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MARI-LIIS VILJUR

# Local and landscape effects on butterfly assemblages in managed forests

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# Local and landscape effects on butterfly assemblages in managed forests

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Department of Zoology, 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 consists of the following articles which are referred by their Roman numerals.

**I** **Viljur, M.-L.** & Teder, T. (2016) Butterflies take advantage of contemporary forestry: clear-cuts as temporary grasslands. *Forest Ecology and Management,* **376**, 118–125.

**II** **Viljur, M.-L.** & Teder, T. (2018) Disperse or die: colonisation of transient open habitats in production forests is only weakly dispersal-limited in butterflies. *Biological conservation*, **218**, 32–40.

**III** **Viljur, M.-L.**, Relve, A., Gimbutas, M., Kaasik, A. & Teder, T. (2019) Dispersal of open-habitat butterflies in managed forest landscapes: are colonisers special? *Journal of Insect Conservation*, **23**, 259–267.

**IV** **Viljur, M.-L.**, Tiitsaar, A., Gimbutas, M., Valdma, D., Õunap, E., Tammaru, T. & Teder, T. (2019) Forest butterfly diversity: effects of local and landscape characteristics. *Manuscript*.

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The participation of the author in preparing the listed publications (* denotes a moderate contribution, ** a high contribution, *** the leading role):

| | I | II | III | IV |
|---|---|---|---|---|
| Original idea | ** | ** | ** | *** |
| Study design | ** | ** | ** | * |
| Data collection | *** | *** | ** | * |
| Data analyses | *** | *** | *** | *** |
| Manuscript preparation | *** | *** | *** | *** |

# 1. INTRODUCTION

Understanding how local communities are assembled from regional species pools continues to be one of the major goals in ecology (MacArthur & Levins 1967; Zobel, 1997; Lessard et al., 2012; Cornell & Harrison, 2014). On the ecological time scale, variation in local diversity is largely governed by a combination of habitat- and landscape-scale mechanisms (Cornell & Harrison, 2014; Ricklefs, 2015). Habitat filtering, comprising a variety of abiotic and biotic components, determines the set of species that can potentially settle in particular environments. However, in contemporary landscapes, landscape effects are playing an increasingly important role in assembling local communities, because natural and semi-natural habitats are becoming more fragmented and isolated (Fahrig, 2002). Dispersal limitation imposed by surrounding landscape may affect colonisation probabilities of different species to a different extent and thus shape local species assemblages.

The habitat loss and fragmentation have hit particularly hard the biodiversity associated with semi-natural grasslands. These species-rich habitats, once widespread and abundant in temperate and boreal agricultural landscapes, have suffered drastic decline due to land-use changes during the past century (WallisDeVries et al., 2002; Bergman et al., 2008; Krauss et al., 2010; Sang et al., 2010). To some degree, novel anthropogenic habitats (e.g. mining areas, railway embankments, power line corridors; Berg et al., 2016; Moroń et al., 2014; Riva et al., 2018) have been shown to mitigate the loss of traditional habitats for grassland species. Open habitats, such as clear-cuts and various linear elements (e.g. power line right-of-ways, road verges), have become increasingly common also in forest landscapes. Evidence is accumulating that these forest openings can also be of benefit to many grassland species (e.g. plants: Aavik et al., 2009; Jonason et al., 2014; butterflies: Öckinger et al., 2012; Blixt et al., 2015; Ohwaki et al., 2018; birds: Zmihorski et al., 2016). The loss and degradation of grasslands has led to a situation where managed forest landscapes may serve as almost the only opportunity for some grassland species to survive. For example, one of the last viable European metapopulations of the critically endangered butterfly species *Colias myrmidone* in Poland is restricted to forest clearings and thus completely depends on forest management (Sielezniew et al., 2019). However, comprehensive analyses systematically investigating the importance of managed forests for grassland species has been missing so far.

Although forest clear-cuts share some basic features in common with semi-natural grasslands, the transient nature of these forest openings makes them suitable as habitats for grassland species only within a short time window. Typically, clear-cuts retain their open nature for up to about 10 years after logging, but the progressing succession makes them unsuitable for open-habitat species thereafter (Fartmann et al., 2013). The ability to track the dynamics of emergence and disappearance of habitat patches is therefore crucial for longterm viability and persistence of open-habitat species in such landscapes. The suitability of clear-cuts as habitats can thus be expected to depend on the dispersal ability of species. The window of opportunity for colonisation is even shorter for species that depend on prior successful establishment of lower trophic levels, plants in the case of butterflies.

At the behavioural level, even such good fliers as open-habitat butterflies are known to perceive forest or even just a dense treeline as a movement barrier (e.g. Cant et al., 2005; Ross et al., 2005; Schultz et al., 2012). Consistently, for diverse open-habitat taxa, movement rates between clear-cut sites connected by open corridors have been shown to be higher than those between sites separated by forest (Haddad et al., 2003). However, the degree to which these behavioural movement patterns of individuals constrain species distributions in forest landscapes has remained unclear.

In addition to landscape context, phenotypic traits may affect dispersal decisions and performance (Clobert et al., 2012). Individuals making the decision to leave a habitat patch and to cross potentially hostile matrix may not represent a random sample of individuals from the population. Dispersal propensity may correlate with a suite of phenotypic traits (Clobert et al., 2009). For butterflies, it has been shown that variation in morphology (e.g. wing traits, body mass) and/or physiology (e.g. metabolic rate) can be linked to behavioural dispersal-related traits like movement distance within habitat (Skórka et al., 2013a), flight activity (Saastamoinen et al., 2012) and flight capacity (Larranaga et al., 2013). Moreover, the probability of emigration decision can also be associated with phenotypic traits, such as wing length and flight performance, as it has been found in an experimental system (Legrand et al., 2015). However, direct empirical evidence linking phenotypic traits with the propensity of inter-patch dispersal in natural environments is scarce (but see e.g. Breuker et al., 2007; Niitepõld et al., 2011, for a few exceptions). Forest landscapes, managed by clear-cutting, provide a highly suitable semi-experimental system for studying dispersal in natural conditions. In such landscapes, habitat patches and matrix are well defined for open-habitat species, and have ecologically meaningful spatio-temporal dynamics.

