Tree species composition of a landscape in north-eastern Germany in 1780, 1890 and 2010

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European forests have been affected by human activities since Neolithic times, especially through fragmentation and conversion into non-native tree plantations. Documenting and understanding why these changes have occurred at fine spatial scales will aid forest management in planning, ecological conservation and restoration activities and will inform scientific research regarding biodiversity. While coarse-scale changes in forest cover on the scale of centuries have been previously demonstrated in mapping and statistical exercises, Europe-wide fine-scale datasets on changes in tree species composition are rare. Here, we demonstrate tree species compositional changes in 1780, 1890 and 2010 at a fine scale in a north-eastern German landscape. The area of forest with available data on the main tree species covered ~80 per cent of the total forest area in 1780, ~90 per cent of the total forest area in 1890 and 100 per cent of the forest area in 2010. Beech (Fagus sylvatica L.) and oak (Quercus robur L. and Q. petraea (Mattuschka) Lieblein) both declined in terms of coverage from 40 to 16 per cent, while the coverage of pine (Pinus sylvestris L.) increased from 36 per cent to more than 70 per cent. The fine scale at which these changes have been documented allows inferences to be made on the likely changes in the herbaceous understory composition and possible socio-economic drivers. The historical maps produced by this study will be of value for both further scientific research and forest management.

Introduction

In Europe, there is a long tradition of documenting long-term changes in land use (>100 years), particularly forest cover, via maps, e.g. Schütler (1921), Ellenberg (1988) and Williams (2000). In fewer cases, maps of forest cover changes as well as information regarding long-term changes in tree species composition or forest vegetation has been published in various parts of the world, e.g. Fensham and Fairfax (1997) for Australia, Dupuis et al. (2011) for Canada and Maries and Mladenhoff (2000) and Hall et al. (2002) for North America. The intention of reconstructing historical forest vegetation is mainly for the generation of basic information for restoration purposes (White and Walker, 1997; Honnay et al., 2002). For Germany, maps at a scale of 1:100 000 were published by Glaser and Hauke (2004) showing the distribution of ancient (habitat continuity >200 years) and recent (habitat continuity <150 years; Hermy et al., 1999) forest areas classified into deciduous, coniferous and mixed stands. Although the map scale is quite useful for obtaining an overview, it is too inaccurate to select sites for ecological research and for forest management planning. Fine-scale maps (with scales of 1:50 000 or more detailed) illustrating changes in tree species composition or forest vegetation are rare in Europe and are usually restricted to relatively small areas, e.g. Siccama (1971) and Dupuis et al. (2011).

According to Yang et al. (2014), reconstruction methods can be grouped according to the data or information that were used, as follows: (1) historical documents, (2) historical maps and pictures, (3) natural archives, (4) modelling and (5) multiple-source data. Foster et al. (1996) stressed that an integrative approach using multiple sources is the most balanced and comprehensive method to overcome the limitations of single methods. Other studies have even stressed the use of multiple historical sources as a necessity to obtain the most reliable basis for the reconstruction of past land-use patterns and changes over time, e.g. Grossinger et al. (2007) and Hohensinner et al. (2013). Here, we used multiple forms of data and information to reconstruct the historical forest vegetation of a region in north-eastern Germany for the eighteenth and nineteenth centuries. As the studied region is located in central Europe, it has undergone tremendous anthropogenic changes, and these impacts are well-documented in various archives.

Past land use is a well-known determinant of patterns and processes in current ecosystems (Farrell et al., 2000; Munteanu et al., 2015) and may have long-lasting effects for decades (Wallin et al., 1994), centuries (Boucher et al., 2013) or even

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millennia (Berglund, 1991). In particular, the global carbon balance has been linked to worldwide historical land use (Houghton, 2003). Land-use legacies have been found in several components of ecosystems, e.g. in the vegetation (Foster et al., 2003; Hermy and Verheyen, 2007) and in the soils (Koerner et al., 1997; Dupouey et al., 2002). Land-use legacies are likely to be revealed in forests, as they are composed of long-lived plant species and thus represent a more-or-less persistent land-cover type. For example, studies have shown greater carbon (C) sequestration in ancient versus recent forest ecosystems (habitats with continuity of >200 or <150 years, respectively) (Koerner et al., 1997; Leuschner et al., 2013, 2014). Several typical forest plant species are associated with ancient forests (Hermy et al., 1999), and the colonization of recent forests may take decades or even centuries (Peterken and Game, 1981). Additionally, without historical maps of tree species composition, we would not know where ancient near-natural forests still exist and where we can find forest habitats that are most suitable for restoration (Swetnam et al., 1999; Bolliger et al., 2004). Moreover, maps are necessary bases against which to analyse long-term and large-scale changes in forest herb-layer diversity (Wulf and Rujner, 2011; Stephens et al., 2015) and to provide spatially explicit advice for the implementation of planning and conservation measures (Hill et al., 2005; Herriegel and Groß, 2014).

