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Immigration limitation of forest plants into wooded landscape corridors

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Press

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 original publications, referred in the text by the Roman numerals:

I Liira, J. & **Paal, T.** (2013) Do forest-dwelling plant species disperse along landscape corridors? *Plant Ecology* **214**:455–470.
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II **Paal, T.**, Kütt, L., Lõhmus, K. & Liira, J. (2017) Both spatiotemporal connectivity and habitat quality limit the immigration of forest plants into wooded corridors. *Plant Ecology* **218**:417–431.
doi: 10.1007/s11258-017-0700-7

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(15)**:3113–3126.
doi: 10.1002/ece3.1163

IV **Paal, T.**, Zobel, K. & Liira, J. Plant traits indicate that various ecological filters limit forest species use of wooded green corridors. Manuscript.

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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 collecting the data and preparing the manuscript;

IV participated in designing the methodology, collecting and analysing the data and preparing the manuscript.

1. INTRODUCTION

Due to agricultural activities, forest cover in Europe has reduced severely (Grigg 1987; Foley et al. 2005). However, in the last decades of the twentieth century, the forest area has been increasing mostly due to afforestation of former agricultural land (European Environment Agency 2009; FAO 2016). Despite the increase in secondary forest cover, repeating short-term clear-cut cycles with reforestations, the intensified silvicultural management of stands, and particularly the still ongoing conversion of forest into arable land have caused a decline in biodiversity in the remaining historical forests patches (Bengtsson et al. 2000; Riitters et al. 2012). This has led to a landscape configuration that comprises small residual ancient (historically continuous) forests and secondary forests that are embedded into an agricultural matrix (Decocq et al. 2016). Small-area forests are prone to edge effects and continuing habitat fragmentation (Bélanger and Grenier 2002; Harper et al. 2005; Liira et al. 2012). This in turn contributes to a high rate of extinction debt in fragmented forest landscapes (Tilman et al. 1994; Vellend et al. 2006). At the same time, newly formed forest stands are secondary habitats by definition, where the formation of suitable habitat conditions for forest-specific species and the arrival of these species takes time (Brunet and von Oheimb 1998; Bossuyt et al. 1999; Lõhmus and Liira 2013). The dispersal of forest species is also limited by the inhospitable surrounding agricultural matrix (Hermy et al. 1999; Butaye et al. 2001).

The concept of the patch-corridor-matrix system (van Dorp and Opdam 1987; Forman 1995; Hess and Fischer 2001) defines green corridors between isolated patches as a means to enhance landscape connectivity. Wooded corridors are defined as linear features in a landscape, structured by trees and/or shrubs, i.e., hedgerows, lines of trees or alleys. The concept of patch-corridor-matrix system has been applied extensively to the movement of animals (Bennett et al. 1994; Laurance and Laurance 1999; Chetkiewicz et al. 2006), but less attention has been devoted to quantify the success of corridors for the dispersal of forest plants (Corbit et al. 1999; Sitzia 2007; Wehling and Diekmann 2009). The concept, however, has not been equivocally accepted (Beier and Noss 1998; Niemelä 2001; Davies and Pullin 2007; Dennis et al. 2013), because many habitat-specific species, including forest plants, seem to have difficulties dispersing into and along wooded landscape corridors (Sitzia 2007; Wehling and Diekmann 2009).

The immigration (dispersal *sensu lato*) of plant species into a habitat patch (or corridor) is a process consisting of two main steps: (1) dispersal (*sensu stricto*) from the source habitat and (2) establishment and persistence in the target habitat. During these processes, several steps of ecological filtering act on species, during which species trait composition will be matched with specific properties of the biotic and abiotic environment (Keddy 1992; Zobel 1997). For instance, dispersal involves the interaction between landscape structure and dispersal traits of plants, but also comprises species availability in the local source species pool. The species pool availability is defined by the presence of historically continuous forest in the landscape and connectivity is supported by the current forest cover (Bellemare et al. 2002; Graae et al. 2004; Brunet et al. 2012). The second stage of species immigration includes filters of establishment and persistence in the target habitat. Establishment success is determined by the interaction between plant traits and the environmental conditions of a habitat (Honnay et al. 1999a; Dupré and Ehrlén 2002).

The distance from source to target habitat and other forms of landscape isolation can amplify the poor dispersal ability of forest plants (Jacquemyn et al. 2003; Flinn and Vellend 2005). Dispersal limitation of forest plants is usually reasoned by relatively large seeds, prevailing adaptation to short-distance dispersal vectors (e.g. myrmecochory, but also clonal movement), a short period of seed dormancy, low seedling recruitment rate, and a long pre-reproductive period (Bierzychudek 1982; Verheyen et al. 2003; Whigham 2004). Accordingly, dispersal success and dispersal related traits have received most attention regarding forest plants (Flinn and Vellend 2005; Hermy and Verheyen 2007).

Wooded corridors, however, are quite atypical habitats for forest plants, and therefore, the ability of corridors to harbour forest plants has been shown to depend also on habitat quality mediated by corridor structure, and plant traits responding to the corridor environment (de Blois et al. 2002; Deckers et al. 2004; Wehling and Diekmann 2008). Wooded corridors are relatively narrow and the elongated shape increases the edge effect, expressed either as increased exposure to light and/or nutrient inflow or disturbances (Hobbs 1992; de Blois et al. 2002; MacDonald 2003). An analogous edge effect can be observed in forest margins, but in contrast to forest margins, wooded corridors are exposed to edge effects from two sides, which creates a more hostile environment for species adapted to shade and stability (Fraver 1994; Honnay et al. 2002b).

In the patch-corridor-matrix system, the initial step of dispersal from source forest to target corridor is considered the most limiting (Wehling and Diekmann 2008; Roy and de Blois 2008; Humphrey et al. 2015). In the long term, however, establishment filters become more evident (Graae and Sunde 2000; Baeten et al. 2009; Liira et al. 2012). Therefore, the relative importance of these two filtering steps, dispersal and establishment, in the process of immigration into wooded corridors is still unclear when the spatial isolation is reduced to a minimum ensuring both dispersal and establishment/persistence filters to act somewhat simultaneously.

The relative quantification of forest species' specificity in comparison with species of other ecological groups is rare (Hermy et al. 1999; De Keersmaeker et al. 2011). The reported immigration success of forest plants (dispersal *sensu lato*) in corridors (Sitzia 2007; Wehling and Diekmann 2009) may be biased by the inclusion of forest generalists in the analyses, as generalists are able to cope with a greater range of habitat conditions and disturbances (Kolb and Diekmann 2005). Therefore, it is essential to distinguish between habitat-restricted and generalist forest plants to maximise the efficiency to extract limiting properties of wooded corridors. However, the difference in ecological limitations between species groups can reduce in the long term (Liira et al. 2012) or in conditions of improved landscape connectivity between species source forests and dispersal target corridors (Wehling and Diekmann 2009).

The landscape level stochastic immigration of forest plants in new habitats takes decades or centuries (Jacquemyn et al. 2001; Liira et al. 2012; Naaf and Kolk 2015), and therefore, successful immigration is determined by the long-term existence of both source forest and dispersal target corridors (Wulf and Kolk 2014; Valdés et al. 2015). Successful immigration requires also stable habitat quality in both source forest and dispersal target (either forest or corridor), particularly as the formation of optimal shade-providing overstory takes decades. Thus, when considering wooded corridors as dispersal enhancing structures of the landscape, spatiotemporal nature of the immigration process should be evaluated in late stages of community formation. However, the question about the relative role of isolation vs habitat quality remains unresolved (Humphrey et al. 2015).

The aims of this doctoral thesis were:

1) to evaluate the overall functionality of wooded landscape corridors as dispersal enhancing elements for forest plants in fragmented forest landscape, and that in the idealistic setting where the corridor is attached to the species source forest (**I**);
2) to estimate the critical set of habitat conditions of wooded corridors and surrounding landscape configuration that limit the dispersal and establishment of forest species (**I**, **II**);
3) to elucidate trait-based ecological filters acting on forest plants during their immigration from forest to corridor (**III**, **IV**).

2. MATERIALS AND METHODS

2.1. Study area

The 190 km × 120 km study region (centroid coordinates: 58°25'42.878", 26°19'45.113"; Fig. 1) is located in central, southern and south-eastern Estonia, in the hemiboreal vegetation zone of Northern Europe, which is the transitional area between the boreal and nemoral (temperate) forest zones (Metzger et al. 2005). The forest flora represents a species mixture of both nemoral and boreal zones. Average annual precipitation varies between 600 and 700 mm, and average temperatures range from –5 to –7.5 °C in February to 16.5 to 17 °C in July (Aunap 2011). The main soil types in the agricultural areas of the region are podzols, luvisols and various gleysols. The regional forest(woodland)-agricultural mosaic landscape is characterised by a relatively stable centuries-old structure. The study region is situated on flat terrain 30–100 m above sea level.

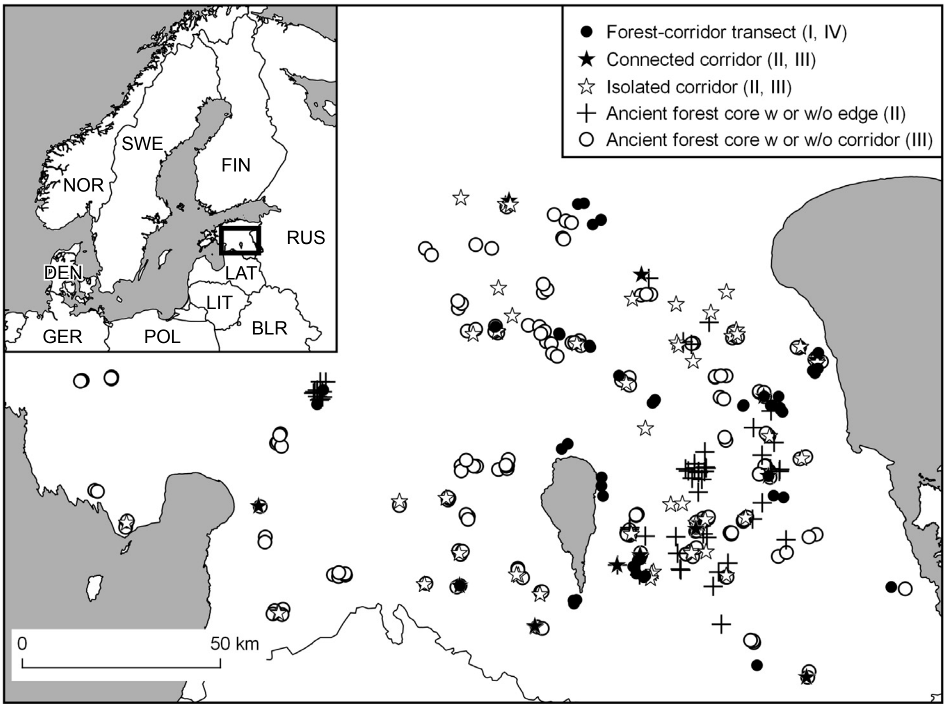

Figure 1. Map of study areas and sampling sites.

