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Imprints of management history on hemiboreal forest ecosystems in the Baltic States

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Citation: Jõgiste, K., L. E. Frelich, D. Laarmann, F. Vodde, E. Baders, J. Donis, A. Jansons, A. Kangur, H. Korjus, K. Köster, J. Kusmin, T. Kuuluvainen, V. Marozas, M. Metslaid, S. Metslaid, O. Polyachenko, A. Poska, S. Rebane, and J. A. Stanturf. 2018. Imprints of management history on hemiboreal forest ecosystems in the Baltic States. Ecosphere 9(11):e02503. 10.1002/ecs2.2503

Abstract. In the Baltic States region, anthropogenic disturbances at different temporal and spatial scales mostly determine dynamics and development phases of forest ecosystems. We reviewed the state and condition of hemiboreal forests of the Baltic States region and analyzed species composition of recently established and permanent forest (PF). Agricultural deforestation and spontaneous or artificial conversion back to forest is a scenario leading to ecosystems designated as recent forest (RF, age up to two hundred years). Permanent forest (PF) was defined as areas with no records of agricultural activity during the last 200 yr, including mostly forests managed by traditional even-aged (clear-cut) silviculture and salvage after natural disturbances. We hypothesized that RF would have distinctive composition, with higher dominance by hardwoods (e.g., aspen and birch), compared to PF. Ordination revealed divergence in the RF stands; about half had the hypothesized composition distinct from PF, with a tight cluster of stands in the part of the ordination space with high hardwood dominance, while the remaining RF stands were scattered throughout the ordination space occupied by PF with highly variable species composition. Planting of conifers, variability in site quality, and variability in spatial proximity to PF with relatively natural ecosystem legacies likely explained the variable compositions of this latter group of RF. We positioned the observations of RF in a classic quantification of site type conditions (based on Estonian forest vegetation survey previously carried out by Lõhmus), which indicated that RF was more likely to occur on areas of higher soil fertility (in ordination space). Climatic and anthropogenic changes to RF create complex dynamic trends that are difficult to project into the future. Further research in tracing land use changes (using pollen analysis and documented evidence) should be utilized to refine the conceptual framework of ecosystem legacy and memory. Occurrence and frequency of deforestation and its characteristics as a novel disturbance regime are of particular interest.

Key words: disturbances; ecosystem legacy; hemiboreal forest zone; land use change; managed forest; manipulated legacy.

Received 4 October 2018; accepted 10 October 2018. Corresponding Editor: Debra P. C. Peters.

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Introduction

Forest ecosystems constitute a globally complex web of interactions and humans are directly or indirectly part of this system. In some areas, forests are directly linked to human livelihoods. Globalization and efforts to come up with ways to alleviate effects and mitigate climate change lead to discussion about ecosystem legacies of natural processes and contemporary management of natural resources, particularly forest vegetation. The concept of ecosystem legacies covers a wide array of relationships among components of the living world and has been proposed as one possible cornerstone of forest management systems (Johnstone et al. 2016, Jõgiste et al. 2017). Ecosystem legacies are biotic or abiotic material or information entities coming from the past. Forest ecosystems are dynamic in time, with temporal trends that integrate the effects of several types of natural and anthropogenic disturbances, which are in turn linked to highly variable editing and conditioning of legacies. Models have attempted to capture the basic and universal components of forest ecosystem regulation (Shugart 1984, Hari et al. 2017). However, modeling is challenged by two main issues: First, the functioning of human-dominated ecosystems that have not been shaped and structured by natural processes is incompletely understood, and second, changing climatic conditions create varied effects on altered and indigenous ecosystems. Therefore, a conceptualization of ecosystem dynamics that highlights changes in ecosystem legacy conditioning by legacy syndromes that result from natural or anthropogenic disturbance regimes could offer a solid basis for further quantification of structural dynamics. Conceptual tools derived from studies of natural and managed forests are needed to fathom the complex pattern of post-disturbance vegetation dynamics, especially from compound disturbances and cascading effects (White and Jentsch 2001, Seidl et al. 2011, Thom et al. 2018).

Ecosystems are affected by multiple, often different disturbances over time. Disturbances vary in their type, intensity, extent, and intervals between disturbances. Anthropogenic influence creates additional interacting patterns with natural disturbances (Frelich et al. 2018). Disturbances interact with the traits of individual species (e.g., shade tolerance, life span, drought tolerance, browse tolerance), so that a post-disturbance ecosystem is reset (to some degree), leading to a new dynamic interplay of different organism types. Ecosystem legacies that remain after a disturbance can affect the direction (trajectory) of the reset through interactions with species traits.

Natural vs. anthropogenic disturbances create different legacies with different longevity and/or strength, where longevity refers to the time that a legacy has an effect and strength to the level of an effect (Jõgiste et al. 2017). Natural disturbances work in sync with species traits; that is, material and information legacies that survive disturbance may lead to rapid recovery (high resilience), and material legacies created by disturbance such as deadwood are integrated into ecosystem function and resilience. In contrast, agricultural land use erases forest legacies, and the material and information legacies created by agriculture are hard to erase, leading to long recovery times. Therefore, changes from agricultural to forestry land use (and the reverse) reveal complex features of ecosystem dynamics in the context of management practice (Foster et al. 1998, Thompson et al. 2016).