With this study in a north-eastern region of Germany, we wanted to illustrate the advantages of using multiple historical sources for the reconstruction of tree species composition. The Uckermark region has large, contiguous forest areas owned by the state, as is typical in Germany. Most of these areas were ancient forest stands that were converted from deciduous into coniferous stands between the seventeenth and nineteenth century. In this respect, the Uckermark region is representative of Germany and much of central Europe (Beckel, 1995). Additionally, fine-scale maps exist from 1780, as well as a handwritten book containing spatially explicit data on tree species in forest districts at that time. Our aim is to inspire ecologists to reconstruct historical landscapes by focussing on the use of different historical sources, with the valuable outcome of furthering ecological research in landscape ecology and the use of maps in forestry management. In particular, we wanted to:

(i) visualize and quantify changes in the tree species composition over a long period of 230 years with digitized fine-scale maps; and
(ii) highlight the benefits of historical tree species composition maps for further scientific research and forest management.

Methods

Study area

The Uckermark region (52°52'N–53°23'N, 13°20'E–14°12'E) is located in north-eastern Germany (Figure 1) and has an approximate area of 391 000 ha within its old boundaries. The current administrative area of Uckermark is 305 800 ha. The region is characterized by a suboceanic to subcontinental climate with mean annual temperatures of ~8.3 °C (Angermünde 1961–1990) to 9.3 °C (Falkenberg 1981–2010). The mean annual precipitation is ~520–550 mm (Angermünde and Prenzlau 1981–2010) (Gränditz et al., 2008; DWD, 2013). Glacial deposits of Weichselian age (12 500 to ~10 000 BP) are widespread, with moraines consisting of sand and loam. In the hilly region, there are also many glacial relicts, e.g. kettle holes and lakes (Lippstreu et al., 1997). The main soil types at higher elevations are haplic luvisols (~40 per cent), calcareous regosols (~25 per cent), cambisols (~15 per cent) and albeluvisols (~6 per cent), with gleysols (~8 per cent) at lower elevations, according to the World Reference Base IUSS Working Group (2006).

The potential natural forest types are mainly various beech stands (F. sylvatica L.), with oak (Q. robur L.) and hornbeam (Carpinus betulus L.) at higher altitudes (c. 85 per cent) and older stands (Alnus glutinosa (L.) J. Gaertn.) at lower elevations (c. 12 per cent) (Wulf and Schmidt, 1996; MUUV, 2005). According to the classification of Hofmann and Pommer (2005), they belong to the communities Maianthemo-Fagetum, Melico-Fagetum, Carpino-Fagetum, Fago-Quercetum petraeae and Corici elongatea-Alnetum. Today, most of the forests in the Uckermark region are pine stands (Pinus sylvestris L.) (~75 per cent). Beech covers an area of ~10 per cent, oak (Q. petraea (Matsuschka) Lieblein and Q. robur L.) constitutes 5 per cent, and alder and birch (Betula pendula and B. pubescens) together represent 10 per cent. The data were extracted from the so-called ‘Forest Data Storage database (Datenspeicher Wald)’, extended version 2 (DSW 2, see Redmann and Regenstein, 2010). Pine planting began in the seventeenth century in Brandenburg (Müller et al., 2002) and peaked at the end of the nineteenth century (Klesmer, 1938).

The land use in former times was characterized by the dominance of manors (equivalent to municipalities in modern terms) owned by noblemen (‘Gutsherrschaf’; Müller, 1965; Melton, 2000; Bayerl, 2006), most likely starting in the eighth or ninth century (Krenzlin, 1952). The so-called ‘Feldmark’ areas of the manors (several 100 ha large) consisted of arable fields, grasslands, forests and other land-use types (gardens, water bodies, etc.) that belonged to the municipality. The area used for agriculture was divided into three ‘Gewanne’, and these three large fields were separately used for summer sowing, winter sowing and as fallow land (Müller, 1965). The manors were characterized by market-oriented estate agriculture (Melton, 2000), including the profitable use of wood. However, the noblemen were also interested in hunting, which is why forests were left on the unproductive soils (Bernhardt, 1872). These forests were mainly used for hunting and obtaining timber for building and to a lesser extent for litter raking and as wood pasture. This may be the main reason why beech stands were still found in large areas in the Uckermark region at the end of the eighteenth century (Gustav Borgstede, 1788).

