

## KERTU LÕHMUS

Colonisation ecology of forest-dwelling  
vascular plants and the conservation  
value of rural manor parks



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Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers that are referred to in the text by Roman numerals:

- I** Lõhmus K, Liira J. 2013. Old rural parks support higher biodiversity than forest remnants. *Basic and Applied Ecology* 14: 165–173.
- II** Liira J, Lõhmus K, Tuisk E. 2012. Old manor parks as potential habitats for forest flora in agricultural landscapes of Estonia. *Biological Conservation* 146: 144–154.
- III** Lõhmus K, Paal T, Liira J. 2014. Long-term colonization ecology of forest-dwelling species in a fragmented rural landscape – dispersal versus establishment. *Ecology and Evolution* 4: 3113–3126.

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Author's contribution to the publications:

- I** participated in designing the methodology, collecting and analysing the data and preparing the manuscript
- II** participated in collecting and analysing the data and preparing the manuscript
- III** participated in designing the methodology, collecting and analysing the data and preparing the manuscript

## I. INTRODUCTION

The European forest landscape has undergone drastic changes in area and habitat quality during recent centuries (Grigg 1987; Foley et al. 2005). As a result, only a small proportion of forest ecosystems has remained in a natural or near-natural state (Hermy & Verheyen 2007; Adermann 2009; Eriksson et al. 2010). During recent decades, forest cover has been increasing again, due mostly to afforestation of former agricultural land (EEA 2009; Hansen et al. 2013). Although these stands are of secondary origin and only partially resemble natural forests, they are expected to function as a habitat for forest species (Brunet & Von Oheimb 1998). However, these forests often contain a lower number of forest species than natural forests (Vellend 2003; Van Calster et al. 2008). The potential of secondary forest to harbour forest species successfully depends on habitat quality and landscape structure, as these two conditions determine the probability of species to colonise a newly formed habitat (Verheyen & Hermy 2001; Jacquemyn et al. 2003b; Brunet 2007).

Secondary forests can be colonised only by species that are already present in the local species pool of the landscape (Eriksson 1993; Pärtel et al. 1996). Species accumulate in continuously existing habitats, defined as historic or ancient habitats, which function as species sources (Zobel 1997; Wulf 2003; Pärtel et al. 2007). Colonisation success further depends on the probability of dispersal to an uncolonised habitat. The patch-corridor-matrix theory predicts that species dispersal is hampered by an unsuitable matrix habitat, while increased by corridors and stepping-stone patches (Opdam 1990; Forman 1995). Indeed, novel forest stands adjacent to old forests are colonized at a faster rate than isolated stands surrounded by agricultural fields (Brunet & Von Oheimb 1998; Brunet et al. 2012). Tree lines and hedgerows can facilitate forest species dispersal (Ehrlén & Eriksson 2000; Liira & Paal 2013). The role of linear woody habitats as dispersal corridors is, however, still debated, as their efficiency depends on regional history, corridor age and connectivity between habitats (Deckers et al. 2004; Roy & de Blois 2008; Wehling & Diekmann 2009b).

Habitat quality, or niche availability, is a significant factor determining the colonisation probability of forest species (Gauslaa et al. 2007; Brunet et al. 2011; Jonsell 2012; Vojta & Drhovská 2012). Forest inventories and monitoring schemes use a wide range of structural characteristics as a proxy of habitat quality (Lindenmayer et al. 2000; Liira et al. 2007; Scheller et al. 2008; Löhmus & Kraut 2010). A forest stand with a complex stand structure provides a large range of available niches, thereby increasing the chance for species colonisation (Norden & Appelqvist 2001; De Sanctis et al. 2010; Jamoneau et al. 2011). Old-growth forest stands, for example, contain a high diversity of microhabitats and can, therefore, harbour a high diversity of forest species (Brunet & Von Oheimb 1998; De Sanctis et al. 2010). Soil conditions are another commonly used indicator of habitat quality, because soil on former agricultural land is often

affected by agricultural activity (Brunet 1993; Honnay et al. 2002; Baeten et al. 2009a; Orczewska 2009). Habitat quality and stand history, therefore, need to be taken into account when assessing species colonisation success.

The colonisation probability of an uncolonised habitat is determined by the trait composition of dispersing species. For example, the low dispersal ability of forest plant species is assumed to be the main limiting factor in habitat colonisation (Brunet & Von Oheimb 1998; Takahashi & Kamitani 2004; Hermy & Verheyen 2007). The dispersal limitation of forest species is often attributed to their relatively large seed mass and poor adaptation for long-distance dispersal (Ehrlén & Eriksson 2000; Jacquemyn et al. 2003b; Verheyen et al. 2003b; Flinn & Vellend 2005). For example, myrmecochory, i.e. the dispersal of seeds by ants, is a common dispersal mechanism among forest species (Brunet & Von Oheimb 1998; Graae & Sunde 2000; Kelemen et al. 2013). Poor competitive ability is considered an additional limiting factor for forest species (Baeten et al. 2009a; Brunet et al. 2011). Generalist species that are good competitors can, therefore, prevent the establishment of forest specialists in novel habitats. The establishment success of species can thus be determined by fundamental niches and resource use strategies of immigrating species.

Disentangling the importance of landscape connectivity, habitat quality, and species traits means that all factors should be evaluated simultaneously (Kolb & Diekmann 2004). Since stand formation and species arrival act at a relatively slow pace, conducting a long-term experiment at a landscape scale is impractical. An alternative would be to survey a range of habitats along a colonisation gradient. For forest plants, this gradient encompasses ancient to recent forest stands, and landscape corridors. In this type of study, young forest plantations on former agricultural land are often used as recent forest stands (Jacquemyn et al. 2003a; Brunet et al. 2012). Such studies often emphasize the importance of time and, therefore, a significant dispersal limitation can be expected for late arrivals. However, when the final resulting community is of interest, rather than the pace of community formation, old plantation stands should be addressed. In this case, old parks can be a model habitat used for forest species colonisation studies. Plantations and parks have many common features, but for forest species even minor structural differences can be critical. For instance, forest plantations are planted and managed to optimize tree growth and to maximize timber production of a single tree species. On such plantations, suitable conditions for forest-dwelling species emerge only during the last stages of stand succession (Flinn & Marks 2007). Parks are planted too, but managed to meet a variety of purposes other than timber production. Planted parks stands are often species rich and include smaller patches of shrubs. Furthermore, parks have a planned structural heterogeneity, which creates various microhabitats for species establishment already in the early stages of park formation.

Old parks stands are not only a suitable model habitat for a long-term observational experiment. In strongly urbanized regions, parks compensate for

the lack of natural habitats and have, therefore, gained considerable research attention (Cornelis & Hermy 2004; Ignatieva & Konechnaya 2004; LaPaix & Freedman 2010). By contrast, studies in rural parks are relatively rare and often focus on a single taxonomic or growth-form group (Jonsell 2004; Kowarik et al. 2013). The traditionally low management intensity of closed-canopy stands in rural parks has created environmental conditions comparable to temperate forests (Cranz & Boland 2004; Abner et al. 2007). Therefore, old park habitats may serve as substitute or refugia habitats, harbouring forest-specific species (Glendell & Vaughan 2002; Jonsell 2012).

***The aims of this doctoral thesis were:***

- to test the hypothesis that rural manor parks, as recently created habitats, are a suitable habitat for forest-dwelling species (**I, II**);
- to test the hypothesis that rural manor parks harbour a high species diversity of forest plants and, thus, contribute to biodiversity at a landscape level (**I, II**);
- to understand the colonisation process of forest plant species in rural manor parks (**II, III**).

## II. MATERIAL AND METHODS

### 2.1. Study area

Estonia is located in a transitional zone between temperate nemoral forests and northern boreal forests, referred to as the hemi-boreal vegetation zone (Ahti et al. 1968). The area is characterised by an average summer temperature of 17 °C in July, an average winter temperature of -6 °C in February, and mean annual precipitation ranging from 600–700 mm (Aunap 2011). The study was conducted in central and southern parts of Estonia (~58°–59° N and 24°–27°30' E). The forests in this area grow mainly on podzols, luvisols and various gleysols, with some on fluvisols (Aunap 2011).

Approximately half of Estonia is covered by forest. These forests serve as an important economic resource for the country. This is illustrated by the fact that the rate of forest stand loss and gain are both high (Hansen et al. 2013). As a result of intensive forest use throughout history, only up to four per cent of forests is in a near-natural state (Adermann 2009). Also, the amount of nemoral forests with broad-leaved trees covers only about five per cent of the total forest area, because nemoral forests on fertile soil were the first to be cut down and converted into agricultural land (Lindbladh et al. 2000; Reitalu et al. 2013). In the last decades, less fertile arable land has been abandoned and reforested, but the fertile soils where nemoral forests could grow still remain in agricultural use.

Estonia has a large number of parks planted around manors in historical agricultural landscapes (Abner et al. 2007). Most manor parks were established during the late 18th or early 19th century on former agricultural land. Traditionally, rural park design kept pace with contemporary gardening trends. For example, parks were regularly redesigned and, therefore, contain elements from different garden styles. Early parks were relatively small and designed to follow the principles of a baroque garden style, which is characterised by geometrical hedges, roads, flowerbeds and regular planning (Thacker 1981). For example, the oldest part of the park was planted close to the manor itself and had regular planning including flowerbeds and lawns, and a structured regular system of walkways. This style supports species from open habitats, while species that prefer closed-canopy stands are rare. By the end of the 18th century, the English landscape park design became fashionable (Abner et al. 2007; Watkins et al. 2007). This design mimics nature in aesthetic terms, but not necessarily in species composition or ecological function (Watkins et al. 2007). Such parks often include a variety of closed-canopy stands in the outer periphery. In 19th-century parks, these two design styles were usually combined. Areas closer to the main building had an organised and managed appearance, whereas stands in the outer periphery were less-intensively managed (Abner et al. 2007). Nowadays parks consist of a combination of styles providing a broad spectrum of habitats, including forest-like stands. After

Estonia gained its independence in 1918 many of these parks were under-managed or even completely abandoned. Mismanagement continued later during the Soviet era. As a result, many Estonian rural manor parks developed into natural forest-like habitats.