A previous analysis of Baltic hemiboreal forests showed the existence of three legacy syndromes—patterns of legacy abundance and spatial patterns at multiple scales that are distinctively edited by disturbances that fall along a naturalness gradient. These are natural disturbance, traditional silviculture (including clearcuts and salvage after natural disturbance), and afforestation of abandoned agricultural land (Jõgiste et al. 2017). In the current analysis, we refine these to fit a recent forest (RF; with agricultural land use history) vs. PF cover scheme (silvicultural history), both rendering artificial legacies. Recent forest is defined as areas of agricultural deforestation followed by spontaneous or intentional conversion back to forest. Ecosystem dynamics of RF demonstrate strong artificial legacy effects of post-disturbance management on vegetation patterns and dynamics of carbon (C) sequestration. For example, the ground vegetation in forests growing on abandoned agricultural fields suggests more rapid C turnover compared to natural forest (Hari et al. 2017). In the frame of this study, PF is defined as the areas where no written records of agricultural activity exist (Verheyen et al. 2003 refer to PF as ancient forest), including mostly traditional even-aged silviculture using clear-cuts and also a small amount remaining of natural forest with marginal human impacts, at least within the short historical perspective of the last two centuries.

Although most PF has been affected by forest management, we nevertheless expect that artificial legacy effects on forest composition will be relatively small (low strength) and that differences will exist in tree species stand composition when comparing them to RF. We assume that forest sites that have been in agricultural use were situated on more fertile soils in the first place, and they demonstrate a continued higher nutrient turnover and biomass production, which should be reflected in forest inventory and permanent plot observations. Furthermore, RFs fall into certain ecological categories, including dominance by hardwood species rather than conifers (Lõhmus 1973). This scheme applies to the hemiboreal forests of Estonia, Latvia, and the northern part of Lithuania as these forests share common species and recent land use history.

The objective was to verify the existence of an artificial legacy signal in the forest inventory database: both post-agriculture afforestation in the case of RF and silvicultural legacy in PF (pre-commercial thinning, timber harvesting and salvage). Therefore, we hypothesized that artificial legacies of past human impacts (of relatively short length or time span, up to 200 yr) are of sufficient strength that they can be detected and distinguished in recent and PF using ordination techniques. More specifically, we hypothesized that areas of former agricultural lands will show hardwood dominance.

Materials and Methods

Ecological conditions of Baltic forests

Forests of the Baltic States belong to the hemiboreal forest zone (Ahti et al. 1968, Hytteborn et al. 2005). The climate is predominantly influenced by continental air masses except for a strip with maritime influence near the Baltic Sea. The regional average temperatures range from 20°C in July to –6°C in February, and mean annual precipitation varies from 500 to 930 mm. The Baltic States are part of the East-European Plain, an area characterized by low relief with small absolute and relative elevations. The highest point is the hill Suur Munamägi (318 m) in southeastern Estonia (Raukas 2009).

The Baltic States are unique in Europe, having had large areas of their landscapes remaining under forest cover for a long time. Nearly half of Estonia and Latvia are covered by forest, while approximately one-third of Lithuania is forested (Jõgiste et al. 2016, Fig. 1). The main tree species in the Baltic region are Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* [L.] Karst), birches (*Betula pendula* Roth and *B. pubescens* Ehrh. and hybrids), alders (*Alnus incana* [L.] Moench and *Alnus glutinosa* [L.] Gaertn.), common aspen (*Populus tremula* L.), pedunculate oak (*Quercus robur* L.), European ash (*Fraxinus excelsior* L.),

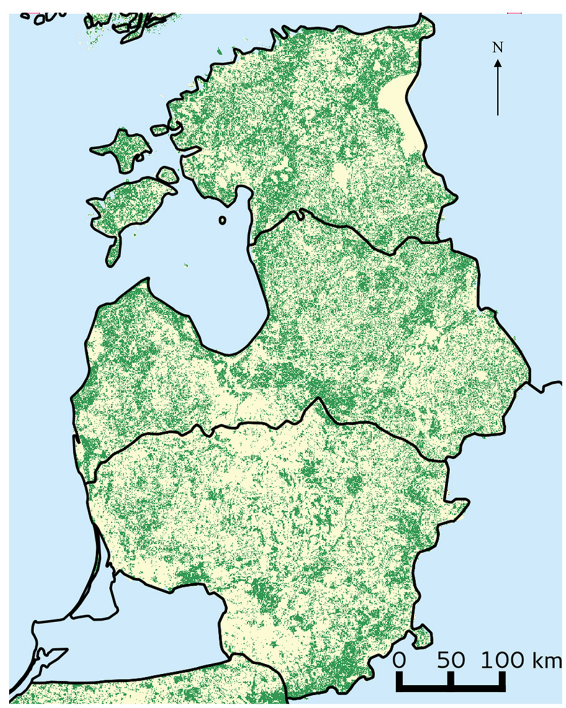

Fig. 1. Forest vegetation cover of the Baltic States as of 2006 (Estonia, Latvia, Lithuania, from north to south).

and small-leaved linden (*Tilia cordata* Mill.). Oak is more frequent in Lithuania. Mixtures of conifers and broad-leaved tree species are frequent.