Search for historical sources and preparation of digitized maps

In total, we checked ~200 maps and nearly the same number of archival documents, books, unpublished works and publications in the ‘grey’
literature. Most historical sources were found in two main archives (Supplementary Material A) but also in five local archives. It was usually not difficult to gain access to all sources, but very large historical maps could not be scanned, and we therefore had to make sketches from the original maps while remaining in the archive and examining the original maps.

**Historical maps of the eighteenth and nineteenth centuries**

We used old map series from the late eighteenth and nineteenth centuries showing the main land-cover types (arable fields, grasslands and forests) in detail. The first series (presenting forest areas of the entire Uckermark in detail) was the hand-drawn Schmettau map (1767–1787; scale 1:50,000), and the second series was the Prussian Land Survey from Brandenburg (undistorted; 1879–1902; scale 1:25,000). In this study, the dates of these map series are referred to as 1780 and 1890, respectively. Both map series (sheets rectified and digitized) were used by the Eberswalde Forestry Forestry Centre of Excellence (LFE) to reconstruct the locations of historical forest areas in Brandenburg (http://www.brandenburg-forst.de/webgis; Verch et al., 2013). To map the contemporary forest landscape (2010), we used biotope maps (scale 1:10,000) provided by the Ministry of Rural Development, Environment and Agriculture of the Federal State of Brandenburg (MRDA, 2009).

The Schmettau map (1780) did not have a legend that provided information on tree species, but toponyms (i.e. the names of specific sites and villages) gave clues to species identity in some cases. For example, ‘Kienheide’ means pine stands, and ‘Elsenbruch’ refers to alder stands in wet sites. The area covered by toponyms represented less than 5 per cent of the total forest area at that time. Therefore, we used two other main sources to derive information on the main tree species. The first is the book of Morgenlaender (1780), a hand-written inventory of all forests stands in the former Kurmark, a region (in 1804) of ca. 1125 km² with the four provinces Old, Middle and UckerMark and the Prignitz. The second is the printed book of von Borgstede (1788), which provides a comprehensive description of the former Kurmark, including an inventory of forest stands. The von Borgstede (1788) book is not as comprehensive as that of Morgenlaender (1780) but proved useful because it was often more legible than the hand-written notes of Morgenlaender. However, in both books, the boundaries of the forest districts were described in the following way, ‘at noon (means south) borders on the Schmorgendorfer Feldmark (fields)’ and were thus were not always exact. We therefore combined this information with several historical maps of the old municipalities (communes) found in the main archive of the Brandenburg Central State Archive and the Secret State Archives Prussian Cultural Heritage (Supplementary Material A) to reconstruct the boundaries of forest districts as precisely as possible. To obtain additional data and information, we searched for historical material in the small archives of churches and town museums and looked for publications on the history of single forests. For example, we found historical maps published in Hausendorf (1940–1941) and Olberg (1943, 1945). We found spatially explicit information on tree species for small forest areas in some publications, e.g. in Schmidt (1931), Rietz (1932), Enders (1986), von Schwerin and Bleich (2007), Krausch (2008) and Ruffer (2015). We then aligned the information from all sources with the forest areas on the Schmettau map and altogether obtained data on ~80 per cent of the 1780 forest area.

The key to the Prussian Land Survey (1890) gave information on deciduous, mixed and coniferous stands but no details on tree species. Fortunately, the boundaries of the forest districts are shown on the maps. Together with the so-called forest address book (Müller, 1926), in which data on tree species are listed for the same forest districts, it was possible to combine the data from the book with the maps. Another source was the so-called ‘Forest Data Storage’ (see the following section), which included all forest stands in the state of Brandenburg (Redmann and Regenstein, 2010). We examined these data for stands and individual trees greater than 120 years old to aid our determination of tree species composition in 1890. Additionally, some reports on botanical excursions into forest districts gave valuable and detailed information not only on tree species composition but also on the occurrences of shrub and herb species, e.g. Gerhardt (1856) and Peck (1865). Together with several old forest stand maps that were often drawn by forestry engineers on behalf of noblemen (owners of the forest), we obtained data for ~90 per cent of the 1890 forest area.

**Data and information on tree species in the twenty-first century**

Contemporary spatially exact data on tree species composition were derived from the Federal County of Brandenburg’s ‘Forest Data Storage’ (Datenspeicher Wald, Version 2; Redmann and Regenstein, 2010). This database was developed in 1965 with annual updates since 1970, and the database has been managed digitally since 1985. Since 2002, it has been a joint initiative between Brandenburg, Mecklenburg-Vorpommern and Thüringen, and the data now include data on individual trees identified to the species level, including diameter at breast height (cm), height (m) and age (years), and the proportions of area covered by different species (per cent) for subsections of ~10–20 ha. This database provides a unique opportunity to derive spatially exact, reliable information on tree species composition across large geographic areas at a fine scale.

