Published in final edited form as:

Reg Environ Change. 2017 February ; 17(2): 501–514. doi:10.1007/s10113-016-1033-0.

Trends and events through seven centuries: the history of a wetland landscape in the Czech Republic

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Abstract

Environmental change can be viewed as the combined result of long-term processes and singular events. While long-term trends appear to be readily available for observation (in the form of temporal comparisons or space-for-time substitution), it is more difficult to gain information on singular events in the past, although these can be equally significant in shaping ecosystems. We examined the past 700 years in the history of a lowland wetland landscape in the Czech Republic with the help of palaeoecological, ecological, landscape archaeological, and archival data. Macrofossil and pollen data were compared to known drainage works in the area and historical climatological data. Trends and events in habitat conditions were assessed using species indicator values. Results showed that ecological succession was the general process in the study area, detected as a trend towards eutrophication, desiccation and vegetation closure. Short-term events influenced development at the sites mainly from the second half of the 19th century. This is consistent with drainage history, although bias related to sample frequency cannot be excluded. On the whole, long-term trends and discrete events were complementary on different scales. We conclude that humans facilitated and accelerated background processes, which can be most likely associated with the succession of open wetlands towards terrestrial ecosystems.

Keywords

human impact; macrofossils; pollen; species indicator values; vegetation development; drainage channels

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Introduction

The interactions between nature and human society are played out on many spatial and temporal levels from global to local and from millennial to short-term (Sayre 2005; Szabó and Hédli 2011). Environmental change can be described by long-term trends, probably the best-known example of which is recent global warming (Parmesan and Yohe 2003). However, in many cases short-term events can modify the effects of long-term processes. Such events can be highly localized (such as the drainage of a fishpond) but potentially global as well (such as the 1815 eruption of Mount Tambora) (Stothers 1984; Oppenheimer 2003). Both trends and single events can be periodically recurring (such as the coming of ice ages or the eruption of volcanoes), which makes them to a certain extent predictable, or more stochastic (such as the human agency behind global climate change) (McNeill 2000). Separating trends from discrete events is in itself a matter of temporal resolution. A useful method is to look at abruptness, which is “a function of magnitude over duration, best described relative to the life cycles of the organisms of interest or the successional speed of the ecosystems in which they occur” (Jentsch et al. 2007; White and Jentsch 2001).

Any long-term environmental change is arguably the combined result of underlying processes and singular events. It is to be noted that the effects of trends and events can markedly differ (Jentsch et al. 2007). However, whereas long-term trends appear to be readily available for observation (in the form of temporal comparisons or space-for-time substitution, Pickett 1989), many past singular events are simply not known (Rackham 2006). If the impacts of such unknown events reinforce long-term trends, they will be attributed to them by default, but if they counteract them, they may lead to false hypotheses. It is therefore of primary importance in the study of environmental change to have information both on long-term processes and on short-term, discrete events.

In this paper we examine the long-term history of a lowland wetland landscape. Lowland wetlands are among those ecosystems that have been the most influenced by human activities. In this respect, they are one of the most sensitive indicators of environmental change. They have undergone a marked decline on a pan-European scale (Brander et al. 2012). The remaining wetlands are usually confined to forests or meadows. Sometimes they occur in arable fields as well, where they provide important transitional refugia for wetland-associated organisms (Némethy et al. 2014). Wetlands are threatened by changing water regimes and eutrophication, both of which can be considerably modified by intentional or indirect human activities, such as in-site restoration or atmospheric nitrogen pollution (Bobbink et al. 1998). Nowadays, most Central European lowland wetlands represent shallow, eutrophic to hypertrophic systems that are highly dynamic in terms of basic factors, such as water depth, amount of nutrient and oxygen, and water temperature (Pott and Remy 2000; Khan and Ansari 2005; Čížková et al. 2013). Traditional uses, such as extensive grazing by livestock and domestic fowl, or mowing the reed beds and tall-sedge stands for use in industry and agriculture have only occasionally survived until the present. Eutrophication and management abandonment have resulted in the accumulation of large amounts of dead biomass, changes in nutrient cycling and water retention, and biodiversity loss related to the extinction of competitively poor, disturbance-dependent plant species (Middleton et al. 2006; Keddy 2010).

