 10, 12) and Alter Rachelsee (Fig. 14) increased again in zone 10a after their scarcity in zone 9, both of crops (Cerealia-type, *Secale*) and pasturing (*Plantago lanceolata*, *Rumex* both types). At the same time open lands expanded slightly (AP decrease, NAP increase). Around Rachelsee, late-successional silver fir, spruce and beech forests were not markedly affected, whereas open land mostly expanded at the cost of disturbance-adapted shrubberies and woods (decline of *Alnus* and *Corylus*). Around Rachelsee, ferns (Monolete fern spores) declined strongly in zone 10a and were partly

replaced by grasses (Poaceae) and partly by ombrotrophic bog (*Sphagnum* spores, *Andromeda* and *Scheuchzeria* macrofossils). Low but consistent values of industrial soot (Spherical carbonaceous particles) in Alter Rachelsee mire (Fig. 14) indicate air pollution. The later appearance of industrial soot in Rachelsee cores RAA and RAS is likely an artefact, caused by the difficulty of recognizing isolated soot particles among the more abundant, pretty similar-looking pyrite-like particles in lake sediments. This contrasts with the earlier appearance of industrial soot in core RA0 also from the lake, in Zone 9 already, which is possibly the result of sediment mixing related to the modest water depth (ESM Table 2).

Forest destruction around Stangenfilz and Alter Rachelsee after AD 1910

In Stangenfilz SFC2 (Fig. 6), a comparison of zone 10 with zone 8b shows that sometime during the hiatus (AD < 1800–1950) *Abies* and *Fagus* collapsed around the site and Poaceae expanded at the cost of ferns. In Alter Rachelsee (Fig. 14), *Abies* and *Picea* declined and Poaceae increased around AD 1910 (zone 10b). This is suggestive of localized forest grazing, which around Rachelsee did not affect the trees but it did increase soil erosion (*Coenococcum*, Fig. 11), possibly at the lake shore caused by animal husbandry. In other parts of the forest, grazing may have been one of the factors that weakened the forests, thus facilitating the historically known major bark-beetle infestation of the 1930s following devastating storms in 1925 and 1929. However, this event did not noticeably affect the relatively remote forest around Rachelsee, where the forest was resilient likely because it consisted mostly of mixed fresh regrowth (*Abies*, *Picea*, *Fagus*) during the 19th century (zone 9, Figs. 8, 10, 12). The strong decline of *Amphitrema flavum* in Alter Rachelsee mire around AD 1950 in spite of the continued presence of its host *Sphagnum* may have been caused by air pollution (industrial soot).

Abies and *Fagus* decline after AD 1960

Abies and *Fagus* declined after about AD 1960 (zone 11a), *Abies* most strongly around Rachelsee (Figs. 10, 11, 12), *Fagus* most strongly around Alter Rachelsee (Fig. 14). Increased influx of all trees in Alter Rachelsee indicates that forest thinning was here considerable, as locally increased wind speeds and lowering of the forest canopy could bring in more pollen, especially of *Picea* that was abundant in the surroundings (Fig. 15, Prentice 1985). This was not the case around Rachelsee where influx did not increase (Fig. 13). The different developments may be explained by the declaration in AD 1950 of Rachelsee and its surrounding forest as a conservation area. Several causes may have contributed

to the *Abies* and *Fagus* decline: forest disturbance (e.g. excessive browsing, see e.g. marked *Sporormiella* peak at ca. 1960 associated with *Abies* and *Fagus* declines at Alter Rachelsee, Fig. 14), selective logging, and air pollution (see industrial soot curve). Around Stangenfilz *Abies* and *Fagus* were already very scarce and no further decline occurred (Fig. 6). *Urtica* expanded after about AD 1960, but because there are hardly any *Urtica* plants growing at the elevation of the sites today it indicates a general increase of nutrients in lower-lying areas.

Isoëtes occurred in Rachelsee since 8500 BC until after the 1970s when it disappeared (zone 11b in RA0) probably due to water acidification (industrial soot). It was, however, never found by botanists here. *Isoëtes* occurs still today in a few other lakes on the Czech side of the same mountains (Procháska 2000; Weilner 2016: *Isoëtes lacustris* in Černé Lake, *I. echinospora* in Plěsné Lake), and fossil spores were found in three other lakes (Břízová 2011: Stará Jímka, Prášilské and Čertovo Lakes). *Fagus* recovered somewhat in the past few decades (zone 11c). The impact of the recent major bark-beetle infestation of the forests, following heavy storms in 1983 and 1984 does not show up in the pollen curves.