## 2.2. Sampling design

I selected historic manor parks located in agriculture-dominated landscapes, which included a closed-canopy stand (tree canopy closure > 0.5) with an area of at least 0.5 ha. Selected stands consisted of mature trees (age > 80 years). Parks in close proximity to each other were avoided to minimise the potential effect of spatial autocorrelation. Adjacent parks were surveyed only if there was a distinct contrast in either their internal structure or in the abundance of surrounding forest.

Based on the map data, about 81% of the selected parks can be confirmed to have had open land cover at some point in history. Ten per cent of parks were probably wooded meadows or have an unclear origin of shade-providing habitat. Early map data was not available for 9% of manor parks. The land cover change in the park sampling points is presented in Table 1.

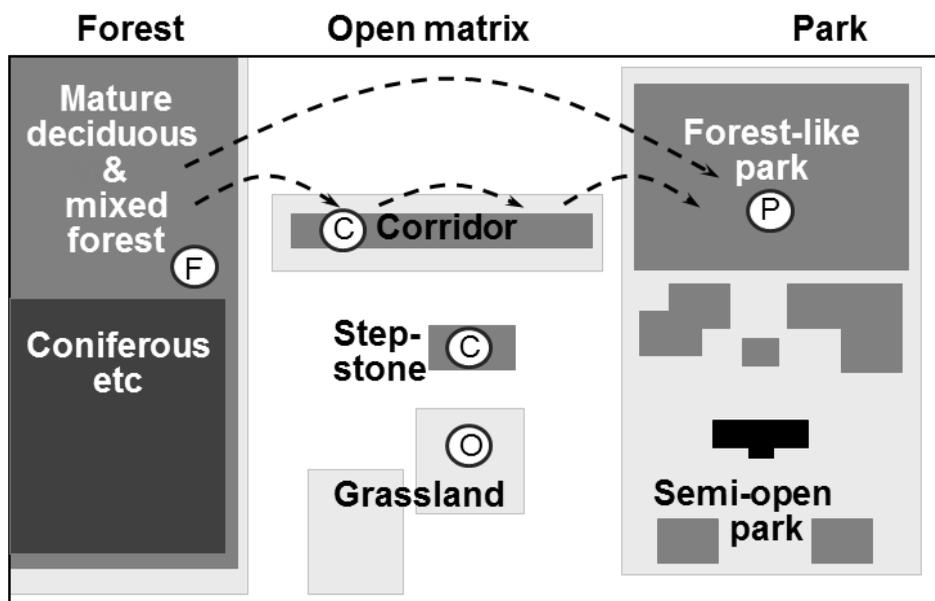
**Table 1.** Proportions of land cover type in the park sampling points throughout history. N = number of parks that had a classified land cover type at some point in history; <sup>1</sup>based on detailed maps of parks; <sup>2</sup>detailed maps of parks and one verst map of the Russian Empire

End year of time interval	Land cover					Number of parks
	Agricultural land	Lawn or open garden	Regular (open) park	Closed- canopy park	Woodland	
1700	56	32	–	2	10	59
1850	27	27	18	23	5	22
1900 <sup>1</sup>	18	12	14	53	2	49
1918 <sup>2</sup>	–	3	14	80	4	74
1945	3	–	4	93	–	67
1960	–	1	–	99	–	74
1980	–	–	–	100	–	74
2009	–	–	–	100	–	74
N	42	27	16	74	10	74

I selected deciduous-tree-dominated stands from the surrounding landscape to provide a comparison group for park stands. Suitable forest stands had an area of >0.9 ha and a first layer tree age of >75 years. I selected forests growing on a similar soil type as parks in order to minimize potential side effects in park-

forest comparison. I sampled forests growing primarily on ancient forest land. This means that the area was marked as forest land on maps from the 17th to mid-19th centuries, depending on the maps available in the map collections of the Estonian Land Board and Estonian Historical Archives. About 79% of selected forest stands had history of being continuously forested land. The remaining 20% of forests were located in old semi-open woodland areas, and 1% was of secondary origin. The latter was sampled only because ancient mature forests were not available within a reasonable distance from the park.

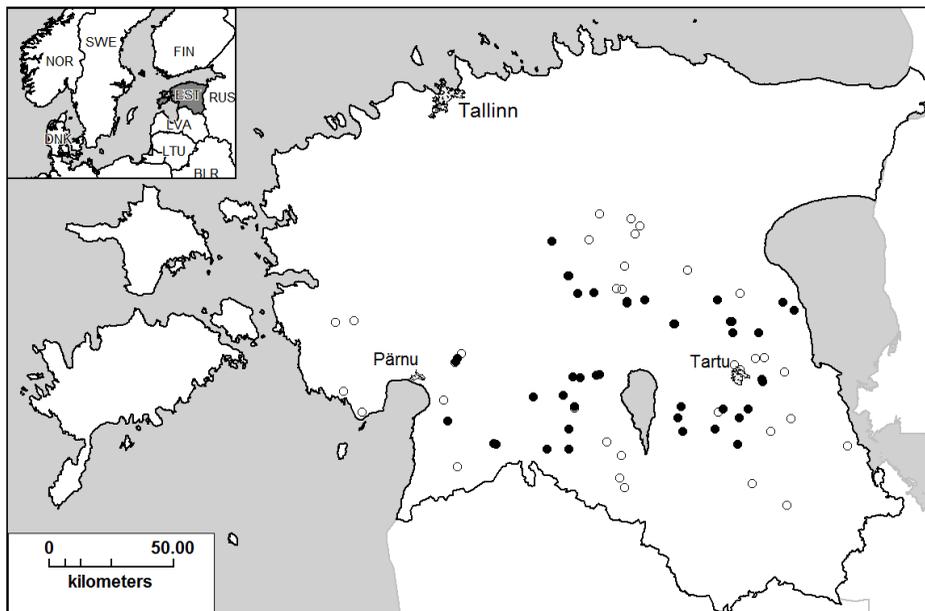
Linear wooded habitats, such as hedgerows, tree lines and a few tree stands, were sampled as corridor habitats to estimate the ability of forest species to thrive in different habitats. These corridor habitats ranged in age from relatively young hedgerows to centuries-old allées. Grasslands were sampled as reference habitats to obtain a species list and a species trait pool from open habitats.



**Figure 1.** Theoretical scheme of forest species dispersal into parks, and the sampling design to evaluate dispersal. Sampled habitats and sampling points in parks (P), deciduous forests (F), corridor habitats (C), and grasslands (O) are marked on the scheme. Coniferous forest and semi-open parks were not sampled and are merely shown to illustrate the general landscape and park structure.

The general sampling design comprised four habitat types: rural parks, forests, corridors, and grasslands (Fig 1). I used a subset of 74 parks and 93 neighbouring forests in paper **I**, using their full variable list of community structure. With emphasis on herb layer plants, I used a subset of 40 parks, 70 forests and 103 corridor habitats in paper **II**. In paper **III**, I used the complete dataset of 74 parks, 230 forests, 151 corridors, and 97 grasslands (Fig 2).

Based on historical maps, the landscape around planted manor parks had changed little since the 17th century. Most parks were planted on old agricultural land, whereas the majority of the forests (79%) were located on ancient forest land or woodland (20%; wooded grassland or pasture forest) (I). The history of corridor habitats was occasionally available since the end of 19th century, but mostly since the 1950s, depending on map precision and object size. As I sampled the oldest-looking corridor or stepping-stone type habitat, most of the sampled corridor habitats in the landscape could be considered as older than 30–50 years. Old allées were at least one century old, some even older. Presently, crop rotation field is the dominant land use type in the agricultural matrix of the study region. The composition of land cover within a 1-km radius of manor parks was agricultural land – 23.5%–84% (average 58.5%); forest land – 1.1%–62.1% (average 20.4%) and buildings with enclosed yards, average 11.6%.



**Figure 2.** Map depicting the location of studied rural manor parks in central and southern Estonia. For paper II only the sites depicted with closed circles (●) were used. For papers I and III, the same sites were used plus the sites depicted with open circles (○).

## 2.3 Data collection

The herb layer survey was carried out from late May to early August 2008–2012 when both spring and summer plants were visible. In parks and forests, I used a 30-m radius study circle from which I compiled a species list of vascular plants growing in the herb layer. At each park site, I sampled an additional 10 randomly distributed plots (2 × 2 m) within each 30-m study circle to characterise herb layer coverage and species richness (II). In corridors, I sampled the area under the canopy's projection on the ground in a 30-m section at a minimum distance of 50 m from adjacent forest or park (II, III). Since grassland habitats were used only as a reference habitat to filter out grassland species and to provide scaling estimates, I recorded all the observed herb layer species (III).

I characterised each stand of park (I, II, III) and forest (I) with various structural variables. At the centre of each 30-m study circle, I recorded the basal area of trees at two intervals of diameter at breast height (DBH): DBH = 8–40 cm and >40 cm, using a Bitterlich relascope. The proportion of each tree species was recorded. I characterised stem diameter diversity as the number of trunk diameter classes present in the stand (<2 cm; 2–8 cm; 8–20 cm; 20–40 cm; 40–80 cm; >80 cm). To evaluate the vertical canopy structure, I visually estimated the cover of coniferous and deciduous foliar layers at three height intervals (1–4 m; 4–10 m; >10 m). The basal area of lying logs or downed dead trees was measured using a methodology similar to the DBH recording. Specifically, I counted logs longer than 1.3 m and with a diameter greater than 8 cm, 15 cm and 40 cm in concentric circles around the central point with a radius of 0–5 m, 5–10 m and 10–30 m, respectively. I also recorded the presence of wind-thrown or wind-broken trees, the decay classes of dead wood (early, medium, or late decay), and the number of fresh and decaying stumps. Understorey composition was described in a 100-m<sup>2</sup> circle by estimating the proportions of shrub layer coverage and counts of tree saplings by species (DBH < 8 cm and height between 1.3 m and 25% of stand height). I also recorded signs of management, such as mowing, and cutting of trees and shrubs. I recorded the presence of several old-growth forest indicator groups: (i) epiphytic bryophyte species *Neckera pennata* and *Leucodon sciuroides*, and epiphytic lichens *Lobaria pulmonaria*, long-bodied *Usnea* and *Bryoria* species as indicators of ancient nemoral or mixed-nemoral forests, (ii) common forest bryophytes *Homalia tricomanoides* and *Radula complanata*, and stem-base lichen *Peltigera* species to test for basic habitat suitability, (iii) large insect holes and cavities in tree trunks, (iv) fungi on trees, and (v) signs of woodpecker activity. To calculate the management intensity index (chapter 2.4), signs of management activity were recorded within a 30-m and a 60-m radius.