The Baltic States were covered with a continental ice sheet during the last glaciation 21,000–18,000 calibrated ^{14}C years before present (YBP). The ice retreated from the region between 18,000 (southern Lithuania) and 13,000 (northern Estonia) YBP (Rinterknecht et al. 2006). Quaternary glacial deposits (moraines, glaciolacustrine, and glaciofluvial sediments) with varying thickness cover the bedrock (Raukas 2009). However, the presence of bedrock and its basic properties determine soil characteristics in many cases (Fig. 2). The first tree species migrated to the area shortly after retreat of the ice. Pollen and macrofossils record the presence of typical boreal trees (*Betula*, *Pinus*, and *Picea*) in the Baltic States dating back to 14,000–13,500 YBP (Heikkilä et al. 2009, Veski et al. 2012). During the next millennia, boreal woodlands (dominated by *Betula* and *Pinus)* were gradually replaced by a temperate broad-leaved forest (dominated by *Quercus*, *Tilia,* and *Ulmus*), due to further warming of the climate. While relatively high fire frequencies have been recorded for post-glacial pine-dominated forests, the amount of natural disturbances was low in temperate forests. The general climatic cooling during the last 6000 yr has increased the importance of boreal components (mainly *Picea*) and diminished the role of temperate broad-leaved taxa, especially in the northern part of the region. As is typical for a hemiboreal forest (sometimes referred as boreo-nemoral forest), the potential natural woodland cover of the region is over 90%, and the open areas are commonly associated with hydrologically challenging conditions (too wet or dry). Anthropogenic deforestation, mainly small-scale episodes in the surroundings of hunter-gatherer settlement sites, has been recorded since 11,000 YBP (Poska and Veski 1999, Stančikaitė et al. 2004). Cereal farming was introduced to the area ca 6000 YBP, but the transition to an agrarian production-based society took place about two millennia later, during the Bronze Age (3800–2500 YBP; Poska et al. 2004). The widespread usage of extensive agrarian techniques (e.g., slash-and-burn agriculture) led to a considerable increase in the proportion of open land and a rise in deforestation frequency. In sandy areas, such long-term land use caused soil impoverishment and acidification, and led to heathland development (Savukynienė et al. 2003). An abrupt intensification of farming and associated deforestation is observable in pollen records since ca 1000 YBP, and soon reached values similar to the contemporary landscape. The maximal anthropogenic deforestation of the region was reached 200–100 YBP, when the forest area was half that of today, and this happened somewhat later compared to the rest of Europe (Poska et al. 2014).

As with many forested areas in Europe, natural and anthropogenic disturbances in this region are mixed over time and space. Successional patterns include processes after first deforestation and later abandonment of arable land. This makes it difficult to describe natural forest

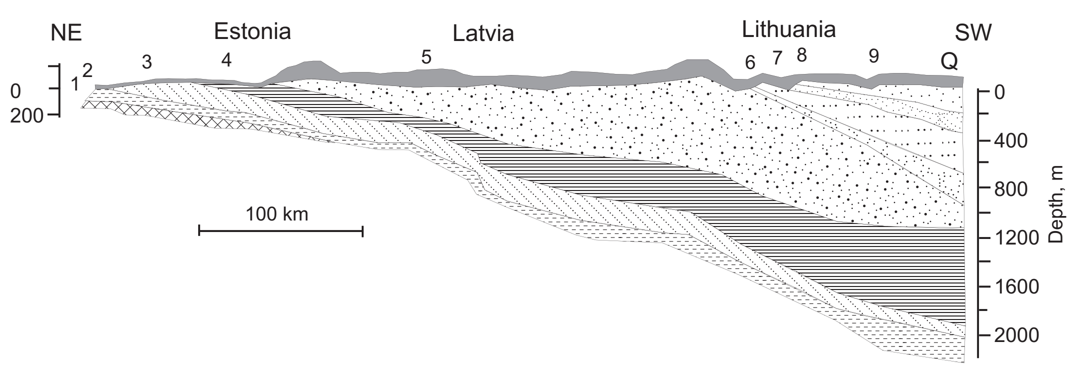

Fig. 2. Stratigraphic cross section of Baltic States from North to South: simplified geological profile. Abbreviations are Q, Quaternary; 1, Ediacaran; 2, Cambrian; 3, Ordovician; 4, Silurian; 5, Devonian; 6, Permian; 7, Triassic; 8, Jurassic; 9, Cretaceous.

development (Laarmann et al. 2009). Natural disturbance regimes in forest ecosystems can be distinguished based on severity (Kuuluvainen 2009): Stand-replacing and gap-forming regimes create the extremes of the gradient, with intermediate (partial) disturbances constituting the varying conditions in between. Despite anthropogenic influences on disturbance regimes in the Baltic States, these two extremes in natural disturbance regimes can be found. High severity disturbance is linked mostly to fire on poor soils close to the Baltic Sea (Parro et al. 2015, Köster et al. 2016). The spatial pattern of fires (historical incidence, frequency, intensity) can be complex, and good evidence can be found only from the sedimentary record in larger lakes (Koff et al. 2000). For example, during the Holocene the average fire return interval in the Baltic region was ~280 yr and there have been shifts in fire regime due to climate-induced changes in vegetation (Feurdean et al. 2017). Lowland forests and forests on fertile moraine or rendzina soils have a gap phase disturbance regime, driven by dynamics of wind, pathogens, and insects (Köster et al. 2009, Adamson et al. 2015, Vodde et al. 2015).

The intensity of land management (both agricultural and forestry use) has varied greatly in recent history; more intensive periods of deforestation for agriculture from ~1700 to 1900 AD (Brūmelis et al. 2005, Tērauds et al. 2011) and a reversed course with a return of forest cover during the 20th century (Fig. 3; Lazdinis et al. 2009, Jõgiste et al. 2016, Poska et al. 2018). Historically, Baltic forestry is juxtaposed between two contrasting approaches to forest management: German influence that favored artificial regeneration and Russian reliance on natural regeneration after timber harvest (Angelstam et al. 1995, Carlsson and Lazdinis 2004, Liira and Kohv 2010). The impact manifests itself as an ecotone of management gradient: the transition from intensive management in the west to a natural regeneration pattern in taiga forest in the east. In commercial forestry of the Baltics during the twentieth century, most attention was given to controlling stand composition in favor of conifers, primarily Scots pine on sandy soils and Norway spruce on more fertile soils. In artificial regeneration, seedlings of these species have mostly been planted, but direct seeding (mainly for Scots pine) has been used as well. Non-native tree species (e.g., *Larix* sp.) have been used occasionally (Sander and Meikar 2004). Areas of changed land use (former farmland and mining areas) with the first generation of woody vegetation represent novel ecosystems where the dynamics depend on management decisions (Laarmann et al. 2015, Jõgiste et al. 2016).

