

LY LINDMAN

The ecology of protected
butterfly species in Estonia



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butterfly species in Estonia



UNIVERSITY OF TARTU
PRESS

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Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in zoology at the University of Tartu on December, 14, 2015 by the Scientific Council of the Institute of Ecology and Earth Sciences, University of Tartu.

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Commencement: Room 301, 46 Vanemuise Street, Tartu, on 12 February 2016 at 10.15 a.m.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu



European Union
European Social Fund



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ISSN 1024-6479

ISBN 978-9949-77-030-4 (print)

ISBN 978-9949-77-031-1 (pdf)

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University of Tartu Press

www.tyk.ee

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers which are referred to in the text by their Roman numerals.

- I. **Lindman, L.**, Johansson, B., Gotthard, K. & Tammaru, T. (2013). Host plant relationships of an endangered butterfly, *Lopinga achine* (Lepidoptera: Nymphalidae) in northern Europe. *Journal of Insect Conservation*, **17**, 375–383.
- II. **Lindman, L.**, Remm, J., Saksing, K., Sõber, V., Õunap, E. & Tammaru, T. (2015). *Lycaena dispar* on its northern distribution limit: an expansive generalist. *Insect Conservation and Diversity*, **8**, 3–16.
- III. Meister, H., **Lindman, L.** & Tammaru, T. (2015). Testing for local monophagy in the regionally oligophagous *Euphydryas aurinia* (Lepidoptera: Nymphalidae). *Journal of Insect Conservation*, **19**, 691–702.
- IV. Tiitsaar, A., Kaasik, A., **Lindman, L.**, Stanevičs, T. & Tammaru, T. Host associations of *Coenonympha hero* (Lepidoptera: Nymphalidae) in northern Europe: microclimate rather than plant species. *Submitted manuscript*.
- V. **Lindman, L.**, Remm, J., Meister, H. & Tammaru, T. Host plant and habitat preference of *Euphydryas maturna* (Lepidoptera: Nymphalidae, Melitaeinae): evidence from northern Europe. *Manuscript*.

The author was responsible for designing the experiments, data collection, data analyses, writing the papers (I, II, V), and contributed to designing the experiment (III, IV), data collection and writing the papers (III, IV).

I. INTRODUCTION

Biodiversity is decreasing worldwide: unprecedented rates of species' extinctions form a complex response to continuing human-induced changes in the global environment (Sala et al., 2000; Tilman et al., 2001; Jones and Neelson, 2005; Rosenzweig et al., 2008; Butchart et al., 2010). The loss of biodiversity has also been and continues to be a major environmental problem at a European level (Hanski, 2005; Alkemade et al., 2009). Insects – the animals which comprise 80% of the world's biodiversity – are not left unaffected (New, 1995; Schultz and Chang, 1998). Various European butterfly species are known to have suffered a dramatic decline during recent decades (Van Swaay et al., 2006; Van Dyck et al., 2009; Fox et al., 2010). In fact, the situation could even be poorer than previously thought (Van Swaay et al., 2010). Indeed, it has been estimated that as much as one third of European butterfly species are currently declining (Van Swaay et al., 2010).

Primary causes for the widespread decline of many European butterflies include habitat loss, habitat fragmentation, and habitat degradation (Saunders et al., 1991; New, 1997; Debinski and Holt, 2000; Maes and Van Dyck, 2001; Van Swaay et al., 2006, 2010; Krauss et al., 2010; Nakamura 2011; Fox, 2012). For butterflies, the availability of suitable habitats frequently appears to be crucially limiting (Dennis and Eales, 1997, 1999; Thomas et al., 2001; Fleishman et al., 2002; Dennis et al., 2006). For this reason, decrease in habitat quality is perhaps the primary factor behind the decline in countless species (Tilman et al., 2001; Benton et al., 2003; Chase and Leibold, 2003). Indeed, there are numerous examples of dramatic effects of habitat loss on population viability (Schultz and Chang, 1998; Bourn and Thomas, 2002; Van Swaay, 2002; Gardiner, 2003; Wenzel et al., 2006; Dover and Settele, 2009; Krämer et al., 2012; Pennekamp et al., 2013). Nevertheless, proximate factors determining the suitability of the habitat have often remained unclear (Brückmann et al., 2010a). Such a deficient knowledge is a major obstacle for efficient conservation actions (Freese et al., 2006).

The cornerstone of a successful conservation practice is understanding the basic ecological needs of the endangered species: primarily, the set of parameters defining a suitable habitat (Van Swaay and Warren, 1999; Sang and Teder, 2011; Tiitsaar et al., 2013). Regrettably, we know surprisingly little about numerous threatened insect species (Van Swaay and Warren, 1999). This gap in our knowledge frequently causes the situation where a conservationists' understanding of how a favourable habitat looks is based on a "gut feeling", but the actual elements essential for the target species, may largely remain unknown (Dolek et al., 2005; Brückmann et al., 2010a). Still, in the practice of conservation work, a critical mistake would be to assume that species' niches are wider than they actually are. Indeed, there are a number of cases where butterfly conservation has failed due to such errors (Thomas, 1980, 1995; New et al., 1995; Pullin, 1996). The successful management of rare and endangered

butterfly species has to consider all of its life stages and the entire spectrum of necessary habitat requirements (Dennis et al., 2003).

For herbivores, the presence of an acceptable host plant species is a primary determinant of habitat quality (Grundel et al., 1996; Brommer and Fred, 1999; Turlure et al., 2009a). In practice, therefore, suitable habitats for insect herbivores have often been defined as larval host plant patches (Weking et al., 2013; Pennekamp et al., 2013, 2014). The importance of the host plant in a habitat is different for mono-, oligo-, or polyphagous insects (Cates 1981). The crucial role of the host plant is quite obvious in monophagous insects (Cates, 1981), such as *Polyommatus coridon* (Brückmann et al., 2010b), *Iolana iolas* (Rabasa et al., 2008) and *Parnassius apollo* (Nakonieczny et al., 2007). The role of the abundance of different potential host plant species is not necessarily clear for species which may feed on numerous hosts. This is, however, not the only problem. Understanding the determinants of habitat quality in a conservation context (Thomas et al., 1998, 2001) can be complicated due to the lack of sufficiently detailed information about the role of various factors related to host plant (Kawecki and Mery, 2003; Forister et al., 2013).

In particular, the suitability of a host plant individual is not determined by its species only: factors such as plant size (Courtney, 1982; Wiklund, 1984; Küer and Fartmann, 2005), phenology (Thomas and Elmes, 2001), abundance (Pennekamp et al., 2013, 2014; Weking et al., 2013; Vilbas et al., 2015), and microclimate (Shreeve, 1986; Thomas et al., 1998; Roy and Thomas, 2003) may also play an important role. Butterflies might not be able to detect scarce plant specimens even if the species is a host for the butterfly in other habitats (Beccalon and Symons, 2000). For instance, at the landscape level, occupied and unoccupied patches were found to differ only in the abundance of host plants in studies on *Euphydryas desfontainii* in Portugal (Pennekamp et al., 2013, 2014) and *E. aurinia* in Denmark (Tjørnløv et al., 2015).

In various butterflies, females have been shown to search for host plant individuals that affect habitat suitability through determining the microclimate allowing for successful larval development (Renwick and Chew, 1994; Weiss et al., 1988; Anthes et al., 2008; Körösi et al., 2012; Eilers et al., 2013; Weking et al., 2013; Örvösy et al., 2013). This type of selectivity can also limit the set of host plants used for oviposition (Anthes et al., 2008; Gibbs and Van Dyck, 2009; Bennie et al., 2013): only some of the potential host species may grow in conditions supporting larval development. Consequently, only a fraction of the total host plant population in a patch may be suitable for oviposition (Dennis et al., 2006). Selection of a host plant therefore often involves a complex trade-off between several biotic and abiotic factors (Courtney, 1982; Wiklund, 1984; Küer and Fartmann, 2005).

Microclimate has indeed been frequently shown to be the crucial aspect of habitat suitability (Shreeve, 1986; Thomas et al., 1998; Roy and Thomas, 2003; Turlure et al., 2009b; Bonebrake et al., 2010; Eilers et al., 2013; Lawson et al., 2014). The essential role of microclimate may imply that even butterflies that are generalists at the larger scale can be functionally specialist due to abiotic

factors restricting oviposition sites. For instance, among satyrines, microclimatic conditions appear to be a primary criterion for oviposition site selection in the false ringlet *Coenonympha oedippus*: spring temperatures must be high enough for successful development of the larvae (Örvösy et al., 2013). *Zerynthia cassandra* females prefer to oviposit on lower specimens of *Aristolochia rotunda* in more open and thus warm areas exposed to the sun (Vovlas et al., 2014). On the other hand, a study from Slovenia (Čelik, 2013) has shown that ovipositing females of *Leptidea morsei* prefer plants growing in shady conditions.

The situation is further complicated by the frequently observed geographic variation in the host-herbivore relationship (e.g. Singer, 1971; Hanski and Singer, 2001; Braschler and Hill, 2007). Perhaps the best known examples of geographic variation in host plant use are provided by various checkerspot butterflies (e.g. *Euphydryas editha*, *Melitaea cinxia*) in which host plant preference may vary even at a limited geographic scale: different host plants can be used by local populations separated by just a few kilometres from each other (Singer, 1971; Kuussaari et al., 2000; Hanski and Singer, 2001; Singer and Wee, 2005). Furthermore, for such a generalist as *Polygonia c-album* it was recently confirmed that its host use varies considerably throughout Europe (Braschler and Hill, 2007), and numerous examples from herbivorous insects other than butterflies exist (e.g. Fritz and Simms, 1992; Salvatore, 2006; Zovi et al., 2008; Logarzo et al., 2011). In addition to the differences in host species, the level of specialisation may also vary. For example, *Coenonympha arcania* was found to use 11 different host plants in mainland Europe, in contrast to using only one in Sweden (Nylin and Bergström, 2009).

Host plant use is especially likely to differ in populations that are close to the geographical range limits compared to more central populations (e.g. Lesica and Allendorf, 1995; Cassel-Lundhagen et al., 2009; Hill et al., 2011; Therry et al., 2014). In particular, peripheral populations have been frequently found to have a higher host specificity towards species distribution margins (e.g. Martin and Pullin, 2004; Schmidt and Hughes, 2006). Therefore, investigating host use at a local level also appears necessary when deciding about appropriate conservation measures (e.g. Samways, 2007; Reudler Talsma et al., 2008; Strausz et al., 2012; Czekeš et al., 2014). Knowing the local host plant use of endangered butterfly species is thus vital for effective conservation management.

In my thesis, I focussed on exploring the role of host plants as determinants of habitat quality in five butterfly species considered endangered at the European level: *Lopinga achine* (I), *Lycaena dispar* (II), *Euphydryas aurinia* (III), *Coenonympha hero* (IV), and *E. maturna* (V) (Van Swaay and Warren, 1999). These species are five out of seven butterfly species which are legally protected in Estonia on the basis of the European Community Habitats Directive. Selecting these five out of seven relies on the fact the remaining two – *Parnassius mnemosyne* and *Phengaris arion* – have already been subjected to ecological research in the country (Kuusemets et al., 2005; Liivamägi et al., 2005; Meier et al., 2005; Vilbas et al., 2015). My work had thus an applied goal

to provide information about the ecology of these species, necessary for designing conservation actions for these species in Estonia. Moreover, as these species still have a favourable conservation status in Estonia and are abundant enough, experimental studies on them are more feasible here than in places where the extinction threat is real.

To determine host plant preferences of the butterflies, we tested the females in simultaneous multiple-choice trials (**I**, **II**, **III**, **IV**), sequential single choice trials (**III**, **V**), and single substrate oviposition trials (**IV**). To figure out the suitability of different host species for larvae, we explored larval host plant preference (**I**, **IV**) and performance (**I**, **II**, **III**, **IV**, **V**) in the laboratory. Additionally, we observed host plant use in the wild (**II**, **III**) and performed a larval performance experiment in the field (**II**) using naturally growing host plants.

