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Vegetation changes in boreo-nemoral forest stands depending on soil factors and past land-use during an 80-year period of no human impact

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Abstract

Information on the long-term changes in plant communities that occur without human interference is limited, due to insufficient studies where vegetation can be resurveyed. In 1912, a strict nature protection reserve, with non-intervention management, was established on Moricsala Island in Latvia, located in the boreo-nemoral forest zone. Prior to establishment of the nature reserve, part of the island area was used for agriculture. The island is now covered almost entirely by forest dominated by *Quercus robur* and *Tilia cordata* on sandy soils. Resurvey was conducted in 2011 in seventeen plots in which tree layers and the understory vegetation had been described in 1930. The plots were classified into two groups based on tree species composition in 1930, to determine changes in species composition. Differences in understory and tree canopy composition between these groups persisted over the period between the studies, in relation to soil factors and past stand history. Considerable turnover of species occurred, with decrease of species typical of open habitats and replacement by species typical of nemoral (temperate deciduous) forest plant communities. In the past, *Quercus robur* had likely established in open habitats created by agricultural land-use or past fire, but is presently not regenerating in the understorey.

Keywords: management, understory vegetation, conservation, succession, regeneration.

1. Introduction

In densely populated regions of Europe, the legacies of land-use have profoundly affected forest fragmentation and biodiversity (Hermy and Verheyen 2007). In regions where much of the existing forest area has been previously used for agriculture, differences between plant communities in secondary forests and woodland that has been forested for a long time (ancient forest) can persist for a long time (Baeten et al. 2010) due to seed dispersal constraints and altered soils (Hermy et al. 1999). Soil properties of parent material and relief form a template governing development of understory vegetation, but canopy type is an important soil forming factor (Jenny 1994). Coniferous and deciduous tree stands differ in humus quality, humus accumulation rate, decomposition of litter and formation of a forest floor layer ((Vesterdal and Raulund-Rasmussen 1998; Vesterdal 1999; Vesterdal et al. 2008;). *Picea abies* litter accumulation promotes soil podzolization, which can be reversed under deciduous trees (Bonifacio et al. 2008). Therefore, changes in forest management that affect tree composition cause changes in understory plant communities not only directly by altering light regimes, but also indirectly via soil characteristics (Van Calster et al 2007). Thus, knowledge of the changes in understory vegetation in relation to soil formation processes, tree canopy composition and past land-use is required for development of biodiversity conservation strategies.

Few areas exist where natural plant successions (tree canopy and understory vegetation) in woodland undisturbed by man can be studied. Most old-growth “noble broadleaved” forest of the nemoral (temperate deciduous) zone has been converted to agricultural land-use in Europe, and reference natural woodland occurs only as small

remnants in reserves (Peterken 1996). The Bialowieza reserve in Poland is one example of natural nemoral woodland that has been minimally undisturbed by humans, but even there the effects of past management in the late 1800s-1900s can still be observed, i.e., facilitation of expansion of *P. abies* (Falinski 1988). Also, abundant *Quercus robur* regeneration in the past in the reserve is considered to be due to past human land use and game management (Bobiec 2012). Paleoecological data suggests that the structure of a historical temperate forest shared some of the mosaic attributes of traditional wood pasture, such as canopy gaps of various size (Bradshaw and Hannon 2004). Wooded meadow landscape has been a common feature in the boreo-nemoral transition forest zone of Northern Europe for centuries. However, much of this area has overgrown to forest, which raises the dilemma of whether restoration of traditional land-use by cutting encroaching trees around the remaining ancient trees of the past agricultural landscape is necessary (Palo et al. 2013). Among the typical “noble broadleaved” tree species (*Quercus robur*, *Fraxinus excelsior*, *Tilia cordata*, *Acer platanoides*, *Ulmus glabra* and *Ulmus laevis* and *Acer sp.*), *Q. robur*, which has a special value for cultural heritage and biological diversity in wooded meadow, is known for lack of ability to regenerate in densely shaded stands (Brūmelis et al. 2011, Palo et al. 2013). Therefore, natural forest development in the long-term can lead to a loss of the biological value associated with the previous land-use. However, *Q. robur* can successfully outgrow pioneer tree species in large canopy gaps created by windthrow in *Picea abies* woodland (Götmark and Kiffer 2014).

Identification of the factors governing changes in tree canopy composition and the understory vegetation can be attained by resurvey of territories that have been studied earlier (Kirby et al. 2005). These types of long-term studies can provide a wealth of

information on natural tree stand development. A detailed ecological study was conducted in 1928-1930 (Grošinskis 1932) on the plant communities in plots located in various forest types in the Moricsala (Island) Nature Reserve in Latvia. The study included data on herbaceous and woody plants in the understory, forest mensuration data and soil profile descriptions. Since 1912, the reserve has had strict restrictions on access, and hence no human impact for a period of over 100 years. Prior to establishment of the reserve in 1912, part of the island was used for hay collection and represented a wooded meadow landscape with various nemoral forest types dominated by *Q. robur* and *T. cordata*, and also stands with *Picea abies*, *Pinus sylvestris*, *Betula pendula*, *B. pubescens* and *Populus tremula*. Resurvey of the forest stands studied in 1928–1930 was conducted to determine if changes in understory vegetation could be predicted by past stand history and tree species composition, in relation to soil characteristics. It was hypothesized that 1. regeneration of *Q. robur* was not occurring, but that other nemoral species had increased dominance in the canopy, 2. development of plant communities typical of noble broad-leaved woodland would not occur under a *P. abies* tree canopy, due to unsuitable soil conditions, and 3. loss of species typical of open habitats had occurred in plots during the period between studies.

2. Materials and Methods

2.1. Site description

Moricsala Island (Fig. 1) is located in Lake Usmas (total area 34.7 km²), in Kursas lowland of the Western part of Latvia. The size of Moricsala Island is 82.3 ha (length 1700 m; width in narrowest part 200m). It is part of the Moricsala Nature Reserve. The reserve was founded in 1912 on the initiative of Karl Reinhold Kupffer with the support of the Naturalists' Society of Riga (Kupffer 1931). Since establishment of the reserve,

the management policy has been complete non-intervention, with visitation allowed only by permit for specific reasons, such as research. Before creation of the reserve, about 30% of the island was used for harvest of hay and grazing in summer, and wood was removed for firewood and building (Kupffer 1931). However, in view of the human footprint already at that time, Moricsala was considered to be the best relict of oak-lime forest in the eastern Baltic region. The only hay meadow today (1.1 ha) is around the previous ranger's house on the north-western portion of the island.