Remnants of forest with minimal signs of management or with natural conditions are scarce. Most areas have been logged and silvicultural techniques were applied to improve stand productivity and vitality. In the Baltic States, clearcuts are usually <5 ha in size and regeneration has often been natural. Harvest rotation periods are shorter (e.g., *Picea abies* 80–100 yr, *Betula* sp. 70–80 yr in Estonia) than return intervals for natural disturbances as well as the average lifespan of the main tree species. Nevertheless, conventionally managed forests in many aspects resemble a natural ecosystem, although structural features such as deadwood presence can be drastically lower (Köster et al. 2005). In Estonia, 55,000 ha (2.3% of the total forest cover) is estimated to be near-natural forest where no land use change is assumed to have taken place and ecosystems are shaped by natural disturbances and occasional forest management interventions (Anonymous 2014). Changed vegetation is typical for coastal areas (pastures covered with *Juniperus communis* L.) and inland woody meadows (Poska et al. 2004). Over time, many of these communities will become woodlands (Laasimer 1981, Pärtel et al. 1999).

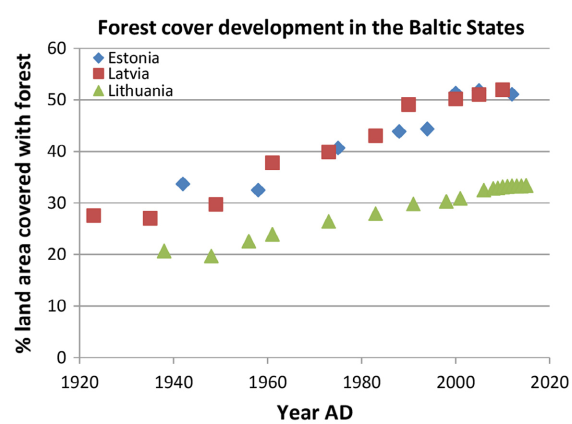

Fig. 3. Forest cover change over 100 yr in the Baltic States (Anonymous 2017).

Database of growth and yield studies: Ordination of forest site type

Data from the Estonian Network of Forest Research Plots (ENFRP; Kiviste et al. 2015) were used to compare sites of different land use history: RF with records of land use change vs. PF. We assume that the plots also represent Latvian and Lithuanian hemiboreal forest because of their shared forest management history. We used 534 plots from the most recent survey as the dataset for analysis (planted forests are also included). The plots marked as RF (54 plots) had records of change in land use in the dataset. The tree species proportion (relative basal area, RBA) of the stand, the generalized share of deciduous trees (DEC), stand age (A), site index, and total number of tree species in the canopy were calculated. If single taxa represented <2%, we pooled these taxa into a single category of others.

We used nonmetric multidimensional scaling (NMDS) to depict similarities and differences in species composition and generalized share of deciduous trees. We used power transformation to standardize the plot-level RBA within all plots. We used the Sørensen (Bray-Curtis) distance measure. Nonmetric multidimensional scaling ordination revealed two axes, the first axis described 85% of the data variation and the second 11%. The stress plot revealed a good fit (final stress factor was 9.9) of the species component in the analysis. All analyses were conducted in PC-ORD version 7.02. The significance of grouping factors (recent or PF) was tested using Multiple Response Permutation Procedure (MRPP). Multiple Response Permutation Procedure is a nonparametric procedure that tests the hypothesis of no difference in compositional similarity among two or more groups (McCune and Mefford 1999).

Plots of the RF from the ENFRP database were screened against the Estonian Forest Site Type classification that is based on an ordination of site conditions (Lõhmus 1973, 2004). For ENFRP plots, the ground vegetation data were not available. However, for each plot the database contains a record of site type as was determined by the surveyor at the time of plot establishment (Table 1). We used the ordination scheme of ground vegetation created by Lõhmus (1973, 1974, 2004) as an approximation of Baltic forest conditions. The typology of forest site type classifications of Latvia (Bušs 1997) and Lithuania (Karazija 2008) resembles that presented in

Table 1. The distribution of forest site types in the dataset of Estonian Network of Forest Research Plots (ENFRP; number of plots) and total forest land of Estonia (%).

Forest site type	Number of plots in ENFRP: Permanent forest	Recent forest	Sum	Representation of forest site type in Estonian forest area† %
Filipendula	15	1	16	9.4
Oxalis	65	35	100	18.0
Oxalis-Myrtillus	42	4	46	9.7
Oxalis-Rhodococcum	42	2	44	2.1
Galamagrostis-alvar	21	1	22	2.2
Polytrichum-Myrtillus	6	—	6	1.5
Calluna	10	—	10	0.1
Polytrichum	1	—	1	0.2
Arctostaphylos-alvar	1	—	1	0.1
Myrtillus	56	—	56	6.1
Aegopodium	24	6	30	10.0
Rhodococcum	109	—	109	3.8
Hepatica	43	3	46	9.7
Cladonia	33	1	34	0.1
Vaccinium	1	—	1	0.2
Transitional bog	1	—	1	2.3
Carex-Filipendula	4	—	4	5.1
Carex	6	1	7	0.7
Other	—	—	—	18.7
Total	480	54	534	100.0

† Anonymous (2017). Yearbook Forest 2016.