For the largest part of the forest area, we only obtained data or information on the occurrence of one main tree species rather than the complete stand structure including the first and second tree layer or proportions of mixed tree species. Therefore, the maps were kept relatively simple with respect to the legend. To compare among time periods, we worked with only one unified legend for all three maps (1780, 1890 and 2010). Thus, we distinguished between alder/birch (A. glutinosa (L.) Gaertn. var. B. pendula Roth or B. pubescens Ehrhr.), beech (F. sylvatica L.), beech/oak (F. sylvatica L./Quercus petrea (Mattuschka) Liebl. or Q. robur L.), oak, pine (P. sylvestris L.), pine/beech and pine/oak stands.

**Results**

**Land-use changes in the Uckermark region between 1780 and 2010**

For at least the last 230 years, the Uckermark region has been covered by a higher portion of arable fields (50 per cent) on average compared with Germany and the European Union (EU; 24 per cent arable fields; 41 per cent forests and 13.5 per cent grasslands; Martino and Fritz, 2008) as well as by large forest areas (~30 per cent). Figure 2 shows that the pattern of forest to non-forest areas (mainly arable fields) has not changed much in the Uckermark region since 1780. We assumed the ownership structure and economic interests to be the main reasons for the relatively stable pattern. Prior to land reform in Germany as a whole (law on land reform in 1920), the forests mainly belonged to noblemen and thereafter to the Prussian State.

**Tree species composition in 1780, 1890 and 2010**

The forest area in 1780 covered 111 171 ha (28.4 per cent, Table 1) of the Uckermark region, but the tree species composition could only be derived for 88 320 ha (79.5 per cent) of the forest area (Figure 3). In 1890, the total forest cover in the
region had declined to 93,999 ha (24.1 per cent), but access to more reliable data sources meant we could identify the main tree species composition in 89.9 per cent of this area (84,509 ha). We could derive data on tree species composition for the entire area in 2010, and the overall forest cover has now slightly surpassed the 1780 levels (111,362 ha).

Based on Figures 3–5 and Table 1, deciduous tree species were widely distributed in the southwestern part of the Uckermark region 230 years ago but had declined to a large extent by 110 years later (1890), with some recovery in the following 120 years. This decline in deciduous forests between 1780 and 1890 is in line with the increase in coniferous stands over the same period, which has been maintained to this day. This is even more pronounced if one takes into account that most of the ‘others’ category in Table 1 was likely dominated by coniferous tree species. These coniferous stands are dominated by pine.

Although beech/oak forests declined in extent over the studied time period (Table 2), beech-dominated forests have markedly increased in the last 120 years, and oak-dominated stands have proportionally recovered to 1780 levels. Alder and birch stands markedly increased in the last 120 years. The simultaneous rise in

![Figure 2](https://academic.oup.com/forestry/article-abstract/90/2/174/2527531)

Figure 2 Development of forest non-forest areas in the Uckermark region within the last 230 years. Ancient (forest continuity >220 years), old (forest continuity >150 years) and recent (forest continuity <100 years) forests and open land (mainly arable fields) in the Uckermark region.

<table>
<thead>
<tr>
<th>Land cover type</th>
<th>1780</th>
<th>1890</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest area</td>
<td>111,171</td>
<td>93,999</td>
<td>111,362</td>
</tr>
<tr>
<td>Deciduous forests</td>
<td>48,390</td>
<td>13,204</td>
<td>27,178</td>
</tr>
<tr>
<td>Mixed forests</td>
<td>54,36</td>
<td>15,085</td>
<td>3004</td>
</tr>
<tr>
<td>Coniferous forests</td>
<td>34,495</td>
<td>56,220</td>
<td>56,279</td>
</tr>
<tr>
<td>Others</td>
<td>22,851</td>
<td>9490</td>
<td>24,901</td>
</tr>
<tr>
<td>Non-forest area</td>
<td>277,292</td>
<td>295,325</td>
<td>279,639</td>
</tr>
<tr>
<td>Missing area</td>
<td>2538</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total area</td>
<td>391,001</td>
<td>391,001</td>
<td>391,001</td>
</tr>
</tbody>
</table>

Table 1 Changes of forest and non-forest area within the last 230 years

1 Mixed deciduous and coniferous tree species.
2 Most of these areas were wetlands sparsely scattered with trees in 1780, but young pine plantations or pine stands mixed with several other coniferous tree species in 1890 and 2010.
3 The outline of the study area is equal in all Figures 3–5, but the historical maps did not cover the whole area.
beech and alder/birch stands accounts for the increase in deciduous forests from their 1890 minima. Mixed forests (coniferous and deciduous tree species) were relatively rare in the 1780 landscape but had markedly increased in extent by 1890. However, they have subsequently declined, with the loss of area accounted for by a transition into the ‘others’ category (mainly coniferous (pine) stands in 2010) or through the recovery of beech or birch/alder stands.