About a quarter of the European butterfly fauna are directly dependent on woodland habitats, i.e. their larvae feed on forest plants. Although the total area of forests in Europe has not decreased in recent decades, a number of forest butterfly species are declining (Van Swaay et al., 2010). However, unlike for many other taxa, relying on intact forests may not be the best approach to maintain and enhance their diversity. In particular, similar to open-habitat butterflies, adults of most forest butterflies feed on nectar, and many of these species therefore require mosaic landscapes with open spaces within or adjacent to forests rather than forest stands without disturbances (Van Swaay et al., 2006). Moreover, butterflies associated with forest landscapes have often been treated as woodland butterflies without much further distinction regarding their habitat requirements. More detailed knowledge on habitat characteristics and landscape context affecting their local assemblages is thus urgently required to tackle their declines.

This thesis consists of studies evaluating the importance of managed forests as habitats for both open-habitat butterflies and forest butterflies in Northern Europe. More specifically, the aims of my thesis were (1) to assess the proportion of the regional species pool of open-habitat butterflies that benefit from clear-cuts and to examine the factors affecting their local assemblages in managed forests (I); (2) to investigate the role of dispersal limitation in shaping the assemblages of open-habitat butterfly species in forest landscapes (II, III); and (3) to analyse the effects of habitat characteristics and landscape context on the local diversity of forest specialists (IV).

# 2. MATERIAL AND METHODS

## 2.1. Study area

Habitat and landscape effects on butterfly assemblages and dispersal phenotypes were studied in managed forest landscapes of Estonia in Northern Europe. Estonia belongs to the non-oceanic section of European hemiboreal zone, located at the transition from coniferous boreal forests to deciduous north-temperate forests (Ahti et al., 1968). Forest land covers approximately 51% of the country (Raudsaar et al., 2018). Managed forests make up about 87% of the total forest area, most of these being harvested by clear-cutting. There are also plenty of linear open elements in Estonian forest landscapes that together with clear-cuts form a network of early-successional habitats (Fig. 1). Such linear elements, e.g. compartment lines, road verges and powerline right-of-ways, are kept open by more or less regular mowing and/or removing bushes/trees, whereas clear-cuts lose their open nature due to regeneration of trees and bushes. Most of the Estonian managed forests are naturally regenerated with native tree species and thus can be regarded semi-natural (Lõhmus et al., 2013).


**Fig. 1.** An example of Estonian forest landscape, managed by clearcutting. Clear-cuts can be distinguished by their lighter green vegetation or by light brown colour if the vegetation is sparse (due to recent clearcutting). Linear elements are either forest roads (whitish) or forest compartment lines (light green). Orthophoto: Estonian Land Board (accessed: 11 June 2017).

## 2.2. Selection of clear-cuts

Altogether 35 clear-cuts were chosen from among the ones in main forest areas in the study region to evaluate the share of the regional species pool of open-habitat butterflies inhabiting clear-cuts, and factors affecting their distribution patterns in managed forests (I). Clear-cuts directly adjacent to semi-natural grasslands were avoided to minimize any direct influence of these nearby butterfly habitats on the clear-cuts' fauna (I). Clear-cut sites were chosen from forest areas representing one of three most common groups of forest site types (oligo-mesotrophic boreal, mesotrophic boreal and eutrophic boreo-nemoral forests; names of forest site type groups sensu Paal, 2002) in the region, roughly proportionally to the share of these forest site type groups in the study area (I).

The effect of dispersal limitation on local butterfly assemblages – species richness and composition – was evaluated in eighteen pairs of clear-cut sites (II). Each pair of study sites in this semi-experimental setup consisted of an isolated and a non-isolated clear-cut (control site; see Figure 2 in II). A clear-cut was considered isolated if it was completely surrounded by a belt of forest stand. In terms of isolation by forest, sites selected by this criterion were assumed to be among the most inaccessible open patches for butterflies in this forest landscape. By contrast, a non-isolated clear-cut was directly connected to the network of other open habitats by linear open elements – most commonly wide verges of forest roads, but in a few cases also by powerline right-of-ways. As the primary focus was on evaluating the role of dispersal limitation in structuring local butterfly assemblages, clear-cut sites forming a pair were aimed to be of similar age, area and forest site type. The average ages of isolated and non-isolated clear-cuts were 4.8 and 6.2 years, respectively. The area of the clear-cuts ranged from 0.3 to 2.5 ha, with an average of 1.2 ha for both isolated and non-isolated sites. Most pairwise sites were reasonably closely located: the average distance between the clear-cuts of the same pair was 1,515 m (min 150 m, max 4,720 m), so that in most cases, they were surrounded by the same network of open habitats.