Lõhmus (2004). The data on forest site types from Lõhmus' (1973) original work were also used for an ordination by Kusmin and Jõgiste (2006). According to Lõhmus (1973), the *x*-axis and z-axis can be interpreted as soil water table and soil acidity, respectively (Fig. 4). The *y*-axis did not clearly correspond to any soil characteristic. The humus composition (C/N ratio) and root nutrition were suggested as possible explanations of the *y*-axis (Lõhmus 1973).

Results

Recent forest plots had two distribution patterns in the NMDS ordination. About 50% of the plots were scattered throughout the ordination space, mirroring the distribution of PF plots. However, the remaining 50% had unique species composition and were tightly clustered at the left side of the ordination and clearly dominated by hardwoods as indicated by the ordination vectors (Fig. 5). Vectors for tree species in the genera *Salix*, *Alnus*, and *Betula*, which are pioneer species known to spontaneously regenerate on abandoned farmland, pointed toward this cluster. An additional hardwood species not usually associated with recolonization of abandoned farmland, *Tilia cordata*, was also represented within the natural afforestation vectors. A MRPP test revealed significant differences between PF and RF groups. The factor stand age (A) was slightly negatively correlated to this cluster.

Part of the afforested agricultural lands contains sites where coniferous tree species were planted. This reflects a situation where artificial regeneration was directed toward restoration of natural conditions (Jõgiste et al. 2017).

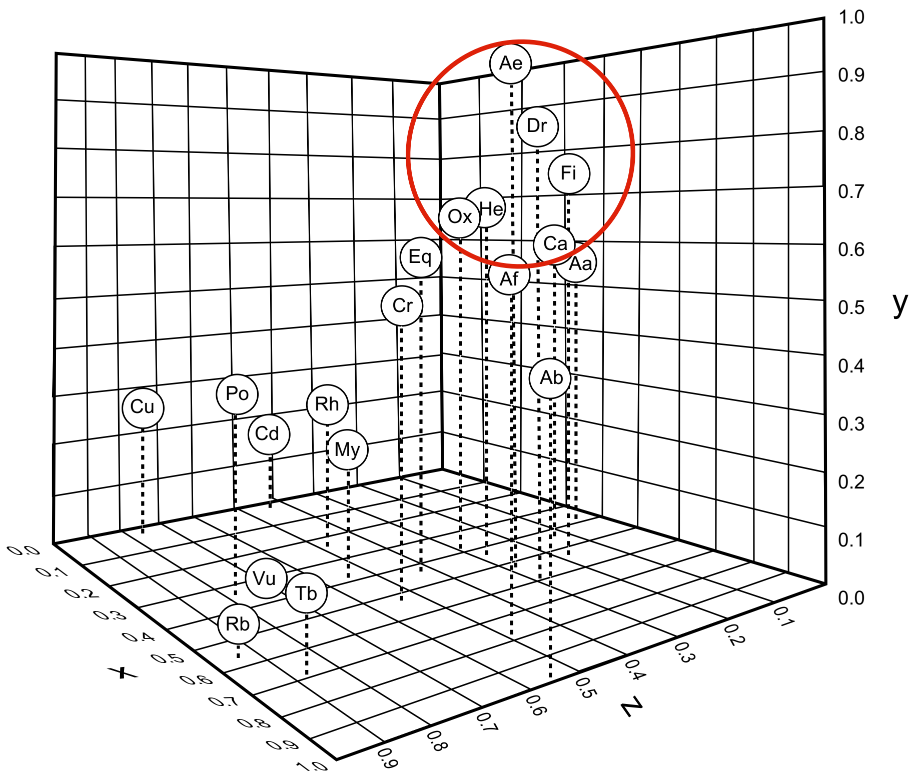

Fig. 4. Three-dimensional ordination of forest vegetation in Estonia by Lõhmus (1973). Abbreviations are Aa, *Arcostaphylos*-alvar; Ae, *Aegopodium*; Ab, Alder-birch (eutrophic-mesotrophic) swamp; Af, Alder (eutrophic) fen; Ca, *Calamagrostis*-alvar; C, *Cladonia*; Cr, *Carex*; Cu, *Calluna*; Dr, *Dryopteris*; Eq, *Equisetum*; Fi, *Filipendula*; He, *Hepatica*; My, *Myrtillus*; Ox, *Oxalis*; Po, *Polytrichum*; Rb, Raised (oligotrophic) bog; Rh, *Rhodococcum*; Tb, Transitional (mesotrophic) bog; Vu, *Vaccinium uliginosum*. The red circle indicates the site types with higher representation of recent forest plots.