The historical and present-day landscape configuration for each landscape window was measured as the area per land-cover type from historical maps (1890–1934) and present-day maps (2009). For the time period 1600–1900, I used historical maps available from the Estonian Historical Archive

([www.ra.ee](http://www.ra.ee)), and for 1890–1965, the map sources of the Estonian Land Board ([xgis.maaamet.ee](http://xgis.maaamet.ee)).

Plant trait data were obtained from online databases, such as BiolFlor (Klotz et al. 2002), LEDA (Kleyer et al. 2008), BioPop (Poschlod et al. 2003), SID (Kew 2014), and floras (Kukk 1999; Leht 2010). I collated species trait data for (i) life-strategy traits including Ellenberg's indicator values (Ellenberg et al. 1991), hemeroby level (Jalas 1955; Sukopp 1969), and Grime's plan strategies (Grime 1979); (ii) resource acquirement related traits including average height, specific leaf area, growth form, leaf form, and presence of petiole; (iii) dispersal related traits including flowering period, colour of flowers, pollination vector, reproduction strategy, average seed mass, maximum dispersule mass, and dispersal syndrome. Plant nomenclature followed Kukk (1999), while synonyms were identified using The Plant List (2010) database.

## 2.4. Compound indices

A detailed record of management and disturbance history of park stands is hardly ever available. Instead, I used a forest-specific management intensity index (Liira et al. 2007; Liira & Sepp 2009). This management intensity index considers the regional and community-specific spectrum of disturbances, and avoids potential assessment bias based on single trait estimation (e.g. the number of cut stumps). The index can be interpreted as a quantified judgement of an expert, assessing the disturbance rate by combining the presence of various visible signs of anthropogenic disturbance. These visible signs are cut stumps, wood piles, forest tracks, roads, neighbouring clear-cut areas, ditches, trash, fences, soil mechanical damage etc. Signs were recorded at two distance intervals: in the study circle ( $r = 30$  m), and in the outer buffer zone ( $r = 30\text{--}60$  m). Each sign of anthropogenic activity was given a score describing its proportional effect (1 = weak; 2 = strong) in the outer buffer zone, and double weighted (2 = weak; 4 = strong) for the 30-m study circle. The management intensity index is the sum of these weighted scores. A management index of 0 indicates no anthropogenic disturbance within a 60-m radius, and can be as high as 50 in the case of a clear-cut area with soil damage, trash pollution, intersecting ditches and roads, surrounded by neighbouring arable fields or buildings. For example, a typical deciduous forest with moderate forest activities has a management index value of 25 (Liira & Sepp 2009). Since parks are managed quite different from forests, I divided the management index of each park stand into sub-indices to obtain an index for understory management, small roads, mowing and landscape management.

Estimating the nature value of a stand is a complicated task. Here, I proposed three single-value indicator composites describing (i) the stand structure quality, (ii) the quantity and quality of dead wood, and (iii) the level of biodiversity. Each composite was calculated as the sum of the presence-absence data of stand

structural characteristics or individual biodiversity indicators (Table 1). The values of these indicators range, depending on the number of indicators included, from 0 to 6, 7 or 8. I then summed these three composites into a single nature value indicator (value range: 0–21).

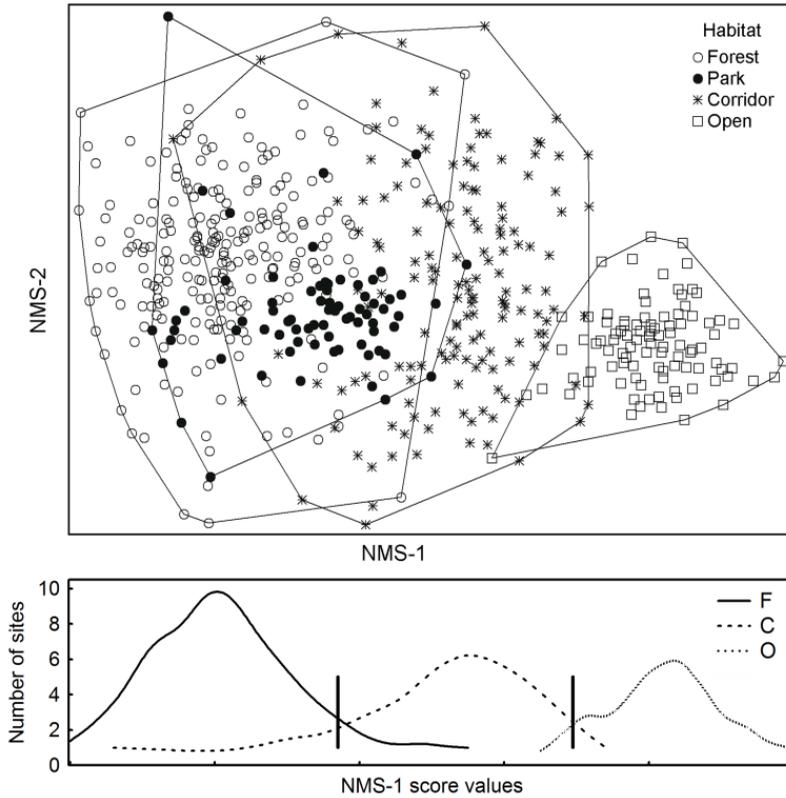
**Table 2.** Characteristics used to calculate nature value indicator composites. Table modified from appendix A, paper I.

Characteristics	Description
<b>Index for stand structure</b>	
Basal area of large trees >5	Basal area of trees with DBH >40 cm is larger than 5
Deciduous tree species >2	More than two broad-leaved deciduous trees in the stand
Natural shrub species >2	More than two naturally occurring shrub species in the stand
Extremely large trees (DBH >80 cm)	Trees with diameter at breast height >80 cm
Many large trees	More than two trees with diameter >80 cm
Foliage layer 4–10 m cover >4%	Foliage cover at the height of 4–10 m is >4%
<b>Index for dead wood</b>	
Standing dead wood	Presence of standing dead trees in the stand
Snags	Broken dead trees with height >1.3 m
Dead branches on trees	Dead branches with diameter >8 cm on living trees
Lying dead wood	Lying logs with diameter >8 cm
Standing dead wood counted in basal area	Presence of standing dead trees in the basal area estimate
Wind damage	Wind-broken or wind thrown trees in the stand
Large diameter dead wood	The presence of lying dead wood with diameter >40 cm
<b>Index for biodiversity</b>	
<i>Neckera pennata</i>	A widely-used bryophyte indicator species of old stands
<i>Homalia trichon</i>	A widely-used bryophyte indicator species of old stands
<i>Lobaria pulmonaria</i>	A widely-used lichen indicator species of old stands
Insect holes >10 mm	Visible insect holes with diameter >10 mm
Woodpecker	Signs of woodpecker activities
Cavity trees	Hollow trees and trees with cavities
Fungi on wood	Fruit bodies of fungi on dead and living trees
Natural forest species >3	More than three natural forest species defined in Sepp & Liira (2009)
<b>Total nature value indicator</b>	Sum of above

## 2.5 Forest species classification

In study **I** and **II**, I defined common forest species as forest-specific or shade-tolerant species that are adapted to regional climate conditions and the soil types. These are abundant in forest landscapes around parks and are, therefore, potentially able to produce a sufficiently large number of diaspores to ensure the likelihood of species inhabiting the closed-canopy habitats in parks. I defined a common forest species as a species present in at least 10% of all studied forests. I further characterised the ecological profiles of common forest species by comparing their occurrence distribution pattern among three habitat types with Indicator Species Analysis (ISA; Dufrêne & Legendre 1997). I only used common forest species that had a minimum frequency of 33% in at least one of the three habitat types to emphasize affiliation patterns. I then classified these common forest species into three categories: (i) generalist species common in all three studied habitat types (ISA test of three groups non-significant, but a frequency 33% in all habitat types); (ii) forest-park distribution type of species or ‘from-patch-to-patch jumpers’, i.e. species common in both forests and park fragments, but not in linear woody habitats (ISA test of three groups and park-corridor pair-wise test was significant); (iii) low-dispersal forest specialist species or forest-delimited species that were common only in forests (ISA test of three groups was significant).

In study **III**, I analysed the variation of species occurrence patterns between forest, park, corridor, and open habitats using Non-metric Multidimensional Scaling (NMS). I used Sørensen distance, random starting configuration, and 50 iterations with real data in PC-ORD v6.05 (McCune & Mefford 2011). Based on 118 iterations, the final two axis solution had a stress value of 20.57 and an instability of <0.0001. I used NMS instead of an Indicator Species Analysis to obtain a habitat affiliation for all species, so as not to limit my results to statistically significant indicator species. The NMS ordination included park habitats to ensure that the species composition of parks was sufficiently similar to forests to consider parks as potential habitats for forest species. I then distinguished three species groups: (i) forest specialists, (ii) corridor specialists, and (iii) open habitat specialists. Species were classified according to species scores along the first axis. I used the median score of sites in the ordination space where point clouds of habitats overlapped as the cut-off value (Fig 3).



**Figure 3.** The Nonmetric Multidimensional Scaling ordination graph of sampling sites and the distinction of specialist groups for each habitat based on NMS score values. The median score of sites in overlapping areas were used as cut-off values in the classification and are indicated with vertical lines.

## 2.6 Statistical analyses

To illustrate the structural composition of parks and forests, I used a Principal Component Analysis (PCA) on stand structural traits (**I**). An artificial sample site of the theoretically generated idealistic old-growth forest with all respective indicators present was included in order to give a scaling reference point on the ordination graph (**I**).

Herb layer compositions in forest, park and corridor habitats was analysed using Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980) on the species presence-absence data of common forest species (**II**). I excluded infrequent species that were recorded less than 10 times to reduce noise variation in the data caused by non-representative species. I also excluded cultivars since I was interested only in describing the colonisation ecology of indigenous species.