A similar pairwise setup of isolated vs. non-isolated patches was applied for investigating dispersal phenotypes of colonisers (III). In this case, three pairs of clear-cuts were selected to compare recent colonisers (i.e. individuals from new isolated clear-cuts) with individuals from older non-isolated control habitats within the same forest landscape. All isolated clear-cuts chosen were 2 years old, i.e. undergoing their second vegetation period. In the first year after logging, the vegetation is sparse, and butterflies are scarce. In the second year after logging, the vegetation has become denser and more diverse, thus creating conditions for colonisation by open-habitat butterflies. The control sites, chosen from the proximity of the corresponding isolated clear-cuts, consisted of a clear-cut and adjacent road verges by which they were directly connected to the network of other open habitats in the landscape. Thus, making the decision to cross the boundary between open habitat and forest was not necessary to colonise the control sites, while it was unavoidable to reach the isolated clear-cuts. The control sites were clearly older (> 5 years) than isolated sites but still not overgrown.

To inspect the roles of habitat and landscape factors in shaping local assemblages of forest butterflies, altogether 402 clear-cuts were surveyed in the framework of the project "Estonian butterfly distribution mapping" (IV). These clear-cuts represented 19 forest site types from nine natural and one anthropogenic group of forest site types. These forest site types cover 99% of the Estonian forest land.

## 2.3. Environmental data

Most of the data on habitat and landscape characteristics were obtained from the database of the State Register of Forest Resources (http://register.metsad.ee/avalik/) and from orthophotos and topographic maps provided by the Estonian Land Board (http://xgis.maaamet.ee). These data included information about surveyed clear-cuts (forest site type, area, age (= years since logging), level of isolation by forest) as well as information on the surrounding landscape (area of forest land in the surrounding landscape, proportions of different forest site types in the surrounding forest land, and distance to the nearest semi-natural grasslands or other open habitats). Clear-cut age and level of isolation were further confirmed by field observations (II, III). Nectar plant abundance and matrix permeability were also assessed in the study sites (II).

Throughout the thesis, the classification of forest site types by Lõhmus (2004) was followed. Twenty-seven forest site types are routinely distinguished on the basis of this classification. These site types are determined by a set of environmental variables including geomorphological and edaphic factors, as well as the composition of plant communities. A particular combination of relative soil pH and moisture level can be associated with each forest site type. The values of soil pH and moisture for selected clear-cuts and surrounding forest land were derived from the ordination scheme of forest site types by Lõhmus (2004) (I, IV). The heterogeneity of forest site types in the surrounding landscape was measured as the sum of weighted dispersions of soil pH and moisture in the circular buffer around the centroid of a clear-cut (IV).

## 2.4. Butterfly surveys

Repeated surveys were carried out to examine the species composition and richness of butterfly assemblages in clear-cuts (2012–2015: I, II; 2016–2017: IV). Each clear-cut was surveyed three times, either within one or two consecutive years so that the flight time of most butterfly species was covered. Timed surveys, instead of more traditional Pollard's transect walk (Pollard & Yates, 1993), were used to quantify butterfly diversity in clear-cuts, as the primary aim was to obtain possibly complete lists of butterflies for each study site (Kadlec et al., 2012).

To investigate among-individual variation in dispersal-related morphological traits, six common open-habitat butterfly species were chosen (III). These species were *Aphantopus hyperantus* (Linnaeus, 1758), *Brenthis ino* (Rottemburg, 1775), *Boloria selene* (Denis & Schiffermüller, 1775), *Coenonympha arcania* (Linnaeus, 1761), *C. glycerion* (Borkhausen, 1788; all Nymphalidae) and *Ochlodes sylvanus* (Esper, 1777; Hesperiidae) (Fig. 2). Butterflies were collected from the study sites in the summer of 2015. Each site was visited two times during the flight time of these butterflies. The sites belonging to the same pair (i.e. an isolated clear-cut and a control site, see above) were always visited consecutively in a random order, usually within the same day. During two hours of active collecting in each site, all encountered butterflies were captured and maintained for further measurements. To examine among-individual variation in dispersal-related phenotypic traits, individuals of six open-habitat butterfly species were collected in 2015. In the laboratory, they were sexed, and wing length and wing area were measured (III). A further characteristic of wing morphology – wing aspect ratio – was calculated as squared wing length divided by wing area.

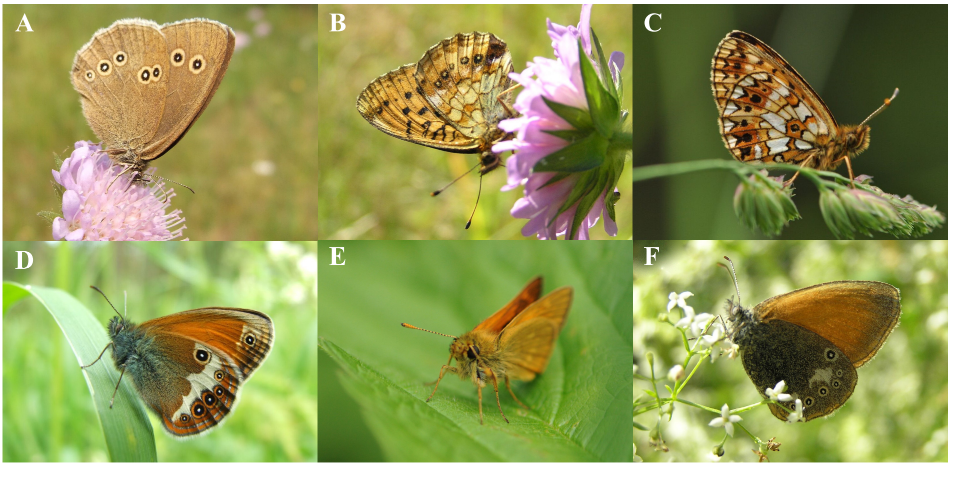


**Fig. 2.** Species chosen to investigate among-individual variation in dispersal-related morphological traits: A) *Aphantopus hyperantus*; B) *Brenthis ino*; C) *Boloria selene*; D) *Coenonympha arcania*; E) *Ochlodes sylvanus*; F) *C. glycerion*. Photos: Anu Tiitsaar.