Figure 6 was reduced to show only beech/oak stands, pine stands (pure and mixed with deciduous tree species) and others because all tree species combinations exceeded more than 300 possibilities with many tiny areas. The forest areas with beech/oak stands at all three time points cover only c. 5500 ha, while those with pure and mixed pine stands reach c. 43 500 ha (Figure 6 and Table 3). Beech-dominated stands covered fewer than 320 ha in 1780, 1890 and 2010 (Table 3).

Due to the high number of possible tree species combinations, not all are presentable in Figure 6, and we provide more detailed information on the ‘others’ category in Table 3. All former and current forest areas have been separated into only deciduous and coniferous stands to make the overview as clear as possible. Table 3 demonstrates that a large area (>10 000 ha) has been converted from coniferous to deciduous stands in the current time, whereas the area converted from deciduous to coniferous stands is quite small (less than 2500 ha).

Discussion

Changes in tree species composition over 230 years

The change from deciduous (mainly beech and oak) to coniferous stands, particularly pine, in northern Germany between 1780 and 1890 is a well-known fact (e.g. Hesmer, 1938) and was usually explained by (1) the devastation of forests through the exploitation of timber and firewood, (2) their excessive use as wooded pasture, and (3) litter raking (Hilf, 1928; Ellenberg, 1988; Küster, 2008). An additional reason for the decline in oak is the
introduction of potatoes, making acorns from oak superfluous as fodder for pigs. This led to the sale of oak timber to the Dutch for shipbuilding (Cornelius, 1995; Küster, 2008). These intensive uses caused high nutrient removal over time, such that the soils became low in plant-available nutrients. Only tree species that are adapted to such soils, e.g. pine, were able to grow under these conditions. Because pine is also a fast growing tree species, a very good seed producer and easy to sow, the cleared, previously oak forest areas became dominated by this tree species (Ellenberg, 1988). Our findings confirm the results of Hesmer (1938), who documented the overall dominance of pine stands in northern Germany at the end of the nineteenth century in overview maps.

However, it is surprising that deciduous tree species have been preserved in several forest areas, especially since Peck (1865) reported extensive clearing of beech stands in the area surrounding Templin (located in the north-western part of the Uckermark region, Figure 1) a few decades before his publication. Additionally, the road and rail infrastructure in the region improved, making the transport of timber easier. Given the demand for beech and oak in international markets, we expected a continued decline in the area of deciduous forest. We ascertained why this was not observed based on the historical sources. For instance, in the northwest area of the region, a deciduous forest patch (‘Kiecker’ of ~260 ha, Figure 1) survived because of ownership disputes. Elsewhere, the topography led to the preservation of deciduous stands. Large altitudinal differences (several climbs and drops of up to a difference of 25 m in elevation within a distance of 300 m) and the high rock/stone content of the soil made the sites less attractive for use as arable fields and even for the conversion to pine stands (Stockmann, 2015). Other forest areas also show large altitudinal differences at a (very) small scale, making any kind of land use or forestry difficult. We assume that this is the main reason for the survival of deciduous species-dominated stands (beech and oak) over the long time period (Scamoni, 1955; Wulf and Schmidt, 1996).

Atmospheric pollution caused by industrial complexes led to forest dieback in the 1980s, which particularly affected the

Figure 4  Map of the tree species composition in 1890 (original scale 1:25 000).
coniferous tree species of fir (Abies alba Mill.) and spruce (Picea abies (L.) Karsten). An increase in close-to-nature silvicultural practices resulted in larger beech stands in recent decades (BMEL, 2014). We are unable to explain the increase in alder/birch stands in recent times, but we assume that the failure of cost-efficient drainage (in the 1970s) for agricultural use has led to the abandonment of wet sites. It is likely that alder/birch may have spontaneously established, as seen in the more eastern Prignitz region (Wulf, 2004).

Benefits of historical tree species composition maps for scientific research

The number of studies that have used historical maps in any form is large (e.g. Fensham and Fairfax, 1997; Dupouey et al., 2002), and they cannot be considered here in an exhaustive manner. However, we discuss two ways in which such maps have already been used in scientific studies and how they will be applied in current projects:

(i) as base maps for the targeted choice of sample sites and
(ii) as base maps for the synthesis with other thematic maps to elucidate possible driving factors for long-term land-use changes and their consequences for patterns and processes in ecosystems (including biodiversity) and landscapes.