There is great variability in the origin and structural properties of wooded corridors in Estonia. Corridors structured with trees usually originate from historical alleys planted around rural manors at the end of the 19th century, or from windbreaks planted at field boundaries in the mid-20th century. Corridors dominated by shrubs and small trees situated along drainage ditches or stream banks are of stochastic origin. In western and northern Estonia, hedgerows have formed along stone fences. Many spruce hedgerows are planted parallel to main roads as shelterbelts to provide protection from snow. Wooded corridors are usually not managed, except for the trimming of planted hedgerows along roads, occasional mowing in alleys and cutting during the maintenance of ditches.

2.2. Study design

The surveys were carried out in the years 2008 to 2014 from late May to early August, a period when both spring ephemerals and summer plants were visible. The overall study design comprised two main habitat types – source forest and wooded corridor. In addition, forest edge, as the connecting point between forest and corridor, was sampled in studies **I** and **IV**, and as a comparison habitat in study **II**. Manor parks and surrounding grasslands were sampled in study **III**, but they are not explicitly considered in this thesis, as the main focus is on estimating the immigration of forest plants between forest and corridor. The selection of forests and corridors was done according to strict predefined criteria (Table 1). The final dataset consisted of 47 forest-to-corridor transects in study **I**, 91 forests, 93 forest edges and 80 wooded corridors in study **II**, 230 forests and 151 corridors in study **III**, and 50 forest-to-corridor transects in study **IV** (Fig. 1).

Table 1. Criteria for site selection. Unique requirements for a study are marked with bold roman numerals.

<table>
<tr><th colspan="2">Criteria for a site location (I, II, IV):</th></tr>
<tr><td colspan="2">• Historically continuously existing edge between forest land and open agricultural land (**II**)
• Corridor’s location cannot be on former forest land within the last century (corridor cannot be the remnant of earlier forest)
• Present surrounding matrix habitat type is arable field or rotational grassland
• Soil type is similar between forest and corridor, and suitable for (boreo)nemoral species
• Consisting mainly of deciduous trees (forest, corridor) and/or shrubs (corridor)
• Same type of habitat at least 150 m apart and structurally or historically contrasting
• Sites could contain drainage ditches</td></tr>
<tr><th>Criteria for forest:</th><th>Criteria for corridor:</th></tr>
<tr><td>• Minimum area 1 ha
• Historically continuous forest land
• Overstorey trees at least 50 years old</td><td>All corridors:
• Length at least 100 m
• Width of at least one tree/shrub canopy
• Minimum woody plant height – 2 m
Connected corridor (**I**, **II**, **IV**):
• Orientation perpendicular to the forest margin
• Continuous canopy of woody vegetation from forest to corridor
Isolated corridor (**II**, **III**)
• At least 100 m from the nearest forest</td></tr>
</table>

The forest-to-corridor transect sampled for studies **I** and **IV** consisted of eight sections along each transect – in the forest core, at the forest edge (at the connection point between forest and corridor), and at six locations along the corridor (Fig. 2, a). Forest core (i.e., the species pool in the seed source forest) vegetation was recorded in a 10 m radius plot. These forest plots were also used in study **II** together with extra plots. In the case of study **III**, forest core was sampled in a 30 m radius plot. Forest edge vegetation (**I**, **IV**) was sampled at the attachment point of the corridor to the forest in a 20 m long and 1–2 m wide strip. Forest edge in study **III** was sampled in an elongated plot of 20 × 1–5 m; the width depended on the width of the edge confined to the area under tree canopies. The corridor sampling locations for study **I** and **IV** were positioned with an approximately exponential distance step – 5, 10, 15, 25, 50, and 100 m from the forest edge. An increasing step size was selected for corridor sampling because the probability of plant occurrence has been shown to decrease exponentially in proportion to absolute distance (Honnay et al. 2002b; Wehling and Diekmann 2009; Brunet et al. 2012), and in the analyses, the exponential distance was converted into an equivalent step after logarithmic transformation. In study **II** and **III**, recording of species in the corridors was done underneath a projection of canopy on the ground in a 20–30 m section at least 50 m away from the nearest stand (Fig. 2, b). In sites where a road passed through the corridor (e.g. in alleys), species from equal widths on both sides of the road were recorded. In sites containing a drainage ditch, the lower half of the ditch was excluded from sampling to minimise moisture-related bias.

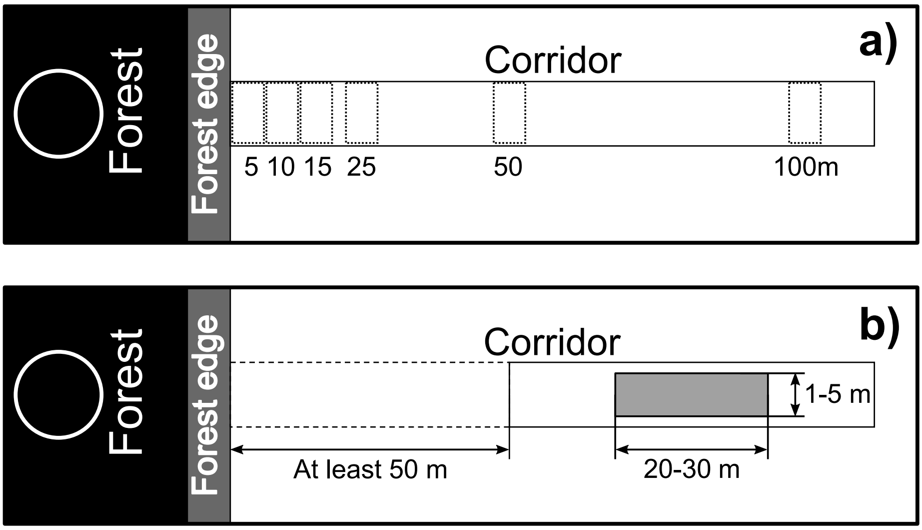

Figure 2. Schematic illustration of the sampling design for studies a) **I**, and b) **II, III** and **IV**. In study **III**, the forest edge was not sampled.

2.3. Data collection

In the field, I recorded several structural characteristics at each sampling location (forest core, forest edge, corridor): overstorey canopy cover, the diameter of the largest tree, understorey cover (shrubs and small trees), habitat width (for edge and corridor), signs of disturbance and management (i.e. cutting of trees, small-scale soil disturbances), the presence of a ditch (large-scale soil disturbance) (**I, II**), and the presence of a road (**II**). The canopy cover and understorey cover of woody plants was estimated visually in forests, edges and as an average per corridor.

In study **II**, I used LiDAR data (provided by Estonian Land Board) to calculate the average height of the tree canopy and its variation, and the length of the outer canopy edge of wooded structures (height above 3 m) in a 50 × 30 m area around each site. Canopy edge length was estimated to reflect the intensity of the edge effect.

In all studies, the soil type and texture in each sampling location was estimated using soil maps of Estonian Land Board (1:10000; xgis.maaamet.ee). Soil types were generalised into four groups reflecting forest site-types of the Estonian forest classification (Lõhmus 2004) – *Filipendula*, *Oxalis-Aegopodium*, *Oxalis-Vaccinium* and *Hepatica* (**II**). Soils were classified by moisture as fresh or moist, and by texture as sandy or clay (**II**).

The historical continuity of shade conditions (i.e. the age of woody structures) was estimated using historical maps and aerial photos, and was re-evaluated in the field. Map data for the periods 1888–1913, 1907–1939, 1945–1952, 1978–1989, 1990–2000, and 2003-present day were provided by the Estonian Land Board. The GIS-based estimate of corridor age was adjusted during field work using tree diameter or rings on the cut trunks of the largest trees. The correction was made upward only if the tree-based estimate suggested the habitat to be older than the GIS-estimated age. A threshold of 50 years was used to distinguish between young and old corridors in study **I**, because it has been shown that approximately 50 years is a critical age for forest species to be able to populate new forest patches (e.g. Brunet et al. 2011).

In study **II**, the historical configuration of forest landscape was estimated as the percentage of forest area within 100 m and 250 m radius buffers using historical maps from 1888–1913 and 1907–1939 (Estonian Land Board digital and paper archive; xgis.maaamet.ee). I categorised sampled corridors according to their connectivity to neighbouring ancient forests – (1) historically continuously connected corridors, and (2) historically isolated corridors. The defined connection of corridor to forest had to be persistent throughout the last century. The existence of a direct connection of a corridor to the nearest historical species source forest was designated by the presence of historical forest within the 100 m buffer (considering the imprecision of historical mapping). As old maps have different systems of land-cover classification, we used two forested area interpretations: forested area *sensu stricto* (henceforth ancient forest area) and forested area *sensu lato* (henceforth ancient woodland area); the latter included forest, wooded meadows and thickets. The current landscape structure around sample sites (**II**) was estimated in 100, 250, and 500 m buffers, as the percentage cover of forested area, agricultural land, permanent grassland, and residential area (buildings and associated courtyards), as well as the length of ditches and both paved and unpaved roads. As a result of map analysis, we classified 28 corridors as historically connected and 52 as isolated.

2.4. Species classification

Three types of species classification were used: on the basis of (1) transect (habitat)-scale distribution pattern (**I**, **IV**), (2) expert provided classification from literature (**II**), (3) landscape-scale pattern based on ordination of habitats (**III**).

In studies **I** and **IV**, species were classified hierarchically in two steps. In the first step, species were categorised as common forest-dwelling species (in at least 10% of forests) and common corridor/open-land species (rare in forest, but in at least 10% of corridors) of the region. Common corridor-dwelling open-land species (henceforth O-species; **I**, **IV**), are species that use corridors frequently as habitats but are not able to establish in forests. In the second step, within the common forest-dwelling species, the distinction was made between forest-restricted (F-species) and forest-dwelling generalist species (G-species) by estimating species' frequency distribution profiles along transects by using log-transformed distance from forest as a predictor in linear and second-order polynomial regression models. Species with the highest frequency in forests while significantly reducing in frequency along the corridor were classified as forest-restricted species (F-species). Species with either (1) positive linear trend, (2) non-significant trend in frequency (flat profile with average frequency greater than 10%), (3) species with a U-shaped profile (plants having a high frequency both in the forest and in the distant part of the transect), and (4) species with a J-shaped profile (significantly increasing in frequency from forest to corridor) as forest-dwelling generalists (G-species). None of the common forest-dwelling species had a reversed U-shape, i.e. maximum occurrence frequency in the first meters of the corridor. The ecology of G-species can be generalised as shade tolerant species with good dispersal ability and/or species with broad ecological niches, but they definitely contrast to F-species in their ecology due to their use of corridor habitats, and probably some other semi-natural habitats in the landscape. Therefore, the dispersal direction of G-species, whether from forest to corridor or vice versa, cannot be uniquely defined. In study **IV**, some F-species were reclassified as G-species because they have been reported as agro-tolerant species in the region, i.e. they able to use open agricultural landscape as a habitat (e.g. *Aegopodium podagraria, Ranunculus repens, Stellaria media, Urtica dioica*; Aavik et al. 2008; Aavik and Liira 2010). Among residual species that were not defined as common forest-dwelling species, we extracted species observed in at least 10% of corridors and classified them as common corridor-dwelling open-land species (O-species). Later we used them as a reference group.