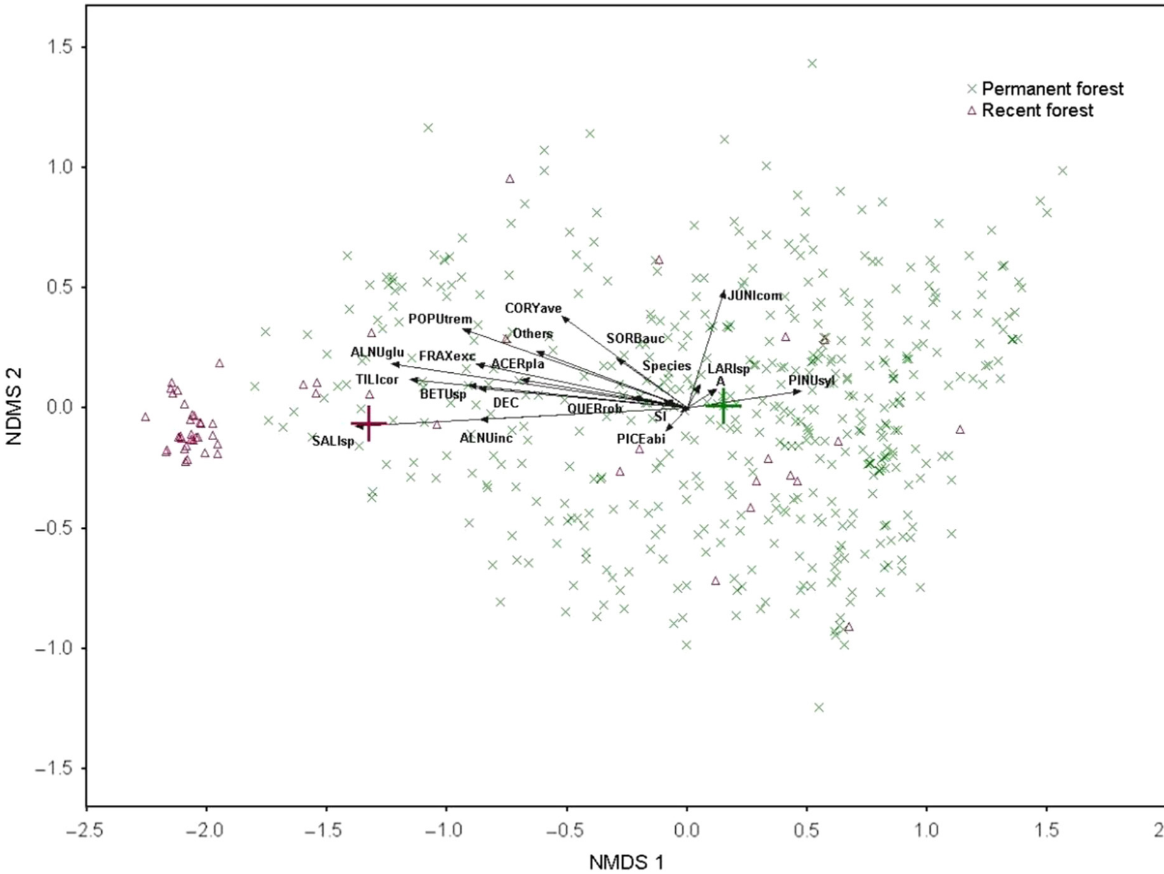

Fig. 5. Nonmetric multidimensional scaling (NMDS) ordination of overstory tree species on 534 Estonian Forest Research Network plots in the categories permanent forest (PF, crosses) and recent forest (RF, triangles), the central points of each cloud represented by a plus (+) sign. Vectors represent tree species proportions (abbreviations listed below), site index, deciduous proportion (DEC), stand age (A), and number of species (Species) with NDMS analysis. Abbreviations are ACERpla, *Acer platanoides*; ALNUglu, *Alnus glutinosa*; ALNUinc, *Alnus incana;* CORYave, *Corylus avellane*; FRAXexc, *Fraxinus excelsior*; JUNIcom, *Juniperus communis*; PICEabi, *Picea abies*; PINUsyl, *Pinus sylvestris;* POPUtrem, *Populus tremula*; QURErob, *Quercus robur*; SORBauc, *Sorbus aucuparia*; TILIcor, *Tilia cordata*; BETUsp, *Betula* sp.; LARIsp, *Larix* sp.; SALIsp., *Salix* sp.

The RF plots appear to have a higher density in the most fertile site types in the ordination space based on ground-layer vegetation (Lõhmus 1973): the *Aegopodium*, *Oxalis*, *Filipendula*, and *Hepatica* site types (Fig. 6). Note, however, that no conclusions can be drawn about the fertile *Dryopteris* site type, since no plots were located in that type, as it is relatively rare in Estonia. For comparison, the area of Lõhmus' original 1973 ordination where the recent plots occur is circled in red (Fig. 4). The highly represented *Aegopodium* site type (most productive) in the database provides evidence of agricultural use in the past (Tomson et al. 2018).

Discussion

The hypothesis that artificial legacies of RFs are of sufficient strength to be apparent in forest inventory data analyzed via ordination is supported by the distinct composition of a cluster of RF sites (Fig. 5). Ordination of species composition can reveal human impacts (Paulson et al. 2016). The management influence (or naturalness) is one possible ordination factor mentioned by several authors (Curtis 1959, Frey 1973, Lõhmus 1973, Cottam et al. 1978, Paal 1997, Šaudytė et al. 2005, Leito 2008). The distinct