The storage of carbon and nutrients in forests is a slow process and is influenced by (among other factors) tree species identity (Compton and Boone, 2000; Jandl et al., 2007; Leuschner et al., 2013). Deep-rooted broadleaved trees accumulate soil organic carbon mainly from deep soil layers, while shallow-rooted conifers tend to do so from the forest floor (Jandl et al., 2007). To determine whether tree species identity plays an important role in long-term carbon sequestration, the sampling of sites with a well-known stand history, including tree species composition and

Figure 5 Map of the tree species composition in 2010 (original scale 1:10 000).
forest management, is required (Compton and Boone, 2000). We used the map of the historical tree species composition of the Prignitz region (NE Germany, Wulf and Rujner, 2011) in a former study to select stands fulfilling the following criteria: (1) the existence of data and information regarding past management, (2) having more or less the same age, and (3) growing on similar geological substrates. Without such maps, it would be impossible to compare the potential carbon sequestration of ancient and recent deciduous forests (habitat continuity of >200 years or <150 years, respectively) with that of ancient and recent coniferous forests (Leuschner et al., 2013, 2014). Leuschner et al. (2013) found that C storage in the organic layer was ~75 per cent greater in recent and ancient pine stands compared with ancient beech stands but that the total C stock in the soil (organic layer and mineral soil to 100 cm) was ~25 per cent larger in the beech forests. This was explained by higher C concentrations in the 0–50 cm depth of the mineral soil. The comparison of ancient (>230 years of continuity) and recent beech stands (50–128 years of continuity) shows an average of 47 per cent more organic C in the soil of ancient beech stands compared with recent beech stands. Compton and Boone (2000) also found lower forest floor C in cultivated sites (90–120 years after abandonment following agricultural use) than in forests with long habitat continuity. However, they found no difference between coniferous and hardwood stands.

The current project TERENO, TEREstrial ENvironmental Observatories – Northeastern German Lowland Observatory

### Table 2  Main tree species at time points 1780-1890-2010

<table>
<thead>
<tr>
<th>Tree species</th>
<th>1780</th>
<th>1780</th>
<th>1890</th>
<th>1890</th>
<th>2010</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ha</td>
<td>%</td>
<td>ha</td>
<td>%</td>
<td>ha</td>
<td>%</td>
</tr>
<tr>
<td>Alder/Birch</td>
<td>2985</td>
<td>2.7</td>
<td>1092</td>
<td>1.2</td>
<td>9013</td>
<td>8.1</td>
</tr>
<tr>
<td>Beech</td>
<td>9985</td>
<td>9.0</td>
<td>1331</td>
<td>1.4</td>
<td>12,296</td>
<td>11.0</td>
</tr>
<tr>
<td>Beech/Oak</td>
<td>30,496</td>
<td>27.4</td>
<td>9354</td>
<td>10.0</td>
<td>432</td>
<td>0.4</td>
</tr>
<tr>
<td>Oak</td>
<td>4925</td>
<td>4.4</td>
<td>1427</td>
<td>1.5</td>
<td>5437</td>
<td>4.9</td>
</tr>
<tr>
<td>Pine/Beech</td>
<td>291</td>
<td>0.3</td>
<td>1834</td>
<td>2.0</td>
<td>2342</td>
<td>2.1</td>
</tr>
<tr>
<td>Pine/Oak</td>
<td>5144</td>
<td>4.6</td>
<td>13,250</td>
<td>14.1</td>
<td>662</td>
<td>0.6</td>
</tr>
<tr>
<td>Pine</td>
<td>34,494</td>
<td>31.0</td>
<td>56,220</td>
<td>59.8</td>
<td>56,279</td>
<td>50.5</td>
</tr>
<tr>
<td>Subtotal</td>
<td>88,320</td>
<td>79.4</td>
<td>84,509</td>
<td>89.9</td>
<td>86,461</td>
<td>77.6</td>
</tr>
<tr>
<td>Others¹</td>
<td>22,851</td>
<td>20.6</td>
<td>9,490</td>
<td>10.1</td>
<td>24,901</td>
<td>22.4</td>
</tr>
<tr>
<td>Total</td>
<td>111,171</td>
<td>100</td>
<td>93,999</td>
<td>100</td>
<td>111,362</td>
<td>100</td>
</tr>
</tbody>
</table>

¹Most of these areas were wetlands sparsely scattered with trees in 1780, but young pine plantations or pine stands mixed with several other coniferous tree species in 1890 and 2010.