Latvia is located in the boreo-nemoral zone. The climate of Western Latvia is characterized as mild coastal with mean annual temperature is 5.5-5.8°C and the annual precipitation is 700-800 mm (data from the Latvian Environment, Geology and Meteorology Centre). The nature protection values of the island are associated with natural mixed nemoral forest with oak *Q. robur* and lime *T. cordata* tree, as well as mixed coniferous forest with spruce *P. abies* and pine *P. sylvestris* (Brūmelis et al. 2011). Areas of lower depression are covered by black alder *Alnus glutinosa* woods.

2.2. Location of plots

A dissertation was defended in 1932 by V. Grošinskis (1932) on forest types on Moricsala Island. In 1928–1930, vegetation and tree structure and composition were described in plots, the locations of which were mapped and noted in the dissertation. The historical maps were rectified to produce a digital map with coordinates of the plots using Geographic Information System ArcGIS 10.0 with Spatial Analyst 10.0. A full description of the maps used and methods for rectification are given as supplementary material. The Pearson's correlation coefficient between matrices of inter-distances of control points on the historical and new images was 0.999 ($p < 0.001$, Mantel test), which confirmed validity of the used method.

Geographical coordinates obtained from the produced digital map base were used to locate the historical plots in the field during 2010-2012 field trips, after receiving approval by the Latvian Nature Conservation Agency. Historical field descriptions by V. Grošinskis of plot location could be used to verify correct locations in the field. For several plots, the chosen locations by coordinates exactly matched the earlier descriptions in the dissertation. For example, locating the plots by coordinates, two plots in small wet *Alnus glutinosa* stands (data from these plots not used in the present study) were precisely located in the middle of depressions, with plot sides extending almost to the edges of the wet area. Two plots in a previously small burnt area had visible subsurface charcoal. Also, sides of other plots that bordered on topographical slopes matched the earlier descriptions. Thus, we are confident that the established plots were located in at least the same forest stands, and that they at least partly spatially overlapped with the historical plots.

2.3. Field data collection

The earlier methods for description of tree canopy structure and composition, and woody and herbaceous understory vegetation, were used in a repeated survey of the plots in July 2010-2012 (mostly July 2011). We restricted the study to 17 plots located on similar dry sandy soil parent material. Three wet plots on hydromorphic soils were excluded. Of the 17 plots, 15 had size 50*50m and the other two were smaller with size 50m*20m. All trees with diameter at breast height (DBH) > 10 cm was measured in each plot. In the earlier study, also age of selected overstory trees was estimated from cores obtained using a Pressler increment borer. Tree saplings and seedlings (all stems <10 cm DBH) and tall shrubs were counted in the previous study in four to ten 4*4m subplots.

However, in the dissertation (Grošinskis 1932), the form of presenting sapling densities varied: 1) counts of saplings and shrubs in the plots and as densities ha^{-1} , 2) only as densities ha^{-1} , 3) only as qualitative descriptors (few, many, etc) and 4) combinations of the above qualitative and quantitative approaches. For plots where only qualitative descriptors were used, the number of saplings ha^{-1} could be estimated by qualitative values based on information from plots where both qualitative and quantitative values were given. The following conversion factors (number of saplings per ha^{-1}) were used to replace qualitative values: very sparse – 270 ha^{-1} , sparse – 1175 ha^{-1} , medium – 3890 ha^{-1} , medium to dense – 4250 ha^{-1} , good – 8030 ha^{-1} , and very good – 16600 ha^{-1} . In the resurvey, ten 4*4m subplots for counting samplings were used in all plots, randomly selected by throwing a stick (earlier method for selection not described).

In the previous study, the understorey herbaceous plant communities were described in ten 1*1m subplots in the larger plots. Complete lists of species in the plots were recorded and frequency of occurrence in the subplots was estimated. We repeated this method. Cover of each species was also estimated in both surveys, but it was considered that cover estimation was not repeatable accurately and was not used for analysis.

In the present study, in consideration of minimizing effect on the habitat, soil profiles were unearthed beside vegetation plots in the closest location without fallen trees and dense shrubs. Soil profiles were described according to the FAO (Food and Agriculture Organization of the United Nations) WRB (World Reference Base for Soil Resources) soil classification system (IUSS Working Group WRB 2014). The soil morphology descriptions and symbols of soil horizons are given according to the Guidelines for Soil Description (FAO 2006). Soil samples in 3 replicates were taken as grab samples from the litter O horizon and the surface mineral topsoil Ah horizon (identified by accumulation of

organic matter). Depth to which samples were taken depended on the depth of the horizon. The samples were placed in plastic bags and transported to the laboratory, where they were immediately processed. In the previous study, the methods used for description of soil morphology vastly differed. However, qualitative descriptions of horizons allowed to cross-reference O and Ah horizons, and as depths of these horizons were measured in both studies, we include this data in the analysis.

2.4. Soil analysis

Laboratory analyses were conducted according to standard methods used in ICP (International Co-operative Programme) Forest monitoring methods (Cools and de Vos 2010) to determine soil texture, soil pH_{KCl} value, total nitrogen (%), total organic carbon (%) and total nitrogen concentrations and total organic carbon/nitrogen concentration ratio of the O and Ah horizons.

The mineral soil samples were dried at air temperature and sieved using a 2-mm mesh. Material from the litter layer was sieved using a 4-mm mesh. Soil fractions were determined by pipetting method (van Reeuwijk 1995) after treatment with 0.1 M NaOH to break down aggregates. The soil fractions were defined by particle size according to the USDA soil texture classification (Cools and de Vos 2010): sand – 0.063 to 2.0 mm, silt – 0.002 to 0.063, clay – <0.002 mm. The percentages of sand, silt and clay were calculated from fine earth (<2 mm fraction). Soil textural classes were determined according to the Guidelines for Soil Description (FAO 2006).

Soil pH was determined with a glass electrode in 1 M KCl solution (10 g soil and 50 ml solution in 3 laboratory replicates). Total nitrogen concentration (%) was determined using a CHNS-O Elemental Analyzer “Eurovector” EA3000 Series and total organic carbon concentration (%) was determined using a total organic carbon analyzer

“Shimadzu TOC-Vcsn” and “Solid Sample Module SSM – 5000 A”, where soil samples were heated at 900° C (ISO 10694 1995; ISO 13878 1998; Cools and De Vos 2010). Analysis of soil samples was conducted using 3 replicates.