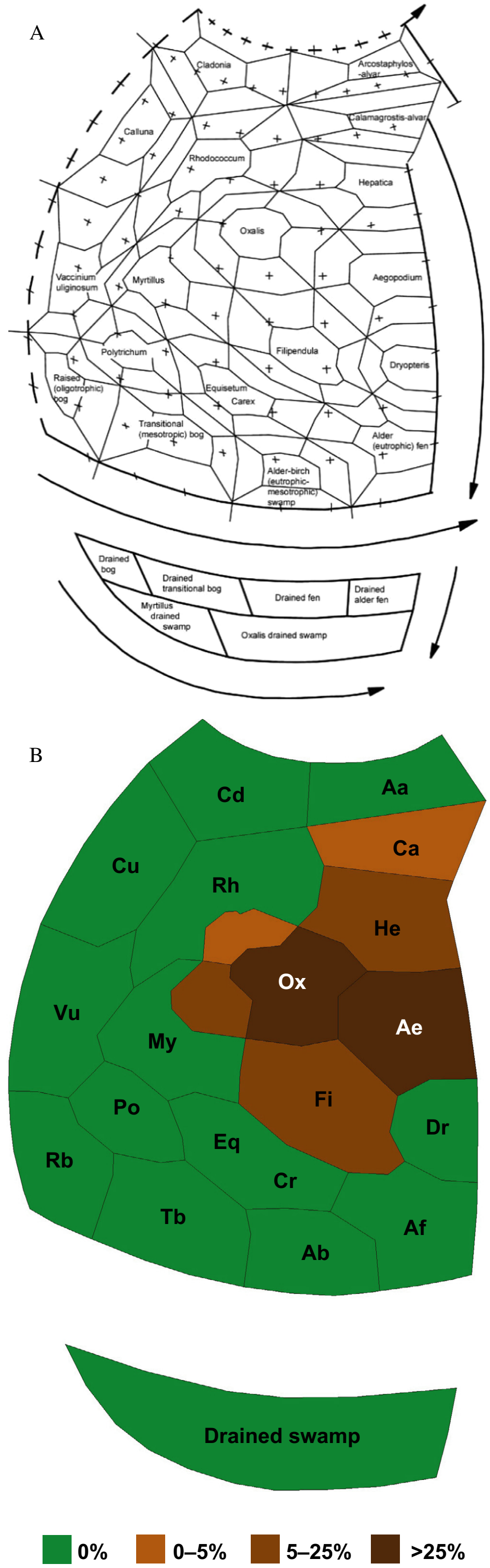

Fig. 6. Polar ordination of forest site types according to two dominant axes of floristic divergence: soil water

(Fig. 6. *Continued*)
table (vertical axis arrow) and acidity (horizontal axis arrow). (A) Forest vegetation arrangement as a result of polar ordination transformed onto two axes of floristic divergence (Lõhmus 1973, 2004). The highest quality site types occur on the middle right side with high pH and mesic hydric conditions. (B) Recent forest proportion: green = 0%, light-brown = 0–5%, medium brown = 5–25%, dark-brown >25%. Abbreviations of forest site types as in Figure 4.

cluster of RF plots was associated with the expected early-successional pioneer tree species with long-distance seed dispersal and ability to grow rapidly in full sunlight, including *Populus*, *Betula*, and *Alnus* species. The negative correlation with stand age (A) also corresponds with this result. Surprisingly, *Tilia cordata* was also associated with spontaneous regeneration in farmlands. Although this species is not commonly thought to be early successional, it does have moderately long-distance seed dispersal via wind, and ability to germinate and establish in full sunlight; although it can tolerate poor sites, it grows most rapidly on relatively rich, high pH sites like those in the RF cluster (Fig. 5).

Equally as striking as the cluster of RF with distinctive broad-leaved composition was the divergence in composition of RFs—about half of the RF plots exhibit the same distribution of species compositions as the PF matrix within which they are embedded. This indicated that factors other than pioneer species status and seed characteristics were responsible for composition of some RF plots. For example, the appearance of conifer-dominated stands was evident in the ordination space between vectors of coniferous species (*Pinus sylvestris* and *Picea abies*) on Fig. 5, possibly due to management (planting *Picea abies*) after cessation of agricultural land use. Because the Baltic States have influences from both the central European (planted regeneration) and Russian (natural regeneration) silvicultural practices, it is not surprising that some locations were planted with shade-tolerant, late-successional conifers. This type of human-made borealization has also occurred in other parts of the European hemiboreal zone (Lindbladh et al. 2013). In these circumstances, the artificial legacy (Jõgiste et al. 2017) is comprised of forest structural features shaped by silviculture (pre-commercial thinning, planting). In addition, some sites cleared for agriculture probably were small in area and close to the surrounding PF. Alternatively, some of these locations were on poor sites that were abandoned after a short time in agriculture (shifting cultivation), allowing rapid return to conditions similar to the PF.

Stands under PF cover in the Baltic States have widely varying composition (Figs. 4–6), which arises from variability in site quality, but also from a hybrid disturbance regime comprising natural and human disturbances. These forests were influenced by management, including planting and other legacy manipulations (e.g., Kangur et al. 2005, Dzerina et al. 2016). Both anthropogenic and natural disturbances create temporal changes in forest vegetation composition (Ilisson et al. 2006, Vodde et al. 2011). Advance regeneration provides a component cohort of shade-tolerant species (Metslaid et al. 2005*a*, *b*, Szwagrzyk et al. 2018), which has also been mentioned in other boreal or hemiboreal regions (Valkonen et al. 1998, Girard et al. 2014). The range of disturbance severities for these hybrid disturbance regimes also determines the recovery and resilience mechanisms of the forest ecosystem (Nagel and Diaci 2006, Kuuluvainen 2009, Swanson et al. 2011, Sass et al. 2018).

Partial damage has been regarded as a successional mechanism creating a precocious stand structure (Donato et al. 2012), which is also common in the Baltic States and helps to create and maintain the widely varying stand composition seen in Fig. 5. Furthermore, salvage logging after natural disturbance (although not part of this study) is a removal of material legacy that occurs in the managed forest matrix (Jõgiste et al. 2017). In the context of recent and PFs, salvage of disturbed areas serves as an equalizing factor because it is applicable and allowed in most areas: Salvage creates very similar post-disturbance forests in either recent or PFs. Still, the difference between salvage and clearfelling at forest management rotations creates a variety of legacies on the naturalness continuum for disturbances in the Baltic States. Further, partial salvage is also possible and may mimic intermediate disturbance intensity or selective cutting methods. Salvage or clearfelling create complex overlaps in natural and human disturbance: Harvest at any time before a natural disturbance occurs can have a pre-emptive effect and save commercial timber, whereas salvage is an action feasible only after disturbance (Frelich et al. 2018). The overall effect of the hybrid human and natural disturbance regime is that it maintains a mosaic of diverse stand development and successional stages across the landscape for PF and some RFs. The cluster of RF plots with distinct composition is an exception and, due to its unique artificial legacy, does not seem to fit within this dynamic.