The presence of the host plant is a factor determining habitat suitability, to a greater or lesser extent. Consequently, to weigh the importance of the presence of the host plant against other habitat parameters, we conducted habitat occupancy analyses, using data from field work (**II**, **IV**, **V**), previously published distributional data (**II**), data derived from topographic maps (**II**, **V**), and host associations at the microhabitat level (**IV**). In addition to contributing to local knowledge about the butterfly species available for conservationists in Estonia (with the potential of transfer to other regions), the information gathered must also be useful for predicting the distribution of the species in other contexts, e.g. considering the anticipated range shifts in connection to ongoing climate change (**II**, **V**).

2. MATERIALS AND METHODS

2.1. Study species

All the species explored in my thesis are considered endangered in most of Europe and are included in the Annexes II and/or IV of the Habitats Directive of the European Union (Council Directive 92/43/EEC, 1992). In the Estonian Red Data Book *L. achine*, *E. maturna* and *E. aurinia* are labeled as 'rare', whereas *L. dispar* and *C. hero* are considered 'vulnerable' species (Eesti Punane Raamat, 2008). Due to the formal status of these butterflies, local information about the species is being collected continuously at the European level. The states have to report ranges, population sizes, habitats, future prospects, as well as overall assessments of conservation status and trends in it. Every EU member state – including Estonia – has the responsibility to protect the species through habitat preservation, and report the status of the species. My thesis will make a contribution to this task.

The woodland brown, *Lopinga achine* (Nymphalidae: Satyrinae; Fig. 1) is distributed from central Europe, European Russia and north-central Asia to the Amur region and Japan (Kudrna, 2002; Eliasson et al., 2005), and to northern Africa in the south (Ebert and Rennwald, 1991). The distribution of the butterfly species has drastically declined in western Europe as well as in Japan (Bergman, 2001; Bergman and Landin, 2001). In northern Europe, *L. achine* adults fly from June to July in one generation per year (Bergman, 1999; Settele et al., 1999; Bergman, 2001; Bergman and Kindvall, 2004) and the species hibernates in the larval stage (Tolman and Lewington, 1998; Bergman and Kindvall, 2004). This species prefers half-open woodlands (Bergman, 1999, 2005; Bergman and Landin, 2002; Bergman and Kindvall, 2004; Schiess, 2004; Konvička et al., 2008). Habitat deterioration is believed to be the main threat to the species (Bergman and Landin, 2002; Schiess, 2004); the loss of suitable habitats is caused by land use intensification through deforestation, as well as residential and road construction (Bergman, 2001). On the other hand, another threat factor for the species is overgrowing of clearings and grasslands



Fig. 1. An Estonian *Lopinga achine*
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in forest landscape which is caused mainly by the ongoing decline in grazing and mowing (Bergman, 2001; Bergman and Kindvall, 2004; Schiess, 2004).

The butterfly is believed to use different plant species from the families Cyperaceae and Poaceae, like *Carex fritschii*, *C. michelii* (Konvička et al., 2008), *C. montana* (Bergman, 1999, 2000), *C. sylvatica* (Bergman, 1999, 2001), *Melica nutans*, *Festuca ovina*, *Calamagrostis canescens*, *Deshampsia flexuosa*, *Brachypodium pinnatum* (Konvička et al., 2008). However, systematic studies on host plant associations are scarce. In Sweden, *L. achine* was considered specialized on *C. montana* (Bergman, 1999, 2000). Therefore, one might suspect that the populations from the floristically similar western Estonia, may also be specialized on *C. montana* while the populations from eastern Estonia – where *C. montana* is rare – must use different host plants.

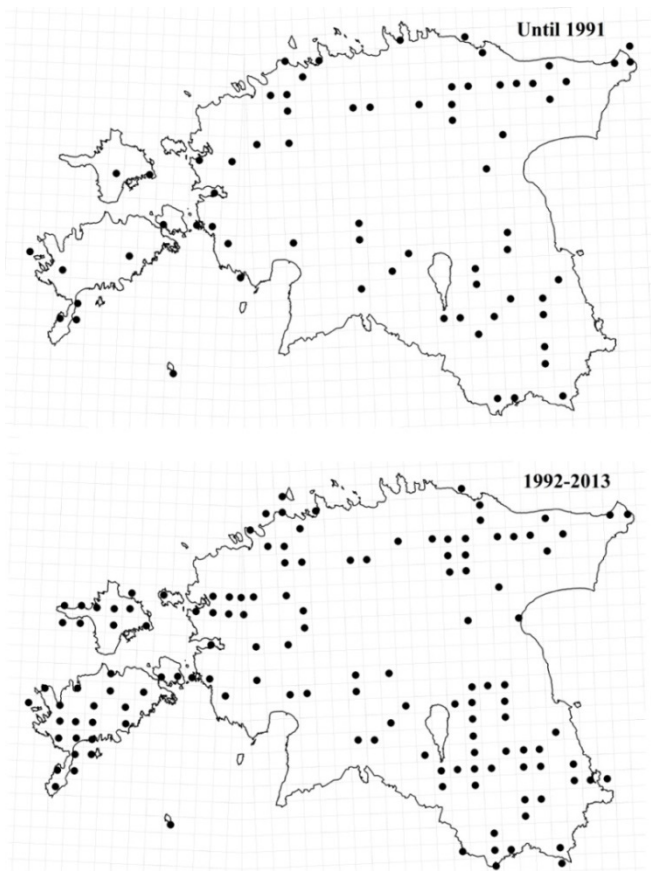


Fig. 2. The known distribution of *L. achine* in Estonia until 1991 (data is retrieved from Kesküla, 1992) and from 1992 to 2013 (the map is compiled on the basis of the data published in the Estonian lepidopterological periodical Lepinfo, interviewing active amateur lepidopterists and the data in Vilbaste, 2004). The data are presented by 10×10 km UTM squares

In Estonia, the earliest sources reported the species to be widespread in the country's deciduous forests, although it had not been found on Saaremaa (Petersen, 1924), the largest island in western Estonia. In 1992, Kesküla (1992) reported several records from Saaremaa, which suggests that the species has been spreading in Estonia. The original distribution map relying on data 1992 to 2013 shows that it has been found in most UTM grid cells where active butterfly faunistic research has conducted (Fig. 2). The increase in the number of observations probably reflects accumulation of the data, and I believe that no qualitative changes in the distribution and abundance of the species have occurred (Lindman et al., 2011a), with the possible exception of colonisation of Saaremaa. Nevertheless, as forest cover of Estonia has increased about twofold during the last 100 years, a positive trend in *L. achine* as a forest species cannot be excluded either.

The Scarce Heath, *Coenonympha hero* (Nymphalidae: Satyrinae; Fig. 3) is a widespread species in the eastern part of its European range, but in most of western and central Europe, the species is very scarce being restricted to a few sites of good quality habitat, definitely declining in the area (Van Swaay et al., 2012). It is reported as extinct in Belgium, Czech Republic, Denmark, Luxembourg, Switzerland and the Netherlands. Declining distribution or population size (more than 30%) has been reported from Germany and Ukraine. 6–30% declining has been reported from Austria, France, Latvia, Lithuania, Norway, Poland and Sweden (data provided by the national partners of Butterfly Conservation Europe; Van Swaay et al., 2010). The species typically inhabits seminatural bushy meadows and woodland clearings. The main threats to the species are believed to be drainage, agricultural improvements and changing grassland and woodland management (Van Swaay and Warren, 1999).

C. hero is univoltine with the flight period starting from early June and lasting to early July in northern Europe. The grass-feeding larvae overwinter in their third instar in a grass tussock, growth resumes in spring, and the larvae pupate having gone through 5 instars (Cassel-Lundhagen and Sjögren-Gulve, 2007; Van Swaay et al., 2010). *C. hero* is believed to be a generalist feeding on various grasses (Cassel et al., 2001; Cassel-Lundhagen and Sjögren-Gulve, 2007; numerous field guides).



Fig. 3. An Estonian *Coenonympha hero*
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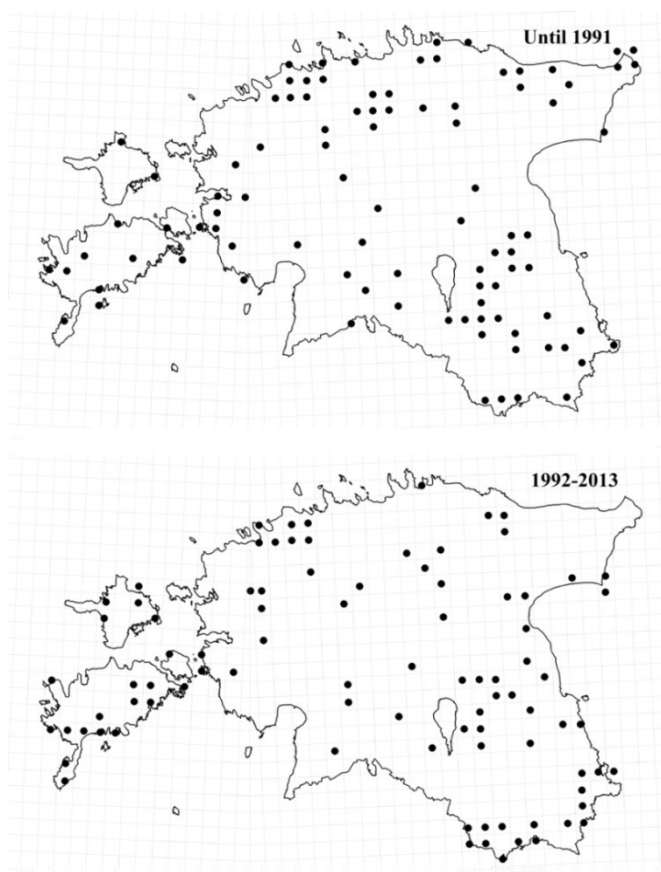


Fig. 4. The distribution of *C. hero* in Estonia until 1991 and from 1992 to 2013 (see Fig. 2 for details)

C. hero is considered a widespread species in Estonia. During the last 20 years the species has been found in more than 60 UTM 10×10 km grid cells (Fig 4). The scarcity of findings in central Estonia is likely explainable by the low intensity of lepidopterological research in that area. Still, the distribution of the butterfly is probably even wider: *C. hero* is considered such a common species among lepidopterists so that the findings are often not reported. There is no reason to suspect qualitative changes in the distribution of the species during last 100 years (Vilbas et al., 2011a). The status of *C. hero* in Estonia is favourable compared to its status in western Europe probably due to the high share of managed forest in the country. The butterfly species appears to thrive on forest clearings with a suitable moisture regime (Vilbas et al., 2011a) and in other half-open landscapes with moderate anthropogenic pressure (Krauss et al., 2010; Sang et al., 2010; **IV**)

The large copper, *Lycaena dispar* (Lycaenidae: Lycaenini; Fig. 5) has a large but discontinuous Palaearctic distribution, ranging from western Europe across temperate Asia to the Amur region and Korea (Ebert, 1993; Pullin et al., 1998; Kühne et al., 2001). The rapid decline of its wetland habitat in north-western Europe has drawn attention to its vulnerability (Pullin et al., 1998). However, the status of *L. dispar* is divergent: the species is still widespread throughout central and eastern Europe (Pullin et al., 1998) and has even expanded its range to new areas in north-eastern Europe including Estonia, (Lai and Pullin, 2004; Saarinen, 2010; Kudrna et al., 2011; II).



Fig. 5. An Estonian *Lycaena dispar*
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L. dispar primarily colonizes wetland habitats (Pullin et al., 1995; Webb and Pullin, 1998; Pullin et al., 1998, Nicholls and Pullin, 2003; Martin and Pullin, 2004), particularly fenlands (Shreeve et al., 2001; Werner and Möller, 2003; Loritz and Settele, 2006), riverside and lakeside areas, as well as wet meadows (Bąkowski et al., 2010). In central Europe, *L. dispar* also uses drier areas such as fallows and urban wastelands (Strausz, 2010). The predominant causes of the decline are identified as wetland reclamation for agricultural purposes (Pullin et al., 1995) and intensive management of grasslands, such as early mowing (Loritz and Settele, 2006).