## 2.5. Species classification

Based on expert opinions, the list of butterflies was compiled for the study region (I). Further, using expert opinions and literature, the species were classified into four groups with respect to their known habitat use in the study region. The following categories were distinguished (1) grassland species, i.e. species for which semi-natural grasslands are considered the primary habitat, (2) open-habitat generalists, i.e. species known to inhabit a wide spectrum of various open habitats, (3) bog species, i.e. species feeding on bog plants, and (4) forest species, i.e. species inhabiting mainly woodlands and feeding on forest plants in the larval stage. All grassland species were ranked according to their relative abundance in grasslands in the study region. Based on expert opinions, abundance estimates were given on a scale of 1–5, where 1 denotes a very rare species and 5 a highly abundant species.

From among aforementioned species groups, all but forest species were considered as open-habitat species for which forest s. str. was assumed to be non-suitable habitat, potentially impeding dispersal. Presumed mobility of recorded butterfly species was described by two widely used mobility proxies: 1) mobility indices by Bink (1992) on a scale from 1 (sedentary species) to 9 (migratory species); 2) average wingspan.

## 2.6. Data analyses

Generalised linear mixed models (GLMMs) were applied to analyse the effects of dispersal limitation (II) and environmental parameters (IV) on butterfly species richness. To analyse if forest-imposed isolation filters species by their presumed mobility, mobility proxies (mobility indices by Bink, 1992 and average wingspan) were separately averaged over the species recorded in each clear-cut. These site-specific mobility scores were used as response variables in separate GLMMs (II). Information-theoretic approaches based on Akaike's Information Criterion were applied for model selection and multimodel inference (II, IV). General linear models were used to analyse differences between individuals from recently colonised isolated clear-cuts and individuals from control sites (III).

Constrained ordination methods – redundancy analysis (RDA) and canonical correspondence analysis (CCA) – were applied to examine the associations between species composition and environmental parameters (I and IV, respectively). Non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances was applied to visualise dissimilarities in species composition between forest site types (IV). The statistical significance of the ordination models and its components were tested using permutation tests (I, IV).

# 3. RESULTS

## 3.1. Clear-cuts as habitats for open-habitat butterflies (I)

Clear-cuts in routinely managed forest landscapes appeared to be remarkably species rich in butterflies. More than four-fifths (81%) of species of the regional species pool were detected in spite of a moderate number of clear-cuts surveyed (35 sites; just 0.1% of the clear-cut area in the study region). Importantly, the list of recorded species contained a very high proportion (79%) of regionally occurring grassland species.

The average number of grassland species recorded per clear-cut was 9.0 (median 9, minimum 6, maximum 14). The frequency of presence of particular grassland species in the surveyed clear-cuts was strongly correlated with their relative abundance estimates in the study region ($R_P = 0.73$). Only 7 of the 33 grassland species occurring in the region remained undetected. Most of the missing species are regionally very rare, described by experts as a 1 on the relative abundance scale of 1–5.

As indicated by the RDA, the distribution of grassland butterfly species among clear-cuts was not random. Clear-cuts belonging to the same forest type group showed clustering by species composition. Among the environmental variables analysed, soil moisture was the strongest determinant of butterfly species composition in clear-cuts.

## 3.2. Dispersal of open-habitat butterflies in managed forests (II, III)

A pairwise comparison of butterfly species richness between isolated and non-isolated clear-cuts showed only a slight difference (about one species, on average). Across the sites, the subset of isolated clear-cuts examined (altogether 18) harboured most open-habitat species of the entire regional species pool. The frequencies of individual species in isolated and non-isolated clear-cuts were strongly correlated (Spearman correlation: $R_S = 0.88$), indicating that factors other than site isolation determined species occurrence in clear-cuts. A few open-habitat species that remained unrecorded in isolated clear-cuts were also rare in non-isolated clear-cuts, most of such species were detected only once. Similarly, a few infrequent species were spotted only in isolated sites. Almost none of the more frequent species were proportionally overrepresented in non-isolated sites. Signs of decrease in species richness started to appear in clear-cuts surrounded by the widest belt of forest in our sample; however, isolation levels of this extent are uncommon in North European managed forests. Moreover, as based on the analysis of two widely used mobility proxies, butterfly assemblages in isolated and non-isolated clear-cuts did not differ in mobility of their constituent species.

No convincing evidence was found for dispersal-related variation in wing morphology of open-habitat butterflies in forest landscapes managed by clear-cutting (III). Across species, none of the three wing traits measured (wing length, wing area and aspect ratio) differed significantly between the recent colonisers of new isolated clear-cuts and individuals inhabiting continuous habitat patches in the same forest landscape. The results were consistent among males and females.

### 3.4. Local and landscape effects on forest butterfly assemblages (IV)

The species richness of forest butterflies in clear-cuts was significantly affected by soil moisture (estimated from forest site type) of local sites. The number of species was highest in forests characterised by medium soil moisture levels and lower in forests located on driest and most humid soils. The species composition of forest butterflies differed significantly among clear-cuts located in different forest site types, with the differences being most pronounced between site types with contrasting soil characteristics. The results of CCA confirmed that the distribution of forest butterflies is associated with the gradients of soil moisture and pH.

At the landscape scale, the area of forest land in the surrounding landscape had a considerable positive effect on the species richness of forest butterflies in clear-cuts. Among the four spatial scales (250–2000 m) at which the area of forest land was measured, the largest (2000 m) was the best to predict the species richness of forest butterflies. There was almost no effect of site type heterogeneity (estimated as dispersion in soil moisture and pH) in the surrounding landscape on the local species richness.