A crucial question is: What is the length of this artificial legacy, or at least how long can it be detected? Masing (1979) defines forest site types according to their permanent nature. Different schools of forest site type ordination have tried to include dynamic aspects (shorter or longer historical influences) in defining the PF (Karazija 1989, Mahatadze 1989, Manko 1989). Laasimer (1981) suggested that convergence back to a situation similar to our PF occurred in a time span of two forest generations (ca 100 yr), but it depends on the tree species involved, duration of the previous artificial legacy and other factors. Disturbance return cycles in nearby Russian forests similar to Baltic forests are about 150 yr (Manko 1989). Tomson et al. (2018) report only minor differences of ancient (>200 yr) slash-and-burn sites in Estonia, when compared to the natural disturbance cycle: They are mostly similar to PF.

The antecedent conditions transmitted via legacies (species and structures preserved from before previous events) define the concept of ecological memory (Ogle et al. 2015, Johnstone et al. 2016) that we have broadened in the concept of ecosystem memory to include land use and management legacies (Jõgiste et al. 2017). Although pre-disturbance stand conditions can determine ecosystem reactions to disturbances (Kosugi et al. 2016), RF and PF may differ in their response to disturbance (Lindbladh et al. 2013, Gardiner et al. 2016, Thom et al. 2018). Some studies have found that artificial legacies such as those found here can last several centuries (Foster et al. 2003), essentially becoming novel ecosystems that cannot go back to their original condition (Stanturf 2015). The idiosyncratic nature of forests generated and magnified by human intervention sets the scene for non-equilibrium conditions (Mori 2011) and novel ecosystems. Multiple changes in the environment, including climate change, fluctuating numbers of invasive species and large, browsing ungulates add to the contingency of ecosystem development, resulting in difficulties for projecting future forest conditions, or they could also lead to maintenance of a novel ecosystem (Frelich and Reich 2010, Frelich et al. 2012, Hall 2018, Stanturf et al. 2018). The range of physical and chemical variables of soils indicating high fertility attracted the types of land use that led to the RFs with artificial legacies, which may also allow multiple alternative states and the possible emergence of novel ecosystems.

Conclusions

The present vegetation carries some distinct influences from the past (Rackham 1980, Verheyen et al. 2003). Our aim was to gain deeper understanding of the effects of disturbances by investigating basic stand variables. We found evidence of a highly manipulated artificial legacy of hardwood forests on former agricultural sites —the distinct cluster of RF points in the ordination space—which could develop back to typical hemiboreal mixtures with conifers, or possibly lead to novel ecosystems.

The forest can be managed without loss of forest vegetation, even when human disturbance is of a stand-replacing nature, such as clear-cutting. However, disruption of forest cover by land use change introduces several structural and functional legacy components causing uncertainty when projecting further changes. The tendency of hardwood dominance in RF has different causes; life history traits of pioneer species are seemingly most important, but initial absence of competing conifers (possibly entering at later successional phases) can also be regarded as an artificial legacy.

Legacy manipulation causes ecosystems to follow trajectories that may be hard to predict without knowledge of site history, resulting in non-equilibrium dynamics and possible emergence of novel ecosystems. Management of legacies drives the process if we practice silviculture, or carry out conservation planning or restoration measures (De Grandpre et al. 2018). Natural resource planning can be substantially guided by ecosystem legacy management unless disturbances become so severe that legacy strength is overridden.

A warming climate may create such conditions whereby existing legacies are largely irrelevant. Increasing dominance by temperate hardwoods in the hemiboreal zone may be occurring in the Baltic States. This change may require a shift in forestry management doctrines toward more artificial regeneration in order to maintain the dominant hemiboreal species. Alternatively, the changed nature of the managed forest may be accepted, requiring new management strategies. Under either future scenario, ecosystem legacies will continue to affect the trajectory of post-disturbance recovery and legacy management will be an option for managers to direct the recovery. Therefore, we recommend continued efforts using potential techniques (pollen analysis, ^{14}C-dating, historical documentation) to reveal the links between past land use and current forest ecosystem structures and function.

Acknowledgments

We are most grateful to Barbara Scott Murdock and Gordon Murdock for comments on an early version of the manuscript. Comments by Rupert Seidl have substantially contributed to the development of ideas presented here. Piret Trei did a substantial part of the editing. Mait Lang gave help with the forest map and Tiit Hang advised on the figure representing the geological profile. The manuscript benefitted significantly from the profound comments of two anonymous reviewers. This study was supported by a grant from the Estonian Environmental Investment Centre and by the Estonian Ministry of Education and Research grants (SF0170014s08, institutional research funding IUT21-4 and IUT1-8), by the Estonian Research Council grant PUT (PUT715), and by the projects of the Estonian University of Life Sciences P180024MIME and P170022MIMB. Considerable amount of work was done in the frame of the FORDISMAN network, the activity of which was financed by SNS-EFINORD. The grant to Kalev Jõgiste from Metsämiesten Säätiö is acknowledged.

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