To compare the structural characteristics of parks and forests, I used General and Generalized Linear Mixed Model analyses implemented in the MIXED and GLIMMIX procedures in SAS v.9.2 (Littel et al. 1996). The extended landscape window, defined as the combination of intersecting buffer areas of a 1-km radius around parks and forests, was included as a random factor to take into account the spatial relatedness of neighbouring study sites. In GLIMMIX, I compared two-state characteristics (presence-absence), using a binomial error distribution and a logit-link function, and correcting for over-dispersion with a random factor 'Landscape window'. To reveal the ecological reasons for the presence of biodiversity indicators, I built extended ecosystem models for biodiversity indicators. I used a two-way stepwise selection and the Akaike information criterion (AIC) to select the best explanatory set of environmental factors.

In study **II**, I calculated the percentage of common forest species in the species list of each park, expecting that this variable characterises the optimum of a park's environmental conditions for forest species. The colonisation success was quantified as the percentage of common forest species present in the park relative to the local species pool in the 1-km radius. Similar percentages were calculated for each neighbouring complex of forests and corridors. I then compared these proportions in park, forest and corridor using Repeated-measures Analysis of Variance (ANOVA) with Tukey's post hoc test. I tested the responses of the percentage estimates of common forest species to sampled gradients of park area, anthropogenic disturbances and environmental variables with multi-factorial General Linear Model (GLM) analyses.

To quantify the trait pattern differences between species groups and habitat types, I used General Mixed-effect Models (MIXED; **III**). For these tests, I used the average trait value per species group in a site as a response variable and species group as a repeated factor. Since some habitat replicates were in relative close proximity to each other, and thus cannot be considered as independent replicates in space, all habitats were nested within a local landscape window. These landscape windows consisted of a 2-km buffer zone around sample points whereby intersecting buffer zones were merged into the same landscape window. I tested only the average trait values between forest and corridor specialists in closed-canopy habitats, such as forests, parks and corridors. Open habitat specialists were only used as a comparison group for scaling trait value general trends.

To determine the probability of species colonisation in parks, I fitted Generalized Mixed-effect Model (GLIMMIX; **III**). As model predictors, I included factors such as species dispersal traits, niche-related species traits, habitat quality characteristics, and landscape structure metrics. Landscape window and species were included in the model as random factors to account for potential spatial auto-correlation within a landscape or species. Species that were potentially available, but absent from park habitats, were determined from cumulative species lists for each 2-km landscape window around a given park.

## III. RESULTS

### 3.1. Stand structure

The general mixed-effects model showed that canopy closure ( $0.74 \pm \text{SE } 0.01$ ) and tree density ( $20.8 \pm 1.0 \text{ m}^2 \text{ ha}^{-1}$ ) in parks were similar to that in forests growing on similar soils throughout Estonia (**II**, based on literature  $0.72$ ;  $26.1 \text{ m}^2 \text{ ha}^{-1}$ ), and to adjacent forests (**I**,  $0.72 \pm 0.01$  and  $21.3 \text{ m}^2 \text{ ha}^{-1}$ ). This similarity confirmed that park stands resembled forests at least in some basic light conditions and stand statistics. In contrast to forests, park stands contained more trees with a large diameter ( $7.6 \pm 1.1 \text{ m}^2 \text{ ha}^{-1}$  in parks and  $17.5 \pm 1.0 \text{ m}^2 \text{ ha}^{-1}$  in forests). The proportion of broad-leaved trees (*Tilia* spp., *Quercus robur* and *Fraxinus excelsior*) was greater in parks ( $76\% \pm 2.4$ ) than in forests ( $23\% \pm 2.9$ ). At the same time, the proportion of conifers was about three times that in forests ( $12.7\% \pm 1.8$  in parks and  $38.3\% \pm 2.8$  in forests), where typical boreal forest tree species, *Pinus sylvestris* and *Picea abies*, grew together with deciduous species characteristic of post-clear-cut forests (*Populus tremula* and *Betula* spp). Even though the proportional abundance of the dominant tree species in a stand was about the same ( $46.4\% \pm 2.4$  in parks and  $52.1\% \pm 1.8$  in forests), park stands were richer in tree species with an average of two more tree species per sample area. Average values of stand structure characteristics in parks and forests are presented in study **I**, Table 1.

Forest stands had higher species richness of undergrowth trees ( $0.9 \pm 1.1$  species in parks and  $2.0 \pm 1.0$  species in forests) and shrub layer ( $0.6 \pm 1.0$  species in parks and  $2.2 \pm 1.0$  species in forests). Shrub cover was  $39.2\% \pm 3.2$  in forests and  $7.9\% \pm 1.9$  in parks. Also, the foliage cover at a height of 1–4 m was twice as much in forests ( $59.1\% \pm 2.7$ ) than in parks ( $27.8\% \pm 3.0$ ), whereas the foliar cover at 4–10 m was similar ( $43.9\% \pm 2.3$  and  $49.4\% \pm 2.3$ ). In parks, the foliar layers at 1–4 m and 4–10 m were dominated by deciduous species (deciduous-coniferous ratio  $7.5 \pm 1.1$  and  $6.8 \pm 1.1$ ) whereas in forests, the foliar layer 4–10 m was distinguished by the equally balanced mix of deciduous and conifers (deciduous-coniferous ratio  $2.6 \pm 1.2$ ).

Compared to parks, forests had a greater total basal area of dead wood ( $43.9 \pm 2.3 \text{ m}^2 \text{ ha}^{-1}$  in parks and  $49.4 \pm 2.3 \text{ m}^2 \text{ ha}^{-1}$  in forest) and diversity of decay types ( $2.3 \pm 0.2$  types in parks and  $3.2 \pm 0.2$  types in forests). Specifically, more than half (53%) of forests had medium decay coarse woody debris present, compared to 23% of parks. Late decay stage was present in 35% of forests and in 15% of parks. By contrast, more parks had large-diameter dead branches on trees (in 68% of parks, 29% of forests) and large diameter lying logs (in 23% of parks, 10% of forests).



**Figure 4.** Illustration of contrasting features in stand structure between parks and forests (Table 1 in **I**).

The first two PCA axes extracted from the analysis on stand structural characteristics accounted for 13.9% and 12.2% of the total variance in the composition of stand structure characteristics. A structural distinction between park stands and forests is evident (**I**, Fig 1), with a very loose continuum between these two habitat types. Most of the tested structural characteristics that were distinct between parks and forests were correlated with the first PCA axis, and sometimes with the second axis as well. Characteristics such as dead wood types and the number of diameter classes had a slightly stronger correlation with the second axis, indicating general trends over habitat types. Variables such as canopy closure and the basal area of trees that had similar average values in parks and forests did not correlate with the PCA axes.

### 3.2 Management

The average value of the management intensity index in parks was 1.4 times higher than in forests (Table 1 in **I**). A common disturbance in all habitats was ‘neighbouring an open area’ (in 85% of parks and 86% of forests), indicating a widespread edge effect (Table 2). Edge effect was increased by various types of roads crossing or intersecting stands with similar frequency in parks (83.8%) and in forests (86.0%). Selective cutting was common in both habitats, as indicated by the nearly equal counts of stumps in both habitats, on average 3 ( $\pm 0.53$  SE) fresh stumps and 5 ( $\pm 0.50$ ) old stumps in forest plots, and 1 ( $\pm 0.31$ ) fresh and 5 ( $\pm 0.76$ ) old stumps in parks.

**Table 2.** Frequency of selected indicators of management and anthropogenic disturbances within a 60-m sampling radius, except for logging, which is sampled only within a 30-m radius. This table is modified from Appendix A, Table 3 in **I**.

Selected indicator groups	Park%	Forest%
Logging (30-m radius):		
Fresh, single tree (1–10 stumps)	32	36
Fresh, selective (>10 stumps)	0	8
Old, single tree (1–10 stumps)	70	66
Old, selective (>10 stumps)	10	11
Piles of logs	43	42
Understory management	62	43
Soil mechanical damage	60	36
Garbage	69	72
Footpaths	82	44
All roads	84	86
Forest roads	41	56
Roads	69	59
Linear open corridors/power lines	7	22
Neighbouring open areas/clear-cut areas	85	86
Drainage ditches	23	44
Fences	35	12
Stone piles	30	23
Mowing	66	3
Unclassified signs of disturbance	62	29
Bird nest boxes	41	9

### 3.3. Biodiversity indicators

An old-growth forest indicator, the *Lobaria pulmonaria* lichen, was present in seven parks but only in one forest (**I**, Table 2). *Usnea* and *Bryoria* spp. were equally rare, occurring in five forests and four parks. Stem-base growing *Peltigera* spp. were equally present in 25% of forests and 17% of parks. The epiphytic indicator moss *Neckera pennata* was more frequent in parks than in forests, but, as the lower AIC-value of the ecological model showed, this contrast was determined by the stand composition and the number of large trees (**I**, Table 2). The indicator moss *Leucodon sciuroides* was mostly present in parks, but its presence was supported additionally by the abundance of broad-leaved trees (**I**, Table 2). Common forest epiphytes *Homalia trichomanoides* and *Radula complanata* were equally successful in both habitats, indicating equal opportunities, even though the occurrence of *H. trichomanoides* was

evidently determined by the proportion of deciduous trees (**I**, Table 2). Woodpeckers, cavities in trees and saproxylic insects were more common in parks, whereas fungi on trees and wind damage were more common in forests. However, as the ecological model results showed, the presence of cavities and fungi was largely determined by stand structure (**I**, Table 2).