In study **II**, I targeted only common forest-dwellers, i.e. species that were observed in at least 10% of forests, forming the active pool of forest species. Then I classified them into forest specialists and forest generalists according to the expert knowledge published in the German forest species classification system (Schmidt et al. 2011) as: (1) category 1.1 "species mainly in closed forest" as forest specialists, and (2) category 1.2 "species mostly at forest edges and clearings" and 2.1 "species in forest and also in open land" as forest generalists. The categorisation was adjusted according to the habitat information provided in the Estonian plant guide (Leht 2010). In addition, four species quite frequent in forest were excluded from the dataset as they are categorised as "species inhabiting also forest, but preferring open habitat" (category 2.2; *Anthriscus sylvestris, Dactylis glomerata, Galium album, Stellaria media*; Schmidt et al. 2011).

In study **III**, first, infrequent species (<10 observations per species) and cultivars were excluded. Secondly, species affiliation with forest, corridor, and open habitat in contemporary landscape was analysed on the basis of occurrence patterns using Nonmetric Multidimensional Scaling (NMS) with Sørensen (Bray-Curtis) distance with 50 iterations from a random starting configuration in PC-ORD ver. 6.05 (McCune and Mefford 2011). We then used habitat scores from NMS to define three emergent groups of species: (1) forest specialists, (2) corridor specialists, and (3) open habitat specialists, without considering data from parks. A cut-off value between point clouds of habitats along the first axis was set so that equal proportions of sites would have been misclassified. That would also allow equal misclassification of species at the borderline between two neighbouring habitat types.

In this thesis, I use only the data of species that are common in at least one specific habitat type (in at least 10% of sampled locations of a specific habitat type), and therefore, the label "common" is not used further in the text before the response group. Across papers, five terms have been used to define the forest-related response groups of interest, three of them define different ecological or classification types of forest plant species and two terms the main comparison group (shade tolerant but widely distributed species in the landscape):

1) **Forest-dwelling plants** – all plant species common in regional forests: F+G species of studies **I** and **IV**, or forest specialists in study **III**;
2) **Forest-restricted plants** – forest-dwelling plants that have limited success in colonising corridors (either limited by dispersal or establishment or both), reflected by their distribution pattern (**I**, **IV**);
3) **Forest(-dwelling) generalist** plants – forest-dwelling plants that are frequent in forests and also in corridors (**I**, **IV**); or expert based classification of forest-dwelling plants that are affiliated to forest edges, clearings or open habitats (category 1.2 and 2.1 *sensu* Schmidt et al. (2011) with regional adjustments *sensu* Leht (2010); **II**).

4) **Forest specialists** – expert based classification of forest-dwelling plants that are specially affiliated to closed forest (category 1.1 *sensu* Schmidt et al. (2011) with regional adjustments *sensu* Leht (2010); **II**);

In addition, I defined an outer reference group, frequent species in corridors and open habitats. In paper **I** and **IV**, this group is labelled O-species (common corridor-dwelling open-habitat species), in study **III**, the group is referred to as 'corridor specialists'. Additionally, in study **III**, 'open-habitat specialists' are used as a comparison group – species common in regional semi-natural grasslands. Plant nomenclature follows Leht (2010).

2.5. Species traits

I addressed traits that are related to plant dispersal, establishment, persistence and regeneration. Information on trait values for species was gathered from internet databases (Fitter and Peat 1994; Klotz et al. 2002; Kleyer et al. 2008) and different published studies (appended reference lists in **I**, **III**, **IV**). Complex requirements of species describing realised niche were described in terms of Ellenberg's ecological indicator values (Ellenberg et al. 1991) and Grime's plant strategies (Grime et al. 1988). In cases where trait information for a species was not available, estimates of the most taxonomically similar species available was used.

2.6. Statistical analyses

2.6.1. Habitat and landscape characteristics

To analyse the change in species richness along forest-corridor transect (**I**), I used a linear mixed model considering the autocorrelation within transect and response groups. Log-transformed species richness was used as a dependent variable, and distance class (forest core, forest edge, 5 m, 10 m, etc), response group (F-species and G-species) and their interaction term as independent variables. Transect ID was included as a random subject first within the response type, and secondly within the transect section using the type AR(1) setting (spatial autocorrelation intensity with autoregressive change) (Littell et al. 1996). Homogeneity groups between factor levels were tested using the Tukey HSD test. The analysis was carried out in SAS ver. 9.2.

To estimate the effect of corridor structural characteristics on the species richness of the response groups (F-species and G-species; **I**), I used linear mixed models in SAS ver. 9.2 with the same random subject configuration as in the previous analysis and only data from the corridor sections were used (distance sections 5–100 m). Structural data, which were entered in the model as independent factors, were carefully selected to avoid collinearity. All structural characteristics were analysed as two-level categorical predictors.

Corridor width was classified as narrow (<10 m) or wide (≥10 m), canopy cover as open (closure <75%) or closed (closure ≥75%), and corridor age as young (<50 years) or old (>50 years).

I used non-metric multidimensional scaling (NMDS) in study **II** to analyse the composition of all four habitat types (forest core, forest edge, connected corridor and isolated corridor). I used a presence/absence data matrix. The ordination was performed with the metaMDS function of the vegan package (Oksanen et al. 2013) in R ver. 3.3.1 using Bray-Curtis distance measure.

In study **II**, I used generalised linear models (GLM) with type III estimation of sum of squares (F-statistic was calculated with function Anova of the car package; Fox and Weisberg 2011) in R ver. 3.3.1 to test the effect of habitat structure and surrounding landscape configuration on the species richness of response groups in forest edges and wooded corridors. GLM models were fitted to untransformed count data using the negative binomial distribution family for errors and log-link function (function glm.nb of the MASS package; Venables and Ripley 2002). We built separate models for forest specialists and forest generalists. A combination of forward and backward stepwise selection was used to construct the most parsimonious model. All continuous variables were also tested for a second order polynomial trend in the model. For each explanatory variable we also tested the interaction term with the factor 'Habitat connectivity type' (levels: forest edge, connected corridor, isolated corridor). On the basis of the final models, I also calculated linear versions (square-rooted response variable to approximate model residuals to a Normal distribution) of both species group models to be able to estimate partial-η^2 for each independent variable as a measure of their relative effect size (Richardson 2011). Partial-η^2 of each variable was scaled to match the models adjusted R^2.

2.6.2. Ecological filtering of traits

General mixed models in SAS ver. 9.2 (SAS Institute Inc.) were used to quantify trait differences between species groups and habitat types (**III**). In these analyses, the average value of each trait per species group in a habitat (forest, park and corridor) was used as a response variable and species group (forest specialist and corridor specialist) as a repeated fixed factor. As 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. The landscape window was defined as a 2 km radius buffer zone around a group of sampled habitats (park, forest, corridor and grassland) and intersecting buffer zones were merged. Grassland species were used only as a comparison group for general trends on graphs. Homogeneity groups were compared with Tukey HSD test.

To illustrate changes in average trait values along corridor transect (**IV**), I used one-way repeated measures ANOVA with function lmer (package lme4; Bates et al. 2014) in R ver. 3.3.1 (R Core Team 2016). Fisher's LSD test was used for post-hoc pair-wise comparisons (function glht in multcomp package; Hothorn et al. 2008). The data table consisted of nine artificial factor levels – seven levels representing the subsets of F-species at each distance step (0 m – forest interior and forest edge pooled, and 5, 10, 15, 25, 50 and 100 m along the transect), and two levels representing reference groups (G-species and O-species). The trait levels of G- and O-species consisted of per transect averages calculated from the pooled species list. We also analysed F-species separately (at seven distances) to estimate the general statistic of trait change and the p-value without inference from reference groups. All nine factor levels (seven distance steps for F-species + transect averages for G-species and O-species) were defined as repeated measurements within the transect, and transect ID was used as random factor defining an error term to estimate F-statistic.

In study **IV**, we devised a statistical metric (CD-index) to define F-species' trait reactions along the distance out of the forest compared to reference species groups. The change of trait distribution among the filtering subset of F-species relative to reference groups was defined either as convergence with or divergence from reference group(s). We considered trait convergence when the average trait level of the subsets of F-species in the corridor became more similar to the average level of the reference group compared to the original level in the subset of F-species in the source forest. Similarly, trait divergence was considered when the subsets of F-species in corridors became more different from the reference group than the subset of F-species in the source forest. We considered G-species as the main reference group, because of their greater similarity to F-species in habitat use. O-species were used as a secondary reference group to obtain extra confirmation of the filtering effect. We also expected contrasting trait changes relative to reference groups, i.e. convergence with one and divergence from the other reference group. This would indicate that the interpretation of the filtering effect of that specific trait is not straightforward, and in that case, an educated guess should be applied.

The CD-index combines two trends into one: (1) the change of average trait value among the subsets of F-species along a transect, and (2) comparison of the change of average trait value to the average trait level of a reference group. The backbone of the analysis is a correlation analysis evaluating the strength of monotonous change of traits within the group of F-species relative to reference group level (of G- or O-species) along the distance from forest to corridor, but the sign of that estimate is modified to represent the direction of trait change relative to a reference group – becoming either more similar to or more dissimilar from the average trait level observed among species in the reference group. In calculations, we used a data matrix of trait averages of F-species at each distance step on a transect (distance sections: forest+edge as distance zero, and six distances along corridor at 5, 10, 15, 25, 50 and 100 m), and the per transect average trait values of reference groups (i.e. one estimate per transect). In all analyses, data only from those factor levels were used where the species groups were represented by more than one species.

As the first step for estimating the CD-index, we calculated the difference between the average trait values of the subset of F-species in all distance sections and the transect average of reference groups, i.e. trait contrast as $\Delta\mathrm{trait}_{\mathrm{FG,Dist}}$ and $\Delta\mathrm{trait}_{\mathrm{FO,Dist}}$, where Δtrait denotes difference, FG or FO species group comparison pairs, and Dist denotes the distance section. As the second step, Spearman rank correlation analysis was applied to quantify the directional change of calculated differences of trait levels along the distance, emphasising on a monotonous (but not necessarily linear) change of trait contrast estimates (with function cor.test of stats package in R). In correlation analysis, a negative estimate of the Spearman rank correlation coefficient (r_S) would usually indicate convergence and a positive correlation divergence. However, as the average trait level of F-species can cross the reference level (the average of a reference group), i.e. the differences between species groups can change sign along the distance, the sign of the initially calculated correlation coefficient would be incorrect. Instead, the final sign should be applied to the absolute value of a correlation estimate post hoc, using the sign of difference between absolute mean values of trait contrasts of F-species in corridor and in forest. The convergence/divergence metric as a formula is as follows:

$$\mathrm{CD}_{\mathrm{F,Ref}}=\mathrm{sgn}\left(\left|\overline{\Delta\mathrm{trait}_{(\mathrm{F,Ref})_{\mathrm{corridor}}}}\right|-\left|\overline{\Delta\mathrm{trait}_{(\mathrm{F,Ref})_{\mathrm{forest}}}}\right|\right)\times|r_S|,$$

where $\mathrm{CD}_{\mathrm{F,Ref}}$ is the continuous estimate between −1 and 1 indicating the strength of convergence (estimate between 0 and −1) or divergence (between 0 and 1) or no change of trait difference (around 0); sgn denotes the sign function, $\Delta\mathrm{trait}_{(\mathrm{F,Ref})\mathrm{corridor}}$ denotes the trait contrasts between F-species averaged over all corridor distance steps and transect average trait level of the reference group (either Ref=G-species or Ref=O-species), $\Delta\mathrm{trait}_{(\mathrm{F,Ref})\mathrm{forest}}$ denotes the difference in average trait value between the subset of F-species in source forest (distance zero) and transect average trait level of a reference group, and r_S is Spearman's correlation coefficient between $\Delta\mathrm{trait}_{(\mathrm{F,Ref})}$ at each of the seven sampling steps and the distance value. As we use the standard statistical procedure, the statistical significance of convergence/divergence can be obtained from the significance test of r_S.