The actual host plant use and the degree of specialisation are known to vary across the range of the butterfly (Pullin et al., 1998; Kühne et al., 2001; Werner and Möller, 2003; Loritz and Settele, 2006). The species is known to utilise *Rumex hydrolapathum* (Bąkowski et al., 2010; Kühne et al., 2001), *R. crispus* (Loritz and Settele, 2006), *R. obtusifolius*, *R. conglomeratus*, *R. sanguineus*, *R. aquaticus*, *R. acetosa* throughout its range (Ebert and Rennwald, 1991; Pullin et al., 1998; Kühne et al., 2001; Werner and Möller, 2003; Loritz and Settele, 2006). The butterfly appears to be monophagous on *R. hydrolapathum* in the Netherlands (Pullin et al., 1998; Webb and Pullin, 2000; Martin and Pullin, 2004), but oligophagous on various *Rumex* species in e.g. Germany and Austria (Kühne et al., 2001; Werner and Möller, 2003; Loritz and Settele, 2006; Strausz et al., 2012).

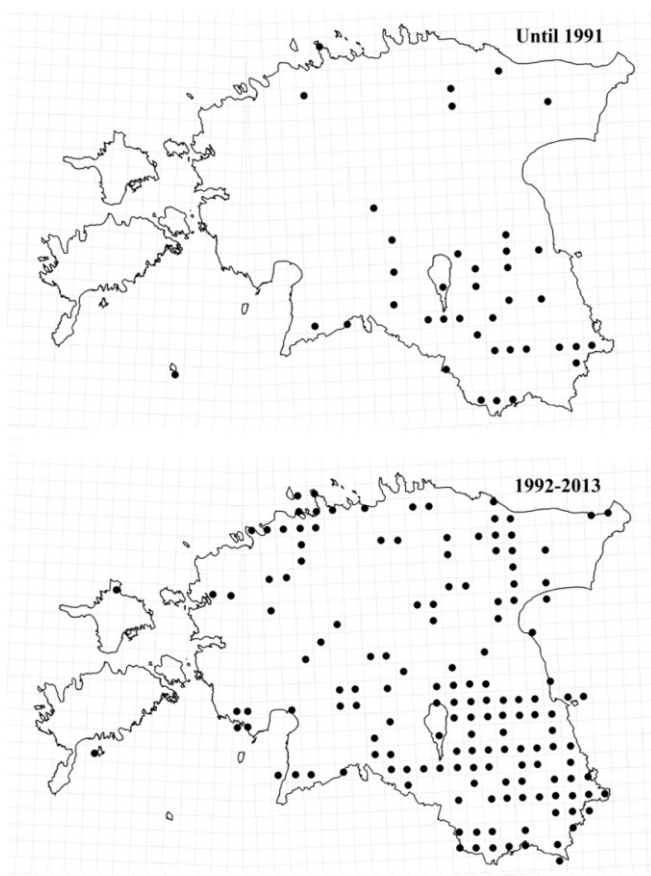


Fig. 6. The distribution of *L. dispar* in Estonia until 1991 and from 1992 to 2013 (see Fig. 2 for details)

In Estonia, *L. dispar* colonizes primarily wet meadows but is also observed in a wide variety of other habitats (Õunap and Tartes, 2014; *pers obs*). The species is a newcomer in the Estonian butterfly fauna, with the first record having been made in 1947. By 1992, the species was distributed mainly in south-eastern Estonia (Fig. 6, Kesküla, 1992). The map from 2013 shows that the species is widespread on the Estonian mainland. It has been found in most UTM grid cells where active butterfly faunistic research has been carried out, with the marked exception of the western Estonian archipelago. There is no doubt that the butterfly species has also been clearly expansive during the last 20 years (Vilbas et al., 2011b).

The scarce fritillary, *Euphydryas maturna* (Nymphalidae: Melitaeini; Fig. 7) is distributed from France across central and eastern Europe to Siberia and Mongolia. It has always been described as local in Europe (Vogler, 1980; Essayan, 1999), but has declined dramatically in many countries during the past few decades (Van Swaay and Warren, 1999), having become extinct in Belgium and Luxembourg and critically endangered in Germany, France, Sweden, the Czech Republic and Austria, where populations have decreased by over 75% (Van Swaay and Warren, 1999).

E. maturna appears to have highly specific habitat requirements (e.g. Kühnert, 1967; Weidemann, 1986, 1988; Settele et al., 1999). The species is an open woodland specialist (e.g. Kühnert, 1967; Weidemann, 1986, 1988; Settele et al., 1999; Benes et al., 2002; Freese et al., 2006): it inhabits forest edges, openings within forests, and forest tracks (Marttila et al., 1991; Somerma, 1997; Wahlberg, 1998, 2000a, 2001a; Freese et al., 2006), where it occurs in small colonies which form metapopulations (Weidemann, 1988; Eliasson, 1991; Marttila et al., 1991). The decline of *E. maturna* in central and western Europe is believed to be related to its dependence on light and sparse deciduous forests (Weidemann, 1986; Benes et al., 2002; Konvička et al., 2005), historically maintained by coppice management. As coppicing was largely abandoned during the 20th century, the butterfly retreated to a handful sites coppiced for conservation purposes (Höttinger and Pennerstorfer, 1999; Van Swaay and Warren, 2006) or to localities where open clearings have continuously been available.

Females of *E. maturna* lay their egg-batches in early summer; larvae hatch and start feeding in groups in silk-woven nests (Cizek and Konvička, 2005). Eggs are generally laid on woody plants, where the pre-hibernation larvae develop communally in silk-woven nests until late summer and diapause in the leaf litter until early spring (Cizek and Konvička, 2005; Freese et al., 2006; Dolek et al., 2013). The principal host plant of the species appears to be *Fraxinus excelsior* (Weidemann, 1988; Ebert and Rennwald, 1991; Eliasson, 1991; Vrabec and Jindra, 1998; Pletcher, 2000; Konvička et al., 2005). Still, there are records that the species has been also found on other plants such as *Fraxinus angustifolia* (Tolman and Lewington, 1997), *Ligustrum vulgare* (Konvička et al., 2005; Dolek et al., 2013), *Viburnum opulus* (Eliasson, 1991, 2001; Eliasson and Shaw, 2003; Dolek et al., 2013), *Veronica longifolia* (Wahlberg, 1998, 2000a, b) and *Populus tremula* (Weidemann, 1988; Ebert and Rennwald, 1991; Tolman and Lewington,



Fig. 7. An Estonian *Euphydryas maturna*
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1997; Pretcher, 2000), but there do not seem to be any verified observations of pre- or post-diapause larvae feeding on the last plant species (Wahlberg, 2001b). However, the situation appears to be different in Finland, where the butterfly species is monophagous on *Melampyrum pratense*, (Eliasson, 1991, 1999; Wahlberg, 1998, 1999; 2000a, b, 2001a; Wahlberg et al., 2002).

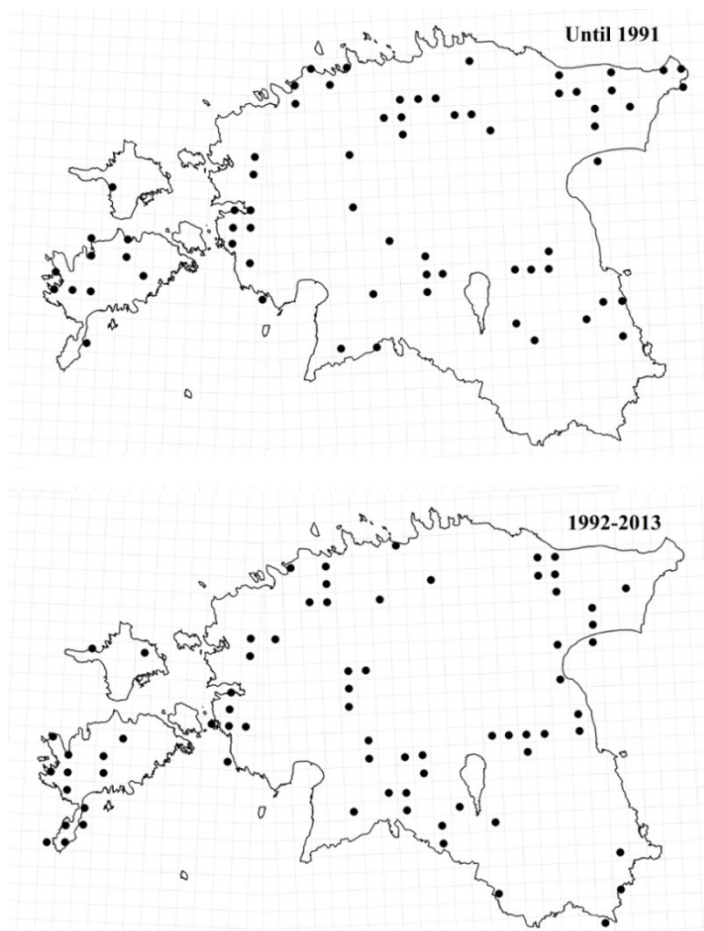


Fig. 8. The distribution of *E. maturna* in Estonia until 1991 and from 1992 to 2013 (see Fig. 2 for details)

In Estonia, the species inhabits deciduous forests and wooded meadows (Õunap and Tartes, 2014; *pers obs*). According to the distribution map of *E. maturna* published in 1992 (Kesküla, 1992) the butterfly species is widespread in the country though not ubiquitous (Fig. 8). The gap in central Estonia is likely explainable by the low intensity of lepidopterological research there. The comparison of distribution maps from different time suggests that, during last

100 years, no qualitative changes in the distribution and abundance of the species have occurred (Lindman et al., 2011b).

The marsh fritillary, *E. aurinia* (Nymphalidae: Melitaeini; Fig. 9) is a widespread species, occurring from the Iberian Peninsula through most of Europe and across temperate Asia eastwards to Korea; it is found in most European countries (Liu et al., 2006; Bulman et al., 2007; Kudrna et al., 2011) being absent only from Iceland, Norway, and the Mediterranean islands (De Prins and Iversen, 1996). Despite its large geographic range, numerous local populations are considered endangered (Schtickzelle et al., 2005; Fox et al., 2010; Smee et al., 2011).

E. aurinia primarily inhabits semi-natural meadows, including fen meadows (Van Swaay and Warren, 1999; Anthes et al., 2003; Betzholtz et al., 2007; Sigaard et al., 2008; Reid et al., 2009). However, forest clearings, woodland edges and areas under power lines (Saarinen et al., 2005; Betzholtz et al., 2007) can also be populated. Most of the threats have been found to rise from direct human activities: open habitats falling out of use, inappropriate habitat maintenance methods, overgrazing or mowing in unsuitable time period, with habitat fragmentation as a frequent side effect (Joyce and Pullin, 2003; Saarinen et al., 2005; Fowles and Smith, 2006; Wang et al., 2007).

E. aurinia has a univoltine life cycle (Wahlberg, 2000a), with the larva as the overwintering stage. The females lay their eggs in several clutches (average of 270 eggs per clutch) on the lower surface of a host plant leaf (Wahlberg, 2000a; Stefanescu et al., 2006; Švitra and Sielezniew, 2010) from the last days of May to the end of June (Hula et al., 2004). The species has geographical variation in the use of host plants (cf. Descimon et al., 2001; Singer et al., 2002), using *Succisa pratensis* (Wahlberg et al., 2002; Norberg et al., 2002; Eliasson and Shaw, 2003; Konvička et al., 2003; Saarinen et al., 2005; Singer et al., 2002; Sigaard et al., 2008; Tjørnløv et al., 2015), *Knautia arvensis* (Warren, 1986, 1994; Eliasson and Shaw, 2003; Schtickzelle et al., 2005), *Lonicera implexa* (Mikheyev et al., 2013; Stefanescu et al., 2006) and several other plant species in different regions (e.g. Table 1 in III).