# 4. DISCUSSION

The conservation of forest biodiversity has increasingly shifted from relying on protected areas alone towards maintaining and enhancing forest biodiversity in managed landscapes (Lindenmayer et al., 2006). There is increasing evidence that managed forest lands may also provide habitat for a considerable share of biodiversity that have been associated with open habitats in agricultural landscapes. My thesis adds strong support to this view, showing that managed forests in Northern Europe provide habitat for a remarkably high proportion of open-habitat butterflies. The list of open-habitat species recorded in clear-cuts contained also the majority of regionally occurring species that have been traditionally considered as grassland specialists (I). Several arguments suggest that most of the recorded grassland species form resident populations in managed forest landscapes. First of all, the potential effect of semi-natural grasslands in the surrounding landscape on clear-cuts' fauna was minimised by selecting the sample of clear-cuts deliberately from forest-dominated areas. Secondly, all chosen clear-cuts were located in the forest interior and many of them were more than half a km away from the nearest grassland. Thirdly, clear-cuts provide essential resources for the majority of butterfly species during their entire life cycle – diverse nectar plants for adult butterflies and host plants for larvae of most species (pers. obs.). Finally, the ordination analysis revealed that the distribution of grassland butterfly species among clear-cuts was significantly associated with the environmental characteristics of sites, soil moisture in particular. This non-random pattern of species composition would emerge from the distribution of locally breeding individuals rather than dispersive individuals tracking nectar resources (I).

In contrast to the essential role of habitat filtering, my thesis points to the relatively minor effect of dispersal limitation on local assemblages of open-habitat butterflies in North European managed forests (II). There was only a slight difference in the species richness (about one species on average) between isolated (fully forest-surrounded) and non-isolated (connected to other forest openings by open corridors) clear-cuts. Moreover, even the smallest species and those considered to be most sedentary were frequently present in isolated clear-cuts. Dispersal between non-isolated clear-cuts along open corridors may result from frequent routine movements associated with resource exploration. By contrast, reaching a fully forest surrounded clear-cut requires special dispersal movements across hard habitat boundaries (Van Dyck & Baguette, 2005) that have been found to be perceived as dispersal barriers by individual butterflies (Cant et al., 2005; Ross et al., 2005; Skórka et al., 2013b). Nevertheless, the minor effect of dispersal limitation on the composition of local butterfly assemblages indicates that patterns of individual movement behaviour do not necessarily scale up to assemblage level patterns of colonisation. As suggested by the results of this thesis, inter-patch movements are likely to occur often enough in managed forests to allow most open-habitat butterfly species to colonise newly emerged habitat patches even if completely surrounded by forest.

Individuals that colonise new isolated patches may not necessarily be a random sample of individuals from the population, but may represent specific dispersal-related phenotypes. However, no compelling evidence was found for colonisers of new isolated clear-cuts to differ from individuals inhabiting continuous open habitats in the same forest landscape (III). Across the six open-habitat species studied, none of the three dispersal-related morphological traits measured indicated distinct dispersal phenotypes of colonising individuals. A possible explanation may lie in the dynamic nature of the forest landscapes managed by clear-cutting as a whole. Indeed, temporal variation in the carrying capacity of habitat patches has been widely predicted to increase dispersal propensity (Comins et al., 1980; Travis & Dytham, 1999; Bowler & Benton, 2005; Blanquart & Gandon, 2011). Frequent, deterministic events of habitat loss and formation in forests managed by clear-cutting may imply that virtually all phenotypes in such landscapes represent "dispersal phenotypes". It should, however, be noted that wing traits and dispersal parameters in butterflies have found to be unrelated also in other landscapes (Hanski et al., 2002; Sivakoff et al., 2016; Turlure et al., 2016). Moreover, it has been recently shown that flight ability and performance may not be related to dispersal propensity (Reim et al., 2018). Thus, even if wing morphology is associated with dispersal ability, it may not be reflected in dispersal propensity. On the other hand, dispersive and resident individuals have been found to differ in phenotypic traits that were not examined in this thesis, such as physiological characteristics and thorax mass (Hill et al., 1999a; Hill et al, 1999b; Niitepõld et al., 2011).

Although managed forest landscapes support the majority of open-habitat butterfly fauna in the study region, relying solely on conventional forest management for butterfly conservation would be definitely inadvisable. Firstly, clear-cuts are unlikely to serve as suitable habitats for all open-habitat species. Butterflies that are in complex ecological interactions with other species, such as e.g., obligately myrmecophilous species, may not be able to take advantage of these transient forest openings due to the lack of time available for colonisation. Successful colonisation of newly-emerged clear-cuts may also be impeded in species whose host plants have poor dispersal ability. Secondly, despite the minor effect of dispersal limitation on the diversity of open-habitat butterflies found in this thesis, movements of some sedentary open-habitat specialists in forest landscape may still be insufficient for long-term metapopulation persistence (Sielezniew et al., 2019). Thus case-specific critical evaluation of the conservation potential of managed forest landscapes as well as an assessment of the need for special actions is required when developing conservation plans for particular species of conservation concern. Nevertheless, identifying the share of open-habitat species that are able to form resident populations in forest openings will help to set conservation priorities, and will allow one to canalise research and conservation effort to these open-habitat species that cannot take advantage of the routinely managed forest landscapes.