2.5. Data analysis

In addition to a vegetation matrix of plant frequencies of occurrence in subplots, a matrix consisting of ecological characteristics of plots was produced with the following variables: weighted mean Ellenberg values of plants (weighted by frequency of occurrence) for pH, N and light, obtained from Ellenberg et al. (1991), and relative frequencies of plants in plots by Raunkiaer life form, C-S-R plant strategies and dispersal type, obtained mostly from the Bioflor (see supplementary material in Kühn et al. 2004) and Ecological Flora databases (Fitter and Peat, 1994). Barochorous species were combined together with autochorous species. In addition, species were grouped by their characteristic habitat: forest, grassland, other open habitats (forest edges, clearings, clearcuts), and both forest and grassland. Other matrices produced consisted of data on basal area of trees by species and counts of saplings by species calculated as densities in 4*4 m subplots.

Classification of plots into groups was made using cluster analysis (Ward’s method with correlation distance measure) using PCORD version 5. For comparison of values between these groups, a permutation test was chosen for herb relative frequencies, ecological characteristics, species richness, soil variables, tree basal area and sampling densities, since most of these variables did not correspond to a normal distribution and tests showed heteroscedasticity of variance. To compare changes in variables between studies, a paired

permutation test (herb relative frequencies, ecological traits, species richness, O and Ah horizon depths, tree basal area and sampling densities) was used. Significant differences in the proportion of plots occupied by herb and sapling species between years and plot groups were determined using a test for equality of proportions. All tests were performed using program R 3.1.3 (R Core Team 2015), with permutation tests as implemented in library coin of this program (Hothorn et al. 2008). A non-metric multidimensional scaling ordination (NMS) of the vegetation matrix was performed using PCORD version 5 (McCune and Grace 2002).

3. Results

3.1. Tree species composition

Cluster analysis of plots based on basal areas of tree species in 1930 classified the plots into a larger group of 8 plots, all dominated by *Q. robur*, and three small groups of 2, 3 and 4 plots dominated by different combinations of *Picea abies*, *Pinus sylvestris* and pioneer species (*Betula* sp. and *Populus tremula*). The estimated age of the canopy trees in the *Q. robur* stands in 1930 was 90–100 years (Table 1). Five of the eight plots (plots 2, 3, 4, 5, and 6) contained old or dead *P. tremula*, which in one plot had been cut (plot 3). The three small groups included plots that had regenerated after use as wooded pasture (plots 11 and 12), after a fire in about 1900 (plots 8 and 20), after a bark beetle outbreak (plot 8) or after selective cutting (plots 9 and 6). Thus, it was considered that the three groups represented an early to mid secondary succession stage after a major disturbance or land-use change. Field descriptions of two of the stands (one dominated by *P. tremula* (plot 21) and the other by *P. abies* (plot 18) did not include notes on the past disturbance, but in the cluster analysis were included in two of the three secondary succession groups.

In further analysis, the three small groups were combined to form a larger group containing stands that contained variable composition of conifers and pioneer tree species, and which mostly represented an early to mid successional stage after a major disturbance or land-use change (further called the conifer/pioneer-dominated group).

Comparing the two defined groups, in 1930, the *Quercus*-dominated plots had significantly larger basal area of *Q. robur*, *T. cordata* and *A. platanoides* (Table 2). In 2011, comparing the two groups, the conifer/pioneer-dominated group had significantly larger basal area of *P. sylvestris*, *P. tremula* and *Betula sp.* (Table 2) and higher shrub layer densities of *Q. robur* and *P. abies*. Between the two years of study, basal area of *A. platanoides* and *Betula sp.* significantly decreased in the conifer/pioneer-dominated group (Table 2). In the conifer/pioneer species group, basal area of *Q. robur*, *T. cordata* and *A. platanoides* increased by 2-6 times, but non-significantly (Table 2), while density of *Q. robur* in the understory had significantly decreased (Table 3).

Comparing the two defined groups, in 1930 the conifer/pioneer-dominated group had higher occurrence of *P. tremula* in the overstory (Table 3). Between the two years of study, occurrence in plots of *P. tremula* and *Betula sp.* significantly decreased in the *Quercus*-dominated plots (Table 2). In the conifer/pioneer species group, occurrence of *Q. robur* in the understory had significantly decreased between years (Table 3); in both groups, *Q. robur* was no longer found in the understory in 2011.

3.2. Soil characteristics

In 1930, the thickness of the O horizon did not significantly differ between the two groups of plots. However, in the period since 1930, the thickness of the O horizon had significantly increased in the conifer/pioneer tree species plots. Based on data from soil

pits studied in 2011, soil in the plots had sandy soil texture in the topsoil with weakly (Arenosols and Cambisols) to well formed soil horizons (Podzols). Depth to silty loam parent material mostly occurred in the soil profiles at a depth >100 cm (Table 4), but was less than 50 cm in two plots. Depth to free carbonates (CaCO_3) was less than 1 m in three plots. Charcoal was found in the O, Ah, Bs or Bt horizon in 13 of the 17 plots (Table 1). While the soil texture of the topsoil in all plots of the two tree composition groups was sand, several soil variables significantly differed between the groups. The pH of the O horizon and N concentration of the Ah horizon were significantly higher in the *Quercus*-dominated plots (Table 4). Thickness of the O horizon, C concentration and the C/N ratio in the O horizon, were higher in the conifer/pioneer-dominated group.

3.3. Ecological characteristics

In comparison with the conifer/pioneer species group, in 1930 the *Quercus*-dominated group had greater relative frequency of chamaephytes (plants with resting buds close to soil surface), species with autochorous (self) seed dispersal and species with an intermediate competitive stress-tolerant ruderal CSR strategy (Table 5). In 2011, chamaephytes remained relatively more frequent in this group. In addition, the weighted mean pH and N Ellenberg values were higher in this group, and ant-dispersed myrmecochorous (ant-dispersed) species and those characteristic of both forest and grassland were relatively more frequent. Between the two times of study, relative frequency of plants with a competitive-stress tolerant CS strategy and autochorous seed dispersal mechanism had decreased, while species characteristic of moist habitats had higher frequency (Table 6).