Due to the highly unstable conditions at such sites, the vegetation of shallow lowland wetlands is usually composed of vascular plant species of relatively broad ecological range and high eco-morphological plasticity (Balátová-Tuláková 1976; Hejný and Hroudová 1987). However, even if these species are able to survive under a broad range of local environmental conditions, their ecological niche optima (i.e. the conditions in which the species occurs and reproduces most frequently) are usually narrow. At the level of vegetation composition this means that smaller changes in environmental conditions are reflected by fast and pronounced changes in the quantitative representation of individual vascular plant taxa rather than by overall species composition change. By contrast, overall changes of species composition in wetlands are usually associated with considerable shifts in trophic status, and in the timing, duration and frequency of mechanical disturbances or climate-related events (Hejný et al. 1982; Rintanen 1996; Czerepko 2008; Strohbach et al. 2009).

We investigate the past 700 years in the history of a small forest wetland. We apply a historical ecological approach (Swetnam et al. 1999; Egan and Howell 2001; Szabó 2015), which combines research methods from the natural sciences and the humanities in multi-proxy research. Interdisciplinarity was a prerequisite in our work, because anthropogenic influence was one of the probable drivers of change. We used data and methods from four disciplines. *Quaternary palaeoecology* traditionally focused on ecosystem development in the Quaternary and especially in the Holocene (Birks and Birks 1980; Cappers and Neef 2012). Palaeoecologists usually put more emphasis on older periods, and research analysing the past few centuries is still relatively rare, although especially with the coming of ^{210}Pb dating there is no methodological reason for this to be so (Walker and Walker 2005).

Ecology mostly focuses on recent patterns in species, populations and ecosystems. Knowledge of species niche, the ecological space potentially or actually occupied by individual species, can be used for an indirect assessment of environmental conditions (e.g. Chase and Leibold 2003; Wildi 2016). This can include the reconstruction of past environments wherever suitable fossil resources are available. *Landscape archaeology* deals with all periods of human history and prehistory, but, as opposed to traditional archaeology, more recent periods have always played a prominent role in it (Aston 1985). Last but not least, *archival research* on landscape history in Europe can reach back to the 8th century (e.g. Sonnlechner 2004) although environmental historians have predominantly dealt with the 19th and 20th centuries (Szabó and Hédli 2011). Combining the methodological opportunities offered by the individual disciplines, seven centuries appear to be a temporal scale for which relatively high resolution can be achieved to which each discipline can significantly contribute.

Through the combined interpretation of palaeoecological, ecological, landscape archaeological, and archival data, we ask the following interconnected questions: (i) how did the ecological conditions change at the study site in the past 700 years, and which factors induced such changes? (ii) do long-term trends significantly differ from site history reconstructed in higher temporal resolution?

Material and Methods

Study site

Dúbrava Wood (3600 ha) is located in the northwestern edge of the Pannonian Basin in the southeastern part of the Czech Republic (17°05'00"E, 48°52'40"N) next to the town of Hodonín on the fringes of the alluvium of the Morava river. Tree cover in the core area of the Wood has been stable for at least four centuries, although approximately one third of the current forested area along the edges of the Wood was converted to pastureland for several decades in the early 19th century (Jamrichová et al. 2013; Szabó and Hédli 2013). The site is mostly flat, altitude varies between 164 and 242 m a.s.l. Climate is temperate subcontinental with ca. 9°C of average annual temperature and 500–550 mm of annual precipitation (Tolasz et al. 2007). The Wood lies on eolic sands of Pleistocene origin of varying thickness. Soils are generally arenic dystic cambisols; in places with prolonged waterlogging gleyic soils occur (<http://mapy.geology.cz/pudy/>). The soils are mostly nutrient poor, slightly acidic and prone to desiccation in dry periods (Novák and Pelíšek 1943). Water conditions fluctuate during the year, in spring many sites are waterlogged. Within the forest matrix, there are dozens of wet depressions of up to ca. 100 m in diameter.

Field sampling and palaeoecological sample processing

We collected three profiles from three different wet depressions in Dúbrava Wood (Fig. 1). The sites named MS3, MS4 and MS15 were chosen out of 15 locations surveyed in 2008 through 2012. The sites are ca. 0.5 km from each other (Fig. 1) and reflect the same climatic, substrate and topographic conditions. However, the shape of sites and their vegetation cover differs.

- MS3 was sampled from an oval-shaped treeless depression, which is ca. 100 m in diameter. This depression is covered with dense reed (*Phragmites australis*) vegetation and a shallow pool can be found in the middle part, where organic sediment is wet and about 50–60 cm deep.
- MS4 was extracted from a treeless depression of ca. 30–40 m diameter. Organic sediment is only about 30 cm deep and relatively dry for most of the year. Vegetation is composed of shrubs and small trees (*Salix caprea*, *Alnus glutinosa*, *Betula pendula*); herbs include dominant *Phragmites*, then *Juncus*, *Agrostis* and rare sedges, such as *Carex lasiocarpa* or *C. elata*, indicating formerly wetter conditions. *Sphagnum* is also present.
- MS15 differs from the other two sites by the depth and age of its organic sediment, which is 0.9 m and over 10 thousand years, respectively. The site is a treeless glade of about 25 m in diameter. The surrounding forest is composed of *Betula pendula*, *Alnus glutinosa*, *Quercus robur* and *Salix* sp. The inner part of the site is dominated by grasses and forbs (e.g. *Polygonum hydropiper*), not reed as at the other two sites. Organic sediment is finely structured, moist but not waterlogged for most of the year.