Discussion and conclusions

Holocene climate setting and effects on vegetation composition

At the onset of the early Holocene, ca. 11,500 years ago (9500 BC), temperatures in southern Central Europe rapidly increased by about 3–5 °C within a few decades to centuries to approximately reach modern summer temperature conditions (e.g. von Grafenstein et al. 1998; Ammann et al. 2000; Lotter et al. 2000; Heiri and Millet 2005; Larocque et al. 2010; Heiri et al. 2014, 2015). Early Holocene winters were considerably cooler than today, most likely because of reduced winter insolation as resulting from orbital forcing (Schwörer et al. 2014; Marsicek et al. 2018). Vegetation in Central Europe rapidly adjusted to the increased temperatures by the establishment of the first temperate tree and shrub stands including *Fraxinus excelsior*, *Tilia*, *Ulmus*, *Acer*, *Corylus* and *Quercus* (empirical limit reached at Rachelsee between 9500 and 8500 BC, Fig. 3). In our area the first *Picea* stands also established during this period, though it took about 1,000 years for the temperate tree taxa and *Picea* to outcompete *Pinus sylvestris* and *Betula* (cf. *pendula*) communities; the latter communities had established in response to Late-Glacial climate warming at the onset of the Bølling interstadial ca. 12700–12500 BC (Lotter et al. 2012; Ammann et al. 2013).

In the Bavarian Forest NP early Holocene climatic conditions (hot summers, cold winters, rather dry conditions) fostered the establishment of continental temperate forests in which the boreal species *Picea abies* was prominent after ca. 8000–7000 BC (e.g. Figs. 3, 4), specifically in the mountains (> ca. 800–1,000 m a.s.l.). We assume that the spread of *Picea* was connected to increasing summer moisture availability, as also inferred for other areas of Central Europe including the Alps (Henne et al. 2011). Still abundant late frost may have impeded the expansion of other mesophilous trees such as *Fagus* and *Abies*. This suddenly changed at 6200 BC, when *Abies alba* and *Fagus sylvatica* populations established (empirical limit) synchronously over wide areas of southern Central Europe, ranging from western Switzerland to eastern Bavaria, most likely in response to mid-Holocene climate reorganizations involving more oceanic conditions (summer moisture increase, winter temperature increase, less late frost; Tinner and Lotter 2001, 2006; Giesecke et al. 2011).

Subsequent Holocene climatic changes were less pronounced than those triggered by climate reorganization around 6200 BC, but they nevertheless had impacts on European vegetation (Giesecke et al. 2011). However, we assume that at the latest by 6000–5000 BC the forest tree species pool of the Bavarian NP forests was comparable to today (see empirical pollen limit of *Abies* at Rachelsee and Stangenfilz, Figs. 3 and 4). With the advent of agriculture ca. 5500 BC, human impact on vegetation and the fire regime became important in Central Europe; however, human impacts and climate change are difficult to separate after the establishment of farming societies (Giesecke et al. 2017). Indeed at latest during the Late Holocene, specifically in the Bronze Age, human impact had established as the first driver of vegetational and fire-regime change (Tinner et al. 2005; Molinari et al. 2013).

Comparison with REVEALS-based results at Rachelsee

Carter et al. (2018) used the REVEALS model for pollen-based estimates of land-cover abundance of the three dominant trees in the region of the Bavarian Forest and Šumava. For the last period with near-natural high-montane forest (2000–500 BC, Bronze Age), they reconstructed that on a regional scale *Picea* covered on average ca. 45% of the surface, which is 4.5 times more than estimated for *Abies* (10%) and more than twice than estimated for *Fagus* (20%). Rachelsee has for this period average pollen values of *Picea* 17.6%, *Abies* 13.3% and *Fagus* 26.2%, but it depends on relative pollen productivities (RPP) how this translates to land-cover proportions. Estimated RPP values vary widely among studies (e.g. Broström et al. 2008) and these values for *Abies* and *Fagus* are scarce. However our field and