Fig. 9. An Estonian *Euphydryas aurinia*
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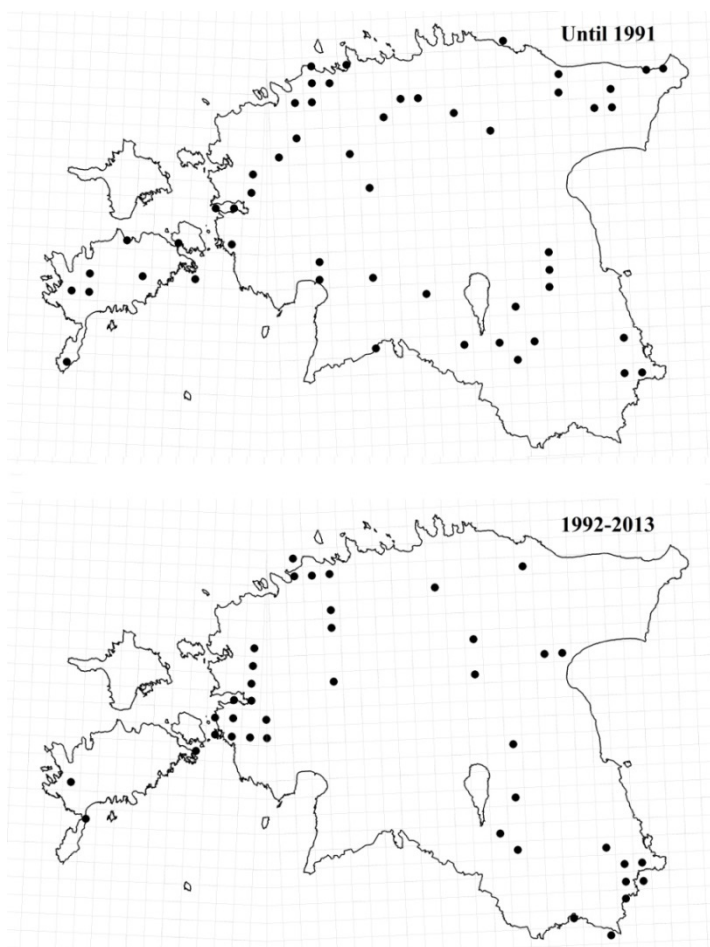


Fig. 10. The distribution of *E. aurinia* in Estonia until 1991 and from 1992 to 2013 (see Fig. 2 for details)

In Estonia, the species inhabits smaller meadows in forest landscapes and forest clearings (Õunap and Tartes, 2014; *pers obs*). According to the distribution map of *E. aurinia* published in 1992 (Kesküla, 1992) the butterfly species is relatively widespread in Estonia. A comparison of maps from different periods (Fig. 10) suggests no qualitative changes in the distribution (Lindman et al., 2011c), though a negative trend appears slightly more likely than in the other species, considered in the present work.

2.2. Methodology

Oviposition experiments

Simultaneous multiple-choice trials (e.g. Wiklund, 1975; Janz and Nylin, 1997) were conducted with wild caught females of *L. achine*, *C. hero*, *L. dispar*, *E. maturna*, and *E. aurinia*. Each female was simultaneously offered similarly sized plant sections from different plant species (3 to 5), placed at equal distances from each other. The order of the plants was randomized in each replicate. Sugar-water solution was offered as food for the female using damp tissue paper located at the middle of the box. The eggs laid were counted and removed from the plants once a day. The females were housed individually in transparent boxes with size 50×50×50 cm (I), 45×45×55 cm (II), 25×25×15 cm (IV), 1 litre (III), and 0.5 litre (IV) for 48 or 72 hours (IV) or until the death of butterflies (I, II, III). The experiments took place at approximately 25 °C (I) or 27 °C (II, III, IV), with LD 16:8h (I) or 18:6h (II, III, IV) photoperiodic regime.

Sequential single choice trials were performed with *E. maturna* and *E. aurinia*. These tests have specifically been designed for studying oviposition preferences in checkerspot butterflies. This is because these insects are frequently observed not to behave normally during multiple choice tests in enclosures (Singer, 1982; Ehrlich and Hanski, 2004). In such tests, candidate plants are presented to the female one at a time just for short time periods, and the behavioural responses of the butterflies are recorded in detail. Moreover, sequential choice tests allow us to obtain more information per individual compared to, for example, standard simultaneous-choice tests.

In the original protocol of the sequential choice tests (Singer, 1982, 2004), whether the butterfly shows interest towards the presented plant is recorded, the 'interest' being defined as protruding the ovipositor to the lower surface of a plant leaf at least three times within a three minute trial. After every trial butterflies are kept deprived of a plant for fifteen minutes before presenting the next plant species. Oviposition *per se* is precluded to ensure that the motivation to oviposit would not fall to zero. In the experiments, we observed protruding ovipositors just in a few cases, likely as a result of suboptimal ambient conditions. In particular, due to unfavourable weather during the experimental period, our experiments had to be conducted in the laboratory setting under artificial light conditions, contrary to natural light recommended by the original protocol. Nevertheless, we were able to distinguish between butterflies showing, and not showing 'interest' in a 'softer', slightly modified sense – towards the plant presented. In particular, behavioural acts such as the female walking on both sides of the leaf, extracting her ovipositor and probing the leaf with labial palpi were all considered indications of showing interest in the plant presented.

Experiments took place from 11 am to 4 pm (V), or to 5 pm (III), coinciding with the timing of oviposition events in the field; and lasted for at least a day for each butterfly. Host species known to be used in neighbouring countries were

incorporated in the experiments with *Betula pendula* included as a control plant (treated in the same way as the other host plants), i.e. a plant certainly not used as a host by the focal species. Visually similar sized plant sections (a leaf or a branch, depending on the species) were offered to the butterfly in a randomized order which was, however, kept constant for each individual during one day. Sixteen (V) or eighteen (III) trials (exposing one plant to a butterfly) were conducted with each butterfly every day, i.e. each specimen was tested on the same set of plant species four (V) or six times (III) a day.

In the **single substrate oviposition trial** with *C. hero* (IV), wild caught females were placed singly in 0.5 litre transparent boxes, accompanied with a bunch (or twigs) of one out of three plants: two suggested host species and *Picea abies* as a control. The selection of the substrates offered was motivated by the results of the multiple choice tests. After 72 hours, the experiment was terminated, and the eggs were counted. Single substrate trials are considered complementary to the multiple choice trials as in the latter ones, the signals from other candidate plants present nearby may elicit oviposition on hosts which would not have been accepted otherwise. Single substrate trials, though not directly testing for host plant choice, are free from this problem, with the number of eggs laid on each type of substrate characterising its acceptability (Tammaru et al., 1995).

Preference and performance of the larvae

The host plant preference of neonate larvae was tested with *L. achine* and *C. hero* (I, IV), i.e. the species in which the females do not (always) attach their eggs to the plant, and finding a suitable host is thus the task of the larva. The tests were run using a set of potential host plant species. In the trials, sections of two plant species were offered simultaneously to neonate larvae, various pair-wise combinations of host species were used. A Petri dish was prepared with damp filter paper at the bottom and equally sized (ca 3 cm) leaf sections from each plant were placed on the opposite sides of the dish, with a newly hatched caterpillar in the middle of it. Over 24 hours, larval preference was recorded on the basis of caterpillar location and eating marks. In the typical case, the caterpillar was found resting on the host plant it had preferred; only rarely it was necessary to determine the preference by inspecting feeding marks. The cases when larva had died during the trial were excluded. Laboratory temperature was kept at 25°C (I) or 23°C (IV) during the experiment.

Larval performance on different potential host plants was investigated in laboratory rearing experiments with all the five butterfly species using potential host plants of the species. A newly hatched caterpillar (I, II, IV) or a group of caterpillars (IV, V) were reared on growing potted host plants (I, III) or on fragments of host plants (I, II, III, IV, V). The host plant leaves were renewed and moisture was increased by providing a piece of damp cotton wool every day (IV), every second day (II, V), every third day (I, III) or when plant fragments started to show signs of deterioration (I). Growth performance was expressed as

survival and body weight at the age of one (IV), two (II), three (I, III, V) or six weeks (I) since hatching. The relatively short test periods were chosen because all studied species overwinter in the larval stage. Arranging suitable hibernation conditions for such species in the laboratory is known to be problematic (Friedrich, 1986), and was not attempted. The experiments were carried out in the laboratory at a constant temperature of 17 °C (I), 19°C (I), 23°C (II, III, V) or 24°C (III) and 17:7h (I) or 18:6h (I, II, III, IV, V) photoperiodic regime.

Field studies

Host plant use. To confirm the results of laboratory experiments, we also studied host plant use in the field in two species *L. dispar* (II) and *E. aurinia* (III). In addition to observations and field censuses of both eggs and larvae (II, III), in the case of *L. dispar* a larval growth performance experiment was conducted in the field: we reared larvae hatched in the laboratory, on natural host plants in a natural habitat (II).

Habitat occupancy analyses. For *E. maturna*, transect counts were conducted to understand the relative importance of the abundance of a potential host plant relative to other habitat characteristics (V). As the adults of *E. maturna* often feed and bask on umbellifers and are not easily startled, it is highly feasible to count them. For the field work, we selected 30 transects in a forested area inhabited by this species. Each transect was walked twice and the number of *E. maturna* individuals was counted. The values of several predictor variables were also recorded (for example, the abundance of potential host species *F. excelsior*, the percentage of umbellifers, weather parameters) or derived from topographic data-bases (moisture, forest age, length of roads and edges).

Landscape occupancy analysis, relying on previously published distribution data, was performed for *L. dispar*. Distribution data were based on records published in the Estonian lepidopterological bulletin Lepinfo, recorded by 10×10 km UTM squares. Predictor variables related to the parameters of water bodies, forest cover and human settlement were derived from topographic data bases.

To explore host plant associations of *C. hero* at the microhabitat level (V), we systematically searched for resting *C. hero* adults in a number of habitat patches on the islands of Saaremaa and Muhu. We recorded the exact resting points of observed butterflies, and control points within the same habitat patch, 10 metres apart from the points occupied by the butterflies. All the field data were collected during active flight time of butterflies: from 9.30 am to 7.00 pm, temperature above 16°C, and a minimum of 60% of sunshine. Vegetation parameters were recorded within a circle with a radius of one metre around each point. Cover of all the vascular plant species present and shrub cover were estimated visually for both the occupied and the control points. Vegetation height was measured as average height of dominant herbs in the circle. Ellen-

berg light and moisture indices were derived from the data on floristic composition of the spots studied.

2.3. Data analyses

To determine oviposition preference in the multiple choice (**I**, **II**, **III**, **IV**) and single choice experiments (**IV**), the number of eggs laid was tested as dependent on plant species in respective mixed general linear models, with the identity of the female as a random variable. In the experiments (**III**, **V**) conducted using sequential single choice trial method, we analysed the dependence of the binary response variable (interest towards the host plant observed or not during each 3 minute period) on host species, applying mixed generalized linear models for binary variables. In the field, the number of eggs laid on each plant in each trial (**II**) was analysed as dependent on the plant species using a Poisson mixed model accounting for over dispersion. To explore host plant preference (**I**, **IV**), as well as performance and survival (**I**, **II**, **III**, **IV**, **V**) of the larvae on different host plants, mixed generalized linear models were constructed, brood (offspring of one female) identity was always included as a random factor. In the habitat occupancy analyses, to compare models with different sets of predictors (**II**, **V**), we used the variable ranking procedure based on the Akaike information criterion (as described by Anderson et al., 2000; Burnham and Anderson, 2004; Johnson and Omland, 2004). Mixed generalized linear models for binary data were constructed to discriminate the occupied points from absence points in *C. hero* (**IV**), with 'site' being included as a random variable. The inference was, once again, based on the Akaike information criterion. Data of all the laboratory and field experiments were analysed using SAS (SAS institute Inc., 2008), or respective packages in the R environment (R Core Team, 2014).