The results of my thesis allow me to argue that forests managed by clear-cutting retain their suitability as habitat also for butterflies considered as forest specialists (I, IV). Indeed, nearly all forest butterfly species were recorded both in the regionally restricted (I) as well as the country-level subset of clear-cut sites (IV). My thesis suggests that different forest site types contribute to the regional species pool of forest butterflies in a partly complementary manner. The peak frequencies of presence and peak abundances of different species were distributed across multiple site types, indicating that habitat preferences widely vary among species, and functional habitat availability for many forest species is considerably lower than could be inferred from the total proportion of forest land in the landscape. Forestry practices reducing forest heterogeneity, such as shifts towards plantation forestry and practices potentially decreasing soil heterogeneity (e.g. fertilisation), may pose a considerable threat to the diversity of forest butterflies. There was also a considerable positive effect of the proportion of forest land in the surrounding landscape on the local species richness of forest butterflies, indicating the importance of landscape context. Importantly, the results suggest that the loss of species diversity with the decreasing proportion of forest land may start at a relatively high landscape-scale forest land cover. Surprisingly, however, forest heterogeneity in the surrounding landscape had no discernible effect on the local species richness. The lack of this effect may indicate that forest butterflies are rather sedentary, and rarely move away from their preferred habitat. The findings of my thesis thus imply that both the extent as well as the diversity of forest land are important for maintaining the diversity of forest butterflies.

Main conclusions of my thesis:

- Forest landscapes managed by clear-cutting can substantially improve the conservation prospects for butterflies and other organisms that have traditionally been associated with grasslands and other open habitats in agricultural landscapes.
- Most open-habitat butterfly species can colonise transient forest openings, even if these are isolated in the forest matrix. Most species thus can take advantage of routinely managed forest landscapes without further costly actions, such as creating open dispersal corridors.
- Forest landscapes managed by clear-cutting retain their suitability as habitat for forest-dependent butterflies. However, both the extent of forest land in the landscape as well as heterogeneity of forests are important for maintaining and enhancing the diversity of forest butterflies.

# SUMMARY

## Local and landscape effects on butterfly assemblages in managed forests

The conservation of forest biodiversity has increasingly shifted from relying on protected areas alone towards maintaining forest biodiversity in managed landscapes. There is accumulating evidence that managed forest lands may also provide habitat for a considerable share of biodiversity that has traditionally been associated with open habitats in agricultural landscapes. While semi-natural open habitats in agricultural landscapes have severely declined during the past century, the global area of forests has been rather stable or even slightly increased in some regions (e.g. Europe and North America). Most of the forests are managed for timber harvesting and clear-cutting is widely practiced for that purpose. Therefore, contemporary managed forests are typically mosaic landscapes with many open elements, clear-cuts in particular.

My thesis shows that grassland butterflies are among these organisms that take advantage of anthropogenic disturbances in managed forests. Repeated surveys showed that clear-cuts were inhabited by a remarkably high share of regionally occurring grassland butterfly species (I). However, the distribution of grassland butterfly species among clear-cuts was not random but affected by local forest characteristics. Soil moisture, strongly influencing local vegetation of clear-cuts, had the strongest effect on local butterfly species composition (I). Managed forest landscapes may thus substantially mitigate the detrimental effects of the ongoing loss and fragmentation of natural and semi-natural open habitats for open-habitat species in general, and grassland species in particular.

Besides local characteristics, landscape effects are likely to play important role in assembling local communities. Dispersal limitation imposed by surrounding landscape may affect colonisation probabilities of different species to a different extent and thus shape local species assemblages. In particular, grassland butterflies are known to perceive forest as a dispersal barrier at the behavioural level. Such dispersal limitation at the individual level might possibly lead to colonisation limitation of clear-cuts at the level of entire butterfly assemblages. To examine the effect of potential dispersal limitation at the assemblage level, the species richness and composition of open-habitat butterflies in clear-cuts that were completely surrounded by forest were compared with those in clear-cuts connected to the network of other open spaces within the same forest landscapes (II). Contrary to expectations, the differences in species richness and composition between isolated and non-isolated clear-cuts were negligible. Even the smallest species and those considered to be most sedentary, were present in isolated clear-cuts.

Dispersal of butterflies may exhibit also a considerable amount of intraspecific variation. The variation in dispersal ability and emigration propensity can be associated with various morphological and/or physiological traits. Yet, direct

empirical evidence linking phenotypic traits with the propensity of inter-patch dispersal in natural environments is scarce. In my thesis, dispersal decisions were investigated with regard to flight morphology, again applying the semi-experimental setup consisting of isolated and non-isolated clear-cuts. No significant relationship between flight morphology and realised dispersal decisions appeared – recent colonisers of isolated clear-cuts (fully surrounded by forest) did not differ from individuals of surrounding non-isolated habitats in any of measured wing traits. The lack of difference between recent colonisers of isolated clear-cuts and individuals from non-isolated habitats may imply that virtually all phenotypes in dynamic forest landscapes represent "dispersal phenotypes". The results of my thesis (II, III) thus indicate that dispersal is unlikely to be limiting factor for effective colonisation of open patches in conventionally managed forest landscapes.

About a quarter of the entire butterfly fauna in Europe are feeding on trees or forest understorey plants at larval stage, and are thus directly dependent on forest habitats. The results of my thesis allow to argue that forests managed by clear-cutting retain their suitability as habitat also for butterflies considered as forest specialists. Nevertheless, a comprehensive country-wide dataset used shows that different forest site types contribute to the regional species pool of forest butterflies in a partly complementary manner. Forestry practices reducing forest heterogeneity may therefore pose a considerable threat to the diversity of forest butterflies. Also, there was a clear positive effect of the proportion of forest land in the surrounding landscape on the local species richness of forest butterflies, indicating the importance of landscape context. Maintaining a high proportion of forests in the landscape may therefore be a necessary prerequisite to effectively conserve forest specialists.