pollen work related to modern pollen studies in mountains that have these three trees today such as the Monts du Forez (Lutgerink et al. 1989), the Vosges Mountains (Tamboer-van den Heuvel and Janssen 1976), the Swiss Jura Mountains (Mazier et al. 2008) and the Swiss Alps (Lotter et al. 2000; Sjögren et al. 2006, 2008a, 2015) indicates that RPP of *Picea* is slightly to a few times higher than that of *Abies* and *Fagus*, whose RPPs are in the same order of magnitude. For Rachelsee 2000–500 BC this results in coarsely similar tree abundances of *Picea* and *Abies* but higher abundances of *Fagus*, which is quite different from the results of Carter et al. (2018) quoted above. At least two things contribute to the difference. First, their estimates are said to be 'regional' because they are based on lakes, which means that the results are valid for a large region, but the lake Rachelsee lies in such sheltered position (between mountain slopes) that the bulk of the pollen reflects rather a 'local' scale, like the pollen signal of a mire. Second, Carter et al. (2018) use an exceptionally high RPP of *Abies* (12.77), 29 times higher than their exceptionally low RPP of *Picea* (0.47), and an RPP of *Fagus* (1.2) 2.6 times higher than that of *Picea* and ten times lower than that of *Abies*. Low RPP boosts REVEALS-estimated land-cover (*Picea*), and high RPP suppresses it (*Abies*). The quoted RPPs of *Picea* and *Abies* were modified from Soepboer et al. (2007, 2010), who determined them in a low-lying region where *Abies* is scarce adjacent to high mountains where *Abies* is abundant. We suspect that massive *Abies* pollen transport from the mountains during foehn or katabatic winds invalidated their results, because such pollen transport is not taken into account in Sutton's equation used in the estimation of RPPs. A third aspect that possibly contributes to the difference between Carter et al. (2018) estimates and results from Rachelsee is that this site is the only lake in their study that lies SW of the highest mountain ridge, where past vegetation composition was possibly different from the other side. Using realistic RPPs, we estimate that the forests on the mountain plateau around Stangenfilz 2000–500 BC were dominated by *Picea* and *Abies*, with a smaller share of *Fagus*. The difference lies in *Fagus*, which was dominant in surroundings like Rachelsee but subordinate in surroundings like Stangenfilz. Taken together, we relativize the formerly reconstructed strong Holocene *Picea* dominance for the Bavarian National Park (Carter et al. 2018). Our new records Stangenfilz and Alter Rachelsee also show that spatial stand variability was rather high, depending on the environmental and ecological characteristics of the different habitats.

The forests without human impact and with it: searching the natural baseline conditions

The two longer pollen sequences of this study, from the lake Rachelsee (Fig. 3) and the mire Stangenfilz (Fig. 4), show the sequence in which the different tree taxa expanded after the early-Holocene dominance of *Betula* and *Pinus*, and their subsequent history might be used to search the natural vegetation baseline conditions for the Bavarian Forest NP (Stähli et al. 2006; Willis and Birks 2006; Valsecchi et al. 2010, etc.). Quasi-natural conditions existed up to about 5000 BC in the study area. The valley forests were already heavily affected by humans during the Neolithic period with the gradual reduction of important forest trees such as *Tilia, Ulmus* and *Fraxinus excelsior*. Conversely, human impact most likely advantaged disturbance resistant taxa such as *Betula*, *Pinus*, *Corylus*, *Picea* and *Fagus*. In 12 of 13 pollen samples dated between 8350 and 2990 BC, most of the *Tilia* pollen grains were identified as *T. cordata* and ca. 7% as *T. platyphyllos*. This shows that *T. cordata* was the far more abundant *Tilia* species, but also that both species were part of the natural vegetation. While *T. cordata* was probably widespread (e.g. in the oak forests), the likely habitat of *T. platyphyllos* is sheltered gorges, similar to the situation in the Vosges Mountains in France where the tree had a similar (rare) occurrence in the Holocene and still grows today in mixed elm-maple forests (Kalis 1984). The mixed high-montane forests were most likely less affected up to about 500 BC. Only during the 20th century very important high-montane forest constituents such as *Abies alba* were completely destroyed, e.g. at Stangenfilz, or strongly reduced (e.g. at Rachelsee), leaving *Picea abies* as the predominant species.