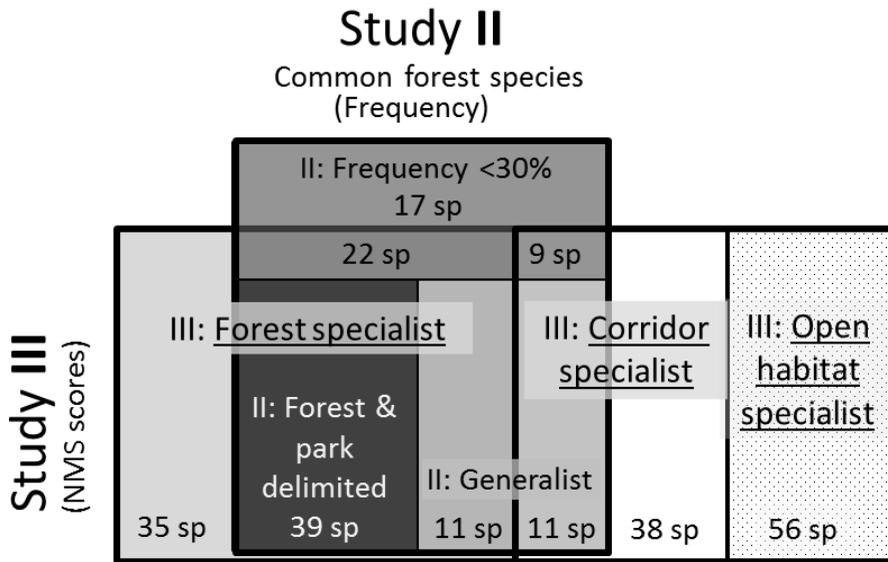
The mean of the total nature value index was 1.2 units greater in parks than in forests (**I**, Table 3). Its three sub-indices had a more heterogeneous pattern; the stand quality and biodiversity level indices were greater in parks, whereas forests had a greater mean for dead wood quality and quantity index. However, the mean value did not describe the distribution of high quality habitat between parks and forests. Therefore, we calculated the proportion of sites above the mid value of the range of index values. Parks largely exceeded forests in stand quality because the stand quality index was greater than the mid value in 64% of the parks and 18% of the forests. The biodiversity level index was above the mid value for 47% of the parks and 30% of the forests, whereas 52% of forests had a greater index mid value for dead wood, but only 35% of parks exceeded the dead wood index mid value.

These results indicate that the stand structure of parks differed generally from that of regional forests. This is also illustrated by the negative correlation of the stand quality index with the first axis of PCA (PCA-1  $r = -0.5$ ;  $p < 0.0001$ ). However, the positive correlation of the dead wood index was much stronger with the second PCA-axis ( $r = 0.9$ ;  $p < 0.0001$ ), showing a parallel trend in parks and forests.

### 3.4 Forest species classification and characterisation

The classification of plant species according to their 10% frequency in forests resulted in 109 species defined as forest species common to the whole study region. Further classification of these common forest species defined 22 species as generalists, 17 species as forest and park species and 22 species as forest-delimited species (Table 3 in **II**).

Alternatively, the classification of species based on NMS scores of a larger data set resulted in 107 forest specialists, 53 corridor specialists, and 56 open habitat specialists (**III**). Some 72 species were classified as forest species in both studies. All species that were defined as forest-park species or forest-delimited species in paper **II** were classified as forest specialist in the NMS-based classification, whereas half of the species defined as generalist species in paper **I** were classified as corridor specialists and the other half as forest specialists. In general, a relatively large overlap between classification results can be seen in Figure 5. The only 17 species from study **II** that do not overlap with study **III** were tree and shrub species that were excluded from the data in study **III**.



**Figure 5.** Schematic overview of the classification difference between study II (common forest species growing in more than 10% but less than 30% of forests; forest and park delimited species and generalist species growing in more than 30% of forests) and study III (forest specialists; corridor specialists; and open habitat specialists). Numbers indicate the number of species (sp) in each group, while the overlap between classifications indicates shared species.

In parks, forest and corridor specialists showed similar trait patterns as in their source habitat, or in some cases had an intermediate trait value. Therefore, most trait patterns are discussed as a comparison between forest and corridor habitats.

Forest specialists had lower Ellenberg's indicator values for light than corridor specialists, and both specialist groups were represented by more light-demanding species in corridors (Fig 4.1 in III). Ellenberg's indicator values for soil productivity were lower among forest specialists than corridor specialists. The soil productivity indicator value increased among forest specialists from forest to corridor, but corridors specialists had higher requirements for soil productivity in forests than in corridors (Fig 4.11 in III).

Forest specialists had shorter plant height in forest habitats than in corridor habitats (Fig 4.4 in III). The specific leaf area estimate was relatively large for both specialist groups and only corridor specialists in corridors had a lower value (Fig 4.2 in III). Corridor specialists were dominated by species with a hemi-rosette growth form irrespective of habitat type (slightly more than half of species, Fig 4.6 in III). The rosette growth form was rare in all specialist groups, only slightly more common among forest specialists in forests (Fig 4.7 in III). The leaf shape type among forest specialists was more constant between habitats than that of corridor specialists. For corridor specialists, the proportion of simple and compound leaves decreased from forest to corridor and were

replaced by species with narrow leaves (Fig 4.8–4.10 in **III**). By contrast, open habitat specialists were dominated by species with simple leaves, whereas the proportion of narrow leaved species was quite low.

Forest and corridor specialists started flowering almost at the same time, but the flowering period of corridor specialists was longer by almost a month (Fig 3.5 in **III**). Forest specialists had a high additional ability for self-pollination (Fig 3.4 in **III**). Many forest specialists used both vegetative and generative reproduction, whereas corridor and open habitat specialists relied more on seeds (Fig 2.1 in **III**). The average seed mass of forest specialists was less than that of corridor specialists, but did not differ between habitats (Fig 2.4 in **III**). Dispersule mass, however, did not differ between species groups, but only between habitat types, as the dispersule weight in corridors was a bit less than in parks, but still greater than in open habitat specialists (Fig 2.5 in **III**). The dispersule based dispersal types prevailed among corridor specialists and open habitat specialists, whereas both propagule types, seed and dispersule, were equal among forest species (Fig 2.3 in **III**). Zoochory was the most prevalent dispersal syndrome for all specialists groups, used by more than half of the species; in corridors it reached the level of open habitat specialists (Fig 2.6 in **III**). Within zoochory, mammals were the most prevailing vector group, particularly among corridor specialists (Fig 2.7 in **III**), whereas bird dispersal played no significant role (Fig 2.8 in **III**). Dispersal by invertebrates was twice as important for forest species as for corridor species (Fig 2.9 in **III**). Among invertebrates, myrmecochory played a small role in all specialists groups, particularly among forest species (Fig 2.10 in **III**). The proportion of species using anemochory was constant over all habitats, except in parks, where anemochory was less common (Fig 2.11 in **III**).

### 3.5 Forest species proportion in park flora

Herb layer richness in parks was on average 36 ( $\pm 1.3$  SE) species. With a smaller sample size of 40 parks (**II**), the average richness per cent of common forest species in the park flora was 87%, but decreased to 75% when all 74 parks, including less-representative park stands, were analysed. In comparison, the average richness per cent of common forest species in neighbouring forests was nearly identical to parks (85% in forests; **II**), whereas it was remarkably lower in corridors (66%; **II**). Park flora consisted of 63% forests specialists and 32% corridor specialists (**III**). Open land species (**III**) were of minor importance (average of  $2.0 \pm 0.3$  species per park) and can be neglected as the stochastic fraction of park biodiversity.

The most frequent species in park stands were also common in woody linear habitats, i.e. *Veronica chamaedrys* (in 98% of parks), *Aegopodium podagraria* (90%) and *Ranunculus cassubicus* (90%), (Table 3, in paper **II**). They could, therefore, be classified as forest-dwelling generalist species. Other generalists

growing in all three habitats were *Rubus idaeus*, *Geum urbanum*, *Geum rivale* and *Poa nemoralis*. Very common species in parks with a forest-park distribution pattern were *Anemone nemorosa* (85%) and *Oxalis acetosella* (75%). Similar forest-park distribution species were *Galeobdolon luteum*, *Paris quadrifolia*, *Stellaria holostea* and *Athyrium filix-femina*. Species of the last group, such as *Dryopteris carthusiana*, *D. filix-mas*, *Maianthemum bifolium*, *Melica nutans*, *Mercurialis perennis*, *Rubus saxatilis* and *Stachys sylvatica* were present mostly in forests and, therefore, can be considered to be forest-delimited species.

According to the results of the GLM analysis, the proportion of forest species in parks depended on the area of forest-like habitat in the park, the area occupied by forest in the surrounding landscape, canopy closure of the stand in the park fragment, the number of large trees in the park and park management intensity (II, Table 2, Fig 4). Specifically, park area predicted a greater proportion of forest species in parks, but levelled off when the park fragment area reached 2.5–3.0 ha. The proportional area of forests in the surrounding landscape had a negative correlation with the proportion of forest species in parks. Two factors had a threshold in their effect on the proportion of forest species. Tree canopy closure had a positive effect until closure attained 0.75, after which the relationship flattened out. The density of large trees predicted an increase in the proportion of forest species until a basal area of 17 m<sup>2</sup> ha<sup>-1</sup> was reached. The effect of understory management on park flora was positive at low intensity values of understory management. Mowing had a significant negative effect on the proportion of common forest species in park flora, indicating sensitivity of forest species to mowing.

### 3.6. Colonisation ecology of forest plant species

The average size of the local species pool of common forest species per park in the surrounding landscape was 66 species (SD = 10.6, ranging between 46 and 91; II). The average proportion of the local species pool that colonised park fragments was 50% (SD = 9.4). Using the larger dataset in paper III, an average of 40.2% (range 12.7–80.6%) of forest specialists from the local species pool was present in parks. In comparison, the average proportion of the local species pool in the neighbouring forest stand was 74% (SD = 11.3) and in the corridor 37% (SD = 11.0) (II).

The General Linear Model analysis showed that the proportion of common forest species pool in parks had some regional variation (Table 2 and Fig 2 in paper II). After considering region-specific variability, the proportion of the local species pool in parks was correlated with the proportional area of forest in the surrounding landscape, stand canopy closure, and the basal area of large trees in the park. The proportional area of adjacent forest land affected the proportion of species pool positively, whereas the distance from the forest did

not occur as a significant independent variable in the model. The effect of two factors, canopy closure and the number of large trees, was non-linear. The proportional colonisation success from a local species pool increased to a closure level of 0.65, after which, the estimates decreased again (Fig 2 in paper **II**). The proportion of species pool present in parks had an almost stable value up to a basal area estimate of  $13 \text{ m}^2\text{ha}^{-1}$ ; at greater values, the proportion decreased.