Material for analysis was collected in August 2009 (MS3, MS4) and in September 2012 (MS15) from the walls of hand-dug pits using metal boxes of 10×10×50 cm. The profiles

consisted of organic sediment with higher amounts of sand and/or clay. The amount of sand increases towards the bottom of each profile (for sediment descriptions, see Online Resources 1, 5 and 6). Organic sediments were sub-sampled at 1 cm (MS3, MS4) or 2 cm (MS15) intervals for pollen analysis, and at 2 cm intervals (MS3, MS4 and MS15) for macrofossil analysis. The upper parts of profiles MS3 and MS4 were sub-sampled at 4 cm intervals because of presence of rhizomes of *Phragmites australis*, which would have made finer resolution technically complicated.

Chronology

The chronology of the profiles was obtained by AMS radiocarbon dating and by ^{210}Pb dating of the upper parts of the cores. Charcoals and seeds were isolated from the selected layers and sent for dating to the Centre for Applied Isotopes Studies, University of Georgia, Athens, GA, USA (UG-). Radiocarbon ages were calibrated using the IntCal13 calibration curve (Reimer et al. 2013). ^{210}Pb dating was done at the Institute of Physics, Silesian University of Technology, Gliwice, Poland (MS3 and MS4) and at the Institute of Geochemistry, Mineralogy and Mineral Resources, Charles University in Prague, Czech Republic (MS15). Dates were obtained from the top 15 cm of MS15, the top 27 cm of MS3 and the top 28 cm of MS4 (Online Resource 2). Depth–age models were created with P_Sequence (a Bayesian model of deposition) implemented in Oxcal 4.2.1 (Bronk Ramsey 2011) (Online Resource 3). The command Boundary was incorporated into the model due to potential changes in sedimentation rate. The model reached the agreement value of 155 (MS3), 180 (MS4) and 115 (MS15). In the text below we use mean values of modelled data within a 95.4 % confidence interval.

Macrofossil analysis

The samples were wet-sieved using a set of sieves with mesh diameter of 1 mm, 0.5 mm and 0.25 mm. No chemical treatment was necessary. Seeds and plant remains were determined according to Cappiers et al. (2006), Velikevich and Zastawniak (2006, 2008) and other available identification literature. They were also checked against the reference seed collection of the Institute of Botany, Czech Academy of Sciences. Values are presented as absolute numbers per sample for countable fossils (mostly seeds).

Pollen analysis

The preparation of samples for pollen analysis followed standard techniques (Faegri and Iversen 1989). Samples containing mineral material were pre-treated with cold concentrated HF for 24 hours and then processed by KOH and acetolysis. At least 500 terrestrial pollen grains were identified using standard key and photo collections (Beug 2004; Reille 1995, 1998); for the determination of non-pollen palynomorphs we used van Geel et al. (1980). The nomenclature of pollen types follows Beug (2004). Pollen data are presented in percentage pollen diagrams constructed in the Tilia software v. 1.7.16 (Grimm 2011). Total pollen sum (TS) was calculated based on terrestrial pollen sum taxa ((semi)aquatics, Pteridophyta, algae, fungi, and the other non-pollen palynomorphs (NPP) were excluded). The percentages of pollen taxa were based on pollen sums of arboreal (AP) and non-arboreal pollen (NAP) ($\text{TS} = \text{AP} + \text{NAP} = 100\%$). The percentages of spores, and NPP were related to the extended sum ($\text{AP} + \text{NAP} + (\text{semi})\text{aquatics} + \text{spores} + \text{NPP} = 100\%$). The pollen diagrams

were divided into developmental phases based on constrained cluster analysis by sum-of-squares (CONISS, implemented in the Tilia program; Grimm 2011).

Full pollen diagrams for profiles MS3 and MS4 were published previously (Jamrichová et al. 2013). For the evaluation of trends and events, we considered taxa related to the development of local mire vegetation (Cyperaceae, (semi)aquatics, spores, green algae, pteridophytes).