Compared with the *Q. robur*-dominated group, in 1930 the conifer/pioneer tree species group of plots had significantly greater relative frequency of hemiphanerophytes

(dwarf shrubs), therophytes (annuals), plants with a CR strategy and wind-dispersed seed, and plants characteristic of open habitats (Table 5). In 2011, higher relative frequency of hemiphanerophytes (buds at or near the soil surface) and species of open habitats had remained higher in the conifer/pioneer species group, but there was also significantly higher relative frequency of plants with a stress-tolerant S strategy and plants characteristic of forest habitats. Between the two years of study, a greater number of significant differences in ecological characteristics of the plant communities occurred in the conifer/pioneer species group than in the *Quercus*-dominated group (Table 6). The relative frequency of geophytes (with an underground storage organ), and species with both geophyte and hemicryptophyte (buds at or near the soil surface) life forms, and species with a S strategy, zoochorous (animal dispersed) seed dispersal mechanism had significantly increased. These changes occurred alongside decreased relative frequency of therophytes, hemiphanerophytes, species with a competitive ruderal CR strategy and species characteristic of both forest and grassland.

3.4. Species composition

Mean species richness did not significantly differ between the two stand groups nor between years of study: 23.5 and 23 species in the conifer/pioneer trees species group and 23.8 and 20.1 in the *Quercus*-dominated group. Of the species that are protected today (there were no protected species lists in the earlier period), only one, *Dentaria bulbifera* was recorded in plots in 1928–1930, but in addition to this species, *Circaea lutetiana* and *Festuca altissima* were recorded in the recent survey.

The conifer/pioneer tree species group was characterized by plant species typical of coniferous forest, like *Vaccinium* species and *Trientalis europaea*, along with species characteristic of open habitats, such as the graminoids *Festuca ovina* and *Deschampsia*

flexuosa, the herb *Melampyrum nemorosum* and fern *Pteridium aquilinum* (Table 7). Compared to the plant communities of the conifer/pioneer tree species group, the *Quercus*-dominated group of plots had higher relative frequency of woodland herbs like *Aegopodium podagraria* and *Paris quadrifolia* (Table 7).

Over the 80-year period between the two studies, species characteristic of open habitats and forest/grassland, like *Fragaria vesca*, *V. chamaedrys* and *M. nemorosum* in the conifer/pioneer tree species and *Athyrium filix-femina* in the *Quercus*-dominated group had decreased in relative frequency. The other plant species showing significant positive or negative change were forest species. Of those, significant increase in relative frequency occurred for *Circaea lutetiana* in both plot groups, *Dryopteris carthusiana* in the *Quercus*-dominated group, and *Galium odoratum*, *Veronica officinalis*, and *Oxalis acetosella* in the conifer/pioneer species group (Table 8). In plots of the *Quercus*-dominated group, species characteristic of perhaps more open forest habitat, like *Geum urbanum*, and also some species of closed deciduous forest habitat, like *Polygonatum multiflorum*, had become less frequent. *Vaccinium* species became less frequent in the conifer/pioneer species group.

The NMS ordination of vegetation data (Figure 2) showed a fairly good separation of the two tree species groups. The two post-fire groups are located at the bottom of the ordination. However, two plots of the conifer/pioneer species group occurred within the cluster of *Quercus*-dominated plots. The plots at the bottom of the ordination show a unidirectional change in species composition to the right side, while the change in the *Quercus*-dominated group is not consistent. The vegetation gradients in the ordination can be explained by the same significant factors (Figure 2B) obtained in the above explicit analysis, for example, greater occurrence of species of open habitats in the

conifer/pioneer species group and species with higher Ellenberg values for pH and N in the *Quercus*-dominated plots. Between the periods, depth of the O horizon and occurrence of stress-tolerant species increased, shown by vectors directed to the right side of the ordination (Fig. 2).

4. Discussion

The present vegetation of the Moriscala Nature Reserve has developed as a result of past land-use and natural and human-caused disturbance interacting with soil formation processes. An intrinsic problem in the study was low number of plots imposed by the plot design in the early part of last century, in relation to the variability in soils and canopy composition and the vast number of characteristics examined. We divided the stands into two groups. The conifer/pioneer tree species group was not homogenous and included various combinations of tree species and different past history. It was not subdivided further as this would not allow statistical comparison. However, it did differ statistically from the *Quercus*-dominated group in canopy, soil and vegetation characteristics, which suggests that this grouping was valid. Also, the NMS ordination indicated fairly good separation of the two groups in vegetation composition. The large number of characteristics examined increased the probability of a chance significant difference between the plot groups, and certainly correcting for chance in statistical analysis led to fewer significant differences. However, groups of plant ecological characteristics and soil variables with significant differences without correction for chance effect did suggest the same overall features that are known to be characteristic of particular communities, indicating their validity. Nevertheless, interpretation requires caution.

4.1. Canopy composition in relation to soil factors

All studied forest stands had similar soil texture, but stands characterized by various combinations of dominance by conifer (*P. sylvestris* and *P. abies*) and pioneer tree (*P. tremula* and *Betula* sp.) species had a deeper, less decomposed (higher C/N ratio) and more acidic O horizon. The conifer/pioneer species group was variable in canopy structure and composition, having developed after different pre-1930 history of fire, forest-pasture use, cutting and natural disturbance. The past disturbance in the stands can explain the greater dominance of the pioneer tree species. The lower pH can be explained by the strong acidifying effect of coniferous litter (Hagen-Thorn et al. 2004), which accelerates podzolization and leaching of soluble organo-mineral complexes and carbon to deeper soil layers (Lundström et al. 2000). Litter from coniferous forests decomposes slower than litter from deciduous forests and accumulates in the forest litter layer (Berg 2000). The effect of coniferous trees on soils of deciduous forests has been previously described in the Białowieża Primeval Forest in Poland (Kwiatkowski and Pedrotti 1994). Increase of the thickness of the O horizon in conifer/pioneer species plots since 1930 indicates ongoing podsolization processes due to coniferous litter accumulation.

Compared to the conifer/pioneer-dominated group, stands in the *Quercus*-dominated group were mixed with other broad-leaved tree species like *A. platanoides* and *T. cordata*. The thinner and well decomposed O horizon, sometimes minimally formed, with higher pH, is typical of this canopy type (van Oijen et al. 2005). These soil features can be explained by additions to the soil of more easily decomposable and nutrient rich leaf litter (Hagen-Thorn et al. 2004), as also indicated by significantly higher N concentration in the Ah horizon. Concentrations of nitrogen, potassium, calcium and magnesium are higher in the canopy of deciduous forests with varying degrees than in canopy in coniferous forests (Bergmann 1988), which results in higher concentration of

exchangeable cations and higher pH value in deciduous forest litter (Binkley 1995). The lower C concentration in the O horizon might be explained by increased invertebrate activity causing mixing of the horizons.