Estimating the change in mean trait values does not, however, describe the case when species with extreme trait values are filtered out, leaving only species with intermediate levels, i.e. the trait average can, but does not have to change along the gradient, and only the variability of the trait decreases. Such a reduction in variability would be expected also in the case of strong convergence or divergence, as species with opposite trait levels would be filtered out. The reduction of trait variability among the subsets of F-species along the distance was quantified as Spearman rank correlation between trait variability (coefficient of variation, CV) among species within a subset of F-species at each distance step and distance along the corridor.

We postulated that the strongest proof of trait-based filtering from source to target habitat is the co-occurrence of the two changes in trait distribution:

(1) trait convergence or divergence of filter-permeated species towards/from the reference group (CD-index significantly different from zero), and (2) the decrease in trait variability (CV correlation with distance being negative). The CD-index and the correlation coefficient between CV and distance were not correlated (r_S=0.01, p=0.97), and this shows that they provide complementary information for the interpretation of F-species reactions during migration from forest to corridors.

3. RESULTS

3.1. Species classifications

The total number of species recorded in studies **I** and **IV** was 272, with an average of 60 species per transect, ranging from 19 to 103 species. The most frequent plant species per transect were *Rubus idaeus* (100% of transects), *Taraxacum officinale* agg. (98%), *Deschampsia cespitosa* (96%), *Fragaria vesca* (96%), *Paris quadrifolia* (96%), *Dryopteris carthusiana* (94%), *Urtica dioica* (94%), and *Dactylis glomerata* (91%).

Of the total of 272 species, 89 were classified as common forest-dwelling species and 40 as common corridor-dwelling open-land species (O-species) in study **I**, and 87 plants as common forest-dwelling species and 37 species as O-species in study **IV**. Based on frequency profiling, the common forest-dwelling plants were classified to 60 forest-restricted species (F-species) and 29 forest-dwelling generalist species (G-species) in study **I**. Later, in study **IV**, we corrected this classification based on additional data and knowledge on agro-tolerant species to 87 F-species and 38 G-species. The correction in classification concerned 15 species, of which 11 F-species and 4 G-species from study **I** were classified as G-species and F-species in study **IV**, respectively. Most of the species still overlapped between these studies.

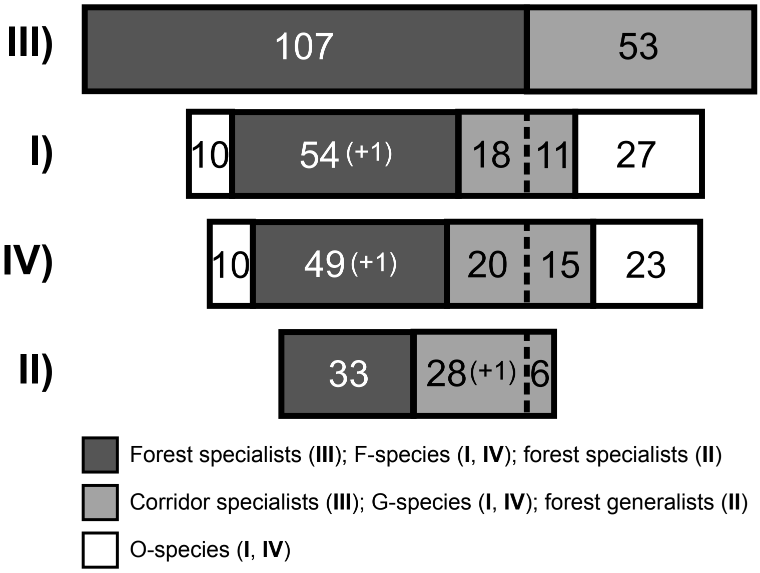

Figure 3. Comparison of forest species classifications between studies (roman numerals). The baseline comparison consists of the species classification of study **III** into forest specialists and corridor specialists (*sensu* distribution pattern in contemporary landscape context). Studies **I** and **IV** represent classifications of forest-dwelling species according to their distribution pattern along the forest-corridor transect. Study **II** represents expert based classification of species common in forests. Numbers with plus signs represent number of species of a certain group unique to the study compared to study **III**.

The final list of 204 plants species recorded in forests in study **II** was classified based on expert knowledge into 34 forest specialists and 35 forest generalists. The classification of species in study **III** based on NMS ordination scores resulted in 107 forest specialists, 53 corridor specialists, and 56 open habitat specialists.

Comparing the classification methods based on frequency (response) profiling (**I**, **IV**), expert knowledge from literature (**II**) and landscape-scale response estimated with ordination of sties (**III**), the greatest agreement in species groups was in forest specialists, as 27 forest specialists overlapped across all studies. The extremes of classifications are the expert based system (**II**) as the strictest and landscape-scale system (**III**) as the most general. The ordination based classification using landscape-scale distribution of species among habitat types (**III**) included all forest-restricted species of other classifications used in studies **I**, **II** and **IV**. Many shade tolerant generalists, particularly from expert based system in **II**, included forest plants of study **III**, emphasising that many of these species do not have an alternative habitat in contemporary landscape. At a smaller scale and in specific landscape setting, i.e. the transect of forest and connected corridor in studies **I** and **IV**, the frequency profiling based response classification agreed largely with literature based classification (**II**) (Table 2). In both systems (**I**, **II**, **IV**), the group of forest generalists also included some corridor specialists of the landscape-scale classification (**III**) (Fig. 3), or vice versa, the group of corridor specialists from study **III** was comprised of some G-species and most O-species from study **I** and **IV**. Thus, the comparison between F-species (**I**, **IV**) and forest specialists (**II**) is most reliable, while forest specialists from study **III** can really be considered as a combination of F-species and G-species from **I** and **IV** or forest specialists and forest generalists (**II**), i.e. forest-dwelling plants *sensu lato*.

Table 2. Comparison of species classifications between the strictest classifications: study **II** (the expert knowledge based) and study **IV** (the frequency profiling based).

		IV		
		F-species	G-species	Unique
II	Forest specialists	29	3	1
	Forest generalists	18	16	
	Unique	4	17	

3.2. Species richness and composition of forest-dwelling species

The species richness of forest-dwelling species (F- and G-species combined) decreased from forest to edge to corridor along the transect (test results in Table 4 in **I**). The average number of forest-dwelling species in seed-source forests was 29, at forest edge 22 and in corridor 13. More than half of F-species (57%, 34 species in study **I**; 55%, 28 species in study **IV**) were recorded in at least 10%

of corridors. There was a significant response group specific pattern of species richness along the distance (the main effect of distance classes and the interaction term with dispersal response groups in the mixed model; p<0.0001). The significant interaction term between distance and response group indicated that the species richness of F-species declined sharply from the forest (21 species) to the edge (13) and to 5 m, and then remained almost constant throughout the corridor (6), while the species richness of G-species was relatively stable along the transect (in average 7 species; Fig. 4).

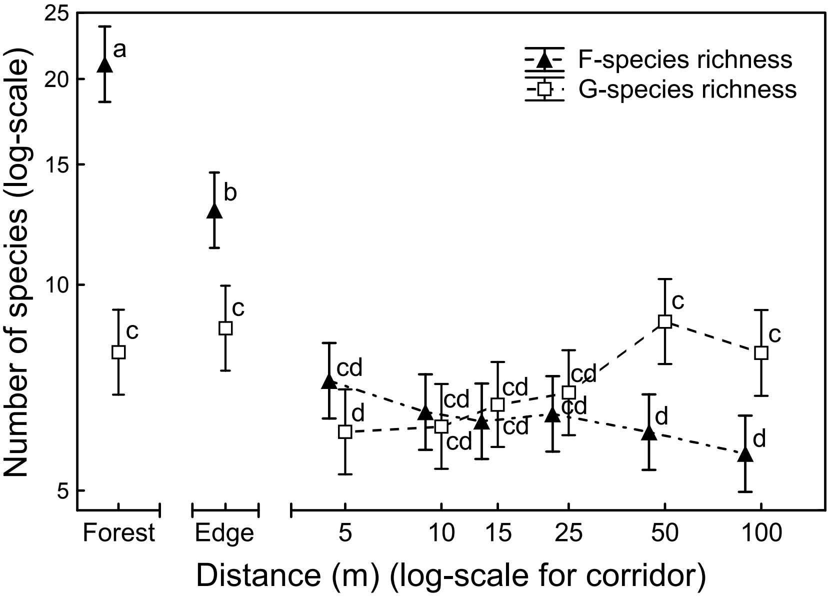

Figure 4. The change in the number of species (F- and G-species) along forest-corridor transect. Letters denote homogeneity groups based on Tukey HSD multiple comparison test. Modified from Fig. 5, study **I**.

NMDS ordination (Fig. 2 in **II**) showed a clear distinction among habitat types (MRPP test A = 0.045; p<0.001; pair-wise comparison test – all different at p<0.001 in **II**). Clusters of forest edges and historically connected corridors overlapped the most, whereas forest cores and isolated corridors had a more distinctive set of species. The centroid of forest specialist species indicates that many species are clustered around forest core sites and some species at forest edges, but the observed 90% distribution range of forest specialist species reaches only connected corridors. The centroid of forest generalists is located at forest edges, but many species were also observed frequently in forest cores. Their observed 90% distribution range covered all habitat types (Fig. 2 in **II**).

3.3. Habitat level filtering

The results of the mixed model analysis in study **I**, when only species richness data from the corridor part (5–100 m) was used, revealed some response group specific effects of corridor structure (test results in Table 4 in **I**). The richness of both response types was uniformly smaller in corridors with an intense tree and/or shrub canopy (canopy closure ≥75%; Fig. 5). The presence of a ditch in corridors had a significant positive effect on species richness only for G-species (Fig. 5, although the interaction term was non-significant, Table 4 in **I**). Corridor width had a significant but response group specific effect on richness (the interaction term significant at p=0.026) – G-species richness was enhanced in narrow (<10 m) corridors, while the effect was marginally insignificant on species richness of F-species, even though wider corridors contained slightly more species. Corridor age had an effect on both response groups, but the effect was reciprocal – the species richness of F-species was greater in older corridors (≥50 years) and the richness of G-species was greater in younger corridors (<50 years). The interactions between distance along the corridor and corridor structural characteristics were non-significant in the model, indicating that none of the structural characteristics enhanced species dispersal along corridors.