Landscape archaeology of channels

Approximately 1000 ha in the southwestern part of Dúbrava Wood were surveyed by fieldwalking for visual remains of drainage and other channels, including woodbanks (based on the methodology of Szabó 2010). Channels were mapped by a handheld GPS device; the results were visualised using the ArcGIS software. The physical remains of channels were also examined as regards basic structure in order to prepare a typology. Where channels crossed each other, we tried to work out a relative chronology of their ages. In addition, relevant historical written sources (for a list, see Jamrichová et al. 2013) were studied to obtain absolute dates for construction and/or desertion. Although some of the features we identified were not originally intended to serve as channels, all were used for that purpose for at least shorter periods of time, therefore we will use the term ‘channel’ throughout this paper to refer to all types of linear hand-dug features observed in the Wood.

Environmental assessment

Trends and events in habitat conditions were assessed by using species indicator values. Indicator values, which reflect the optima of a species’ realised niche, have been widely used in vegetation ecology since the 1970s (for a review, see Diekmann 2003). Water level fluctuation during the growing season is one of the factors that are crucial for the survival and/or reproduction of many wetland plants (Hejný 1957, 1960; Moravcová et al. 2001). The tolerance of aboveground and underground organs to floods, summer drought or frost also influences species composition. Because no indicator values sensitive enough to reconstruct water level fluctuations and related processes were available, we decided to create our own indicator values appropriate for use in wetland ecosystems – wetland species indicator values. These values were based on the long-term field experiences and results of germination/cultivation experiments of one of the authors (K. Š.) as well as on published papers (e.g. Hejný 1957, 1960; Balátová-Tuláková 1968, 1976; Hejný and Husák 1978; Hroudová et al. 1992; Moravcová et al. 2001). We produced indicator values in relation to the following environmental factors: water depth (WD), water level fluctuations (WLF), insolation (IS) and trophic status (TS). We established values for vascular plant species identified in macrofossils using a numerical scale of 0, 1, 2, 3, 4 and sometimes also 5. Only non-woody wetland plant species were selected and used in the subsequent analyses. For species with broader ecological ranges, a range of values was set. Descriptions of scales for each indicator value can be found in Online Resource 4.

Numerical analyses

Species used in the analyses are presented in Online Resource 4. These species represent a selection from the complete macrofossil assemblage (Online Resource 5). Only wetland

vascular plant species were used. Trees, shrubs and species of terrestrial habitats that do not tolerate waterlogging were excluded, because their seeds most probably originated from outside the wetland itself. Bryophyte macrofossils were not determined to the species level and therefore they were not evaluated.

For each sample, we calculated weighted averages for the indicator values of the species present as macrofossils (Ter Braak and Barendregt 1986). Species were weighted according to the width of their niche expressed as the range of indicator values, where species with wider ranges (see Online Resource 4) were given less weight. Although averages calculated from ordinal data received criticism in vegetation ecology (e.g. Podani 2006), a number of recent papers argued in favour of indicator value averages: “Despite their ordinal nature, it has been shown that average indicator values can characterize an area well, and can provide useful ecological interpretation.” (Tölgyesi et al. 2014; see also Wildi 2016). Weighted averages of indicator values for samples were plotted on a time line. Trends were visualized through linear regression. Short-term changes were plotted by a 4-period moving average. Analyses were run separately for each of the three studied profiles to reveal variation among the sites.

Temporal patterns in variation in species composition with respect to indicator values were analysed with ordinations. Redundancy analyses (RDA) were calculated for the three sites separately, with time as an active factor and the four indicators as supplementary variables, which did not affect species composition patterns. The significance of the canonical axis was tested by a Monte-Carlo permutation test (5000 completely random permutations). Completely random permutation removes autocorrelation between the individual observations in time. Macrofossil species assemblages subject to ordination analyses were as in Online Resource 5 including species abundances, which were log-transformed to downweight over-abundant species. In total, 33, 27 and 43 species were included in the ordination analyses of MS3, MS4 and MS15, respectively. The results are presented in the form of ordination graphs; unidentified woody species, unidentified *Bryophyta*, all woody species and less abundant herb species were excluded from the presented diagrams. Ordinations were calculated in CANOCO, version 5 (Ter Braak and Šmilauer 2012).

Results

Trends and events reflected in macrofossils

The detailed results of macrofossil analyses for individual profiles can be found in Online Resource 5. Linear regressions and moving averages through time for the four species indicator values are presented in Figs. 2–5. *Water depth* showed a general downward trend from permanent shallow water to only waterlogged soil. However, differences between sites were apparent. The downward trend was most pronounced for MS3, while at MS15 WD was only slightly decreasing and the trend was almost neutral for MS4. The most visible discrete event (a sudden drop in WD) occurred in ca. 1900 at MS4 and MS15, and approximately half a century later at MS3. *Water level fluctuation* showed a rising trend from stable conditions to larger fluctuations at MS4 and MS15, while MS3 demonstrated the opposite trend. Sudden changes in WLF characterized the period since the end of the 19th century. *Trophic status* showed a rising trend from meso- to eutrophic conditions at each site.