Q. robur is a temperate climate tree species that commonly occurs on alkaline and fertile soils characterized by relatively heavy soil texture and moisture conditions (Jones 1945). However, the species has a relatively wide ecological valence (Lawesson and Oksanen 2002) and occurs in many forest types (European Environment Agency 2006; Ikauniece et al. 2013). The Moricsala Nature Reserve is a case where *Q. robur* occurs on less-fertile sandy soil conditions.

4.2. Canopy composition in relation to past land-use and disturbance

The long-term history of vegetation on Moricsala Island is not known. The reserve was established on the island in 1912 to represent the best noble broad-leaved woodland in the Baltic region (Kupffer 1931), but there is evidence that humans had direct impact on its development. The evidence of charcoal in soil of most plots indicates past forest fire. Considering the past agricultural land-use of the island at the beginning of the 1900s and the traditional slash and burn traditions in the past, it seems likely that humans had cleared the forest by fire at some unknown time. Isolated noble *Q. robur* trees with large diameter and wide crowns were noted by Kupffer (1931) in forest habitat, typical of overgrown wooded meadow. This, along with the relatively young age (90-110) of trees in the *Q. robur* stands in 1930 (Grošinskis 1932), suggests that these *Q. robur* trees regenerated in the early 1800s after agricultural land-use or fire, as its establishment is successful in non-intensively used pasture and hay fields (Vera 2000). We did not determine age of *Q. robur*, but other published (Brūmelis et al. 2011) and unpublished studies in the island give a maximum age of 240 years, with most canopy trees about 180-

200 years, which is in conformity with the earlier study. The noted occurrence of *P. tremula* snags and logs in the *Q. robur* stands in 1930, and subsequent decreases in basal area and/or occurrence of the pioneer tree species *Betula* sp. and *P. tremula*, also suggest past regeneration of pioneer species in open areas and subsequent mortality with canopy closure. The significantly higher density of *Q. robur* in the shrub layer of the conifer/pioneer tree species group in 1930 also suggests that the past land-use created suitable conditions for establishment and recruitment to the canopy layer.

Establishment of *Q. robur* in the understory was still occurring in 1930, but it was lacking in the understory in 2011. Recruitment of *Q. robur* from the understory to the canopy stage is unsuccessful under a deciduous canopy (Falinski 1986, 1988). However, there is evidence that *Q. robur* can successfully establish under conifer canopies, provided sufficiently lit conditions free from competitive vegetation (Götmark et al. 2005). There were few significant changes in total basal diameter of tree species in plots during the 80-year period. Basal area of *Q. robur* had increased, suggesting its continued presence in the tree canopy. Long-term persistence of *Q. robur* in woodland can be explained by its long life span, ecological plasticity in habitat and growth, and ability to survive disturbances (Götmark and Kiffer 2014). However, *T. cordata* has been observed to successfully recruit to the overstory in *Q. robur* on Moricsala Island (Brūmelis et al. 2011), as also was suggested by the large (non-significant) increase in mean basal area of *T. cordata*. Data from five permanent plots established in 1936 in Pino-Quercetum and Tilio-Carpinetum communities in the Bialowieza reserve indicated replacement of *Q. robur* by *P. abies*, *T. cordata*, and *Carpinus betulus* (Falinski 1986).

One of the reasons for poor establishment of *Quercus robur* might be due to seed predation by boar, which was rare in Latvia in the early 1900s. The population has much

increased in Latvia, and groups of 5-6 boars, rarely up to over 30, regularly visit the island for a few weeks in autumn to forage, presumably attracted by acorn crops (Vilnis Skuja, personal communication). In the isolated area of the island, such densities are extremely high and they can cause extensive damage such as uplifting of the soil (personal observation). Currently, however, regulation of the boar population is not permitted in the reserve. Individual roe deer occasionally also visit the island for short periods, but damage to saplings is likely minimal.

Major storms in the early 1900s (Kupffer 1931) and in 1967 and 1969 (Abolina et al., 1979) were documented to have selectively caused extensive mortality of *P. abies* on Moricsala Island. The wide occurrence of pioneer tree species and low success of *P. abies* in recruiting to the canopy can therefore partly be explained by wind disturbance. Its low density in the shrub layer of the *Quercus*-dominated stands suggests that the conservation value of these stands is not threatened in the near future by recruitment to the canopy layer. We noted that throughout the island *P. tremula* was being selectively cut by beaver, an animal that was extinct in the early 1900s. Thus, in contrast with the *Quercus*-dominated stands, disturbance will continue to be a major factor affecting tree and herb species composition in the conifer/pioneer tree species group, and this might provide opportunities for recruitment of *Q. robur*. The future changes in tree species composition on Moricsala Island will be determined by competitive exclusion, tree longevity and disturbance.

4.3. Changes in vegetation in relation to soil and canopy factors

In 1930, the vegetation of the conifer/pioneer tree species stands differed from the *Q. robur* stands in higher abundance of species with ecological characteristics (therophyte, hemiphanerophyte, ruderal strategy, and wind dispersed) of open habitats. In

2011, species of open habitats were still more abundant in this group, but species characteristic of forest habitats, geophytes, plants with both geophyte and heimicryptophyte life form, and a stress-tolerant strategy, which are features that are characteristic of ancient forest species (Hermy et al. 1999), had increased in occurrence.

In the *Q. robur* stands, few significant differences in the period between studies occurred in ecological characteristics of the vegetation, suggesting general stability of the vegetation communities. Abundance of species typical of moist habitat increased, as might be expected after less light exposure due to canopy closure. Chamaephytes, which have sensitive buds located slightly above the soil, had higher occurrence in the *Q. robur* stands, compared to the conifer/pioneer tree species group, in both years of study. These species have been observed to increase in abundance after cessation of the previous human impact (Roovers et al. 2005), which can explain their lower occurrence in the disturbed stands. In 2011, species with seed dispersal by ants, which is at small distances, had higher occurrence in the *Q. robur* stands, suggesting that greater time would be needed for these species to colonize the disturbed stands. Dispersal by ants at short distances is a plant trait described to be common of old deciduous woodland, as recovery of typical woodland communities after agricultural land-use occurs after a long time due to dispersal constraints (Ikauniece et al. 2013). The decrease of abundance of plants with a competitive stress-tolerant strategy and autochorous seed dispersal in the *Q. robur* stands is difficult to explain and might have occurred by chance. In line with the differences in soil variables between the stand groups, *Q. robur* stands had greater abundance of species with higher Ellenberg pH and N values. However, this difference occurred only in 2012, which might suggest an effect of richer leaf litter on soil nutrient regime favouring growth of competitive species, like *Aegopodium podagraria*, which was

more common in the *Q. robur* stands in both years. Use of semi-permanent plots for study of plant communities has shown that the abandonment of coppicing as a traditional form of management has led to increased shading, causing shifts from more thermophilous towards more nutrient demanding species (van Calster et al. 2008; Hédél et al. 2010). This was also observed on Moricsala Island, with species of open habitats decreasing in the conifer-pioneer tree species group, and nutrient-demanding species becoming more frequent in the *Q. robur* stands.