# KOKKUVÕTE

## Elupaiga ja maastiku mõjud päevaliblikakooslustele majandatavates metsades

Ökoloogia üheks keskseks eesmärgiks on jätkuvalt koosluste mitmekesisust mõjutavate mehhanismide väljaselgitamine. Elupaigalaigu liigirikkus ja liigiline koosseis sõltub nii laigu enda kui ka seda ümbritseva maastiku omadustest. Ümbritseva maastiku mõju olulisus on kasvanud tõusujoones, sest looduslikud ja poollooduslikud elupaigad killustuvad üha enam ning jäävad sageli teistest eraldatuks. Seejuures võib maastik toimida filtrina, „selekteerides“ liike levimisvõime alusel, sel viisil mõjutades nii elupaigalaikude liigirikkust kui ka liigilist koosseisu. Levimispiirangute rolli koosluste kujunemisel on raske uurida, mistõttu on enamik levimisega seotud uurimusi loomadel keskendunud isendite liikumiskäitumisele. Siiski ei ole isendite käitumismustrite põhjal võimalik automaatselt teha järeldusi elupaigalaikude liigilise mitmekesisuse kohta.

Elupaikade kadumine ja killustumine on eriti tõsiselt puudutanud poollooduslike niitude elurikkust. Maakasutuse muutuste tõttu on niitude pindala viimase sajandi jooksul drastiliselt vähenenud. Tasapisi süveneb arusaam, et majandatav metsamaastik oma mitmekesiste avamaastiku elementidega (raiesmikud, sihid, teeservad, kõrgepingeliinide trassid) võib lisaks metsaliikidele pakkuda alternatiivset elupaika ka paljudele niiduliikidele. Käesolev doktoritöö näitab, et avamaastikupäevaliblikad on ühed neist, kes inimmõjutustega metsamaastikust võidavad. Selgus, et raiesmikud on elupaigaks väga suurele osale regionaalsest päevaliblikafaunast. Uurimistöö käigus ilmnes ka, et liblikate liigilist koosseisu raiesmikel mõjutab metsa kasvukohatüüp. Olulisimaks kasvukohatüübiga seotud keskkonnatunnuseks osutus mulla niiskus, mis taimestiku vahendusel määrab, millistes kasvukohatüüpides millised liblikaliigid sagedamini esinevad.

Raiesmikud on Põhja-Euroopa majandatavate metsamaastike tavalisimaks avatud maastikuelemendiks ja avakooslustena mitmete omaduste poolest niitudele sarnased, kuid on erinevalt niitudest lühiajalised. Raiesmikud püsivad avatuna umbes kümmekond aastat, mistõttu selliste avakoosluste toimivus avamaastikuliblikatele elupaigana sõltub liikide võimest raiesmikke selle aja jooksul metsamaastikus leida ja asustada. Samas on varasemast teada, et isendite käitumise tasemel on mets avamaastikuliblikatele oluliseks liikumis- ja levimistakistuseks. Doktoritöö eesmärgiks oli selgitada, kuivõrd isendi tasemel käitumismustrid avalduvad avamaastikuliblikate liigirikkuses ja liigilises koosseisus raiesmikel. Täielikult metsaga ümbritsetud ja avatud elupaikadega ühendatud raiesmike võrdluse tulemusena selgus, et metsa mõju raiesmike asustamisele on tagasihoidlik – metsaga piiratud raiesmike liigirikkus ei erinenud märkimisväärselt teiste avakooslustega ühendatud raiesmike liigirikkusest. Metsaga ümbritsetud raiesmikele olid teiste seas jõudnud ka väikeste mõõtmetega ja vähemobiilseteks peetavad liigid. Minu doktoritöö tulemused näitavad, et avamaastiku päevaliblikad levivad raiesmikele (isegi kõige isoleeritumatele) ka suhteliselt madala raiekoormuse juures (päevaliblikatele sobivas vanuses raiesmike pindala Eestis uurimisperioodil oli umbes 1,4 korda väiksem kui 2018. aastal).

Isendite levimiskäitumine võib varieeruda päevaliblikatel ka liigisiseselt. On leitud seoseid isendite levimiskäitumise ning morfoloogiliste ja füsioloogiliste tunnuste vahel. Enamik vastavasisulisi uurimusi on aga teostatud tehistingimustes. Majandatav metsamaastik sobib elupaik-maatriks süsteemina hästi ka isendite levimise uurimiseks looduses. Doktoritöös uurisin, kas täielikult metsaga ümbritsetud raiesmike esmaasustajad erinevad levimisega seotud morfoloogiliste tunnuste poolest liigikaaslastest, kes püüti pikemaajalise asustusega elupaikadest naabruskonnas. Kuue niiduliigi isendite võrdlusel ilmnes, et koloniseerijad ei erinenud kontrollgrupist ühegi uuritud tunnuse osas. Doktoritöö tulemustest võib järeldada, et tõenäoliselt pole majandatavas metsamaastikus olulisi levimispiiranguid, mis takistaks sealsete avatud elupaikade asustamist (II, III).