The results of Generalized Linear Mixed-Effect Model analysis on data of the occurrence of 160 species in parks showed that colonisation success of species was explained by a combination of habitat conditions, plant traits related to life-history, and the use of resources and landscape configuration. The landscape effect consisted of two factors: the proportion of historical forest land and the proportion of agricultural land in the area. The proportion of historical forests predicted an increase in the probability of colonisation of both forest and corridor species, whereas the proportion of agricultural land predicted increased colonisation success only of corridor specialists (Table 1 in paper **III**).

Management intensity index of parks, as a generalized descriptor for anthropogenic disturbances on a stand, had a positive effect on the colonisation success of both species groups. In addition, mowing increased the probability of colonisation of corridor specialists. Understory cover, i.e. young trees and shrubs at foliage height 1–4 m, predicted an increase in the probability of establishment of forest specialists and suppressed the colonisation of corridor specialists. Species traits, which predicted species colonisation in parks, were related to resource acquisition. Specifically, successful colonisers had earlier flowering time and were more shade tolerant (lower Ellenberg's indicator value for light), and at the same time, had a higher requirement for soil nutrients (Ellenberg's indicator for soil nutrients) and the R-strategy.

## IV. DISCUSSION

### 4.1. Habitat suitability

The structural characteristics of a forest stand (Lindenmayer et al. 2000; Scheller et al. 2008; Löhmus & Kraut 2010) can be used as an efficient means to evaluate habitat quality and biodiversity value of parks. In the present study, forest and park stands had similar tree density and canopy closure, resulting from similar light regimes in both habitat types (I, II). In addition, park stands were sufficiently dominated by broad-leaved deciduous tree species to create seasonality in understory light intensity and microclimatic conditions favourable to forest-dwelling species (Brunet et al. 2011; Ellis 2012). Moreover, the presence of old broad-leaved trees in park stands played an important role as a substrate for epiphytic forest species. In fact, the old-growth forest indicators *Neckera pennata* and *Lobaria pulmonaria* were more frequent in park stands than in forest stands. This was mostly because large broad-leaved trees were more abundant in park stands than in the surrounding forests (I). These results indicate that structurally-diverse park stands are likely to contain the specific habitat requirements for a variety of taxa or ecological guilds that are associated with high habitat quality and biodiversity value.

The amount of dead wood is widely used as an indicator of management history and intensity (Nilsson et al. 2002). Additionally, large-diameter dead wood has been shown to host a large number of red-listed saproxylic insects (Löhmus & Kraut 2010; Jonsell 2012). Due to the specific management of parks, parks are likely to have a lower diversity and less dead wood (I). The scarcity of dead wood in parks, however, was balanced by the presence of large-diameter dead wood, which was rare in contemporary forests.

Contemporary forests are often structurally degraded as a result of recurrent clear-cuts and intensive management (Kohv & Liira 2005; Scheller et al. 2008). For example, I found that forest stands had high proportions of coniferous tree species and post-clear-cut tree species, such as *Populus tremula* and *Betula* spp (I). This means that parks can be even more valuable for nature conservation of nemoral forest species than the best reference stands in a contemporary landscape (I). However, even though many old-growth structural indicators were more common in parks than in forests, both habitat types were still far from the theoretical old-growth forest (I). Therefore, more efforts should be made to attain biodiversity-supporting targets even in the best representatives of both habitat types.

## 4.2. Forest species properties

Biodiversity conservation can be effective only when the object of interest and its limiting factors have been properly recognized. Therefore, in the present study much effort has been put into identifying forest specialist species and their specific habitat requirements. A forest specialist is traditionally characterised as a shade-tolerant species with poor competitive adaptations, and limited dispersal capacity (Graae & Sunde 2000; Flinn & Vellend 2005; Brunet et al. 2012). However, previous studies have often identified forest specialists without using comparison groups. Here, the comparison of forest specialists to corridor and open habitat specialists (**III**) showed that corridor specialists were more similar to forest specialists. They can be defined as shade-tolerant generalists, which have the potential to be forest dwellers, but also use various alternative and perturbed shaded habitats in the landscape. Open-habitat specialists, on the other hand, formed a distinct group with more light demanding species (**III**).

Forest specialists are species best adapted to poor light conditions in forests (Hermy et al. 1999; Brunet et al. 2011). This was supported by their leaf traits, flowering phenology and growth form (**III**). Forest species have been shown to be sensitive to anthropogenic disturbances (Sepp & Liira 2009). Forest species indeed tolerated only low levels of management and were sensitive to mowing (**II**, **III**). Additionally, forest species expressed fairly low competitive abilities, as expected (Baeten et al. 2009b; Brunet et al. 2011). Corridor species, on the other hand, showed a greater investment in competitive strategies as would be expected from their generalist nature (Roy & Blois 2006; Wehling & Diekmann 2009b).

Forest species are considered to have a low dispersal ability (Matlack 1994; Ehrlén & Eriksson 2000; Verheyen et al. 2003b). Dispersal-related traits, however, showed patterns that seemed to contradict earlier understanding, because some forest specialists were well-adapted for long-distance dispersal (**III**). Forest species had smaller seeds than corridor species, which suggests that many seed-size drawn conclusions have been made based specifically on data from early-successional forests. Liira & Paal (2013) suggested that dispersule weight could be used to predict species dispersal ability. Here, the dispersule weight was uniformly larger for forest and corridor species in comparison to open habitat specialists. Previous research indicated that forest specialists have adaptations mostly for short-distance dispersal (Couvreur et al. 2005; Hovstad et al. 2009; Peredo et al. 2013), one of which is myrmecochory (Hermy et al. 1999). Such studies, however, usually do not use a quantitative comparison with species of alternative habitats. In my results, the most common dispersal type in all species groups was zoochory, and its significance increased towards more open habitats among both forest and corridor specialists. Furthermore, wind dispersal, which is a long distance dispersal vector, was equally common in all species groups. Forest species are shown to rely more on vegetative dispersal

(Brunet et al. 2012), but I found that forest specialists were more flexible and used both vegetative and generative reproduction. At the same time, a combined reproduction strategy of generative and vegetative type was of less importance among other specialist groups, as they rely more on generative reproduction, indicating their more opportunistic ecology (MacArthur & Wilson 1967; Pianka 1970; Grime 1979).

An additional adaptation to forest conditions within the generative reproduction type of forest specialists is an early and short flowering period, with the potential deficit of pollinators in the early season being compensated by self-pollination ability (Westoby 1998; Graae & Sunde 2000). Similarly, corridor species had an early onset of flowering, but in contrast to forest species, had a longer flowering period analogous to species of open habitats (III). Interestingly, in an alternative forest-like secondary habitat, such as a park, both forest and corridor specialists had even earlier onsets of flowering. This might indicate selective management pressure (Dufлот et al. 2014) resulting from early summer mowing in parks.

### 4.3 Colonisation ecology of forest plant species

Secondary forest stands often have a reduced number of forest specialists growing in the herb layer (Verheyen et al. 2003a; Sciama et al. 2009). However, several forest-specialist plant species, classified as ancient forest species in Europe (Peterken & Game 1984; Hermy et al. 1999; Schmidt et al. 2003), have found a way to colonise old parks (II, III). Particularly, three forest-specialist species, *Anemone nemorosa*, *Ranunculus cassubicus* and *Oxalis acetosella*, were present in the majority of the parks, with the two first ones even more common in park stands than in forests. Several forest-specialist species, such as *Galeobdolon luteum*, *Paris quadrifolia*, *Stellaria holostea* and *Athyrium filix-femina*, were also found in more than half of the parks, and nine other typical forest species were observed in 30–50% of the parks (II). Most of these species have been observed as characteristic of unmanaged boreo-nemoral stands in Estonia (Sepp & Liira 2009).

Forest-dwelling species have to overcome two critical steps to colonise secondary forests. The first step is dispersal, which depends mostly on habitat connectivity and time allowed for a dispersal event. The time lag in dispersal processes is sometimes also referred to as colonisation credit (Harmer et al. 2001; Jacquemyn et al. 2003b; Brunet et al. 2011). The selected old park stands have existed for at least a century, and this can be expected to be long enough to overcome the colonisation credit (Vellend 2003; Brunet 2007). The second step is the establishment and expansion in a stand, which depends on habitat quality in terms of optimal stand structure and management-disturbance intensity (Hartley 2002; Gauslaa et al. 2007; Vojta & Drhovská 2012). Parks showed to

have at least a sufficient minimum habitat quality to support survival of forest-dwelling species (**I, II**).

The proportion of species from the local species pool in parks was somewhat less than the same estimate in forests (50% versus 74%, respectively), but was still considerably greater than in woody corridor habitats (37%). In study **III**, the proportion of species from the local species pool was about 10% less, because of an extended sampling size toward less-suitable parks. Nevertheless, the 40–50% of the forest species pool growing in parks seems to be an encouraging result in comparison to 23% for recent forests stands observed in Belgium (Butaye et al. 2002).

Landscape aspects of forest plant dispersal predict that geographic distance from the source habitat determines colonisation success (Brunet & Von Oheimb 1998; Bellemare et al. 2002). Contrary to this expectation, the abundance of forest land in the surrounding landscape of parks was the best predictor of successful immigration of forest species. This complements observations from forests in Western Europe (Butaye et al. 2002; De Frenne et al. 2011). This result indicates that the abundance of available seed sources in the neighbourhood is probably the main critical factor compensating the minute probability of a long-distance dispersal event to occur, traditionally termed as the ‘mass effect’ (Shmida & Wilson 1985).

The habitat quality of target habitats has been shown to limit recruitment success and persistence rate in forests (Verheyen & Hermy 2001; Godefroid et al. 2011). However, my results indicate that colonisation success was limited mostly by the habitat quality of a target habitat. Limited light availability and variability are usually considered as the base conditions for the formation of a forest understory community (Dupré & Ehrlén 2002; Bartemucci et al. 2006). The general canopy closure or smaller-scale factors, such as the cover of understory foliage layer (tree saplings and shrubs), were predictors of colonisation success, partly because the specific shade provides site selection. However, the shading effect by understory facilitated forest specialists and suppressed corridor specialists, which can be explained by the greatest shade tolerance of forest specialists (Westoby 1998; Graae & Sunde 2000; Herault et al. 2005).