Compositional differences between recent secondary forest and ancient forest can persist for decades (Baeten et al. 2010). In our study, differences in vegetation between the two tree groups were still evident after 80 years, which can be explained by persisting soil and canopy factors. Nevertheless, the NMS ordination of vegetation data showed a unidirectional shift in vegetation of seven of nine conifer/pioneer tree species stands, due to replacement of open species like *Fragaria vesca*, *Veronica chamaedrys* and *Melampyrum nemorosum* with typical forest species like *Circaea lutetiana*, *Oxalis acetosella* and *Galium odoratum*. The decreased occurrence of species common to boreal woodland, like *Vaccinium* sp, and *Luzula pilosa* might also be explained by increased shading conditions. As distribution of species with different life histories is associated with soil pH, nitrogen mineralization, and amount of organic material in soil (van Oijen et al. 2005), the typical nemoral flora under a broadleaved canopy may be altered by soil and shading conditions that evolve after development of an *P. abies* understory (Ikauniece et al. 2013). However, there was no evidence of significant recruitment of *P. abies* to either of the two groups of stands, which would endanger the value of the reserve as a reference area for the noble broad-leaved tree species stands. The two stands of the disturbed conifer/pioneer tree species group that were misplaced in the NMS ordination

of vegetation data were in 1930 dominated by *P. tremula*, which was replaced by *Q. robur* in 2011, which can explain the similarity of vegetation in these plots with that in other plots of the *Quercus*-dominated group. This suggests that successful recruitment of *Q. robur* in the canopy of the disturbed stands might be possible, along with the development of the typical plant communities.

Changes in the ecological characteristics of plant communities in the *Q. robur* stands showed few changes over time. This suggests the strong role of the canopy and soil in determining formation of the plant community composition from the pool of species that can establish in the existing conditions. However, the NMS ordination showed that trajectories of compositional change in the *Q. robur* stands were unpredictable, perhaps due to a shifting mosaic of ground layer conditions created by tree mortality and perhaps by uplifting of the topsoil by boar. Vegetation composition of the disturbed stands will continue to change, and differences in community composition with the *Q. robur* stands can be expected to continue in the near future.

4.4. Management implications

Management of the Moricsala Nature Reserve since its establishment in 1912 has been by strictly enforcing non-intervention. It has served as a reference area for natural development of woodland after previous land-use for pasture and hay collection. Regeneration of *Q. robur* on the island was likely promoted by past traditional human practices. Although *Q. robur* is presently not regenerating in the understory, it will persist in the canopy due to its longevity. There was no evidence of invasion of *P. abies* in the shrub layer of the noble broad-leaved stands, which would endanger their conservation value. In stands previously dominated by conifer and pioneer trees species, *Q. robur* was the only tree species that showed significantly increased basal area, indicating its ability

to outlive the other tree species. There was little change in composition of herbaceous vegetation in *Quercus*-dominated stands, while the conifer/pioneer tree species dominated stands had decreased occurrence of species characteristic of the past open forest habitats affected by human land-use. Our study showed that there is no reason for changing the non-intervention management regime on the island, with the exception of exerting some control on boar populations in autumn to minimize seed predation and ground disturbance.

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Table 1. Characteristics of forest plots on Moricsala Island (Grošinskis 1932). Evidence of charcoal (in 2011) indicating past fire shown by a “+”. Maximum age of sampled overstory trees in 1928-1930 is given.

Plot no.	Dominant canopy species	Past fire	Age	Comments (Grošinskis 1932)
<i>Quercus robur</i> stands				
2	<i>Q. robur</i> , <i>T. cordata</i> , <i>A. platanoides</i>	+	90	several old <i>P. tremula</i> snags and logs; <i>P. tremula</i> being replaced by lime and maple in the subcanopy
3	<i>Q. robur</i> , <i>T. cordata</i> , <i>A. platanoides</i>	+	110	large decomposed stumps (cut) - two <i>P. tremula</i> stumps and two oak; very decomposed logs and branches
4	<i>Q. robur</i> , <i>T. cordata</i> , <i>A. platanoides</i>	+	90	7 wind-thrown and partially decomposed tall aspen
5	<i>Q. robur</i> , <i>P. tremula</i> , <i>P. abies</i>	+	100	many wind-thrown, decomposed aspen
7	<i>Q. robur</i> , <i>P. tremula</i> , <i>A. platanoides</i> ,	+	100	a few aspen and <i>Sorbus</i> logs
14	<i>Q. robur</i> , <i>A. platanoides</i>	+	110	no human activity, no stumps or dead wood (very dense shrub understorey)
15	<i>Q. robur</i> , <i>A. platanoides</i>	+	110	no human activity, fallen large tree branches
16	<i>Q. robur</i>		110	no human activity, fallen large tree branches and trees
Conifer/pioneer tree species stands				
11	<i>P. sylvestris</i> , <i>Q. robur</i> , <i>P. tremula</i>		120	previous wooded pasture, 3 <i>P. sylvestris</i> stumps and one pine log, on border with meadow
22	<i>P. sylvestris</i> , <i>Q. robur</i> <i>Betula spp</i>		100	previous wooded pasture, some pine stumps; very open <i>P. sylvestris</i> stand; previously without trees
9	<i>P. sylvestris</i> , <i>Betula spp.</i>	+	150	1 oak and 5 <i>P. tremula</i> cut stumps; 5 <i>P. tremula</i> logs; spruce canopy forming
20	<i>P. sylvestris</i> , <i>Betula spp.</i> , <i>Q. robur</i>	+	140	many cut pine stumps; fire about 1900.
19	<i>Betula spp.</i>	+	30	decomposed <i>P. abies</i> , <i>P. sylvestris</i> and <i>Q. robur</i> stumps; fire about 1900.
6	<i>P. tremula</i> , <i>Q. robur</i>	+	100	5 old <i>P. tremula</i> stumps (logs removed); two aspen logs
21	<i>P. tremula</i> , <i>Q. robur</i> , <i>A. platanoides</i>		105	no human activity, no stumps or dead wood
8	<i>P. abies</i> , <i>Q. robur</i> , <i>P. tremula</i>	+	125	in 1900 tall <i>P. abies</i> that later suffered mortality from wind and bark beetle.
18	<i>P. abies</i> , <i>P. sylvestris</i> , <i>Q. robur</i>	+	110	<i>P. abies</i> replacing <i>Q. robur</i>

Table 2. Mean basal area ($\text{m}^2 \text{ha}^{-1}$) of living trees in plots on Moricsala Island. Significant differences between conifer/pioneer tree species and *Quercus*-dominated plots (permutation test) are indicated by different letters (A and B for basal area and X and Y for occurrence in plots). Significant differences between years are shown by bold font (paired permutation test) and for occurrence in plots by italics (test for equality of proportions).