3. RESULTS

Lopinga achine

In *L. achine* (I), we found that oviposition was not selective with respect to oviposition substrate (host plant) offered. Larvae accepted all plant species offered with approximately equal probability, except for *Festuca ovina* which was the least chosen host in the experiment. Of host species tested, *Carex montana*, *C. sylvatica*, *Melica nutans*, and *Calamagrostis canescens* were close to being equally suitable for the caterpillars; only *F. ovina* failed to support larval development in one of the experiments. Thus, *L. achine*, being polyphagous in Estonia, appears not to be specialized on certain host plant species; only *F. ovina* of those plant species tested may not be a suitable host plant in Estonia. There was no evidence of specialisation of either Swedish or western Estonian *L. achine* on *C. montana*, previously suggested to be a principal host plant of the species; neither did the Swedish and Estonian populations differ in their host preference.

Lycaena dispar

In *L. dispar* (II), neither oviposition preference of the females nor the growth performance of the larvae revealed any substantial differences in the suitability of *Rumex hydrolapathum*, *R. crispus*, *R. obtusifolius* or *R. aquaticus*: in the laboratory, all these plant species were equally acceptable/ suitable for the butterfly. In some contrast to the lab based results, field studies revealed significant differences between the two primary host plants, *R. obtusifolius* and *R. crispus*. There were more eggs on *R. crispus* (4.6 eggs per plant) than on *R. obtusifolius* (2.9 eggs per plant) but the difference between these hosts became reversed as the season progressed: there were more mid-growth larvae on *R. obtusifolius* than *R. crispus*, indicating better survival on the former host species. Consistently, field work showed that *R. obtusifolius* provides significantly longer growing time for the larvae than *R. crispus*: the latter dries up before caterpillars reach the developmental stage adapted to hibernation. Both the laboratory and field experiments proved the possibility of the rarely observed second generation of *L. dispar* in Estonia though the selection of developmental pathway did not depend on the used host plant. A country-wide analysis of landscape occupancy revealed that the occurrence of *L. dispar* is positively affected by the density of ditches and human settlements, likely mediated by the abundance of suitable habitat for the *Rumex* species used.

Euphydryas aurinia

The two different oviposition experiments used revealed a preference of the females of *E. aurinia* (III) for *Succisa pratensis*: butterflies showed most interest in this plant, and actually oviposited onto it more often than to other species (*Knautia arvensis*, *Betula pendula*). Larval performance on different

host plants was tested in two years using different group sizes of the larvae. *S. pratensis* was also found to be superior over *K. arvensis* in terms of larval performance: the survival of three week old larvae growing on *S. pratensis* was 12 times higher in one year of the study, and three times higher in another compared to *K. arvensis*. In addition, the average weight of the larvae was significantly higher on *S. pratensis* than *K. arvensis*. The larvae were not able to develop on *Plantago media*, *P. lanceolata*, *P. major* and *Valeriana officianalis*. While surveying larval webs in natural habitats, all nests were found on *S. pratensis* and none on the alternative host plants (*K. arvensis*, *P. lanceolata* and *P. media*) simultaneously present.

Coenonympha hero

We tested the suitability of *Festuca ovina*, *F. rubra*, *Dactylis glomerata*, *Sesleria caerulea*, and *Helictotrichon pratense* for the butterfly species in two different years (IV). In simultaneous multiple-choice oviposition experiments, the number of eggs laid clearly differed between the plants offered: *F. ovina* – a grass with thin needle-like leaves – was strongly preferred over *C. arundinacea*, *C. epigeios* and *D. glomerata*. Surprisingly, in one of the years, the number of eggs laid on the control plant, Norway spruce (*Picea abies*), was equal to the number of eggs on *F. ovina*. In single substrate oviposition experiment, females laid significantly more on *F. ovina*, compared to *D. glomerata* or the control plant *P. abies*; nevertheless, the latter plant also received a considerable number of eggs.

The neonate larvae preferred *F. ovina* over other plants (*C. arundinacea*, *C. epigeios*, and *D. glomerata*), with the least preferred plant species being *D. glomerata*. In another year, the test was repeated to specifically assess the choice between *F. ovina* vs. *F. rubra*: a clear majority of the larvae (77%) selected *F. rubra*. In one year of the study, the larvae reared on *F. ovina*, *D. glomerata* and *H. pratense* were similar in weight whereas larvae reared on *S. caerulea* remained smaller compared to those on *F. ovina*. In the other year larval weights were significantly lower on *F. ovina* compared to either *F. rubra* or *D. glomerata*. In the first year of study, survival of one week old larvae did not differ between the four grasses offered. In the other year, survival on *D. glomerata* and *F. rubra* was significantly higher compared to *F. ovina*. Nevertheless, all grass species offered proved to support larval development, with the differences in larval performance indices between the plants offered being relatively minor.

Exploring host plant associations of *C. hero* at the microhabitat level revealed seven grass species which were most common in the habitats of the butterfly; these were *H. pubescens*, *H. pratense*, *F. rubra*, *F. ovina*, *S. caerulea*, *B. media*, and *P. angustifolia*. However, in the statistical models constructed to explain the occurrence of *C. hero*, only the cover of *F. rubra* appeared among the highly ranked variables. In contrast, the butterfly was more frequently encountered in patches with a higher light and moisture index, and with

presence of shrubs; these environmental parameters being far better predictors of the occurrence of the butterfly than any species of potential hosts.

Euphydryas maturna

Our results (V) provide support for the idea that *Fraxinus excelsior* is the primary host plant of *E. maturna* in Estonia. In the sequential choice experiments, *F. excelsior* was readily accepted by the ovipositing females, as well as supported larval growth well. These indices were, however, equal for another possible host, *Viburnum opulus*, whereas *Melampyrum pratense* clearly proved to be an inferior alternative. The larvae of Estonian *E. maturna* were unable to develop on *Populus tremula*, *Betula pendula* and *Vaccinium myrtillus*. Habitat occupancy analysis based on original transect count data indicated that the abundance of *F. excelsior* is the primary determinant of the abundance of the butterfly. The association between *E. maturna* and *F. excelsior* is also evident from country-wide distribution patterns of these species – the butterfly species has rarely been found in south-eastern Estonia which is an area well studied lepidopterologically but differs from other parts of the country through scarcity of *F. excelsior*. In contrast, the occurrence of *V. opulus* is unlikely an important determinant of the abundance of *E. maturna* in Estonia, just due to the relative scarcity of the plant in the country.

4. DISCUSSION

The work reported in the present thesis allowed us to increase the knowledge about the ecology of five butterfly species – *Lopinga achine*, *Lycaena dispar*, *Euphydryas aurinia*, *E. maturna*, and *Coenonympha hero* – considered endangered at the European level (Van Swaay and Warren, 1999). Though using different experimental designs – due to species-specific differences in adult behaviour – knowledge about host preference of ovipositing females was obtained for all five species. Laboratory-based studies of larval host preference as well as host-specific performance and survival provided further information. Integrating the data on host preference and host-specific performance with results of various field studies and distribution data allowed us to estimate the degree of host specialisation in all the species studied, and to estimate relative ranks of the hosts used by the specialists. Such locally-derived knowledge allows us to make conservational recommendations for preserving and protecting the Estonian populations of these butterflies, and also makes a contribution to the knowledge about these species at a broader geographical scale. Indeed, much of the information gathered on the species' ecology must be of use in regions where the species may be, or may become a conservation concern.

Our results do not support the idea that females of *L. achine* may prefer to oviposit on certain plant species (Bergman, 2000) confirming the conclusions about indiscriminate oviposition behaviour in this species (Settele et al., 1999; Bergman and Kindvall, 2004). Our experiments supported the observations by Bergman (2000) that newly hatched larvae are capable of host plant selection. We agree that *C. montana* is favourable host for the butterfly species but we failed to support the idea (Bergman, 2000) that the plant species is clearly superior over other species, being the main host plant in Sweden.

In fact, we found that north European populations of *L. achine* are polyphagous enough on various grasses and sedges (I), so that the presence of any particular host species cannot be a critical component of habitat quality. As many of the plant species proven to be acceptable are widespread (Kukk and Kull, 2005), host plant is not a limiting factor of the distribution of *L. achine*. There may only be some weak preference for soft- and broad-leaved grasses and sedges (*Carex montana*, *C. sylvatica*, *Melica nutans* in our sample), which may partially explain the tendency of the species to prefer moist forests supporting the idea of strict habitat requirements of the butterfly (Bergman, 2001; Bergman and Landin, 2002). For protecting the species, it appears to be necessary to preserve its habitats in moderately moist forest with half-open elements. Current forestry practices in Estonia appear not to be threatening the species' future.

Our results are in contrast with observations from Britain and the Netherlands (Pullin et al., 1998; Martin and Pullin, 2004) where *Rumex hydro-lapathum* is the only confirmed host species for *L. dispar*. Our results are more

similar to those from Austria (Strausz et al., 2012) and Germany (Loritz and Settele, 2006) but differ in terms of preferring *R. crispus* over *R. obtusifolius*.

The principal host plant species in Estonia appears to be *Rumex obtusifolius* (II). Various other *Rumex* species were shown to be equally acceptable for the larvae in the laboratory but should play a minor role as a host plant due to their relative scarcity. *R. crispus*, an abundant plant of the agricultural landscape, was shown to be less suitable due to the ephemeral character of the above-ground parts of the plant. The landscape occupancy analysis revealed that the butterfly prefers the habitats near ditches and human settlements, which is consistent with an idea that moderate anthropogenic pressure maintains suitable habitats for *L. dispar* through creating favourable conditions for *R. obtusifolius*. Distribution data show that *L. dispar* is an expansive and now already a widespread species in Estonia.

Due to its expansive character, and generalism in both host as well as in habitat use, *L. dispar* is not in the need of active conservation measures at the current northern limit of its distribution. Still, it should be considered that reexcavation of ditches, and mowing tall herbaceous vegetation e.g. on road verges during the larval period (early July – mid August) kills the offspring of the butterfly.

The host use of *E. aurinia* in Estonia appears to be more similar to that in Finland (Wahlberg et al., 2002), the Czech Republic (Konvička et al., 2003, 2005), Denmark (Sigaard et al., 2008) and Italy (Casacci et al., 2014) where the butterfly species is reported to use only one host species. A higher number of hosts – including *Knautia arvensis*, *Valeriana officinalis*, *Lonicera implexa*, *L. etrusca* – are known from Sweden, France and Spain (Norberg et al., 2002; Eliasson and Shaw, 2003; Stefanescu et al., 2009; Mikheyev et al., 2013).

In Estonia, *E. aurinia* appears to be functionally monophagous on *Succisa pratensis* (III). The plant species was the one most preferred by females, the best supported larval growth, and the only plant species on which larval nests were found in the actual habitat of the butterfly: *S. pratensis* remains the only confirmed host of *E. aurinia* in Estonia.

S. pratensis may be adversely affected by abandonment of traditional agricultural practices, and active measures may be needed to preserve local populations. Without grazing, mowing in the habitat of *E. aurinia* is important to keep it open, but doing so at the wrong time of the year may damage the population significantly. For example, in the Czech Republic, late mowing in the larval growth period decimated the number of larval nests in a habitat patch by more than 90% (*pers. comm.*). Therefore, mowing should be done before the beginning of June. Still, there is an alternative way, practised successfully in the Czech Republic (Konvička et al., 2003): the host plant of *E. aurinia* grows in groups, so to avoid the destruction of larval webs, mowing around the groups can be done without damaging host specimens.