Stability in trophic status characterized each site until end of the 19th century, when fluctuation started to increase at MS3 and MS4, while MS15 remained more stable. *Insolation* demonstrated a decreasing trend, referring to the closing of the vegetation around the sites, except at MS4. Open vegetation was typical until the late 19th century, after which marked fluctuations commenced.

The results of RDA are presented in Fig. 6. According to the RDA model, macrofossil assemblages showed a significant trend in species composition through time (MS3: $F=5.4$, $P=0.015$; MS4: $F=3.9$, $P=0.023$; MS15: $F=24.5$, $P<0.001$; for each first canonical axis). The explained time-related variation in species composition is 33% for MS3, 30% for MS4 and 58% for MS15. Common processes were the decrease of *Alisma* sp. (most probably *A. plantago-aquatica*), a species of open, shallow water habitats, which is rather sensitive to substrate desiccation, and the increase of a number of species, mostly graminoids tolerant to relatively dry conditions, such as *Phragmites australis*, *Calamagrostis canescens*, *Juncus effusus*, *Alopecurus aequalis* and *Carex riparia*, but also of nitrophilous herbs, such as *Urtica dioica* and *Oenanthe aquatica*. This change in species composition indicates succession towards increasingly eutrophic, less water-flooded habitats. In addition, the environmental trends revealed by indicator values showed that the deeper the water was, the less its level fluctuated. Trophic status seems to have increased in time and with water level fluctuations, while insolation decreased in time.

Trends reflected in pollen

Percentage diagrams of selected pollen taxa and spores concentrating on local mire development are presented in Online Resource 6. The development of local mire vegetation in Dúbrava could be divided into four main phases (Fig. 7). Stable water conditions characterized the first phase of mire development (Phase 1; AD 1350/1600–1900). At the beginning of the 18th century (transition between Phases 1a and 1b) species indicating more eutrophic conditions started to occur in higher abundances. It should be noted that the internal dividing line between Phases 1a and 1b cannot be dated with much confidence because of the uncertainty in calibrated radiocarbon dates. By contrast, Phases 2–4 were precisely dated with ²¹⁰Pb. At the beginning of the 20th century (Phase 2; ca. AD 1900–1950), several changes in (semi)aquatic macrophytes were recorded. Although these differed among profiles, they probably indicated higher WLF. Changes in mire vegetation composition implied decline in WD at MS4 and MS15, while at MS3 water depth seemed to have increased. From ca. 1950 (Phase 3; ca. AD 1950–1990) increase in trophic status was reflected in all profiles. There were also changes in water depth, which increased at MS4 and MS15. WD at MS3 declined and subsequently (after ca. 1970) increased. The last change in local wetland conditions occurred at the end of the 20th century (Phase 4; ca. 1990–recent), when a significant increase in trophic status was recorded.

Channels and drainage

Approximately 17 km of artificial channels were found in the study area. These represent an unknown fraction of the channels that once existed. Based on their physical structure, channels were grouped into two categories: i) a ditch with a bank on one side only, and ii) a central ditch with banks on either side. Results are visualized in Fig. 1.

i) In this category, we can distinguish between woodbanks and an unidentified structure. The woodbanks of Dúbrava Wood were made in the late 1780s (Moravský zemský archiv [MZA], F 5 kniha 232). They are massive structures, in the best preserved parts as much as 8 m across and 1.5 m high. An unusual bank-and-ditch structure cuts through the eastern half of the study area from the northeast towards the southwest. The bank is towards the east, where the town of Hodonín lies. This construction is smaller than the woodbanks, ca. 4 m across and 1 m deep. The purpose of this channel could not be identified and we could not date it. Nonetheless, it is older than the drainage channels, which, as demonstrated below, were dug at the end of the 19th century and the beginning of the 20th century. A drainage channel cuts across the unidentified channel and is therefore clearly of a later date.