	Mean basal area ($\text{m}^2 \text{ha}^{-1}$)		2011	
	1930			
	conifer/pioneer -dominated	<i>Quercus</i> - dominated	conifer/pioneer - dominated	<i>Quercus</i> - dominated
<i>Quercus</i>	5.2 ^A	12.5 ^B	9.8	15.7
<i>Tilia</i>	0.7 ^A	5.3 ^B	4.7	12.1
<i>Acer</i>	0.9 ^A	7.0^B	2.8	2.0
<i>Picea</i>	5.0	0.7	7.3	1.3
<i>Pinus</i>	10.9 ^A	0.8 ^B	9.8 ^A	0.3 ^B
<i>Populus</i>	5.4 ^X	1.2 ^Y	3.9	0.5
<i>Betula</i>	3.8 ^A	0.6^B	3.1	0.0

Table 3. Densities of tree sapling and shrub species in plots on Moricsala Island. Significant differences between conifer/pioneer tree species and *Quercus*-dominated plots (permutation test) are indicated by different letters (A and B for mean density and X and Y for occurrence in plots). Significant differences between years for sapling densities are shown by bold font (paired permutation test) and for occurrence in plots by italics (test for equality of proportions).

Saplings/shrub species	Mean number stems ha ⁻¹			
	1930		2011	
	conifer/pioneer dominated	<i>Quercus</i> -dominated	conifer/pioneer dominated	<i>Quercus</i> -dominated
<i>Quercus</i>	272^A	31 ^B	0	0
<i>Picea</i>	2423 ^X	188 ^Y	243	55
<i>Tilia</i>	623	1272	602	1196
<i>Acer</i>	1447	688	396	203
<i>Pinus</i>	73	0	0	0
<i>Populus</i>	203	65	521	0
<i>Betula</i>	178	0	14	8
<i>Padus</i>	216	1908	757	4430
<i>Sorbus</i>	1505	375	209	39
<i>Corylus</i>	1653	3062	1201	1954
<i>Frangula</i>	75	0	14	0
<i>Juniper</i>	6	0	0	0
<i>Salix</i>	32	0	14	0
<i>Crataegus</i>	17	0	0	0
<i>Malus</i>	6	6	0	0

Table 4. Characterization of soil properties in Moricsala Island. Mean and range of values in soil pits studied in 2011 are given. Significant differences between conifer/pioneer tree species and *Quercus*-dominated plots (permutation test) are indicated by bold font. * with Bonferoni correction.

		Conifer/pioneer-dominated			<i>Quercus</i> -dominated		
		mean	min.	max.	mean	min.	max.
O horizon	Depth (cm)	5.9	3.0	11.0	3.1	0.5	6.0
	pH	4.3	3.5	5.8	5.4	4.4	6.5
	N (%)	1.4	0.7	2.7	1.0	0.5	1.4
	C (%)	32.4*	18.3	45.0	18.9*	14.7	25.8
	C/N ratio	25.4	15.2	40.2	16.0	11.3	18.9
Ah horizon							
	Depth (cm)	15.8	0.0	52.0	12.9	3.0	20.0
	pH	4.1	3.5	4.8	4.5	3.9	5.1
	N (%)	0.1	0.0	0.2	0.2	0.0	0.2
depth to loam (cm)		149	50	160	125	21	180
depth to free carbonates (cm)		190	100	200	160	100	200

Table 5. Significant differences (permutation test) in relative frequency of ecological characteristics and weighted mean Ellenberg values (pH and N) of conifer/pioneer tree species and *Quercus*-dominated plots on Moricsala Island. Characteristics are given for the plot group with higher value. * with Bonferoni correction.

1930			2011		
Conifer/pioneer -dominated	<i>Quercus</i> - dominated	p value	Conifer/pioneer -dominated	<i>Quercus</i> - dominated	p value
hemiphanerophyt e		0.005*	hemiphaneropyte		0.051
therophyte		0.016	open		0.006*
anemochorous		0.023	S		0.026
CR		0.034	forest		0.036
open habitats		0.054		pH	0.009*
	autochorous	0.031		chamaephyte	0.012
	CSR	0.033		Forest and grassland	0.019
	chamaephyt e	0.010		N	0.030
				myrmecochorous	0.030

Table 6. Significant differences (paired permutation test) between 1930 and 2011 in relative frequency of ecological characteristics of conifer/pioneer tree species and *Quercus*-dominated plots on Moricsala Island.

		increase/ decrease	p
Conifer/pioneer -dominated	variable		
	S	+	0.014
	zoochorous	+	0.017
	forest-grassland	-	0.017
	therophyte	-	0.019
	hemiphanerophyte	-	0.019
	geophyte	+	0.038
	CR	-	0.040
	moist habitats	+	0.040
	geophyte and hemicryptophyte	+	0.047
<i>Quercus</i> - dominated	moist habitats	+	0.015
	CS	-	0.028
	autochorous	-	0.046

Table 7. Significant differences (permutation test) in relative frequency of plants species of conifer/pioneer tree and *Quercus*-dominated plots on Moricsala Island. Placement of species in the conifer/pioneer-dominated versus *Quercus*-dominated columns indicates the plot group in which it had higher relative frequency. Species shown in bold also showed significant differences (test for equality of proportions) in occurrence in plots.