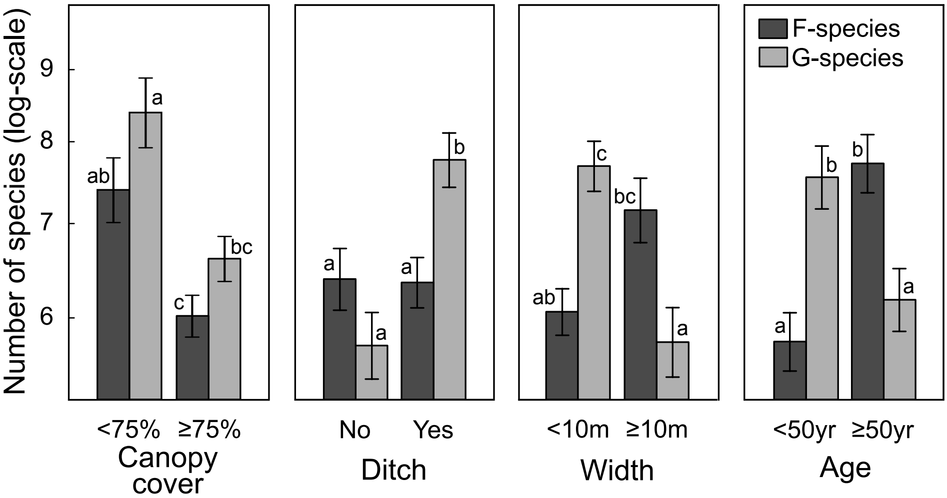

Figure 5. Structural characteristics of corridors affecting the number of species of the F- and G-response groups based on the results of the linear mixed model (Table 4 in **I**). The letters denote statistical homogeneity groups based on the results of post hoc comparisons using the Tukey HSD multiple comparison test, and the letter range is unique for each factor. Error bars denote 95% confidence intervals.

In study **II**, the analysis of corridor suitability for forest plants was limited to old (≥50 years) corridors to emphasise testing landscape level effects (connected vs isolated). The results of generalised linear regression (GLM) models for species richness of forest specialists and forest generalists showed that none of the predictor variables had a specific effect associated with a habitat type (i.e. interaction terms non-significant in the models; Table 1 in **II**). Despite a different classification of species used compared to study **I**, canopy cover, habitat width and presence of a ditch had still significant effects on species (Fig. 6). Similarly to study **I**, canopy cover had an optimum at ca 70–75% cover for both species groups, while the presence of ditch benefited generalists (**II**). However, the effect of habitat width differed slightly between studies; in study **I**, generalist species were supported by narrow (<10 m) corridors and forest specialists by wide (≥10m) corridors, while in study **II**, species richness of both specialists and generalists reacted positively to increasing habitat width (in study **II**, width was a continuous predictor and data included isolated corridors). In addition to effects found also in study **I**, the richness of forest specialists was positively related to tree height and overhanging branches (Fig. 6). The greatest proportion of variation in species richness of forest specialists was explained by habitat connectivity type (partial eta squared = 15.3%) – connected corridors had almost as many species as forest edges, and only historically isolated corridors had significantly fewer forest specialists than connected corridors (Fig. 6). Species richness of forest generalists did not differ among habitat connectivity types. The effect of spatiotemporal connectivity was also shown by a positive effect of historical woodland area in the 250 m radius buffer (6.4% of explained variance) for forest specialists, while the present day area of forest within 250 m around a site (partial eta squared = 6.9%) benefited forest generalists. Habitat structural variables accounted for 25.5% of the model variance in the case of forest specialists, of which canopy cover and presence of overhanging branches had the greatest effect. In the case of forest generalists, habitat structure explained a total of 14.2% of model variance, of which presence of a ditch had the greatest contribution (Fig. 6).

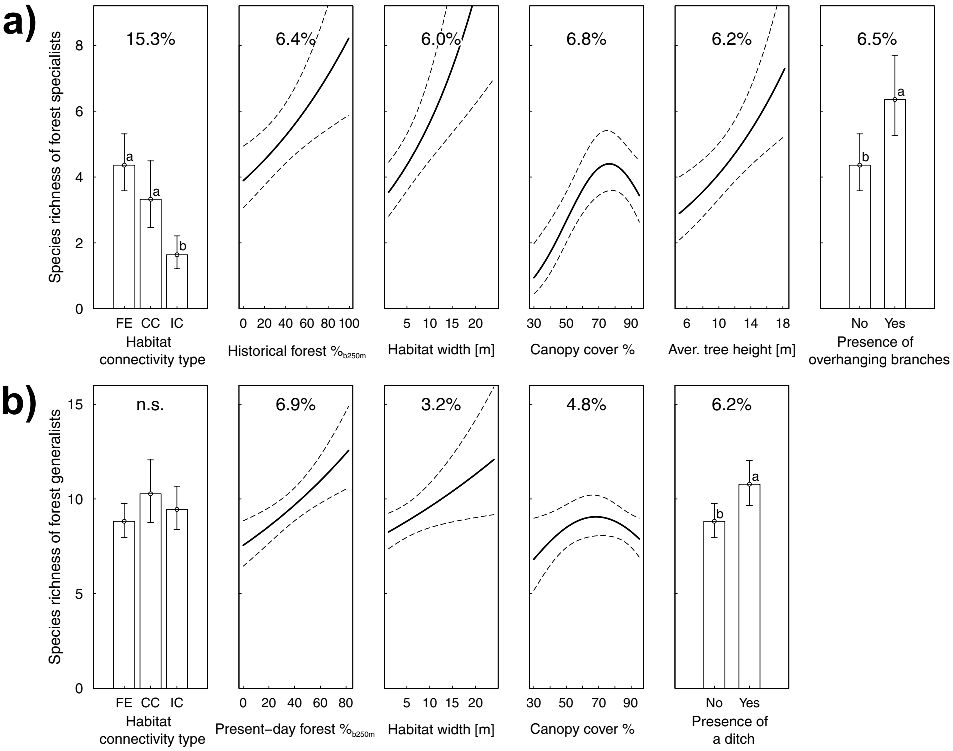

Figure 6. Fitted values of the species richness of a) forest specialists and b) forest generalists related to residual values of the significant predictors in the regression models. FE – forest edge, CC – connected corridor, IC – isolated corridor; b250 – 250 m buffer. Lower case letters denote homogeneity groups according to Tukey HSD test. Percentages show the explained variance of each variable (partial eta squared) and are scaled to R^2_{adj}.

3.4. Trait filtering

During the filtering of forest-restricted species from forest to corridor, 19 traits out of 23 showed a reaction to distance (**IV**). Of those traits, convergence/ divergence within the subsets of F-species was detected in 13 traits, of which 7 traits converged and 6 traits diverged from at least from one reference group (Fig. 7). The reduction of variability among F-species was observed in 16 traits (Fig. 7). In 10 traits, we observed the strongest confirmation of filtering, i.e. co-occurring convergence/divergence with a reduction in variability. Among those 10 traits, convergence with reference groups occurred towards greater proportion of species with hemirosette growth form (plants with both leaf rosette and leaved stem), higher stature, and higher Ellenberg's indicator value for light (Fig. 4 in **IV**); trait divergence from reference groups occurred towards the selection of F-species with greater seed mass and higher Ellenberg's indicator value for soil moisture (Fig. 4 in **IV**). The interpretation of convergence/

divergence of some traits depended on the choice of reference group, as some traits showed contrasting changes relative to reference groups. However, as we defined G-species as the primary reference group, convergence was concluded towards lower proportions of myrmecochory and ballochory, and towards greater proportion of species with ruderal (R) strategy; divergence of F-species compared to G-species was noted by higher proportion of epizoochory and proportion of species dispersing with dispersules (Fig. 7).

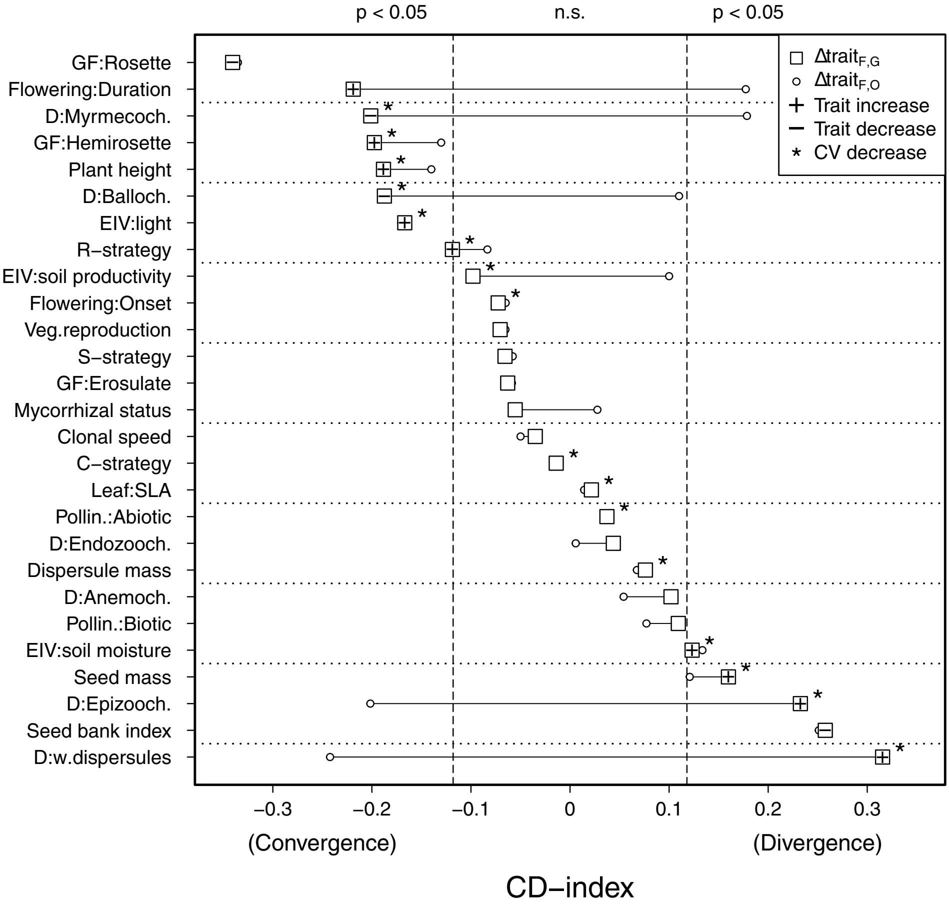

Figure 7. Ranking of traits based on the strength of correlation between difference in average trait values of forest-restricted species and a reference group (CD-index; $\Delta\text{trait}_{F,Ref}$; Ref_1=forest-dwelling generalists and Ref_2=corridor-dwelling open-land species) and distance, expressed as Spearman rank correlation coefficient. The direction of the change in average trait values along transect for forest-restricted species (plus or minus sign; see Fig. 4 in **IV**) is displayed only for significantly converging (negative correlation) and diverging (positive correlation) traits.

Three traits converged/diverged without a reduction in variability and six traits reduced in variability without significant change of mean value (**IV**; Fig. 7): (1) convergence of species groups towards lower frequency of rosette growth form, and divergence of F-species towards longer flowering duration and lower seed bank longevity without a reduction in variability, and (2) only a significant reduction in CV, i.e. Ellenberg's indicator value for soil productivity, flowering onset, SLA, C-strategy, abiotic pollination and dispersule mass (Fig. 7). The rank-ordering of traits based on the strength of convergence/divergence showed that plant growth form (rosette and hemirosette) showed the strongest convergence, while various dispersal traits displayed the strongest divergence from reference groups (Fig. 7).