ii) Two types of channels can be distinguished in this category: fishpond channels and drainage channels. The former include the large channel that runs along the fishponds in the western part of the study area. The earliest records of fishpond construction at the site are from the late 15th–early 16th centuries (MZA F5 karta 2 inv. . 24, karta 3 inv. . 29, karta 11 inv. . 744). The channel in the Wood was a special type of structure dug along fishponds to make the regulation of water levels more sophisticated. This channel was mentioned in the 1691 *urbarium* of the Hodonín estate (MZA F5 kniha 3). Drainage channels are much more frequent but much less robustly built in the study area. They served to drain the many small waterlogged areas in the Wood. Smaller channels led their water either into the fishpond channel or into the woodbanks, which were adapted to this new function. Drainage channels can be dated to the end of the 19th and beginning of the 20th centuries. The 1925 Forest Management Plan (MZA F 263 kniha 1) contains detailed information on the construction and maintenance of drainage channels. In the period 1907–1924 in the whole of Dúbrava Wood 1767 metres of new channels were constructed and 720 metres of existing channels were renovated. This means that on average 104 metres of new channels were dug every year, therefore if all existing channels were renovated between 1907 and 1924 (which is unlikely) then drainage channel construction started in 1900 at the latest. Similar drainage works are known from written sources around the neighbouring villages of Dubany in 1805–1855 (MZA F5 karta 28 inv. . 909) and Lužice in 1901–1910 (MZA F5 karta 28 inv. . 910). The end of channel construction and the abandonment of drainage operations can be roughly dated to the second half of the 20th century. Post WWII sources made no mention of channels, and conifer plantations always disregarded and ruined drainage channels. Currently no functional drainage channel exists in Dúbrava.

Each palaeoecological site (MS3, MS4 and MS15) was drained by drainage channels. MS4 and MS15 lay along the same channel, while MS3 had its own channel. In addition, the unidentified channel (category i) ran in the close vicinity of site MS3. Other than these channels, the sites have no other water outlets.

Discussion

Trends, fluctuations and changes

Long-term development at the sites, as inferred from the species composition of plant remains, showed common trends as well as local differences. The only universal trend, observed in each profile in both macrofossils and pollen, was eutrophication. In addition, the

sites received progressively less light and water got shallower with increasing fluctuations. However, at some sites these trends were not very pronounced and exceptions existed: for example, water level fluctuation decreased with time at MS3 or water depth showed a neutral trend at MS4. Overall, MS4 had a different development from the other two sites, especially with regard to insolation.

Short-term events influenced the study sites mainly from the second half of the 19th century. Especially remarkable are short-term changes in water depth. At MS4 and MS15, water depth suddenly decreased at the end of the 19th century, while the same happened at MS3 approximately half a century later. This is consistent with drainage history. Drainage channels around the sites were dug from the second half of the 19th century and we also reconstructed that MS4 and MS15 had lain along the same channel. This indicates that the channel draining MS4 and MS15 was constructed some time towards the end of the 19th century, while the channel at MS3 a few decades later. Drainage led to a drop in water level, to which plants were quick to react. When drainage channels were abandoned in the later part of the 20th century, water depth bounced back towards previous values. It is also worth noting that the unidentified channel along MS3 cannot be connected to any single event.

A remarkably similar change in sedimentology occurred at all three sites in the 1960s–1970s. The transition from sandy (or somewhat clayey, MS15) sediments to a layer of organic material might have reflected environmental processes. Litter mineralization could be impeded during a period of increased soil wetness, or dead biomass accumulation could be connected to decreasing management activities. Neither explanation is very likely for the study sites. Water depth decreased throughout the entire period (Fig. 2) and no significant changes in management are known from the 1960s and 1970s. More probably, the observed change in soil profiles can be interpreted as a result of pedogenesis (Brady and Weil 2008). The upper 10–12 cm represent the topsoil horizon of humus formation and fresh material from litter continues to contribute to further formation of this organic layer. At the same time, the bottom part of the organic layer gradually mineralizes and the amount of sand increases.

Ecological succession and human influence

The observed processes, mainly the trends inferred from the analysis of species indicator values, can be ecologically interpreted as succession from open water pools to closed vegetation dominated by tall grasses, shrubs and eventually trees. Eutrophication is usually visible in the vegetation with some delay, hence clear indicators of eutrophication such as *Lemna gibba* or *Carex riparia* appeared or strongly increased only in about the 1930s. Succession includes various mechanisms of species interactions, and unless some form of natural disturbance, such as floods or fire occurs, succession is usually understood as a gradual process (Glenn-Lewin et al. 1992). Wetlands, despite their marked interannual variation, show relatively slow development and their succession may last for millennia (Magyari et al. 2001; Lamentowicz et al. 2007). Several abrupt changes in species composition at our study site therefore suggest the existence of an external factor, likely a management impact, which can be supported by archival and landscape archaeological data.

Drainage in the second half of the 19th century contributed to substrate desiccation and probably enhanced the succession process.