Our laboratory experiments and a habitat occupancy analysis confirm the idea (Cassel-Lundhagen and Sjögren-Gulve, 2007) that *C. hero* is a polyphagous butterfly species feeding on various grasses. Consistently, we found

that the females, as is the case in some other Satyrinae species, may not attach the laid eggs onto the host plant, being characteristic for polyphagous Lepidoptera (Tammaru et al., 1995; Janz and Nylin, 1997; Nylin et al., 2000). Nevertheless, oviposition behaviour was not indiscriminate: the most preferred substrates for egg-laying were *Festuca ovina* and, surprisingly, also the control plant Norway spruce (*Picea abies*) (IV). Despite the well expressed host preference, there was no evidence of preference-performance linkage: the preferred *F. ovina* could not be shown to be a host supporting larval development better than its alternatives, and *P. abies* is obviously unsuitable. So, the result that females preferred unsuitable plants with needle-like leaves suggest that their decisions may be primarily based on microclimatic conditions. Indeed, needle-like leaves may give the signal that solar radiation reaches to the ground. According to the field study at microhabitat level, soil moisture and shade provided by shrubs are favoured by *C. hero*, these conditions should ensure that the host grasses do not dry out during the pre-hibernation larval development. The results confirm the idea that *C. hero* is highly sensitive to abiotic environmental conditions during larval development: an aspect of undeniable importance also in the conservation-ecological context. Consequently, to protect local populations of the butterfly, any actions affecting the microclimate like changing the extent of shrubs, or modifying structure of vegetation cover should be performed with extreme care.

E. maturna is known to have at least 24 larval food plants across its European range, although various regionally focused studies have found it to be oligophagous or even monophagous (Dolek et al., 2013). Testing the larvae from an Estonian population does not suggest a broad polyphagy either. Our results agree with those from Sweden, where the butterfly primarily uses *Fraxinus excelsior* and *Viburnum opulus* (Eliasson, 1991 Eliasson and Shaw, 2003).

Our evidence – both the results of habitat occupancy analysis, and the overall distribution patterns in the country – suggest that the occurrence of *E. maturna* is related to the presence of *Fraxinus excelsior* in Estonia (V). Using *Viburnum opulus* – as a host is also possible. Nevertheless, due to the relative scarcity of the plant species in (at least the eastern parts of) the country, a significant influence of *V. opulus* to the distribution of *E. maturna* is unlikely. Although *Melampyrum pratense* is the main host plant of the butterfly in the neighbouring Finland (Eliasson, 1999; Wahlberg, 2001a; Wahlberg et al., 2002), it is unlikely to be suitable for *E. maturna* in Estonia. Indeed, *M. pratense* was a clearly inferior plant species in terms of larval performance. Moreover, this plant primarily grows in dry coniferous forests in Estonia, which are, as a minimum, not the typical habitats for *E. maturna* in the country.

The use of *F. excelsior* as the primary host plant by *E. maturna* raises a specific conservation concern. Though currently in a favourable status, the future of *E. maturna* is uncertain. This is due to the rapid spread of a novel fungal disease – ash dieback – which damages *F. excelsior* and *F. angustifolia* (Queloz et al., 2011) threatening the trees as well as the organisms that depend

on them (Pautasso et al., 2013). Due to the recent nature of the problem, not much is known about ways to handle it. It has, however, been suggested to isolate healthy forest patches from forest parts where the disease already occurs. Once the disease is established, management is practically impossible: not much can be done to prevent the spread of invasive tree diseases. Therefore, only the occurrence of a small fraction of partially tolerant trees constitutes hope for resistance breeding in the future (Gross et al., 2014).

Another threat to the butterfly species could be unsuitable forest management, as has happened in the Czech Republic where opened clearings are replanted by oak or by coniferous species (Konvička et al., 2005; Freese et al., 2006), becoming too shady for the species. Current forestry practices in Estonia do not indicate a similar problem.

Our results demonstrate that the importance of the host plant as a determinant of habitat suitability differs between the studied butterfly species. The satyrines, *L. achine* and *C. hero*, were found to be polyphagous on different grasses and sedges which implies that the presence or absence of any certain plant species in the habitats of the butterflies cannot be critical, confirming the idea that the species of this group are not strongly specialized (Singer and Ehrlich, 1991; Fielder, 1998). All available evidence suggests that micro-climatic factors are of primary importance as determinants of habitat quality in these butterflies, and also have to be considered as such in the practice of conservation. The situation is different in the case of *L. dispar*. As this butterfly species is able to use only hosts from one genus – *Rumex* – the distribution of acceptable host plants must be a critical determinant of habitat suitability. Nevertheless, the primary host plant of the species is abundant enough not to substantially limit the distribution of the butterfly at the scale of the country. The Melitaeini butterflies *E. maturna* and *E. aurinia* represent a clearly contrasting case in which a certain plant species has the crucial role in determining the suitability of the habitats. Both these butterfly species appear to be (nearly) monophagous in Estonia, with the host plants themselves – for different reasons – being sensitive to environmental changes.

Experimental approaches to exploring host plant use are widely used in evolutionary ecology and plant-herbivore studies but perhaps less so in conservation oriented studies. The cause is likely in the tradition of research but we see no reason why these traditions should be continued. From a methodological point of view, the work reported in the present thesis allows one to evaluate several experimental approaches as sources of information on host plant preference, and host-specific larval performance. The simultaneous multiple-choice test is perhaps the most traditional, straightforward and uncontroversial way to determine oviposition choices of female insects (Bossart, 2003; DiTommaso and Losely, 2003; Murphy, 2007; Metspalu et al., 2009). Another advantage of this design is the practical feasibility: the researcher needs not to be continuously involved. No doubts arose with respect to the applicability of this method in the case of *L. dispar*, and our results show that this design can also be used in the case of Satyrinae, at least for *C. hero*. For

species not (always) attaching their eggs to the hosts, it may be advisable to place plants far enough from each other, so it might also be possible to identify which plant was preferred when the eggs are laid next to the plants.

Unfortunately, the simultaneous multi-choice trials frequently do not work in melitaeine butterflies (Ehrlich and Hanski, 2004), likely because the oviposition behaviour of these insects is complex (Singer, 1983), and cannot be fully realized in captive conditions. Indeed, we failed to get useful data in such experiments with *E. maturna*, in which oviposition was hard to achieve, and the clutches were mostly laid not on the host plants presented. However, as a positive surprise, we were able to record female preferences in multiple substrate trials with *E. aurinia*. These preferences were highly consistent with the results of the other experiments, showing that multiple-choice trials are not necessarily useless in this group of butterflies.

To get further information about oviposition preference in *E. maturna* and *E. aurinia*, we used a sequential single choice test specifically designed for checkerspot butterflies (Singer, 1982). This test allows us to get more information per tested individual, though the disadvantage of the design is the higher need for manpower: one person is able to test four butterflies per day as a maximum. The results with *E. maturna* and *E. aurinia* were not as clear as we expected, probably due to the unsuitable weather during the flight time of the butterflies, so experiments took place in the laboratory under artificial light, and not in the field, as suggested. In fact, the butterflies made oviposition attempts (extracted ovipositors) in only a few cases. Our analyses could not have been based on the frequencies of such rare events so we defined the response variable more loosely: as any behaviour interpretable as 'showing interest' in the plant. Analysis of such data revealed patterns clearly consistent with results of the other experiments, advocating the usefulness of such a 'softer version' of the sequential choice trial.

The simplest experiments to reveal oviposition preference are the single substrate oviposition experiments. This approach is based on the assumption that females in tests with more suitable host species are more motivated to lay eggs: more eggs, better plant (Javoiš and Tammaru, 2004, 2006; Gamberale-Stille et al., 2014, Friberg et al., 2015). The method is less time-consuming and labour-intensive compared to the trials discussed above, but does not give as much information per female. Nevertheless, the clearly non-random pattern recorded in the study on *C. hero* indicates that this method perhaps deserves to be applied more widely, also in conservation-ecologically oriented studies on butterflies.

Testing larval host plant preferences appears to be reasonable for species which do not attach their eggs to the host plant. In these species, it is the 'responsibility' of the neonate larvae have to find a plant to feed on. Although the trial is time-consuming, it may provide valuable supplemental information about host selection of a species. In our studies, such experiments appeared technically feasible for the satyrines, *L. achine* and *C. hero*. The choices made by the larvae were clearly non-random, and well correlated with the female

choice. Once again, our results allow us to recommend wider application of analogous experiments.

A traditional (though not necessarily so for conservation-ecological studies) way to get information about the suitability of different plant species as larval growth substrate is to rear the larvae on a certain plant species for a certain period of time. In addition to growth rate, usually expressed as weight gain during the test period, survival is also an informative parameter. Our results with several of the species suggest that host-specific survival is a better index of host suitability than growth rate. This appears to be especially true for species with overwintering larvae as these are not time-stressed in their pre-diapause development, so that their growth rates rather reflect individual developmental decisions than host plant quality.

The traditional transect count method gave valuable data about habitat preferences of the *E. maturna* within the framework of an investigation of habitat suitability. The subsequent habitat occupancy analysis allowed us to find the critical determinants of habitat suitability for the species. In addition to providing to some locally based knowledge about this butterfly species, I believe that the information derived, with some development, could be useful to predict the distribution of the species in changing environments, or to identify sites suitable for (re)colonisation. In the present thesis, I provided examples of similar approaches also at different spatial scales: a small-scale study of host plant association for *C. hero*, and a country-wide landscape occupancy analysis for *L. dispar*. The latter one was based on data accumulated in the course of gathering and publishing amateur lepidopterist records, thereby highlighting the usefulness of this type of data for conservation-ecological research.

The status of the five studied butterfly species appears currently favourable in Estonia, primarily due to the currently good availability of suitable habitats for them. In particular, this is because all these species are highly compatible with, and certainly benefiting from, forestry practices currently being implemented in Estonia (Viljur and Teder, *submitted*). Of landscapes other than managed forests, the semi-natural habitats (in Estonia, primarily, wooded meadows and alvar grasslands with bush cover; Laasimer, 1975) are not only extremely species rich areas floristically (Pärtel et al., 1998, 1999; Helm et al., 2006), but supporting also a diverse butterfly fauna (Krauss et al., 2010; Sang et al., 2010). These habitats are highly suitable for at least four out of five species (with a possible exception of *L. dispar*) dealt with in the current thesis, and the ongoing efforts to preserve such habitats are most welcome from the butterflies' point of view.

SUMMARY

Biodiversity is decreasing worldwide, numerous European butterflies are declining widely, and some of them are already endangered. The cornerstone of successful conservation practice is an understanding of the basic ecological needs of endangered species. The presence of a suitable host plant species is the main need for herbivorous insects, many of these are specialists, feeding on only one or a limited range of host species. Selection of proper host plants made by ovipositing females is therefore crucial for larval fitness. Understanding the factors that determine habitat quality is complicated due to the lack of sufficiently detailed information about the role of host plants as a determinant of suitable habitat. This problem naturally extends to developing effective conservation practices. The importance of the host plant is different for mono-, oligo-, or polyphagous insects as well as in the case of geographic variation in the host-herbivore relationship. It is therefore vital to know whether any endangered butterfly species has locally more specific food preferences than believed for the region (Europe, in our case) as a whole.

In my thesis, I focussed on exploring the role of host plants as determinants of habitat quality for five butterfly species considered endangered at the European level: *Lopinga achine* (I), *Lycaena dispar* (II), *Euphydryas aurinia* (III), *Coenonympha hero* (IV), and *E. maturna* (V). These are five butterfly species out of seven which are protected in Estonia according to the European Community Habitats Directive. The work had thus an applied goal to evaluate the importance of the host plant for the needs of designing conservation actions for these species in Estonia. To find out host plant preferences of ovipositing females, we tested the females in simultaneous multiple-choice trials (I, II, III, IV), sequential single choice trials (III, V), and single substrate oviposition trials (IV). To figure out the suitability of different host species for larvae, we explored larval host plant preference (I, IV) and performance of the larvae on different host plants (I, II, III, IV, V) in the laboratory. Additionally, we observed the host plant use in the wild (II, III) and performed a larval performance experiment in the field (II) using naturally growing host plants (Table 1).

Table 1. An overview of the habitats, host plants, conducted experiments and the results for *Lopinga achine*, *Coenonympha hero*, *Lycaena dispar*, *Euphydryas maturna* and *E. aurinia*.