At the landscape scale, trait filtering among forest specialists from source forest to an isolated corridor was observed in 21 traits out of 34 (**III**). A negative reaction from forest to corridor was observed in dispersal by myrmecochory, abiotic pollination, presence of petiole, and rosette growth form (Fig. 2–4 in **III**). Increased trait values between forest and corridor were observed for proportion of generative reproduction, zoochory (including dispersal by mammals and birds), proportion of bright flowers, biotic pollination vector, flowering onset, length of flowering and end of flowering period, EIV for light and soil nutrients (productivity), plant height, erosulate growth form, hemeroby level, and R-strategy (Fig. 2–5 in **III**).

There were seven traits that showed similar filtering effect among forest plants at habitat scale (**IV**) and landscape scale (**III**) (Fig. 8). Specifically, the proportion of plants with rosette growth form and myrmecochorous dispersal decreased from forest to corridor, while the proportion of plants with longer flowering duration, greater stature, higher EIV for light, R-strategy, and zoochorous dispersal increased (Fig. 8). Some scale-dependent trait reaction was detected for the mass of seeds and dispersules (Fig. 9). Forest plants that colonised distant parts of corridors and isolated corridors (**III**) had lighter seeds and dispersules compared to the average weight across species observed in forest, while connected corridors (i.e. at habitat-scale, **IV**) were more successfully colonised by forest plants with heavier seeds.

The repeated measures ANOVA results (Table 2 and Fig. 4 in **IV**) revealed an abrupt trait filtering of F-species at the forest-corridor transition zone, i.e. the main change in trait distribution occurred between distance steps 0 m (forest and edge combined) and 5 m, and no remarkable changes afterwards in the proportion of myrmecochory and epizoochory, plant height, and Ellenberg's indicator value for light, flowering duration; most of these traits are related to establishment and persistence. The continuous change of traits along corridors was detected for the proportion of species dispersing with dispersules, seed mass, and proportion of species with rosette growth form (Table 2 and Fig. 4 in **IV**), traits related to both dispersal and establishment.

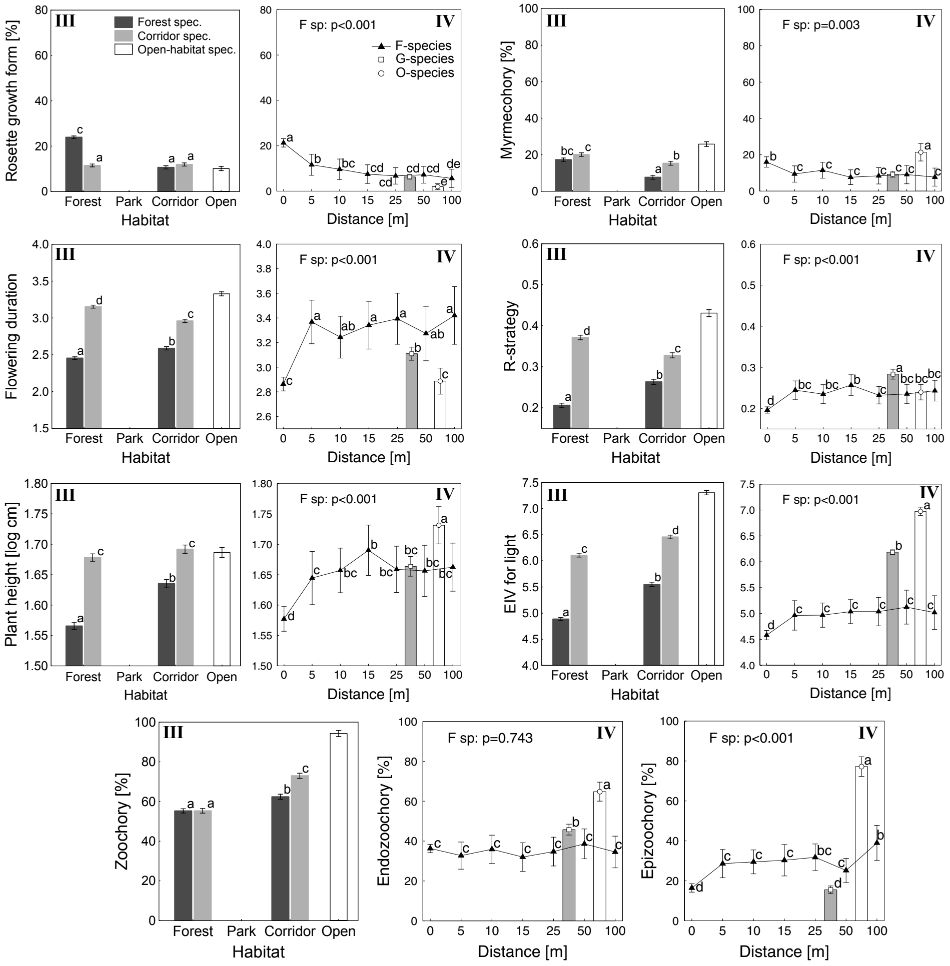

Figure 8. Patterns of functional traits among response types presented as a comparison between study **III** and **IV**. For easier reading, park data are excluded from graphs of study **III**. In **IV**, F sp represent the significance of within F-species trend, without inference from G- and O-species.

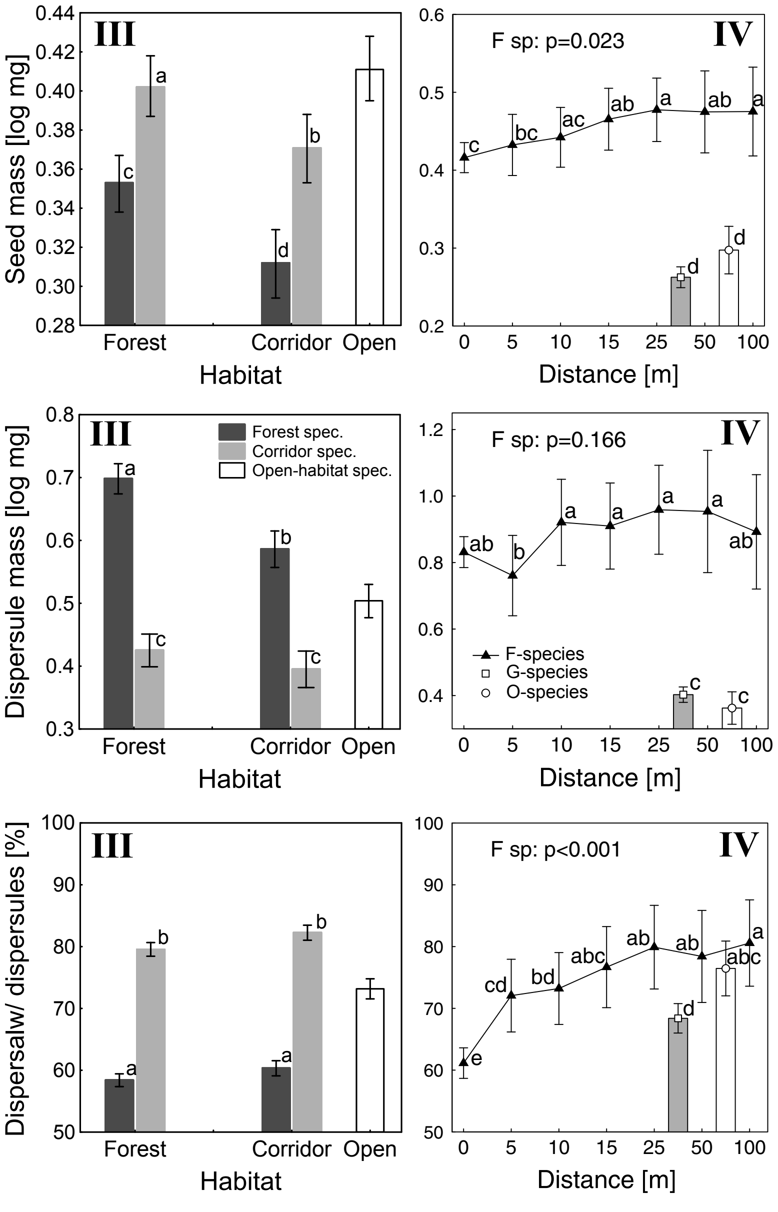

Figure 9. Comparison of seed and dispersule mass of forest plants between study **III** (landscape-scale dispersal) and **IV** (habitat-scale dispersal). Letters denote homogeneity groups based on post hoc multiple comparison tests. Open-habitat specialists are not considered in multiple comparison test in study **III**. In **IV**, F sp represent the significance of within F-species trend, without inference from G- and O-species.

4. DISCUSSION

4.1. Dispersal success into corridor

To improve the connectivity of fragmented forest landscapes with the aid of wooded corridors, forest plants must be able to disperse from source forest to and along corridors. However, we confirmed the extreme immigration limitation of forest-restricted plants into and along corridors (Corbit et al. 1999; Honnay et al. 2002a; Sitzia 2007; Wehling and Diekmann 2009); only a small fraction of the total forest specialists species pool was found in corridors (**I**). A considerable amount of forest-restricted plants were detected only at the edge and in the first meters of the corridor, and it seems that they were not able to disperse farther (**I**, **IV**). Generalist forest species, however, did not show an immigration limitation even into remote corridors (**I**, **II**). Nevertheless, the dispersal pressure of forest-restricted plants out of the forest can be quite substantial, as the species richness at the forest edge was still relatively high (**I**), and many forest-dwelling species were able to immigrate into distant novel forest-like habitats, such as parks (**III**). Therefore, establishment limitation might be more important. These results indicate that overall, wooded corridors at the present state do not significantly enhance the migration of forest plants across the landscape.

4.2. Habitat and landscape structure affecting forest plant migration

What are the specific corridor structure-based restrictions to forest plants? The increased light availability in corridors due to the edge effect has been considered the main driver of habitat quality in corridor habitats (Hobbs 1992; Murcia 1995; MacDonald 2003). Indeed, I found that both forest specialists and generalists showed preference for shaded conditions in corridors (and forest edges); both exhibited most successful immigration at canopy closure around 70–75% (**II**), but the over-intensive shade (>75% cover) from trees and shrubs also caused a resource limitation for both species groups (**I**, **II**, Liira and Sepp 2009; Van Couwenberghe et al. 2011; Liira et al. 2012). However, the specific properties of light/shade conditions are more important for forest specialists (Brunet et al. 2000; Wehling and Diekmann 2008), as in corridors they responded positively also to tree height and to the presence of overhanging tree branches at habitat margins (**II**). Tree height can be interpreted as a combined indicator of tree age (continuity of shade conditions over decades) and structural maturation of the overstorey (i.e. old trees usually exhibit a structurally different canopy) (McElhinny et al. 2005) with the potential for the formation of overhanging tree branches. These hanging branches suppress lateral penetration of irradiance, i.e. one of the components of the edge effect (Wehling and Diekmann 2008; Hamberg et al. 2009). However, these branches are frequently cut off, and therefore, the trait ‘overhanging branches’ could be included into the model as an independent driver.