1930			2011		
Conifer/ pioneer- dominated	<i>Quercus</i> - dominated	p value	Conifer/ pioneer- dominated	<i>Quercus</i> - dominated	p value
<i>Trientalis</i>			<i>Trientalis</i>		
<i>europaea</i>		0.012	<i>europaea</i>		0.015
<i>Vaccinium</i>			<i>Vaccinium</i>		
<i>myrtillus</i>		0.003	<i>myrtillus</i>		0.050
<i>Pteridium</i>			<i>Pteridium</i>		
<i>aquilinum</i>		0.018	<i>aquilinum</i>		0.058
<i>Deschampsia</i>			<i>Mycelis</i>		
<i>flexuosa</i>		0.071	<i>muralis</i>		0.222
<i>Festuca</i>			<i>Oxalis</i>		
<i>ovina</i>		0.083	<i>acetosella</i>		0.039
<i>Luzula pilosa</i>		0.016	<i>Rubus idaea</i>		0.027
<i>Melampyrum</i>				<i>Aegopodium</i>	
<i>nemorosum</i>		0.028		<i>podagraria</i>	0.021
<i>Vaccinium</i>				<i>Paris</i>	
<i>vitis-idaea</i>		0.076		<i>quadrifolia</i>	0.461
<i>Veronica</i>					
<i>chamaedrys</i>		0.031			
	<i>Aegopodium</i>				
	<i>podagraria</i>	0.002			
	<i>Paris</i>				
	<i>quadrifolia</i>	0.012			
	<i>Geum</i>				
	<i>urbanum</i>	0.020			
	<i>Convallaria</i>				
	<i>majalis</i>	0.027			
	<i>Pulmonaria</i>				
	<i>obscura</i>	0.033			
	<i>Melampyrum</i>				
	<i>pratense</i>	0.040			

Table 8. Significant differences between 1930 and 2011 in relative frequency (paired permutation test) and overall occurrence of plant species (test for equality of proportions) in conifer/pioneer tree species and *Quercus*-dominated plots on Moricsala Island.

		Relative frequency		Occurrence in plots	
Species		increase/ decrease	p	increase/ decrease	p
Conifer/pi oneer- dominated	<i>Circae lutetiana</i>	+	0.055	+	0.012
	<i>Galium odoratum</i>			+	0.018
	<i>Veronica officinalis</i>		0.048	+	0.035
	<i>Oxalis acetosella</i>	+	0.036		
	<i>Veronica chamaedrys</i>	-	0.030		
	<i>Stellaria holostea</i>	-	0.013		
	<i>Luzula pilosa</i>	-	0.024		
	<i>Fragaria vesca</i>	-	0.019		
	<i>Melampyrum nemorosum</i>	-	0.034		
	<i>Vaccinium vitis-idaea</i>	-	0.079	-	0.013
	<i>Vaccinium myrtillus</i>	-	0.043		
<i>Quercus</i> - dominated	<i>Circaea lutetiana</i>	+	0.037	+	0.010
	<i>Dryopteris carthusiana</i>			+	0.044
	<i>Geum urbanum</i>	-	0.025	-	0.010
	<i>Polygonatum multiflorum</i>	-	0.041		
	<i>Athyrium felix-femina</i>			-	0.044
	<i>Pulmonaria obscura</i>		0.044	-	0.031

Figures

Fig. 1. Location of study area within (a) Europe and (b) Latvia is shown. (c) Location of 20 sample plots on Moricsala Island is shown, using WGS 84 coordinates.

Fig. 2. Cluster analysis (Ward's method with correlation distance measure) of forest plots. Plot numbers are given as in Table 1. Ovals denote conifer/pioneer species-dominated plots; square denotes *Quercus*-dominated group plots

Fig. 3. NMS ordination of vegetation matrix. A. Vectors indicate direction of change in vegetation composition in plots on Moricsala Island between the years of study (1930 and 2011). B. Open circles — conifer/pioneer-dominated group plots; black circles — *Quercus*-dominated group plots; abbreviations; Ellenberg values for pH and N; life forms chamaephytes (cham), therophytes (ther), geophyte and hemiphanerophyte (geo/hemi), and hemiphanerophyte (hemiphan); habitat types open and forest/grassland (for/grass); myrmecochoorous (Myrm) seed dispersal; and depth of the O horizon (O_hor).

Draft

Supplementary material. Description of methods used for determining coordinates of plots from historical maps.

Historical map drafts and field manuscripts associated with the 1932 work were obtained from the family archives of J.V. Grošinskis (J.W.Grods). These 1932 paper maps were completed to 1:8400 scale with a common reference grid in metres with attached scale bars; these were considered to be drafts of the final map, which has been lost. The key 1932 map of focus, labelled “Moricsalas mežaudžu plāns” (Forest type map of Moricsala), not only delineated ecological polygons, but contained other map entities of plots, soil pits, soil borings (some of which were associated with vegetation plots), earlier cadastral survey lines and several annotated features and notes. This mapping was scanned at a 1:1 resolution set at 300 dpi into Geographic Information System ArcGIS 10.0 with Spatial Analyst 10.0 as a raster image where map entities were digitized. Two additional 1932 maps played a role in rectification of the “Moricsalas mežaudžu plāns” into the 2011 digital base. A base grid map was an earlier draft that illustrated also transects in a north to south azimuth not present on the final draft, along with a base gridded map. In the dissertation (Grošinskis 1932) it is noted that these maps were obtained from R. Meyers who surveyed the island in the period 1912-1915, and that they were used as the basis for construction of other maps; we presumed that the base grid map was a copy of this or the original. Transects and grid lines were determined to be every 100 meters, and the majority of 134 soil borings were aligned on these. According to descriptions in Kupffers (1931) and Grošinskis (1932), mapping of the edges of ecological polygons (including forest stands) stands, established vegetation plots, and soil pits and borings had been made by measuring distances and angles from transects denoted on Meyer’s map, and were marked in the field and located on the Grošinskis map. These survey markers were

not located in the present study and thus there were no exact reference points existing today that could be used for rectification. For georeferencing, an east-west meridian across the island anchored at the island's north-west point was established on the “Moricsalas mežaudžu plāns” map. As the key maps had referenced scales, using the north-west point, the historical map was used to measure the distance from the established meridian point to the first North-South transect line. This transect line was then imposed onto the meridian overlaid onto the recent imagery georeferenced to the LKS92 coordinate system, also a metric based coordinate system. The soil borings and distinguishable ecological features (43 control points) on the present day Moricsala ortho-image were then used to rectify the historical mapping using many iterations to optimize correspondence between the two maps based on a normalized cross correlation matrix, similar to processes outlined by Benavides and Koster (2006) and El-Hussainy et al (2011). Truthing was conducted by measuring the scale present on the transformed historical map and ensuring that transect lines ran North to South. The Pearson's correlation coefficient between matrices of inter-distances of control points on the historical and new image was 0.999 ($p < 0.001$, Mantel test), which confirmed validity of the used method.