Colonisation is usually related to habitat area (MacArthur & Wilson 1967). However, the area of a park stand predicted the proportion of forest species in the park (i.e. community composition), but not the proportion of species present from the local species pool. Such an area effect indicates that the size of the target habitat was of minor importance to species immigration. However, larger stands often have higher habitat quality due to the larger core area being unaffected by an edge effect (Didham & Lawton 1999). The effect of patch area on forest-specialist species has frequently been observed (Dupré & Ehrlén 2002; Kolb & Diekmann 2005), but the critical minimum area in which the boundary effect has a minor impact on forest-like vegetation composition is still undefined. According to the shape of the model prediction profile, I suggest that

the minimum area of a forest-like habitat fragment required to be an efficient habitat for forest species is 2.5–3.0 ha, which is several times greater than the minimum forest patch area suggested in the literature (Honnay et al. 2002; Marozas et al. 2005; Avon et al. 2010).

The establishment of forest and corridor specialist groups was enhanced in parks where management was more sustainable. Even though park management optimises tree and shrub density for visitors, the average shade and intermediate disturbances seem to improve the overall environmental conditions in a stand towards an optimum for all shade-tolerant species (Von Oheimb & Härdtle 2009; De Keersmaecker et al. 2011; Liira & Paal 2013). However, some management treatments, such as intensive early-summer mowing, supported only corridor specialists, probably because corridor specialists with hemi-rosette growth form have a greater tolerance to mowing. This is reflected by the observed pattern of earlier flowering onset of forest species in park habitats in comparison to forest habitats. Another indicator group of forest specialists intolerant of mowing and management are ferns (McEvoy et al. 2006), which were largely absent in habitats where intensive mowing was a component of the local management regime. Only some management traits proved to be statistically significant on forest specific plants. In the context of direct management disturbances, I analysed the intensity of understory management (anthropogenic disturbance rate) and mowing, and found that both affected the proportion of forest species in parks. The negative effect of mowing on forest plants is an expected outcome. The continuous index of understory management intensity, however, revealed a unimodal response of the proportion of common forest species richness in park flora. The negative correlation between forest land proportion in the landscape and park flora can be an indirect indicator of low management intensity in recent decades. Low intensity of understory management allows park stands to become more overgrown by ornamental shrubs or tree saplings, particularly *Padus avium* and *Acer platanoides*, and this has limited the colonisation of herb species in parks. The dense stand conditions suppress competitive light-demanding species (Decocq et al. 2005; Götmark et al. 2005; Wohlgemuth et al. 2008; Sepp & Liira 2009), while the competition created by the surplus shrub-layer and tree recruits after selective management suppresses shade-tolerant species (Bailey & Tappeiner 1998; Liira et al. 2007; Bergstedt et al. 2008).

As suggested by the emerged trait patterns of forest and corridor specialists, the colonisation of a park stand was not limited by species dispersal traits. The prevalence of long-distance dispersal properties and the flexibility to use many reproductive types among forest specialists suggests that dispersal limitation has been an over-estimated factor, particularly considering that colonisation as a long-term process. The dispersal success of forest specialist species is correlated with landscape structure around forests (Verheyen et al. 2003a; Endels et al. 2007; Baeten et al. 2009a), and specifically to historically continuous habitats (Graae et al. 2004; Ewers et al. 2013). I found that the importance of the long-

term availability of seed-source habitats, such as in historical forests in the landscape, was important, but only for forest specialists. By contrast, shade-tolerant generalists, namely corridor specialists, benefited from the contemporary structure of the open landscape, in which secondary habitats, including recently created corridors and woodland edges, might be important (Wehling & Diekmann 2009a; Liira & Paal 2013). Considering the historic use of manors and their parks, the bond with dogs or horses (Heinken 2000; Graae 2002; Couvreur et al. 2004) can be important means of dispersal for many species. At present, foxes and hares are the most common animals in these rural landscapes, and their roles as potential epi- and endozochorous vectors have yet to be revealed (Heinken et al. 2001; Matias et al. 2010; Faust et al. 2011).

#### **4.4. Management recommendations**

The main factor preventing park stands from becoming universal harbours of forest biodiversity is the structural simplification by management to meet the requirements of public use and recreational purposes (LaPaix & Freedman 2010). Management effects on biodiversity are mostly indirect via changes in habitat structure (Liira et al. 2007; Reich et al. 2012; Kohv et al. 2013). With respect to forest biodiversity conservation, specific management principles should be applied in order to enhance the stand complexity. Old and large-diameter trees, snags and fallen trunks should be preserved in parks and forests in order to support epiphytes, saproxylic fungi and insects. In parks specifically, the shrub mosaic should be enhanced in order to provide necessary habitats for birds and small animals, while mowing height and frequency should be adapted to preserve ephemerals and other forest herbs. Biodiversity-targeted management in habitats open to the public, i.e. parks, would consequently increase general awareness of biodiversity issues. Old parks could be upgraded from objects of simple cultural heritage to socio-ecological systems with ecosystem-enhancing sustainable management.

## V. CONCLUSIONS

Old rural manor parks proved to be suitable habitats for many forest-dwelling species (**I**, **II**, **III**). The suitability of parks was confirmed by habitat conditions that were measured using stand structure characteristics (**I**). Park stand structure was largely similar to forests, and old planted stands in manor parks resembled broad-leaved deciduous nemoral forests even more than contemporary forests on ancient forest land (**I**). The habitat suitability of park stands was confirmed by a number of forest biodiversity indicators. Several biodiversity indicators were common in park stands with some of these indicators, for example *Lobaria pulmonaria* and *Neckera pennata*, more common in parks than in forests. These findings indicate that parks can harbour a high level of biodiversity and thus contribute to biodiversity at a landscape level.

Focusing on forest specialist plants and their colonisation ecology in park stands, I identified several characteristics of forest specialists (**III**). Forest specialist plants were characterised as species showing adaptation to intensive shade and lower soil nutrient levels, and intolerance to anthropogenic disturbances, while having a flexible reproductive and dispersal strategy (**III**). Species in corridor habitats were mostly habitat generalists according to their traits; therefore, corridors contribute little to forest biodiversity in agriculture-dominated landscapes (**III**).

Common forest species formed the majority of park flora (**II**). Forest-dwelling species in old secondary stands are supported by sufficient stand area, canopy closure and stand density. To further support forest species, understory management needs to be at an optimal level and intensive mowing should be avoided. Colonisation success of forest specialists into park stands was determined by niche defining plant traits, taking into account the habitat quality of the target habitat and the long-term availability of seed source habitats (**II**, **III**). Therefore, it is important to consider not only the present day status of the habitat and the number of species in it, but also to take into account the habitat history and its surrounding landscape (**II**, **III**).

The primary task of conservation planning should be to preserve the historical habitat patches and to maintain suitable conditions for habitat specialists in these fragments. The biodiversity conservation of old cultural habitats is achievable by focusing on the habitat quality requirements of species with conservation value, or on a more general group of habitat specialists. Adaptive management schemes should be developed to preserve and enhance current biodiversity. To support forest specialists, park management should promote a heterogeneous mid-story with a mosaic understory and a diverse overstory to diversify seasonal variations in light conditions, and avoid mowing early in the season.

## VI. SUMMARY

Forest biodiversity is among the most common, but still threatened habitats in Europe because severe human impact has reduced forest cover and decreased the habitat quality in remaining stands. Even in Estonia, where the forest land covers about half the country, the quality of habitats is often diminished. Rural parks provide a unique study system to disentangle the colonisation ecology of forest species. Even though parks have been shown to harbour indigenous species, little is known of the closed-canopy parts of parks and their ability to function as forest-like habitat. The aim of my thesis was to quantify the ecological value of old rural parks to forest biodiversity and to identify the factors that affect forest species colonisation in forest-like habitats. My first hypothesis was that old rural manor parks are a suitable habitat for forest species. Secondly, I tested whether rural manor parks harbour a high forest species diversity and contribute to biodiversity at a landscape level. I then used parks, as a model system of old secondary habitats that forest species colonised in the past, to understand the long-term colonisation processes of forest plant species.

Estonia has a large number of old manor parks, planted on former agricultural land around manors during the 17th–19th century. After Estonia became independent in 1918, and following the Soviet era, many of these parks were largely undermanaged. Low management levels allowed parks to develop into a more natural looking habitat. Here I sampled more than 70 old rural manor parks across central and southern Estonia. I compared the flora and structure of closed-canopy parts of parks with that of adjacent forests growing on ancient forest land. For this purpose, I described the stand structure and herb layer composition in parks and forests using 30-m radius sampling plots. I also used these forests as species source habitats in subsequent analyses. To identify the biodiversity conservation value of parks, I recorded the presence of biodiversity indicators, such as old-growth indicator species and dead wood quantities. In order to assess human influence, I recorded visible signs of management. To further study the ability of forest species to use different habitats, I sampled linear wooded habitats as dispersal corridors. To adequately describe the plant trait patterns of forest species, I sampled species growing in open habitats as a comparison group. I used various statistical models, such as repeated-measures ANOVA, general linear model and generalised mixed effect model, to analyse these data.

Stand structure measured as stand density and canopy closure was similar in old parks and forest stands. Park stands, however, included more large deciduous trees, whereas forest stands had more dead wood. I found biodiversity indicators from different organism groups, such as bryophytes and lichens, growing in old parks. Even more so, I found more biodiversity indicators in park stands than in forest stands. Several of these indicators were connected to the presence of large deciduous trees, which are common in parks

but rare in adjacent forests. About 87% of species growing in parks were forest plants and approximately half the forest species from the local species pool were present in parks. The proportion of forest species in park flora was explained by environmental conditions and management in parks, but also by park area and the structure of surrounding landscape. The proportion of forest species from the surrounding species pool depended mostly on landscape properties and environmental characteristics of parks, with some regions having higher forest species proportions than others. Forest species differed in their ability to colonise new habitats. Shade tolerant species that had some generalist properties were more successful and could also grow in corridor habitats. However, species colonisation success was affected mostly by the surrounding landscape structure and habitat properties, and less by species-specific traits. Landscapes in which disturbed habitats prevailed supported more generalist species, whereas better habitat connectivity supported forest species. Plant species that were more successful in colonising park habitats had adaptations to shade tolerance and earlier flowering, but also higher requirements for soil nutrients and higher values for a ruderal life strategy.