Our results indicate that prior to the Iron Age, before 500 BC, the *Picea-Abies-Fagus* forests in the higher parts of the Bavarian forest were continuous without any major gaps that were sufficiently large to cause a shift in the relative tree abundances or to develop a replacement vegetation type. This changed after 500 BC: larger forest openings were created from which the pioneer trees *Pinus* and *Betula* benefited, and here and there higher in the mountains *Abies* especially became heavily impacted. A general but temporary forest recovery took place after AD 500, although without a come-back of *Abies*. Human impact intensified after AD 1000 with forest grazing and wood extraction, mainly at lower but increasingly also at higher elevation where *Abies* was strongly affected. This climaxed in the 19th century, with the creation of larger forest openings at high elevation by combinations of forest grazing, wood extraction, air pollution, windthrow and bark-beetle infestations. The historically recorded major bark-beetle infestations since AD 1870 are, however, rarely marked out among the various instances of human-induced forest change. Our results suggest that natural forests were far more mixed than the extant humanized communities, and that higher in the mountains *Picea*, *Abies* and *Fagus* coexisted together in equilibrium in which all the three taxa had large shares. Similar results have been obtained in the Alps and other areas of Central Europe

(Welten 1982; Tinner and Ammann 2005; Colombaroli et al. 2013; Rey et al. 2013; Schwörer et al. 2014).

Past, present and future dynamics of change in the forest

The combined historical and pollen data show that during the Holocene, the forests of the Bavarian Forest National Park have gone through several phases of change triggered by climate change and/or human intervention. While climate change had similar effects over entire Central Europe, direct human intervention was more localized and consisted of forest clearing for food production, forest grazing, charcoal production, wood extraction, reforestation and air pollution. These factors resulted in impoverished forest stands with unnatural, humanized characteristics that were either unnaturally open (widely spaced large trees) or unnaturally dense and even-aged. Humanized forests in the high-montane belt were mostly spruce-dominated and situated in areas where *Fagus* and *Abies* co-dominated the forests before. This anthropogenically-driven change opened the way for indirect effects such as increased sensitivity to windthrow and to large-scale bark-beetle infestation. Our results indicate that the high-montane forests remained in general markedly less dense once they were affected by humans, whereas no periods of forest opening are recorded prior to human impact. This implies that if there were bark-beetle infestations in the mixed and diverse forests prior to human impact, they never occurred at large spatial scales and did not impact forest composition. The indirect human impacts on the forests are now accepted and not further counteracted under the no-intervention management strategy pursued by the Bavarian Forest National Park, and the forest regeneration that follows is now leading towards forests with more 'natural' characteristics such as increased proportions of *Abies alba* and *Fagus sylvatica*, stands of uneven tree age and spacing, and gaps where regeneration is slower. Mixed future *Abies*, *Picea* and *Fagus* forest may prevent further large-scale bark-beetle infestations. Our palaeoecological information may contribute to supporting the future management of the Bavarian Forest National Park.

References

Ammann B, Birks HJB, Brooks SJ et al (2000) Quantification of biotic responses to rapid climatic changes around the Younger Dryas—a synthesis. Palaeogeogr Palaeoclimatol Palaeoecol 159:313–347

Ammann B, van Leeuwen JFN, van der Knaap WO, Lischke H, Heiri O, Tinner W (2013) Vegetation responses to rapid warming and to minor climatic fluctuations during the Late-Glacial Interstadial (GI-1) at Gerzensee (Switzerland). Palaeogeogr Palaeoclimatol Palaeoecol 391:40–59

Bennett KD (1996) Determination of the number of zones in a biostratigraphical sequence. New Phytol 132:155–170

Bentz BJ, Régnière J, Fettig CJ et al (2010) Climate change and bark beetles of the western United States and Canada: direct and indirect effects. Bioscience 60:602–613

Birks HJB, Tinner W (2016) European tree dynamics and invasions during the Quaternary. In: Krumm F, Vítková L (eds) Introduced tree species in European forests: challenges and opportunities. European Forest Institute, Freiburg, pp 20–43

Blaauw M, Christen JA (2011) Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal 6:457–474