However, drainage was probably not the only human influence. The studied wetlands are embedded in a regularly managed forest in the vicinity of human settlements. Several types of biomass removal (e.g. wood cutting or haymaking) almost certainly occurred directly at the site. Species, such as *Carex* spp., *Typha* sp., *Juncus effusus* or *Phragmites australis* were cut as forage, animal bedding or material for producing objects of domestic use. However, archival data provide solid evidence that forest clearing did not occur in the study period. Another potential disturbance, grazing by domestic animals was practised in Dúbrava Wood, but not at the sampled sites (Szabó and Hédli 2013). We may assume that the complex development of the studied wetlands over the past 700 years combined both natural succession (detectable as trends in environmental conditions) and human impact. The latter included systematic factors like drainage and more or less random events connected to the usage of natural resources, mainly biomass.

Potential sources of bias

The interpretation of observed results can be biased by the nature of fossil samples. The three major sources of possible error are taphonomy, sample frequency resulting from unequal sedimentation rate, and the sensitivity of indicator values to real environmental processes. Taphonomy influences the quality of the fossil record. Younger sediment layers are usually better preserved than older ones (Gifford 1981; Fernández-Jalvo et al. 2011) and many species may not be preserved in the fossil record at all. It is virtually impossible to separate this effect from the process of ecological succession, which involves gradual saturation by species (Clements 1916; Prach and Walker 2011). Therefore, the positive correlation of most species with time (see the results of ordination analyses) may be the result of better preservation of plant remains in younger layers. This taphonomic effect may be behind the apparent change in the macrofossil record with the change in sedimentation in the 1960s and 1970s.

This assumed taphonomic effect, however, may also have resulted from differential sampling frequency. This can be demonstrated by the prevalence of short-term events in the past 150 years. Sampling at regular distances (see Methods) resulted in relatively more frequent data from recent layers. Therefore the moving average tended to show more fluctuation than for earlier periods. At MS15, for example, a larger number of samples for the past ca. 400 years resulted in the apparent signal of more short-term events especially for water depth and water level fluctuation. The number of samples we could use mostly depended on accumulation processes at the individual sites. At MS3 and MS4 sediments accumulated very slowly at the beginning (7–8 cm in half a millennium), followed by rapid accumulation (25 cm in 150 years). Because profiles were sampled evenly, fewer samples fell to the pre-19th-century period. Sampling at higher resolution for earlier periods would have been difficult, because the sediment was sandy and not too compact. By contrast, at MS15 accumulation progressed at a more steady rate from the beginning the 17th century. It should also be noted that the sediments were relatively poor in macrofossils, therefore increased sampling resolution is unlikely to have led to more detailed information. Rather small

amounts of macrofossils in terms of plant species number as well as the number of seeds, oospores, etc. were indicated by other authors in various types of lakes throughout Europe (e.g. Bennike 2000; Pokorný and Jankovská 2000; Davidson et al. 2005; Wohlfarth et al. 2006). Some of the profiles presented in literature showed macrofossil assemblages similar to our profiles in Dúbrava Wood, especially with regard to the overall decrease of macrofossils with the increasing age of the layer (Bennike 2000; Pokorný and Jankovská 2000; Rasmussen and Anderson 2005; Davidson et al. 2005). However, other profiles exhibited opposite or mixed patterns, i.e. older layers were richer in macrofossils than younger ones (Wohlfarth et al. 2006; Stankevica et al. 2015) or layers without macrofossils alternated with the layers rich in macrofossils (Väliiranta 2006; Wohlfarth et al. 2006). The interpretations of the absence of macrofossils of aquatic and wetland plants have been highly varied, but they usually referred to abiotic and/or biotic factors at the site which could restrict macrophyte development, e.g. water depth (Davidson et al. 2005), lake drainage (Wohlfarth et al. 2006), low temperatures (Bennike 2000; Väliiranta 2006; Wohlfarth et al. 2006; Stankevica et al. 2015), high water turbidity related to algal bloom or sediment suspended in water (Rasmussen and Anderson 2005) and water chemistry (Bennike 2000; Väliiranta 2006; Stankevica et al. 2015). In some cases, the biological characteristics of individual species were also considered, e.g. limited production of seeds by some species or dispersal-based seed accumulations (Davidson et al. 2005). Somewhat surprisingly, few studies dealt with taphonomy-related issues (e.g. Thompson et al. 1993).