Doktoritöö viimane osauurimus keskendub päevaliblikaliikidele, kellele mets on põhielupaigaks, st. kes röövikuna toituvad metsataimedel. Olgugi, et Euroopa metsade pindala viimastel kümnenditel kahanenud ei ole, on paljude metsaliblikaliikide populatsioonid languses. Metsaliblikate elupaiganõudlusi- ja eelistusi on aga niiduliblikatega võrreldes üsna vähe uuritud. Doktoritöös analüüsisin metsaliblikate mitmekesisust erinevates kasvukohatüüpides asuvatel raiesmikel, samuti uurisin, kuidas mõjutab metsaliblikate liigirikkust metsa osakaal ja heterogeensus ümbritsevas maastikus. Selleks kasutasin Eesti päevaliblikate kaardistamise tulemusena kogutud mahukat andmestikku enam kui 400 raiesmikult. Raiesmikud ei pruugi küll olla metsaliblikatele põhielupaigaks, kuid pakuvad valmikutele nektaritaimi ning seetõttu sobivad hästi ka metsaliblikate loendusteks. Selgus, et kõige liigirikkamad on parasniisked metsad, väga kuivades ja niisketes kasvukohatüüpides on metsaliblikaliike vähem. Oluliseks osutus ka metsamaa osakaal maastikus – mida rohkem oli raiesmikku ümbritsevas maastikus metsamaad, seda enam liblikaliike leidus uuritud alal. Ümbritseva maastiku kõrgem kasvukohatüübiline heterogeensus liigirikkust ei tõstnud, aga et metsaliblikate liigiline koosseis erinevates kasvukohatüüpides lokaalsel tasemel siiski erines, võib vaadeldud muster viidata metsaliblikate vähesele liikuvusele.

Järjest enam pööratakse tähelepanu elurikkuse kaitsele ja säilitamisele väljaspool kaitsealasid. Doktoritöö tulemustest järeldub, et majandatav metsamaastik pakub elupaika suurele osale päevaliblikaliikidest, sh. nii metsaliikidele kui ka traditsiooniliselt poollooduslike niitudega seostatud liikidele. Seega aitab majandatav metsamaastik leevendada niitude kadumise negatiivset mõju avamaastikuliikide populatsioonidele. Seejuures pole puistu avamaastikuliblikatele oluliseks takistuseks raiesmike asustamisel ja täiendavate, levimist soodustavate koridoride rajamine pole majandatavas metsamaastikus nende mitmekesisuse tagamiseks vajalik. Samas leidub kindlasti ka avamaastikuliike, kellele raiesmikud oma lühiajalisuse tõttu elupaigaks ei sobi. Teadmine sellest, millistele liikidele raiesmikud sobivad ja millistele mitte, võimaldab enam looduskaitselist tähelepanu suunata just viimastele. Nii avamaastiku- kui ka metsaliikide mitmekesisuse säilimiseks on aga tähtis, et majandatavas metsamaastikus säiliks looduslike kasvukohatüüpide mitmekesisus.

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# PUBLICATIONS

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**Viljur, M.-L.**, Relve, A., Gimbutas, M., Kaasik, A. & Teder, T. (2019) Dispersal of open-habitat butterflies in managed forest landscapes: are colonisers special? *Journal of Insect Conservation*, **23**, 259–267.

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**Viljur, M.-L.** & Teder, T. (2016) Butterflies take advantage of contemporary forestry: Clear-cuts as temporary grasslands. *Forest Ecology and Management*, **376**, 118–125.

**Conference presentations:**

**Viljur, M.-L.,** Relve, A., Gimbutas, M., Kaasik, A. & Teder, T. Oral presentation 'Butterflies in forest landscape: Are colonisers special?' Butterfly Conservation 8th International Symposium. Southampton, UK, 6th to 8th April 2018.

**Viljur, M.-L.** & Teder, T. Poster presentation 'Where to see grassland butterflies if grasslands are gone?' International Congress for Conservation Biology. Cartagena, Colombia, 23th to 27th July 2017.

**Viljur, M.-L.** & Teder, T. Oral presentation 'No effect of dispersal limitation on butterfly assemblages in forest landscape' The Graduate Seminar of Insect Evolutionary Ecology. Vana-Veski, Estonia 4th to 6th May 2017.

**Viljur, M.-L.** & Teder, T. Oral presentation 'From individual behaviour to patch colonisation: does forest form a barrier for butterflies?' Future 4 butterflies in Europe. Wageningen, Netherlands, 31th March to 2th April 2016.

**Viljur, M.-L.** & Teder, T. Oral presentation 'The effect of variation in species traits on colonisation of isolated patches' Graduate Seminar of Insect Evolutionary Ecology. Kuke, Estonia 17th to 19th May 2015.

**Viljur, M.-L**. & Teder, T. Poster presentation 'Grassland butterflies in a search of new home: Forest openings provide alternative habitats for grassland butterflies' 7th International Conference on the Biology of Butterflies. Turku, Finland, 11th to 14th August 2014.

**Dissertations supervised:**

Epp Valdaru, bachelor thesis, 2018, sup. Mari-Liis Viljur. *The environmental factors that influence the habitat use of forest butterflies.* University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, Department of Zoology.

Auli Relve, master thesis, 2016, sup. Tiit Teder, Mari-Liis Viljur. *Butterflies in forest landscapes – within-species variation in dispersal.* University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, Department of Zoology.

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**Publikatsioonide loetelu:**

**Viljur, M.-L.**, Tiitsaar, A., Gimbutas, M., Valdma, D., Õunap, E., Tammaru, T. & Teder, T. (2019) Forest butterfly diversity: effects of local and landscape characteristics. *Viimistlemisjärgus käsikiri*.

**Viljur, M.-L.**, Relve, A., Gimbutas, M., Kaasik, A. & Teder, T. (2019) Dispersal of open-habitat butterflies in managed forest landscapes: are colonisers special? *Journal of Insect Conservation*, **23**, 259–267.

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**Konverentsiettekanded:**

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Auli Relve, magistritöö, 2016, juh. Tiit Teder, Mari-Liis Viljur. Päevaliblikad metsamaastikus – levimise liigisisene varieeruvus. Tartu Ülikool, Loodus- ja Tehnoloogiateaduskond, Ökoloogia ja Maateaduste Instituut, Zooloogia osakond.

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