Figure 6  Map of continuous beech/oak, pure and mixed pine stands and other stands (see Table 3).
Wulf and Rujner, 2011
Herriegel and Groß, 2014
Honnay Rose, 1999). It was
2429.5 1.6
; (Hermy Wulf and Kolk, 2014 Wulf and Kolk, 2014)). The forestry
22 393.5 14.9
20 945.9 13.9
Schmidt . Among
1780.1 1.2
). Using a
3584.5 2.4
tation (http://www.gfz-potsdam.de/en/scientific-infrastructure/observatories/regional-observatories/), we have selected forest sites with long continuity as near-natural as possible over a long time (>200 years). Such sites will serve as references for soils that have been transformed, particularly by human-induced wind and water erosion. Using our map, we have selected forest sites with long continuity as near-natural beech stands to serve as reference sites.
Other research in the Prignitz region used the information on historical habitat quality from the map of historical forest vegetation (Wulf and Rujner, 2011), which was transformed into a dummy variable for modelling (Wulf and Kolk, 2014). It was assumed that historical habitat quality was a potential explanatory variable for the current distribution pattern of true herbaceous forest species (predominantly tied to closed forests according to Schmidt et al., 2011) (Honnay et al., 1999). Using a hierarchical partitioning approach, we were able to show that for very small forest areas in particular, the historical habitat quality is a significant factor explaining the occurrence of true forest species in the herb layer (Wulf and Kolk, 2014). This result confirmed an observation that we have often made in the field: to reach biodiversity conservation goals, it is important for patches to contain existing remnants of former species-rich forest communities. Connectivity to other forest patches and the size of the forest patch itself are not important if remnant patches are not present. Our results stress the importance of ancient near-natural forest stands for the maintenance of forest species diversity, as has been demonstrated in several studies throughout Europe (Hermy et al., 1999; Rose, 1999).
In the current project, ‘Bridging in Biodiversity Science’ (see http://www.bbib.org/bibs-project.html), we will contribute to the study ‘transitions from natural to domesticated environments and novel communities’ (see http://www.bbib.org/novel-ecosystems.html). The aim of this package is to assess native and non-native biodiversity patterns from the species to genotype level. Using our map, we are able to identify sites with biodiversity patterns that are as natural as possible.

**Benefits of historical tree species composition maps for forest management**
Maps of historical tree species composition can be used for forestry purposes in several possible ways (Peterken, 1993; Axellson et al., 2002; Herriegel and Groß, 2014; Watkins, 2015):

(i) Identification of ancient forests (habitat continuity >200 years). This guarantees the continuity of habitats and biotopes. In many European countries, several plant and animal species have been shown to exhibit significant associations with ancient near-natural forests (e.g. Rose, 1999). Among these species, many are regionally rare or endangered (Hermy et al., 1999). In Brandenburg as well as Mecklenburg-Vorpommern (also a federated state in NE Germany), foresters are aware of the small proportion of deciduous ancient forest stands and therefore rate them as stands with the highest conservation value (MIL and MLU, 2010).

(ii) Using old-growth stands and their study to develop ecologically oriented forestry. Foresters are generally aware of the long-term development of forest stands and are usually highly interested in determining how old-growth stands of native tree species have developed under various circumstances, e.g. different climate, site conditions and management (Herriegel and Groß, 2014).

(iii) Establishment of autochthonous seed stocks. Relatively high genetic diversity can be expected in near-natural ancient forests because several autochthonous trees, shrubs and herbs may occur at these sites (e.g. Peterken, 1993).

(iv) Identification of the most suitable areas for the conversion of forest stands. One of the most pressing forest policy targets in Brandenburg is the increase in close-to-nature stands, particularly the conversion from pine stands to deciduous stands containing beech and oak (MIL and MLU, 2010). The forestry department of Brandenburg planned to reduce the proportion of pine stands in all state-owned forest areas from 75 per cent at present to 26 per cent by the year 2045 (MLUV, 2005). The map can help to identify areas where deciduous stands existed in former times and where they can be re-established.

(v) Decision support for the increase of forest areas. New near-natural forest areas (mainly beech and oak) should be established adjacent to ancient forest sites, which act as sources to develop well-established populations of typical forest plants species (Brunet and von Oheimb, 1998). For this reason, both of the north-eastern states of Brandenburg and Mecklenburg-Vorpommern declared to prioritize the integration

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### Table 3 Continuity of tree species groups