Finally, indication sensitivity may considerably differ among plant species (Lacoul and Freedman 2006). In general, any species can give us environmental information in a certain context. Our estimates show that several of the analysed wetland species have relatively broad ecological optima (Online Resource 4). However, most species exhibit broad ecological optima related to some of the factors but narrow optima (i.e. higher indication sensitivity) in relation to other factors. Sediment samples containing few macrofossils the majority of which belong to species with lower indication sensitivity can be especially challenging. In such cases, several studies recommended a multi-proxy approach (Bennike 2000; Davidson et al. 2005; Wohlfarth et al. 2006; Lamentowicz et al. 2007; Stankevica et al. 2015). In this light, macrofossils and pollen in our study should be understood as complementary rather than mutually exclusive.

Possible effects of climate

Variation in climate, especially precipitation, could also have played its role in site development. There are several hydrometeorological reconstructions available for the past 500 years for the entire Czech Republic as well as southern Moravia based on various proxies including archival documents and tree rings (Brázdil et al. 2002; Brázdil et al. 2012; Büntgen et al. 2011). Dobrovolný et al. (2015) concluded that these reconstructions demonstrated marked yearly and decadal variability in precipitation but did not indicate long-term trends. They could then be useful mostly in the interpretation of short-term changes visible in macrofossil analyses. In the following, we concentrate on possible connections between climate and discrete events at our sites in the 19th–20th centuries, when the most important changes in the fossil material were observed. As far as water depth is concerned, annual total precipitation data (Dobrovolný et al. 2015) and WD since ca. 1850

at our study sites showed a similar development. After a marked decline, precipitation totals steadily increased between ca. 1880 and 1950 (although this trend is not apparent either in seasonal total precipitation data or in southern Moravian draught series (Büntgen et al. 2011)). At MS4 and MS15, water depth also increased in the first half of the 20th century, which we interpreted to have resulted from the abandonment of drainage. While increased precipitation is unlikely to have raised the elevation of the water surface with drainage channels in place, more rain could complement the effects of channel abandonment. Hydrometeorological events could also influence water level fluctuations. Brázdil et al. (2012) noted a peak in extreme events (including floods and torrential rains) from 1821 to 1850 in a region immediately next to our study site. These seem not to have had an impact on water level fluctuation in Dúbrava. This may be due to the fact that Dúbrava lies (by local standards) considerably higher than the floodplain of the Morava and not even large floods (such as the one in 1997: Hrádek (1999)) reach the forest itself.

Conclusions

Drainage history can explain the sudden changes observed in water depth in Dúbrava Wood. Contrary to expectations, variability in precipitation seems not to have affected the sites much, where stability or slow, long-term and unidirectional changes were characteristic until the late 19th century. However, in the critical period of the late 19th century there are some aspects of precipitation history that make it difficult to separate anthropogenic influences from climatic impacts. On the whole, long-term trends and discrete events were complementary on different scales. With some precaution, we may conclude that humans facilitated and accelerated assumed “background” processes, which can be most likely associated with the succession of open wetlands towards terrestrial ecosystems (forests).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

We would like to thank Petr Dobrovolný for his help with climatic data. The research leading to these results has received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013) / ERC Grant agreement no 278065, from the Grant Agency of the Czech Academy of Sciences (project no. IAA600050812), from the Czech Science Foundation (Centre of Excellence PLADIAS, 14-36079G), and from long-term research development project no. RVO 67985939.

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Figure 1.
Map of the study area and its position in Central Europe. Palaeoecological sites (MS3, MS4 and MS15) and artificial channels are shown. Dashed lines represent current forest roads.

Figure 2.

Trends and events in the past 700 years (x-axis) in water depth detected by weighted averages of species indicator values in the samples. Gradient from shallow to deep water is marked on the y-axis. The three sites are MS3 (circles and full lines), MS4 (triangles and hatched lines) and MS15 (squares and dotted lines).

Figure 3.

Trends and events in the past 700 years (x-axis) in water level fluctuation detected by weighted averages of species indicator values in the samples. Gradient from rare to frequent fluctuation is marked on the y-axis. The three sites are as in Fig. 2.

Figure 4.

Trends and events in the past 700 years (x-axis) in trophic status detected by weighted averages of species indicator values in the samples. Gradient from oligotrophic to eutrophic status is marked on the y-axis. The three sites are as in Fig. 2.

Figure 5.

Trends and events in the past 700 years (x-axis) in site insolation detected by weighted averages of species indicator values in the samples. Gradient from shady to sunny conditions is marked on the y-axis. The three sites are as in Fig. 2.

Figure 6.

Redundancy analysis (RDA) diagrams showing variation in species composition over 700 years in macrofossils in the three analyzed cores. Species indicator values are passively projected. Temporal development was statistically significant at $p=0.05$ in all cases. For full species names, see Online Resource 5.

Figure 7.

Comparative table summarising the development of local mire vegetation of all three profiles (MS3, MS4 and MS15) based on pollen analysis.