Břízová E (2011) Quillwort (*Isoëtes*), a mysterious plant from the Czech Republic. Acta Musei Nationalis Pragae Series B 67:25–34

Broström A, Nielsen AB, Gaillard M-J et al (2008) Pollen productivity estimates of key European plant taxa for quantitative reconstruction of past vegetation: a review. Veget Hist Archaeobot 17:461–478

Carter VA, Chiverrell RC, Clear JL et al (2018) Quantitative palynology informing conservation ecology in the bohemian/bavarian forests of Central Europe. Front Plant Sci 8:2268. https://doi.org/10.3389/fpls.2017.02268

Christensen PB, Blackmore S (1988) The Northwest European Pollen Flora, 40: Tiliaceae. Rev Palaeobot Palynol 57:33–43

Colombaroli D, Beckmann M, van der Knaap WO, Curdy P, Tinner W (2013) Changes in biodiversity and vegetation composition in the central Swiss Alps during the transition from pristine forest to first farming. Divers Distrib 19:157–170

Giesecke T, Bennett KD, Birks HJB et al (2011) The pace of Holocene vegetation change—testing for synchronous developments. Quat Sci Rev 30:2,805–2,814

Giesecke T, Brewer S, Finsinger W, Leydet M, Bradshaw RHW (2017) Patterns and dynamics of European vegetation change over the last 15,000 years. J Biogeogr 44:1,441–1,456

Goslar T, van der Knaap WO, Kamenik C, van Leeuwen JFN (2009) Free-shape ^{14}C age-depth modelling of an intensively dated modern peat profile. J Quat Sci 24:481–499. https://doi.org/10.1002/jqs.1283

Hauner U (1980) Untersuchungen zur klimagesteuerten tertiären und quartären Morphogenese des Inneren Bayerischen Waldes (Rachel–Lusen) unter besonderer Berücksichtigung pleistozän kaltzeitlicher Formen und Ablagerungen. Regensburger Geografische Schriften 14. Institut für Geographie an der Universität Regensburg, Regensburg

Heiri O, Millet L (2005) Reconstruction of Late Glacial summer temperatures from chironomid assemblages in Lac Lautrey (Jura, France). J Quat Sci 20:33–44

Heiri O, Brooks SJ, Renssen H et al (2014) Validation of climate model-inferred regional temperature change for late-glacial Europe. Nat Commun 5:4914. https://doi.org/10.1038/ncomms5914

Heiri O, Ilyashuk B, Millet L, Samartin S, Lotter AF (2015) Stacking of discontinuous regional palaeoclimate records: chironomid-based summer temperatures from the Alpine region. Holocene 25:137–149

Henne PD, Elkin CM, Reineking B, Bugmann H, Tinner W (2011) Did soil development limit spruce (*Picea abies*) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model. J Biogeogr 38:933–949

Heurich M, Englmaier KH (2010) The development of tree species composition in the Rachel-Lusen region of the Bavarian Forest National Park. Silva Gabreta 16:165–186

Heurich M, Beudert B, Rall H, Křenová Z (2010) National parks as model regions for interdisciplinary long-term ecological research: the Bavarian Forest and Šumavá National Parks underway to transboundary ecosystem research. In: Müller F, Baessler C, Schubert H, Klotz S (eds) Long-term ecological research: between theory and applications. Springer, Amsterdam, pp 327–344

Kalis AJ (1984) Forêt de la Bresse (Vogezen), vegetatiekundige en pollenanalytische onderzoekingen naar de bosgeschiedenis van een centraal-Europees middelgebergte (Forêt de la Bresse (Vosges), phytosociological and palynological investigations on the forest-history of a central-European mountain range). PhD Thesis, University of Utrecht, Utrecht (with a summary in English)

Kozáková R, Pokorný P, Peša V, Dalielisová A, Čuláková K, Svitavská Svobodová H (2015) Prehistoric human impact in the mountains of Bohemia. Do pollen and archaeological data support the traditional scenario of a prehistoric "wilderness"? Rev Palaeobot Palynol 220:29–43

Lang G (1994) Quartäre vegetationsgeschichte europas: methoden und ergebnisse. Fischer, Jena

Larocque-Tobler I, Grosjean M, Heiri O, Trachsel M, Kamenik C (2010) Thousand years of climate change reconstructed from chironomid subfossils preserved in varved lake Silvaplana, Engadine, Switzerland. Quat Sci Rev 29:1,940–1,949