<table>
<thead>
<tr>
<th>Tree species groups</th>
<th>ha</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beech/Oak</td>
<td>5482.8</td>
<td>3.6</td>
</tr>
<tr>
<td>Pine pure/mixed</td>
<td>43 475.2</td>
<td>28.8</td>
</tr>
<tr>
<td>Others</td>
<td></td>
<td></td>
</tr>
<tr>
<td>conif²</td>
<td>20 945.9</td>
<td>13.9</td>
</tr>
<tr>
<td>conif-conif³</td>
<td>22 393.5</td>
<td>14.9</td>
</tr>
<tr>
<td>decid-conif³</td>
<td>8191.4</td>
<td>5.4</td>
</tr>
<tr>
<td>decid-decid-conif</td>
<td>2366.0</td>
<td>1.6</td>
</tr>
<tr>
<td>decid-decid</td>
<td>53 896.8</td>
<td>35.8</td>
</tr>
<tr>
<td>decid²</td>
<td>31 591.0</td>
<td>21.0</td>
</tr>
<tr>
<td>decid-decid²</td>
<td>3584.5</td>
<td>2.4</td>
</tr>
<tr>
<td>conif-decid²</td>
<td>24 295.9</td>
<td>1.6</td>
</tr>
<tr>
<td>conif-conif-decid</td>
<td>1706.5</td>
<td>1.1</td>
</tr>
<tr>
<td>conif-decid-decid</td>
<td>397.7</td>
<td>0.3</td>
</tr>
<tr>
<td>decid-conif-decid</td>
<td>6389.6</td>
<td>4.2</td>
</tr>
<tr>
<td>decid-decid-decid²³</td>
<td>1780.1</td>
<td>1.2</td>
</tr>
<tr>
<td>Total</td>
<td>150 733.8</td>
<td>100</td>
</tr>
</tbody>
</table>

Conif = coniferous (pine) and decid = deciduous tree species (alder, birch, beech and oak).

²Pure beech stands at all three time points were only 317 ha (0.2 per cent).
³Forest area only in 1780, in 1890 or in 2010.
⁴Other deciduous tree species (alder, alder/birch or birch).
of near-natural ancient stands in biotope network projects whenever possible (e.g. afforestation of agricultural land and reforestation; MIL and MLU, 2010).

There is actually no third-party funded project for which our data will be used by the Brandenburg forestry department, but as in the past, the data will be offered for use in their long-term projects ‘forest conversion’ and ‘maintaining/enhancing forest biodiversity’ (see http://forst.brandenburg.de/). The data exchange between our research institution and the forestry state centre of excellence (LFE) is ensured by a cooperative agreement. Due to this agreement, a former joint project on ‘first afforestation of agricultural land’ (Groß and Wulf, 2005) was conducted. As a result, all forest areas on historical maps have been digitized for the entire federated state of Brandenburg and have been implemented as a basic tool for forestry on the geopolitical ‘forests as reflections of their time’ (Wälder im Spiegel der Zeit) of the LFE (see http://forst.brandenburg.de/cms/detail.php/bb1.c.324201.de (only in German), Wulf and Groß, 2004; Verch et al., 2013).

Reliability of historical sources
Several authors have noted the positive synergetic effects of the multi-data/documents approach for the reconstruction of historical landscapes (Grossinger et al., 2007; Trpaková, 2009; Hohensinner et al., 2013; Yang et al., 2014). We agree with the previous studies, as we had the same experience. Only by combining various historical materials was it possible to reconstruct the spatially exact locations of the main tree species, particularly for the end of the eighteenth century. We argue that this array of different historical data sources led to reliable maps because we found inconsistencies in only a few very cases and for small areas. However, it is important to bear in mind that statements in Morgenlaender (1780) and von Borgstede (1788) were not quantified. For example, they mentioned that a forest district was ‘composed of beech and oak with a bit [of] pine’. In such cases, we decided to identify the forest area as a beech/oak stand while accepting that this simplification leads to a loss of information on pine through generalization.

This is also true for the data and information from 1890. Müller (1926) only listed per cent values for the main tree species of each specific forest district. However, pine was by far the main tree species among conifers, and we assigned all map areas identified by the Prussian government as coniferous stands to pine stands. The widespread occurrence of tar-smoulder ovens (ovens that allowed the warming of wood to obtain tar) on the Schmettau map, together with lists of tar oven locations in various sources until the end of the nineteenth century, e.g. Enders (1986), confirm the likely presence of pine. The operation of a tar oven requires huge quantities of old pine stumps, and it has been well-documented by local vegetation scientists and local historians that they were established in forests dominated by pine stands (Voigt, 1927; Scamoni, 1955; Wendt, 1972).

Conclusion
We reconstructed the spatially exact composition of dominant tree species across an area of north-eastern Germany for 1780, 1890 and 2010 by combining available map series with archival information sources. These maps reveal species compositional changes that had been previously generalized as a loss of deciduous cover at the expense of coniferous species. This detailed knowledge of the changes in species composition can be used to inform forest management practices, including those focussing on maximizing yield, and species conservation, particularly of the herbaceous layer. An example is the designation of near-natural ancient beech stands (Grumsiner forest and surrounding areas, Figure 6) as a UNESCO World Heritage Site (Geisel et al., 2012). Another important aspect for forest management planning is prioritizing the integration of ancient near-natural stands in biotope network projects (e.g. afforestation of agricultural land), as such stands may serve as sources of well-established populations of typical herbaceous forest species (Groß and Wulf, 2005).

Supplementary data
Supplementary data are available at Forestry online.

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Conflict of interest statement
None declared.

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