The results of my study indicated that old planted stands, such as rural manor parks, can make a significant contribution to forest biodiversity. Therefore, in addition to cultural and historical value, the biodiversity conservation value of parks should be emphasised. However, to support forest specialist species, the management level in parks needs to be kept at moderate levels. My results also imply that forest species are able to colonise forest-like habitats given enough time and suitable landscape and habitat conditions. Suitable conditions at a landscape level means ensuring the availability of species source habitats and supporting larger habitat connectivity. At a habitat level, sufficient area and limited light conditions, suitable for forest species, should be provided. However, in addition to the sufficient closure of tree canopy, it is important to have some shading from shrub layer and lower tree layers. How to combine biodiversity value and cultural aspects effectively in manor parks needs further study.

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## SUMMARY IN ESTONIAN

### Metsataimede levikuökoloogia ja mõisaparkide panus metsade elurikkuse hoidmisel

Metsade elurikkus on üks ohustatumaid Euroopas, kuna intensiivne inimõju on oluliselt vähendanud metsade pindala ja halvendanud allesjäänud metsade looduslikku kvaliteeti. Isegi Eestis, kus metsamaa katab umbes poole maismaast, on metsaelupaikade kvaliteet majandamise tõttu sageli vähenenud. Maa- piirkondade mõisapargid pakuvad ainulaadset mudelsüsteemi uurimaks metsaliikide levikuökoloogiat. Kuigi on teada, et parkides kasvab lisaks võõrliikidele ka hulgaliselt pärismaiseid liike, siis varjuliste pargiosade ja nende võime kohta metsaliikidele elupaiku pakkuda teatakse seni suhteliselt vähe. Käesoleva doktoritöö eesmärgiks oli hinnata mõisaparkide ökoloogilist väärtust metsade elurikkusele ja tuvastada tegurid mis mõjutavad metsaliikide asustamist uutes kasvukohtades. Töö esimeseks hüpoteesiks oli, et mõisaparkide taga-osades paiknevad puistud on sobivad elupaigad metsaliikidele. Teiseks, hindasin mõisa-parkide elurikkuse taset, leidmaks kas pargid panustavad elurikkusesse maastiku tasemel. Seejärel kasutasin parke, kui mudel-elupaika kuhu metsaliigid on saanud levida pika aja jooksil, et mõista metsaliikide ajast sõltumatuid asustamisprotsesse.

Eestis on suur hulk vanu mõisapärke, mis on istutatud 17.–19. sajandil endistele põllumaadele mõisamajade ümber. Pärast Eesti iseseisvumist 1918. aastal ja ka hilisemal nõukogude ajal olid mitmed mõisapargid vähe hooldatud või suisa maha jäetud. Vähene majandamine võimaldas parkidel areneda looduslähedaseks elupaigaks. Käesolevas doktoritöös uurisin üle 70 vana mõisapargi Kesk- ja Lõuna-Eestis. Võrdlesin pargipuistute taimestikku ja puistu struktuuri lähedalasuvate püsival metsamaal kasvavate metsadega. Selleks kirjeldasin puistu struktuuri ja rohurinde liigirikkust 30 m raadiusega proovipunktis nii pargis kui ka metsas. Samu uuritud metsi kasutasin ka kui liikide allikelupaiku. Parkide looduskaitse väärtuse hindamiseks registreerisin parkides esinevaid elurikkuse indikaatoreid nagu näiteks vanametsa indikaatorliike ja kõdupuidu esinemist. Parkides ja metsades esineva inimõju hindamiseks märkisin nähtavad majandamistegevuse jäljed. Metsaliikide erinevate elupaikade kasutamise võimet kirjeldasin maastikus esinevate puisjoonte abil. Puisjooned võiksid olla metsataimede levikukoridoriks. Taimetunnuste adekvaatseks hindamiseks kirjeldasin lisaks ka avamaastikes kasvavaid liike. Andmeid analüüsisin peamiselt üldise lineaarse mudeli, üldistatud segamudeli ning ordinatsioonianalüüsi meetoditel.

Puistu struktuur, mõõdetuna kui puistu tihedus ja võrade liitvus, oli sarnane parkides ja metsades. Küll aga kasvas parkides rohkem suuri laialehelisi puid, samas kui metsades esines rohkem kõdupuitu. Mitmed erinevatest organismirühmade indikaatorliigid, nagu samblad ja samblikud, kasvasid vanades parkides. Kusjuures rohkem elurikkuse indikaatoreid leidsin just parkidest.

Mitmed vaadeldud indikaatorliigid olid seotud suurte laialeheliste puudega, mis olid parkides tavalised, kuid metsades haruldased. Umbes 87% parkides kasvavatest rohurinde liikidest olid metsaliigid ja umbes pool maastiku metsaliikide liigifondist oli parkides esindatud. Metsaliikide osakaalu parkides ennustasid pargisisesed keskkonnatingimused ja parkide majandamise tase, kuid samuti ka pargi pindala ja ümbritseva maastiku struktuur. Liigifondist parki jõudnud liikide osakaal sõltus eelkõige maastiku omadustest ja pargi keskkonnatingimustest, kusjuures erinevates piirkondades oli parki jõudnud liikide osakaal erinev. Metsaliigid erinesid uute elupaikade asustamisvõime poolest. Generalistlike omadustega varjataluvad liigid on edukamad ja suudavad kasvada ka koridorelupaikades. Liikide austamisedukus on peamiselt mõjutatud ümbritseva maastiku struktuuri ja elupaiga omaduste poolt, vähem liigispetsiifiliste tunnuste poolt. Maastikud, kus domineerivad häiritud elupaigad toetavad generalistlike liikide levikut, samas kui parem elupaikade ühendatus toetab metsaspetsiifilisi liike. Taimeliigid, mis olid edukamad parkide asustajad olid kohastunud varjataluvusele ja varajasele üitsemisele, aga omasid ka kõrgemat toitainete nõudlust ja kõrgemaid ruderaalse strateegia väärtusi.

Käsesoleva doktoritöö tulemused viitavad, et vanad mõisapargid suudavad anda olulise panuse metsade elurikkuse säilitamisse. Seepärast tuleks lisaks kultuurilisele ja ajaloolisele väärtusele rohkem tähtsustada ka parkide looduskaitsealist väärtust. Toetamaks metsaomaste liikide kasvamist parkides, tuleks majandamise tase hoida parkides tagasihoidlik. Tulemused viitavad ka sellele, et metsaliigid suudavad asustada uusi elupaiku kui neile anda piisavalt aega, sobivad maastikutingimused ja elupaiga kvaliteet. Maastiku tasemel tähendab see piisavate levikuallikate kindlustamist ja elupaikade ühendatust. Elupaiga tasemel tuleb tagada elupaiga piisav suurus ja metsaliikidele sobivad varjulised tingimused. Kusjuures, lisaks võrade liitvusele tuleb tagada ka põõsaste ja järeikasvu olemasolu. Kuidas täpsemalt elurikkust ja kultuurilise aspekte mõisaparkides kombineerida vajab veel edasist uurimist.

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## **PUBLICATIONS**

## CURRICULUM VITAE

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2009, 2010 Estonian Fund for Nature, field worker for the project 'Estonian Mires Inventory completion for maintaining biodiversity'  
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Colonisation ecology of vascular plants, forest ecology, nature value of rural parks

### Publications:

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- Symposium of the International Association for Vegetation Science, 1.–5.09.2014, Perth, Australia.
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- Liira, J., Lõhmus, K., Kalda, R., Suija, A., Jüriado, I. & Jürjendal, I. Biodiversity in Estonian manor parks. *Oral presentation*. Devepark final conference, 29.07.2012, Alatskivi, Estonia.
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- Lõhmus, K. & Liira, J. The usage of woody habitats by forest plants in historically fragmented landscapes. *Poster presentation*. 54<sup>th</sup> Symposium of the International Association for Vegetation Science. 20.– 24.06.2011, Lyon, France.
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- Lõhmus, K., Tuisk, E., Vellak, K., Jüriado, I., Suija, A. & Liira, J. Old manor parks – seminatural forest communities. *Poster presentation*. Baltic Botany XXIII Conference-Expedition. 19.–22.07.2010, Haapsalu, Estonia.
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Lõhmus, K., Paal, T. & Liira, J. 2014. Long-term colonization ecology of forest-dwelling species in a fragmented rural landscape – dispersal versus establishment. *Ecology and Evolution* 4:3133–3126.

Lõhmus, K. & Liira, J. 2013. Old rural parks support higher biodiversity than forest remnants. *Basic and Applied Ecology* 14:165–173.

Liira, J., Lõhmus, K., Tuisk, E. 2012. Old manor parks as potential habitats for forest flora in agricultural landscapes of Estonia. *Biological Conservation* 146:144–154.

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- Lõhmus, K., Paal, T. & Liira J. Patterns of plant traits in wooded habitats of agricultural landscapes. *Suuline ettekanne*. Rahvusvahelise Taimkatteassotsiatsiooni (IAVS) 56. sümpoosion. 26.–30.06.2013, Tartu, Eesti.
- Lõhmus, K., Paal, T. & Liira, J. Patterns of plant traits and ecosystem services in wooded habitats of agriculture-dominated landscapes. *Posterettekanne*. Rahvusvahelise Taimkatteassotsiatsiooni (IAVS) 56. sümpoosion. 26.–30.06.2013, Tartu, Eesti.
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- Liira, J., Lõhmus, K., Kalda, R., Suija, A., Jüriado, I. & Jürjendal, I. Biodiversity in Estonian manor parks. *Suuline ettekanne*. Devepark lõpukonverents. 29.07.2012, Alatskivi, Eesti.
- Lõhmus, K. & Liira, J. Conservation value indicators of forests and forest-like habitats in historic agricultural landscapes. *Suuline ettekanne*. Rahvusvahelise Taimkatteassotsiatsiooni (IAVS) 55. sümpoosion. 23.–28.07.2012, Mokpo, Lõuna-Korea.
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- |      |   |
|------|---|
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- 2014 – Rahvusvaheline taimkatteassotsiatsiooni (IAVS) liige
- 2009 – Pärandkoosluste Kaitse Ühingu liige

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