Lotter AF (1999) Late-glacial and Holocene vegetation history and dynamics as shown by pollen and plant macrofossil analyses in annually laminated sediments from Soppensee, central Switzerland. Veget Hist Archaeobot 8:165–184

Lotter AF, Birks HJB, Eicher U, Hofmann W, Schwander J, Wick L (2000) Younger Dryas and Allerød summer temperatures at Gerzensee (Switzerland) inferred from fossil pollen and cladoceran assemblages. Palaeogeogr Palaeoclimatol Palaeoecol 159:349–361

Lotter AF, Heiri O, Brooks S, van Leeuwen JFN, Eicher U, Ammann B (2012) Rapid summer temperature changes during termination 1a: high-resolution multi-proxy climate reconstructions from Gerzensee (Switzerland). Quat Sci Rev 36:103–113

Lutgerink RHP, Swertz CA, Janssen CR (1989) Regional pollen assemblages versus landscape regions in the Monts du Forez, Massif Central, France. Pollen Spores 31:45–60

MacArthur RH (1957) On the relative abundance of bird species. Proc Natl Acad Sci USA 43:293–295

Marsicek J, Shuman BN, Bartlein PJ, Shafer SL, Brewer S (2018) Reconciling divergent trends and millennial variations in Holocene temperatures. Nature 554:92–96

Mazier F, Broström A, Gaillard M-J, Vittoz P, Buttler A (2008) Pollen productivity estimates and relevant source area of pollen for selected plant taxa in a pasture woodland landscape of the Jura Mountains (Switzerland). Veget Hist Archaeobot 17:479–495

Molinari C, Lehsten V, Bradshaw RHW et al (2013) Exploring potential drivers of European biomass burning over the Holocene: a data-model analysis. Glob Ecol Biogeogr 22:1,248–1,260

Morris JL, Brunelle A (2012) Pollen accumulation in lake sediments during historic spruce beetle disturbances in subalpine forests of southern Utah, USA. Holocene 22:961–974

Prentice IC (1985) Pollen representation, source area, and basin size: towards a unified theory of pollen analysis. Quat Res 23:76–86

Procháska F (2000) Šumavské šídlatky—Mýty a skutečnost: *Quillwort* species in the Czech Bohemian Forest (Šumava Mts)—fables and reality. Silva Gabreta 5:83–92

Reimer P, Bard E, Bayliss A et al (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55:1,869–1,887

Rey F, Schwörer C, Gobet E, Colombaroli D, van Leeuwen JFN, Schleiss S, Tinner W (2013) Climatic and human impacts on mountain vegetation at Lauenensee (Bernese Alps, Switzerland) during the last 14,000 years. Holocene 23:1,415–1,427

Rey F, Gobet E, Szidat S, Lotter AF, Gilli A, Hafner A, Tinner W (2019) Radiocarbon wiggle matching on laminated sediments delivers high-precision chronologies. Radiocarbon 61:265–285

Schwörer C, Kaltenrieder P, Glur L et al (2014) Holocene climate, fire and vegetation dynamics at the treeline in the Northwestern Swiss Alps. Veget Hist Archaeobot 23:479–496

Sjögren P, van Leeuwen JFN, van der Knaap WO, van der Borg K (2006) The effect of climate variability on pollen productivity, AD 1975-2000, recorded in a *Sphagnum* peat hummock. Holocene 16:277–286

Sjögren P, van der Knaap WO, van Leeuwen JFN, Andrič M, Grünig A (2007) The occurrence of an upper decomposed peat layer, or "kultureller Trockenhorizont", in the Alps and Jura Mountains. Mires and Peat 2: Article 5. http://www.mires-and-peat.net/

Sjögren P, van der Knaap WO, Kaplan J, van Leeuwen JFN, Ammann B (2008) A pilot study on pollen representation of mountain valley vegetation in the central Alps. Rev Palaeobot Palynol 149:208–218

Sjögren P, van der Knaap WO, van Leeuwen JFN (2015) Pollen dispersal properties for Poaceae and Cyperaceae: first estimates of their absolute pollen productivities. Rev Palaeobot Palynol 216:123–131