	<i>Lopinga achine</i>		<i>Coenonympha hero</i>		<i>Lycaena dispar</i>	<i>Euphydryas maturna</i>	<i>Euphydryas aurinia</i>
Estonian name	sõõrsilmik		vareskaera-aasasilmik		suur-kuldtiib	suur-mosaikliblikas	teelehe-mosaikliblikas
Habitat	deciduous forests		seminatural bushy meadows and woodland clearings		fenlands, riverside and lakeside areas, wet meadows, urban wastelands	forest edges, openings within forest, forest tracks	seminatural meadows, forest clearings, woodland edges, areas under power lines
Host species in neighbouring countries	<i>Carex montana</i>		generalist feeding various grasses			<i>Viburnum opulus</i> , <i>Melampyrum pratense</i> , <i>Fraxinus excelsior</i>	<i>Succisa pratensis</i> , <i>Knautia arvensis</i> , <i>Valeriana officinalis</i>
Conducted experiments							
Simultaneous multiple-choice	×		×		×		×
Sequential single choice						×	×
Single substrate oviposition trial			×				
Larval host plant preference	×		×				
Larval host plant performance	×		×		×	×	×

<i>Lopinga achine</i>	<i>Coenonympha hero</i>	<i>Lycaena dispar</i>	<i>Euphydryas maturna</i>	<i>Euphydryas aurinia</i>
Host use observations in the field		×		×
Transect counts			×	
Habitat occupancy analyses		×	×	
Host plant at the microhabitat level				
Suitable host species in the laboratory experiments	<i>Carex montana</i> , <i>C. sylvatica</i> , <i>Melica nutans</i> , <i>Calamagrostis canescens</i>	<i>Dactylis glomerata</i> , <i>Festuca ovina</i> , <i>F. rubra</i> , <i>Helictotrichon pratense</i> (<i>S. caerulea</i>)	<i>Rumex. obtusifolius</i> , <i>R. crispus</i> , <i>R. hydrolapathum</i> , <i>R. aquaticus</i>	<i>S. pratensis</i>
Unsuitable host species	<i>Festuca ovina</i>	<i>R. acetosa</i>	<i>M. pratense</i>	<i>Plantago ssp.</i> , <i>Valeriana officinalis</i> , (<i>Knautia arvensis</i>)
Host use in the wild in Estonia		<i>R. obtusifolius</i> , <i>R. crispus</i>	<i>F. excelsior</i>	<i>S. pratensis</i>

The presence of the host plant is one aspect determining habitat suitability. To find out the importance of the host plant as an important determinant of habitat quality for the butterflies, we conducted habitat occupancy analyses, using data from field work (IV, V), previously published distributional data (II), topographic data-bases (II, III), and host associations at the microhabitat level (V).

Our results revealed that *L. achine* is polyphagous in Estonia. The presence of any particular host species cannot be a critical component of habitat quality for the butterfly. As many of the host species are widespread, host plant is not a factor limiting the distribution of *L. achine*. Although all offered *Rumex* species were used successfully in the laboratory, our work shows that the primary host plant species for *L. dispar* in Estonia is *R. obtusifolius*. Using *R. obtusifolius* confirms the results of the landscape occupancy analysis, which showed that the butterfly species prefers areas with ditches and human settlement, both these factors likely creating favourable conditions for *R. obtusifolius*. Suitable habitats for *L. dispar* are thus maintained by moderate anthropogenic pressure. *E. aurinia* appears to be functionally monophagous on *Succisa pratensis*, which has remained the only confirmed host of *E. aurinia* in Estonia. *C. hero* was found to be a polyphagous butterfly species able to feed on various grasses. Even if oviposition of *C. hero* is selective with respect to oviposition substrates, we suggest that cues of the physical environment rather than host plant quality are the drivers behind this pattern. Our evidence suggests that *E. maturna* is related to the presence of *Fraxinus excelsior* in Estonia. Using *Viburnum opulus* as a host is possible but the importance of the plant species as a determinant of the distribution of the butterfly is unlikely. Host plant use clearly differs from the neighbouring Finland: *M. pratense* is the main host plant there, being unsuitable for the Estonian *E. maturna*.

As a methodological contribution, my work shows that laboratory-based experiments can also provide useful data for conservation-ecological purposes. In particular, traditional multiple-choice oviposition preference experiments worked for most butterfly species studied, the one-substrate test provided additional information, and sequential choice trials yielded consistent results. Neonate larvae of the satyrines made non-random choices between the plant sections offered. Survival allowed us to evaluate the quality of plant species better than growth performance, and could be explained by the fact that we used pre-diapause larvae, which do not have time-stress. Country-wide landscape occupancy analyses showed the utility of amateur faunistic data in exploring habitat preferences.

Assessment of the conservation status of the five butterfly species was not among the aims of the present study. However, there is no direct evidence of decline of any of the Estonian populations of the species, and furthermore the ecological information accumulated in the course of the present study revealed no major reasons for concern. *L. achine* and *C. hero* are polyphagous species, able to feed on many different plant species. Even if these satyrines appear to have strict preferences at the microhabitat level, suitable habitats are unlikely to be limiting in Estonia. *L. dispar*, being able to feed on several common *Rumex*

species, is even extending its range, and appears to benefit from moderate anthropogenic pressure. The situation of *E. matura* and *E. aurinia* also seems favourable, though for these host specialists the future looks more uncertain. The host plants, *F. excelsior* and *S. pratensis*, are widely distributed but may be adversely affected by a fungal disease and changes in agricultural practices, respectively. Even if there currently appears to be no reason for prioritising active conservation measures of the studied species in Estonia, local populations of these species may still require attention; also, the information gathered must be used in other regions where these species may be of higher conservation concern.

SUMMARY IN ESTONIAN

Kaitsealuste päevaliblikate ökoloogia Eestis

Elurikkuse kahanemine on globaalne probleem, taandumas on ka paljud Euroopa liblikaliigid ning mitmeid neist on juba põhjust pidada ohustatuteks. Eduka looduskaitse tegevuse nurgakiviks on ohustatud liikide põhiliste ökoloogiliste nõudmiste mõistmine. Herbivoorsetele putukatele on sobiva toidutaime-liigi olemasolu mõistagi peamine keskkonna kvaliteedi komponent, seda seetõttu, et paljude liikide vastsed on spetsialistid, toitudes vaid ühel või piiratud hulgal taimedel. Õige arusaamine elupaiga kvaliteeti mõjutavatest teguritest on siiski keeruline ülesanne, lisaks puudub enamasti ka piisavalt detailne informatsioon toidutaime osa kohta elupaiga sobivuse määrajana. Nimetatud probleem mõjutab ka looduskaitse tegevuste praktikat. Toidutaime olulisus erineb mono-, oligo- ja polüfaagsetel putukatel, samuti komplitseerib olukorda sageli täheldatav toidutaimekasutuse geograafiline varieerumine. Seetõttu on oluline teada, kas mõnel ohustatud liblikaliigil on lokaalselt spetsiifilisemad taime-eelistused kui regioonis üldiselt (käesoleval juhul Euroopas).

Oma väitekirjas uurisin toidutaime rolli elupaiga kvaliteedi määrajana viiel Euroopa tasandil ohustatuks peetaval päevaliblikaliigil. Nendeks olid sõõrsilmik (I), suur-kuldtiib (II), teehe-mosaiikliblikas (III), vareskaera-aasasilnik (IV) ja suur-mosaiikliblikas (V). Mainitud on viis päevaliblikaliiki seitsmest, mis on Euroopa Loodusdirektiivi kohaselt Eestis kaitsealused. Käesoleva töö praktiliseks eesmärgiks oli seega hinnata toidutaime tähtsust nende liikide kaitse planeerimisel Eestis. Uurimaks emaste munemiseelistusi, viisime läbi samaaegse valiku katseid mitmete kandidaattaimedega (I, II, III, IV), järjestikuseid eelistuskatseid (III, V) ja ühe substraadiga munemiskatseid (IV). Hindamaks erinevate taimede sobivust röövikute kasvusubstraadina uurisime röövikute toidutaime-eelistust (I, IV) ja kasvukiirust (I, II, III, IV, V) erinevatel taimeliikidel. Lisaks vaatlesime otseselt toidutaimekasutust looduses (II, III) ning viisime läbi rööviku kasvukiiruse määramise katseid looduslikult kasvatel toidutaimedel (II; tabel 1).

Tabel 1. Ülevaade sõõrsilmiku, vareskaera-aasasilmiku, suur-kuldtiiva, suur-mosaikliblika ja teehe-mosaikliblika eelistatud biotoopidest, toidutaimedest, läbiviidud katsetest ja nende tulemustest.

	Sõõrsilmik	Vareskaera-aasasilmik	Suur-kuldtiib	Suur-mosaikliblikas	Teehe-mosaikliblikas
Ladinakeelne nimi	<i>Lopinga achine</i>	<i>Coenonympha hero</i>	<i>Lycena dispar</i>	<i>Euphydryas maturna</i>	<i>Euphydryas aurinia</i>
Biotoop	lehtmetsad	poollooduslikud niidud ja raiesmikud	sood, jõgede ja järvede kaldaalad, niisked niidud, kultuurmaastiku tühermaad	metsaservad, avatud alad metsamaastikus, metsarajad	poollooduslikud niidud, raiesmikud, metsaservad, kõrgepingeliinide alused alad
Toidutaimed naaberriikides	mägitar	generalist, toitub erinevatel rohttaimedel		harilik lodjapuu, palu-härghein, harilik saar	harilik peetriteht, harilik äiatar, harilik palderjan
Läbiviidud katsed					
Samaegne mitme substraadi valikukatse	×	×	×		×
Järjestikune ühe substraadi valiku katse				×	×
Ühe substraadi munemiskatse		×			
Rööviku toidutaimede valikukatse	×	×			
Rööviku edukus toidutaimel	×	×	×	×	×

	Sõõrsilmik	Vareskaera- aasasilmik	Suur-kuldtiib	Suur-mosaikliblikas	Teelehe- mosaikliblikas
Toidutaim kasutuse vaatlused looduses			×		×
Transektloendused				×	
Elupaiga hõivatuse analüüs			×	×	
Toidutaim mikroelupaiga tasandil		×			
Sobivad toidutaimed laborkatsetes	mägitaru, metstaru, longus helmikas, sookastik	lamba-aruhein, punane aruhein, harilik kastehein, arukaerand	tõmbilehine oblikas, kärnobliskas, jõgiobliskas, vesiobliskas	harilik saar, harilik lodjapuu	harilik peetriteht
Ebasobivad taimeliigid	lamba-aruhein	(harilik lubikas)	hapu oblikas	palu-härghein	harilik palderjan, teelehe perekonna liigid, (harilik äiatar)
Taimekasutus looduses (Eestis)			tõmbilehine oblikas, kärnobliskas	harilik saar	harilik peetriteht

Leidmaks toidutaimede suhtelist olulisust liblikaliikide elupaiga kvaliteedi määrajana, viisime läbi elupaiga hõivatuse analüüsi kasutades originaalseid välitööandmeid (IV, V), varasemalt avaldatud levikuandmeid (II), kaardipõhiseid topograafilisi andmeid (II, III) ja toidutaimeseoseid mikroelupaiga tasandil (V).