In addition to overstorey mediated suppression of edge effects, corridor width also contributes to the improvement of habitat quality for forest plants. It has been suggested that forest plants require a corridor width of at least 10 m (Sitzia 2007; Roy and de Blois 2008), but our results showed that corridor width has no clear threshold for forest-restricted species (**II**, see also Forman and Baudry 1984), and corridor width has not reached the saturation of the species-area effect. More confusing was the reaction of forest generalists that showed opposite reactions to width between studies **I** and **II**, i.e. a negative reaction to wider corridors in study **I** compared to the positive reaction in study **II**. This is probably due to the interaction between different immigration history of generalist species and habitat age. In study **I**, where young corridors were also included, wide and young corridors seem to have specific conditions that limit the quick accumulation of generalists, while in study **II**, where only older (>50 years) corridors where studied, a longer time for dispersal allowed reaching a level of immigration saturation that was reflected by habitat area and suppressed edge effect. Another option is that ancient forest is not the main source of shade-tolerant generalist species and the effect of other sources over a longer time emphasises the positive effect of width. Anyway, as habitat width had only a minor effect in predicting the species richness of species groups, and particularly for forest generalists (**II**), the contradiction can be left to be solved by more specific studies. We conclude that concerning the main group of interest, forest restricted species, the edge effect has a limited range and is suppressed by structural features of a mature overstorey (Matlack 1993; Didham and Lawton 1999; Hamberg et al. 2009).

Many wooded corridors in the study area have established spontaneously along drainage ditches, or a ditch was constructed inside an alley to drain excess rain water from roads. The establishment of forest plants is known to depend on the availability of disturbance created microsites (Baeten et al. 2009; Brudvig et al. 2011); therefore, ditch banks could potentially provide establishment gaps for forest plants. However, I found that micro-habitats with soil disturbance at ditch banks were exploited only by generalist forest species (**I**, **II**). This indicates that the establishment of forest-restricted species is not limited by the availability of disturbance-created microsites. Thus, ditches may promote the establishment of only forest generalists.

Besides habitat physical features, habitat age (i.e. time factor) is commonly seen as a factor supporting the accumulation of forest species richness in newly-formed forest fragments and corridors (Jacquemyn et al. 2003; Flinn and Vellend 2005; Roy and de Blois 2008), even if its effect has not always been evident (Vellend et al. 2007; Wehling and Diekmann 2009; Baeten et al. 2010). We did, however, find that the long-term continuity of shade conditions had a species group specific effect (**I**) – more forest specialist (forest-restricted) species established with increasing corridor age, while generalist forest species were more successful in younger corridors (<50 years). The importance of time is also apparent when considering the effect of landscape scale dispersal of forest plants. The immigration of forest specialists into corridors was supported only by the long-term existence of historical (ancient) woodland around a corridor, while forest generalists reacted positively to recent changes in forest area (**II**). The observed contrasting responses of forest specialists and generalists on habitat age suggests that corridors with long historical continuity will obtain specific qualities which are difficult to define, but somehow support forest specialists, yet do not influence the accumulation of generalist species.

The importance of direct long-term physical shade providing a connection between source forest and linear habitats has been shown to be important for many forest specialists, but not for generalists (Dupré and Ehrlén 2002; Kolb and Diekmann 2005; Peppler-Lisbach et al. 2015). Forest specialists, however, are able to disperse from patch-to-patch as well (i.e. island-type dynamics; Liira et al. 2012; Liira et al. 2014), particularly when novel stands have greater long-term stability and higher habitat quality than surrounding forests (Lõhmus and Liira 2013). However, I found that habitat connectivity explained a considerable proportion of variation in species richness of forest specialists (**II**) – isolated corridors had significantly fewer species than connected corridors. This shows that even if sufficient time has been provided for dispersal and development of high habitat quality, isolated wooded corridors are still not able to function as corridors or stepping-stone habitats for forest specialists.

4.3. Ecological filtering between forest and corridors

The first step of ecological filtering consists of overcoming spatial isolation by dispersal (*sensu stricto*), in this case, from source forest to target wooded corridor. Forest specialists (or "ancient forest plants") are characterised by specialisation to short-distance dispersal (Hermy et al. 1999; Verheyen et al. 2003; Whigham 2004), e.g. myrmecochory, and thus are considered poor dispersers. However, our findings challenge the earlier opinion that forest specialists are adapted mostly to short-distance dispersal, as various types of zoochory were common among forest specialist species (*ca* 50% of all forest specialists) in addition to *ca* 30% of anemochorous species (**III**, **IV**).

In conditions where the spatial isolation driven dispersal filters were minimised, i.e. in well-connected corridors (**IV**), there was still a multi-trait indication of the small-scale dispersal limitation of forest specialists. For instance, we observed a decrease in the frequency of forest-restricted plants adapted to myrmecochory and ballochory from forest to corridor despite the lack of obvious structural limitations to dispersal. Forest species that use long-distance dispersal vectors were well adapted to disperse at small (**IV**) and large scales (**III**). The proportion of forest-restricted species with relatively high rates of specific dispersal modes such as the use of dispersules for dispersal (**IV**), and more specifically, the use of epizoochory (**III**, **IV**), increased from forest to corridor. Also, seed mass, as the most commonly used indictor of dispersal ability

(Westoby 1998; Weiher et al. 1999), diverged from reference groups among those forest-restricted species that migrated from forest to corridors, i.e. forest-restricted species that were able to migrate into corridors had greater seed mass. Contrary to expectation, the importance of seed mass was scale dependent, i.e. at the habitat scale (from forest to connected corridor), species with heavier seeds dispersed farther along the corridor (**IV**), while at the landscape scale (from forest to isolated corridors; **III**) forest species with lighter seeds succeeded. Differences of scale can probably be related to specialisation to zoochory and specific vector species – if they move more at local scale or across the landscape, and which landscape elements do they more frequently use as stepping-stone habitats. For instance, large-seeded forest species have been observed to prevail in small isolated forest(-like) fragments (Lindborg et al. 2011), which was also observed in manor parks (Fig 2.4 in **III**), and therefore, patch habitats are probably preferred by vector species of large seeded plants. Therefore, we tend to conclude that seed mass may not indicate dispersal ability or disability as assumed at smaller scale, but rather the establishment efficiency in conditions of more intensive competition (Weiher et al. 1999; Moles and Westoby 2004). Instead, dispersule mass should be used to predict species dispersal ability, because dispersule mass includes seed conglomerates, dispersal aiding appendices and rewards for dispersal vector animals. Therefore, forest species had uniformly larger dispersules in comparison with open habitat species across all studies and classifications (**I**, **III**, **IV**).

Relatively similar and diverse dispersal adaptations of forest-restricted plants to reference groups suggests that forest-restricted species have higher probability to migrate into distant corridors or isolated forest patches than reflected by their realised distribution pattern. Therefore, it can be assumed that the second stage of immigration, establishment has a more important role than emphasised by earlier studies.

Forest plants are most often defined by their ability to tolerate shade-induced stress (Hermy et al. 1999; Whigham 2004), which causes a trade-off by reducing the competitive ability with light-demanding species in open habitats (Meiners and Pickett 1999; Fahey and Puettmann 2008). Competition for light resources is considered to be one of the primary limitations to establishment, particularly in secondary stands (Elemans 2004; Whigham 2004; Wehling and Diekmann 2008; Brunet et al. 2011). Indeed, forest-restricted species having the lowest Ellenberg's light indicator value (Ellenberg et al. 1991), i.e. adapted to the low-light stress, were filtered out in corridors (**III**, **IV**); the trend was further supported by their constantly low C-strategy and high S-strategy levels. I also found convergence in traits related to the ability to compete for light, such as plant height (**III**, **IV**) and the replacement of the rosette growth form with the hemirosette (**IV**) or erosulate growth form (**III**), and the increased proportion of R-strategy species (**III**, **IV**). The reaction to increased irradiance in corridors was not, however, supported by specific traits of light adaptation, such as SLA, as it maintained its high value among forest-dwelling species across habitats (**III**, **IV**). Still, some filtering did occur, as both C-strategy level and SLA lost some variability among the subset of filtered forest-restricted species (**IV**). This indicates that forest-restricted species are limited by both biotic and abiotic filters in corridors, and specifically those that are associated with increased light levels in corridors and competition with other species in these conditions (Graae and Sunde 2000; Westoby et al. 2002; Brunet et al. 2012).

A wider phenological niche could be an alternative strategy of forest plants to survive in high-competition conditions (**III**, **IV**), as the filtered subset of forest-restricted species in corridors flowered longer than forest-dwelling generalists. In addition, the subset of forest specialists in isolated corridors started to flower later, but the flowering also ended later (**III**). As forest-restricted species are mostly insect pollinated (more than 80%) (Graae and Sunde 2000; **III**, **IV**), a long flowering duration would increase the plant's probability of generative reproduction even if a single individual has established, and particularly when they have a short-term seed bank. While forest species have been shown to rely more on vegetative dispersal (Brunet et al. 2012), we found that forest specialists are more flexible and use both vegetative and generative reproduction (**III**). In addition, the patterns of other flowering traits, such as a larger proportion of species with bright-coloured flowers and biotic pollination vector in corridors (**III**), indicate an evolutional reproduction advantage of insect-pollinated flowers in alternative habitats for forest specialists.

Alternatively, one could expect that establishment filters related to soil properties should also be important, as the soil chemistry and structure in corridors has been altered during the earlier agricultural use of those areas, and is still continuously being affected by adjacent agricultural activities (Honnay et al. 1999b; McCollin et al. 2000; Wehling and Diekmann 2009) and road management. However, we did not detect an effect using Ellenberg's indicator values for soil productivity in the small scale (**IV**), but an increase of the proportion of species adapted to higher soil productivity values when landscape scale classification of forest specialists was applied (**III**). Additionally, we observed divergence of forest-restricted species from reference groups to higher soil moisture preference on forest-corridor transect (**IV**). This hints that increased soil nutrient levels and ditches in our study system may have had a filtering effect for forest-restricted species.

5. CONCLUSIONS

Wooded corridors, in their present state, do not perform well as dispersal enhancing structures in the landscape for forest-restricted plants (**I**, **II**, **IV**). Immigration limitation of forest-restricted plants from forest to corridor was determined by both ecological filters of dispersal and establishment/persistence (**III**, **IV**). Dispersal filters promoted species adapted to long-distance dispersal vectors. Establishment/persistence filters select taller species adapted to higher levels of light, but also that flower longer, whereas short rosette-forming shade and stress adapted species are filtered out (**III**, **IV**). Even when corridors are directly connected to forests, many forest plants are not able to pass ecological filters at the forest edge and in the first 5–10 m of the corridor out of forest (**I**), probably because establishment filtering occurs mostly at the forest edge (the connection point between forest and corridor), while dispersal filtering affects species gradually (traits changed along the corridor) (**IV**).

Species ecological filtering depends on the habitat quality of a corridor and its surrounding landscape. Critical for forest-restricted species are optimal canopy cover (>75%), width (>10m) and age (>50 years), while the opposite was true for forest generalists (**I**). If only older corridors (>50 years) are addressed, such a contrast between species response groups is not evident any more (**II**). In addition, in older corridors, habitat quality for forest specialists was indicated by the structures of the corridor, such as higher and older trees with lateral branches overhanging towards the cropland (**II**), while the presence of a ditch in the corridor supported forest generalists (**I**, **II**). Among landscape conditions, isolation/connectivity matters, but the corridor's ecological value is higher for forest specialists when it is neighboured by historical forest area, while changes in the present-day forest area around the corridor improved the habitat value for forest generalists (**II**). Therefore, when defining corridor's habitat quality, both structural and spatial properties should be considered.