Soepboer W, Sugita S, Lotter A, van Leeuwen JFN, van der Knaap WO (2007) Pollen productivity estimates for quantitative reconstruction of vegetation cover on the Swiss Plateau. Holocene 17:65–77

Soepboer W, Sugita S, Lotter AF (2010) Regional vegetation-cover changes on the Swiss Plateau during the past two millennia: a pollen-based reconstruction using the REVEALS model. Quat Sci Rev 29:472–483

Stähli M, Finsinger W, Tinner W, Allgower B (2006) Wildfire history and fire ecology of the Swiss National Park (Central Alps): new evidence from charcoal, pollen and plant macrofossils. Holocene 16:805–817

Stalling H (1987) Untersuchungen zur spät- und postglazialen Vegetationsgeschichte im Bayerischen Wald. Dissertationes Botanicae 105. Borntraeger, Stuttgart

Stockmarr J (1971) Tablets with spores used in absolute pollen analysis. Pollen Spores 13:615–621

Szidat S, Salazar GA, Vogel E, Battaglia M, Wacker L, Synal H-A, Türler A (2014) ¹⁴C analysis and sample preparation at the new Bern Laboratory for the Analysis of Radiocarbon with AMS (LARA). Radiocarbon 56:561–566. https://doi.org/10.2458/56.17457

Tamboer-van den Heuvel G, Janssen CR (1976) Recent pollen assemblages from the crest region of the Vosges Mountains (France). Rev Palaeobot Palynol 21:219–240

Tinner W, Ammann B (2005) Long-term responses of mountain ecosystems to environmental changes: resilience, adjustment, and vulnerability. In: Huber UM, Bugmann HKM, Reasoner MA (eds) Global Change and Mountain Regions. Springer, Heidelberg, pp 133–143

Tinner W, Lotter AF (2001) Central European vegetation response to abrupt climate change at 8.2 ka. Geology 29:551–554

Tinner W, Lotter AF (2006) Holocene expansions of *Fagus silvatica* and *Abies alba* in Central Europe: where are we after eight decades of debate? Quat Sci Rev 25:526–549

Tinner W, Hubschmid P, Wehrli M, Ammann B, Conedera M (1999) Long-term forest fire ecology and dynamics in southern Switzerland. J Ecol 87:273–289

Tinner W, Conedera M, Gobet E, Hubschmid P, Wehrli M, Ammann B (2000) A palaeoecological attempt to classify fire sensitivity of trees in the southern Alps. Holocene 10:565–574

Tinner W, Conedera M, Ammann B, Lotter AF (2005) Fire ecology north and south of the Alps since the last ice age. Holocene 15:1,214–1,226

Trautmann W (1953) Zur Unterscheidung fossiler Spaltöffnungen der mitteleuropäischen Coniferen. Flora 140:523–533

Valsecchi V, Carraro G, Conedera M, Tinner W (2010) Late-Holocene vegetation and land-use dynamics in the Southern Alps (Switzerland) as a basis for nature protection and forest management. Holocene 20:483–495

Von Grafenstein U, Erlenkeuser H, Müller J, Jouzel J, Johnsen S (1998) The cold event 8200 years ago documented in oxygen isotope records of precipitation in Europe and Greenland. Clim Dyn 14:73–81

Weilner C (2016) Isoëtes im Bayerischen Wald und im Böhmerwald. Hoppea, Denkschriften der Regensburger Botanischen Gesellschaft 77:99–112

Welten M (1982) Vegetationsgeschichtliche Untersuchungen in den westlichen Schweizer Alpen: Bern–Wallis. Denkschriften der Schweizerischen Naturforschenden Gesellschaft 95. Birkhäuser, Basel

Willis KJ, Birks HJB (2006) What is natural? The need for a long-term perspective in biodiversity conservation Science 314:1,261–1,265

Seidl R, Schelhaas MJ, Lexer MJ (2011) Unraveling the drivers of intensifying forest disturbance regimes in Europe. Glob Chang Biol 17(2):842–2,852

Zeppenfeld T, Miroslav S, DeRose J et al (2015) Response of mountain Picea abies forests to stand-replacing bark beetle outbreaks: neighbourhood effects lead to self-replacement. J Appl Ecol 52:1,402–1,411

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