Töö tulemused näitavad, et sõõrsilmik on Eestis polüfaagne kõrrelistel ja tarnadel: ühegi konkreetse taimeliigi olemasolu ei saa olla liblika elupaiga kvaliteeti määravaks teguriks. Paljud tõendatult kvaliteetsed toidutaimeliigid on Eestis laialt levinud, mistõttu ei piira toidutaimede esinemine sõõrsilmiku levikut. Suur-kuldtiiva peamiseks toidutaimeks Eestis on tõmbilehine oblikas, olgugi et röövikud olid võimelised edukalt toituma kõigil katsesse kaasatud oblikaliikidel. Tõmbilehise oblika kasutamine on kooskõlas elupaiga hõivatuse analüüsi tulemustega, mille kohaselt eelistab liblikas kraavide ja inimasustusega alasid, mis usutavasti loovad tõmbilehisele oblikale soodsaid kasvutingimusi. Seega loob ja säilitab just mõõdukas inimõju suur-kuldtiivale sobivaid elupaiku. Teelehe-mosaiikliblikas näib Eestis olevat monofaagne harilikul peetritehel, mis on siiani jäänud ainsaks tõendatud selle liblika toidutaimeks Eestis. Edukalt erinevatel kõrrelistel toituv vareskaera-aasasilnik on polüfaagne liblikaliik. Emaste munemiskäitumine osutus küll selektiivseks, kuid on põhjust uskuda, et eelistust mõjutavad oluliselt rohkem substraadi füüsilised parameetrid kui kui taime liik. Töö tulemuste kohaselt on suur-mosaiikliblika levik Eestis seotud hariliku saare olemasoluga. Hariliku lodjapuu kasutamine toidutaimena on küll võimalik, kuid usutavasti selle taime esinemine liblika levikut ei oluliselt mõjuta. Suur-mosaiikliblika toidutaimakasutus erineb selgelt olukorrast Soomes, kus peamiseks toidutaimeks on palu-härghein, mis on Eesti suur-mosaiikliblikale ebasobiv.

Töö metodoloogiliseks väärtuseks on tõendus, et laboratoorsed katsed võivad anda kasulikke andmeid ka looduskaitseökoloogilistel eesmärkidel. Traditsioonilist mitme alternatiivse substraadiga munemiskatset kasutati edukalt peaaegu kõikide liikide puhul, ühe substraadi katse andis olulist lisainformatsiooni ning ka järjestikuse eelistuskatse abil saadi ühilduvaid tulemusi. Silmikute vastkoorunud röövikud olid võimelised valima pakutud taimede vahel. Röövikute suremus lubas hinnata taimeliigi kvaliteeti paremini kui kasvukiirus, mis võib olla seletatav tõsiasjaga, et kasutasime katsetes talvitumiseks valmistuvaid röövikuid, kellel ei ole ajastressi. Kogu Eesti ala hõlmav maastiku hõivatuse analüüs näitas amatöörfaunistilise andmestiku kasutatavust elupaigaeelistuste uurimisel.

Viie uuritud liblikaliigi ohustatuse hindamine ei olnud küll käesoleva töö otseks eesmärgiks, kuid autorile teadaolevalt ei viita miski nende liikide populatsioonide kahanemisele Eestis. Samuti ei andnud töö käigus kogutud ökoloogiline informatsioon põhjust eeldada ohustatuse kasvu lähitulevikus. Sõõrsilmik ja vareskaera-aasasilnik on polüfaagsed liigid, mis on võimelised toituma paljudel erinevatel taimeliikidel. Kuigi neil silmikutel näib olevat kindel eelistus mikroelupaiga tasandil, ei ole liikidele sobivate elupaikade olemasolu usutavasti Eestis piiravaks teguriks. Suur-kuldtiib, mis on võimeline toituma mitmetel laialt levinud oblikaliikidel, on laiendamas on leviala ning

näib mõõdukast inim mõjust isegi kasu saavat. Suur-mosaiikliblika ja teelehe-mosaiikliblika seisund näib samuti soodne olevat, kuigi nende toidutaime-spetsialistide jaoks võib tulevik olla ebakindlam. Nimelt on nende liikide toidutaimed – saar ja peetrileht – küll laialt levinud liigid, kuid võivad olla negatiivselt mõjutatud vastavalt kiiresti levivast seenhaigusest ja muutustest maakasutuses. Isegi kui hetkel ei tundu Eestis olevat põhjust aktiivsete meetmete rakendamiseks nende liikide kaitseks, võivad kohalikud populatsioonid siiski vajada tähelepanu. Lisaks sellele, et käesolev töö pakub olulist teavet looduskaitseliste meetmete rakendamiseks kohalikul tasandil, on kogutud informatsiooni kindlasti võimalik kasutada ka nendes piirkondades, kus nimetatud viie liblikaliigi looduskaitsealine seisund on halvem.

ACKNOWLEDGEMENTS

It all started with series of coincidences. I did not plan to undergo doctoral studies until I met my supervisor Toomas, or more specifically – he found me. I cannot thank you enough, Toomas, for guiding, supporting and helping me during all these years. You have never given up on me, even on moments when I gave up on myself. Thank you for answering to all those last-minute panics and endless number of stupid questions (which I still like to ask). Jaanus has been my supervisor and my guide in the field of mapping and map analyses, thank you for your patience in explaining to me things over and over again. There were, of course, also other people who were around me during my studies, giving me tips, helping me out during field work or in the laboratory, or just creating scientific atmosphere (in totally random order): Anu Tiitsaar, Robert B. Davis, Toomas Esperk, Tiit Teder, Juhan Jovoiš, Freerk Molleman, Erki Õunap, Ants Kaasik, Virve Sõber, Helen Vellau, Siiri-Liis Sandre, Sille Holm, Margus Vilbas, Andro Truuverk, Hendrik Meister, Mari-Liis Viljur, Kristiina Taits, Madli Pärn, Mark Gimbutas, Laura Tammiste, Ando Vaan, and Liisi Laks – thank you! Thank you all co-authors and reviewers of the papers.

My family has always been there for me. Thank you, mother Marika for causing unintentionally the opportunity to me to start the way I am finishing now. Thank you, my other mother Neringa, my father Urmas and grandmother Meeli for believing in me and for the support you have given to me. Thank you, my brother Leo for being always there for me and encouraging me during the studies to take the plunge when I was hesitating. I have never regretted those dives. Thank you, my little sister Uma for being a star in my heaven. Once you said that you want to be as smart as I am – and you could be much more than that – but you do not like to study. Hopefully you will realize soon that you can't be smart without studying and decide to work for your goal.

There were other people in the background playing different but important roles: Maarja, Rille, Piret, Kermet, Ploom, Tanel, Pille, Väino, Martin, Martin and Triinu, thank you for the support and understanding – I know I have been busy, constantly. Special thanks to Pierre for keeping me smiling.

The studies were performed at the Department of Zoology at the Institute of Ecology and Earth Science, University of Tartu. The study was supported by the Estonian Science Foundation (Grant 9294), Institutional Research Grant IUT20-33, by the European Union through the European Regional Development Fund (Center of Excellence FIBIR) and through the European Social Fund (V. S. Mobilitas postdoctoral grant MJD258) as well as the Swedish research council FORMAS and the Strategic Research Programme Eko Klim at Stockholm University. Permissions to work with the protected butterflies was granted by the Environmental Agency of Estonia and we limited the number of individuals used in the experiments due to conservation concerns.

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Education:

1992–2004 Puurmani Gymnasium (*Silver Medal*)
2004–2005 Mathematics at the University of Tartu (*unfinished*)
2005–2008 Bachelor's studies in landscape protection and maintenance at the University of Life Sciences
2008–2010 Master's studies in environmental protection at the University of Life Sciences
2010– Doctoral studies in Zoology at the University of Tartu

Scientific and research activity

Research interests: butterfly ecology and conservation

Publications:

- Lindman, L., Remm, J., Meister, H. & Tammaru, T. Host plant and habitat preference of *Euphydryas maturna* (Lepidoptera: Nymphalidae, Melitaeinae): evidence from northern Europe. *Manuscript*.
- Tiitsaar, A., Kaasik, A., Lindman, L., Stanevitš, T. & Tammaru, T. Host preference and habitat use of *Coenonympha hero* (Lepidoptera: Nymphalidae) in northern Europe are driven by microclimate. *Submitted manuscript*.
- Meister, H., Lindman, L. & Tammaru, T. (2015) Testing for local monophagy in the regionally oligophagous *Euphydryas aurinia* (Lepidoptera: Nymphalidae). *Journal of Insect Conservation*, **19**, 691–702.
- Lindman, L., Remm, J., Saksing, K., Sõber, V., Õunap, E. & Tammaru, T. (2015) *Lycaena dispar* on its northern distribution limit: an expansive generalist. *Journal of Insect Conservation and Diversity*, **8**, 3–16.
- Lindman, L., Johansson, B., Gotthard, K. & Tammaru, T. (2013) Host plant preferences of an endangered butterfly, *Lopinga achine* (Lepidoptera Nymphalidae) in northern Europe. *Journal of Insect Conservation*, **17**, 375–383.

Conference presentations:

- Lindman, L., Tammaru, T. “*The importance of host plants for four endangered butterfly species*”. The 7th International Conference on the Biology of Butterflies, Turku, Finland, 11.–14.08.2014.
- Lindman, L., Remm, J., Saksing, K., Sõber, V., Õunap, E., Tammaru, T. “*Lycaena dispar in Estonia – an expansive generalist*”. The conference „Butterfly Conservation Symposium“, Southampton, UK, 4.–6.04.2014.
- Lindman, L., Tammaru, T. “*Host plant preference of Lopinga achine*”. The conference “Future of butterflies”, Wageningen, Netherlands, 29.–31.03.2012.

Dissertations supervised:

- Hendrik Meister, Bachelor's Degree, 2011, Ly Lindman. Teelehe-mosaiikliblika (*Euphydryas aurinia*) ökoloogia ja kaitse (*The ecology and conservation of the marsh fritillary (Euphydryas aurinia)*). University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, Department of Zoology.
- Kristiina Saksing, Bachelor's Degree, 2012, Ly Lindman. Suur-kuldtiiva (*Lycaena dispar*) toidutaime- ja biotoobieelistus (*The host plant and biotope preferences of the large copper (Lycaena dispar)*). University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, Department of Zoology.
- Hendrik Meister, Master's Degree, 2013, Ly Lindman. Teelehe-mosaiikliblika (*Euphydryas aurinia*) toidutaime-eelistuse varieeruvus ja looduskaitse Eestis (*The variability of host plant preference and conservation of the marsh fritillary (Euphydryas aurinia) in Estonia*). University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, Department of Zoology.
- Tiina Stanevitš, Master's Degree, 2013, Anu Tiitsaar, Ly Lindman. Vareskaera-aasasilmiku (*Coenonympha hero*) toidutaime- ja biotoobieelistus Eestis (*The host plant and biotope preference of the scarce heat (Coenonympha hero) in Estonia*). University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, Department of Zoology.
- Kristiina Saksing, Master's Degree, 2014, Ly Lindman. Suur-kuldtiiva (*Lycaena dispar*) toidutaime- ja elupaigaeelistus Eestis (*The host plant and habitat preference of the large copper (Lycaena dispar) in Estonia*). University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, Department of Zoology.

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2005–2008 Eesti Maaülikool, maastikukaitse ja -hooldus,
bakalaureuseõpe
2008–2010 Eesti Maaülikool, keskkonnakaitse, magistriõpe
2010– Tartu Ülikool, zooloogia, doktoriõpe

Teaduslik ja uurimuslik tegevus

Peamised uurimisvaldkonnad: päevaliblikate ökoloogia ja looduskaitse

Publikatsioonide loetelu:

- Lindman, L., Remm, J., Meister, H. & Tammaru, T. Host plant and habitat preference of *Euphydryas maturna* (Lepidoptera: Nymphalidae, Melitaeinae): evidence from northern Europe. *Manuscript*.
- Tiitsaar, A., Kaasik, A., Lindman, L., Stanevitš, T. & Tammaru, T. Host preference and habitat use of *Coenonympha hero* (Lepidoptera: Nymphalidae) in northern Europe are driven by microclimate. *Submitted manuscript*.
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- Lindman, L., Tammaru, T. „*Host plant preference of Lopinga achine*“. The conference „Future of butterflies“, Wageningen, Netherlands, 29.–31.03.2012.

Juhendatud väitekirjad:

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- Kristiina Saksing, magistrikraad, 2014, Ly Lindman. *Suur-kuldtiiva (Lycaena dispar) toidutaime- ja ehupaigaeelistus Eestis*. Tartu Ülikool, Loodus- ja Tehnoloogiateaduskond, Ökoloogia ja Maateaduste Instituut, Zooloogia osakond.

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