Both well-connected and isolated wooded corridors support mostly forest-dwelling generalists and rarely forest-restricted plants (**I**, **II**). Environmental conditions in corridors do not vary much with the distance from the forest, and therefore each corridor can be considered a specific and homogeneous habitat unit in the landscape. In conservation planning of wooded corridors, old corridors with structurally mature trees and good connectivity to historical forest areas (as source habitats) should be a priority over planting new corridors. The planting of new corridors into the open landscape will have an extensive time lag before the formation of suitable shaded forest-like habitat conditions. The short-term responses by forest generalists can leave an over-optimistic impression of recently established corridors. Restoration schemes of wooded corridors should prioritise the planting of new tree lines in areas where historically continuous (ancient) forest habitats as species sources are nearby, and the planting of double tree lines (e.g. alleys) is preferable to planting narrow single tree lines or hedgerows. Management of wooded corridors should aim at preserving a dense overstorey of trees, enhancing their arc-type canopy, and maintaining branches overhanging towards the cropland impeding edge effects. Pruning and coppice should be avoided and renovation of corridors should see continuous planting of new trees into formed gaps.

6. SUMMARY

Afforestation-formed new stands, repeating short-term clear-cut cycles with reforestations, the intensified silvicultural management of stands and the still ongoing conversion of forest into arable or rural land have caused the continuing decline in forest biodiversity. This has led to the formation of a landscape that comprises small forest stands with low habitat quality that are isolated by the agricultural matrix. In newly afforested areas, the formation of forest-specific vegetation is impeded by the poor immigration success of forest plants across the inhospitable surrounding agricultural matrix. According to the concept of the patch-corridor-matrix system, wooded landscape corridors are proposed as a means to increase the connectivity between species source and target habitats, therein to enhance the dispersal of forest-specific vegetation in fragmented forest landscapes. Wooded corridors are defined as wooded linear features in a landscape, such as hedgerows, lines of trees or alleys. The function of green corridors, however, has been applied extensively to animal movement, but less attention has been devoted to quantify the success of corridors for the dispersal of forest plants. The concept has not been equivocally accepted, because many habitat-specific species, including forest plants, seem to have difficulties dispersing into and along wooded landscape corridors. The aim of this doctoral thesis was to evaluate the overall functionality of wooded landscape corridors as dispersal enhancing elements for forest plants of deciduous forests and to elucidate ecological filters (either plant trait based or as corridor conditions at habitat and landscape scale) acting during forest plants' migration from forests to corridors.

I sampled numerous wooded corridors with different habitat quality and connectivity. Habitat quality was described as habitat age, structural properties of woody vegetation and corridor's abiotic structures. Connectivity to source forest was defined either as having a direct connection with potential source forest vs isolated in the agricultural landscape, or as the area of ancient forests in the landscape. I recorded the presence of forest plants in ancient forests and in corridors. Common species in forest were classified using different methodology, either according to their frequency profiles or by using expert opinion. Empirical response groups addressed were plants restricted to the forest environment (forest specialists) and forest-dwelling generalist plants (forest generalists). Using statistical models, I analysed the response of the species groups to trait-based ecological habitat filtering, and corridor structure and landscape configuration based limitations to species groups' success in wooded corridors. I used various statistical techniques, such as repeated measures ANOVA, linear mixed models, generalised linear models, and also developed original methods.

I found that forest specialists are very limited in their migration success into wooded corridors, even in conditions where the corridor was directly connected to source forest. Most of forest specialists were filtered out already in the first

5–10 m of the corridor outward from the forest, and in isolated corridors the success of forest specialists was the lowest. In contrast, there was no colonisation limitation observed for forest generalist plants, even in isolated corridors.

Immigration of forest specialists from forest to corridor was determined by both dispersal and establishment/persistence filters. Species adapted to short-distance dispersal, i.e. myrmecochory, ballochory, were mostly filtered out in corridors, but species with long-distance dispersal, i.e. zoochory, increased in frequency. Among establishment filters, taller more ruderal-strategy forest-restricted species that tolerate higher levels of light and flower longer are favoured in corridor conditions, whereas short rosette-forming species adapted to shaded and stressful forest environment were filtered out. Habitat quality of corridors was determined mostly by edge effect mediated light conditions and spatiotemporal stability (age and historic neighbourhood) of the habitat. The success of forest specialists was positively related to high canopy cover (*ca* 75%) and great width. In addition, the edge effect for forest specialists was reduced in corridors by old trees having lateral branches overhanging the cropland. The presence of a ditch in the corridor supported only forest generalists. Among landscape conditions, forest specialists were supported by a historical area of surrounding forest, while the success of forest generalists in corridors was related to the surrounding present-day forest area.

The results of this thesis indicate that wooded corridors in their present state do not perform well as dispersal enhancing structures for forest plants. Only those forest plants that are able to utilise long-distance dispersal vectors, such as mammals or birds, and those that can tolerate the edge effect mediated environment of corridors are able to migrate into and along wooded corridors. Conservation efforts should be focused on corridors that are directly connected to ancient forest, and the structures of those corridors should limit edge effects, i.e. a double tree line with wide-arching mature tree canopies and with lateral side branches. Maintaining and managing existing wooded corridors should be preferred over planting new tree lines, as the formation of suitable habitat conditions takes decades or centuries.

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SUMMARY IN ESTONIAN

Metsataimede levimisedukus avamaastike puiskoridorides

Viimastel aastakümnetel on metsamaa osakaal Euroopas järjest suurenenud vanade põllumaade metsastumise tõttu. Samal ajal on jätkunud vanade ajalooliselt järjepidevate metsade pindala ja elupaigakvaliteedi vähenemine. Suurepinnalise põllumajanduse tõttu on nii sekundaarsed kui ka ajalooliselt järjepidevad metsad maastikuliselt killustunud ja isoleeritud, mis omakorda mõjub negatiivselt metsadega seotud elurikkusele. Et parandada sekundaarsete metsade maastikulist ühendatust ning samal ajal ka nende elupaigakvaliteeti, on pakutud välja ühendada metsatukad omavahel puiskoridoridega. Oma teesides uurisin, kas puiskoridorid toetavad metsataimede levikut ning millised taimede funktsionaalsetest tunnused, koridori struktuursed omadused ja maastiku eripärad määratlevad metsataimede ökoloogilised piiranguid levimisel metsadest puiskoridoridesse.

Käesolevas töös uurisin salu-(ja laane-)metsa rohttaimede liikide levikut nii metsaga ühendatud kui ka avamaastikuga isoleeritud koridorides, eeldades et koridori läheduses olevad ajalooliselt järjepidevad metsad on leviku allikaks. Igas koridoris ja metsas kirjeldasin lisaks taimede liiginimekirjale ka puistu struktuuriparameetrid, näiteks võrade liituvus, põõsarinde katvus, kuivenduskraavide ning maapinnahäiringu esinemine. Lisaks sellele kirjeldasin veel ka koridore ümbritsevat maastikku. Analüüsis keskendusin piirkonna ajalooliselt järjepidevates metsades kõige sagedamini kasvavatele liikidele, klassifitseerides neid eelnevalt erinevaid metoodikaid kasutades kahte rühma – metsaspetsialistid ning metsas kasvavad varjutaluvad generalistid. Analüüsisin liigigruppide tunnusmustrite muutumist metsast koridori kui ka koridori ja ümbritseva maastiku struktuuri mõju liigigruppide levimisedukusele koridoridesse. Statistilistest meetoditest kasutasin korduvmõõtmistega dispersioonanalüüsi, korrelatsioonanalüüsi, üldistatud lineaarseid mudeleid, üldist segamudelit kui ka ordinatsiooni.

Leidsin, et spetsialist-tüüpi metsataimed on piiratud levimisedukusega puiskoridoridesse. Isegi metsaga vahetus ühenduses olevates koridorides kahanes metsaspetsialistide liigirikkus järsult juba esimesel viiel kuni kümnel meetril. Veelgi vähem edukad olid metsaspetsialistid levimisel maastikuliselt isoleeritud koridoridesse. Võrdluseks, generalist-tüüpi metsaliikide levimisedukus oli ühetaoline sõltumata koridori ühendatusest. Koridori elupaigakvaliteet oli suuresti määratud servaefektist tuleneva lisavalguse tingimustest, sest metsaspetsialist taimede liigirikkus oli suurem optimaalse võrade liituvuse (ca 75%) ja võimalikult laia koridori puhul. Lisaks oli oluline servaefekti leevendavaks teguriks ka juba küpses vanuses puudest moodustunud koridor ning eriti kui neil puudel olid alla kaardunud ja varju pakkuvad külgoksad. Kuivenduskraavi esinemine koridoris oli oluline vaid generalist-metsaliikidele. Maastikuskaalas oli oluline koridori ajalooline vanus ja koridori ümbritseva ajalooliselt järjepideva metsamaa hulk. Mõju erines liigigrupiti – metsaspetsialistidele oli oluline sajanditaguse metsamaa osakaal maastikus, kui generalistidele oli oluline metsamaa osakaal tänapäeval.

Uurides taimede funktsionaalsete tunnuste mustri muutumist metsast koridori leidsin, et metsaspetsialistid on mõjutatud nii seemne levikuvektori eripärast kui ka taime asustamist ja püsimajäämist mõjutavatest tunnustest. Need liigid, mis on adapteerunud lühimaalevile, näiteks mürmekohooriale või ballohooriale, ei suuda koridori levida nii edukalt kui zoohoorid. Asustamistunnustest olid metsaspetsialistide edukusega positiivselt seotud ruderaalsemad kõrgema kasvuga taimeliigid, mis suudavad konkureerida teiste taimeliikidega koridoride valgusküllasemates tingimustes. Eriti rosetti moodustavad madala kasvuga liigid, mis on kohanenud stabiilsele ja varjuküllasele metsakeskkonnale, ei suutnud koridori asustada.

Käesoleva doktoritöö tulemused viitavad sellele, et puiskoridorid ei toimi kui metsataimede levimist toetavad maastikustruktuurid. Ainult sellised metsataimed, mille levised kanduvad pika maa taha, näiteks imetajate või lindude abil, suudavad koridori levida. Lisaks suudavad needsamad liigid ka juba järgmisse metsatukka levida ehk neile pole puiskoridoril suurt lisaväärtust. Koridorides suudavad kasvama jääda vaid need metsataimed, mis suudavad kasu lõigata servaefekti tõttu paranenud valgustingimustest. Arvestades ka looduskaitselisi eesmärke, tuleks maastike planeerimisel keskenduda juba olemasolevatele laiadele puiskoridoridele, mis asuvad ajalooliselt järjepidevalt eksisteeriva metsa läheduses ning mille aastakümnete jooksul välja arenenud struktuur suudab leevendada servaefekti mõjusid. Sellised koridorid on näiteks kahe- või enamarealised vanad alleed, millel on juba väljakujunenud kaarjas võrastik ning külgmised allalaskuvad oksad. Praktikas tuleks eelistada olemasolevaid puiskoridore ning nende sujuvat noorendamist uute alleede istutamisele, kuna sobivate struktuursete tingimuste moodustumiseks kulub aastakümneid.

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