

MARGUS VILBAS

Biotic interactions affecting
habitat use of myrmecophilous
butterflies in Northern Europe



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

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Supervisor: PhD Toomas Esperk, University of Tartu, Estonia
PhD Tiit Teder, University of Tartu, Estonia

Opponent: PhD Piotr Nowicki, Jagiellonian University in Kraków,
Poland

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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. **Vilbas M**, Teder T, Tiitsaar A, Kaasik A & Esperk T (2015) Habitat use of the endangered parasitic butterfly *Phengaris arion* close to its northern distribution limit. *Insect Conservation and Diversity* 8:252–260.
- II. **Vilbas M**, Esperk T, Teder T (2016) Host ant use of the Alcon blue butterfly at the northern range margin. *Journal of Insect Conservation* 20:879–886.
- III. **Vilbas M**, Esperk T, Edovald T, Kaasik A & Teder T (2016) Oviposition site selection of the Alcon blue butterfly at the northern range margin. *Journal of Insect Conservation* 20:1059–1067.
- IV. **Vilbas M**, Teder T, Tiitsaar A, Kaasik A, Tammaru T, Esperk T (2018) Two obligately myrmecophilous butterflies regularly share habitat despite different host ants. *Manuscript*.

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

	I	II	III	IV
Original idea	***	***	***	**
Experiment design	***	***	***	**
Data collection	***	***	***	***
Data analyses	***	***	***	**
Writing the paper	***	***	***	***

1. INTRODUCTION

Halting the fast decrease of global biodiversity has become the major challenge facing conservation biologists today. Populations of numerous species are suffering significant declines or have even gone to extinction, mainly as a consequence of human-induced habitat destruction and fragmentation (e.g. Diamond et al 1989; Sala et al 2000; Tschardt et al 2002; Fahrig 2003; Van Dyck et al 2009; Butchart et al 2010). Moreover, unambiguous evidence on adverse effects of climate change is rapidly accumulating (e.g. Dillon et al 2010; Doak & Morris 2010; Pereira et al 2010; Beaumont et al 2011; Parmesan et al 2011), with most major groups of organisms being affected (e.g. Dirzo & Raven 2003; Parmesan 2006; Hunter et al 2010; Bellard et al 2012; Tseng et al 2018).

Protection of habitats alone is often insufficient to prevent ongoing declines and extinctions (e.g. Thomas et al 2009; Hallmann et al 2017). Long-term survival of populations may require knowledgeable management in focal habitats (e.g. Bergman 2002; Thomas et al 2009; Rosin et al 2011; Weiss et al 2013; Bubova et al 2015; Kelly et al 2015; Ma et al 2017). Nevertheless, caution must be taken while planning and implementing conservation strategies as species and populations may respond differently to environmental changes. Profound understanding of species' ecology, evolution and life-histories is therefore vital in developing successful conservation strategies. Indeed, fundamental life-history differences may exist among closely related species (e.g. Gutierrez et al 2001; Wahlberg et al 2002; Wang et al 2004; Körösi et al 2012) and even among distinct populations of the same species (Schtickzelle et al 2006; Sielezniew et al 2010a, 2010b, 2010c; Tartally et al 2014). Ignoring such ecological variation could easily lead to erroneous understanding of species habitat requirements and hamper their successful conservation (e.g. Thomas 1980; New et al 1995; Pullin 1996). Accordingly, not rare are the cases when population declines have resulted from inappropriate management of otherwise healthy habitats (Balmer & Erhardt 2000; Waring 2001; Konvička et al 2008).

Narrowly specialized species engaged in complex interactions with other species are expected to be particularly vulnerable to environmental changes (e.g. Warren et al 2001; Filz & Schmitt 2015). Habitat degradation may affect such species either by impacting their habitat requirements directly, or disrupting their interspecific interactions (Munday 2004; Stefanescu et al 2011; Edwards et al 2013). Moreover, conservation of such species can be further complicated by often considerable geographic variation in their ecology and habitat use (e.g. Thomas et al 1999; Sielezniew & Stankiewicz 2008; Casacci et al 2011). Accounting for region-specific ecological requirements is therefore essential for successful conservation management, but is also valuable for understanding species' biogeography and evolutionary ecology (e.g. Settele et al 2005).

Peripheral populations deserve special attention as they hold key insights into the limits of realized niches (Holt & Keitt 2005; Bahn et al 2006). For example, the northern distribution limits of many herbivorous insect species have been shown to be primarily determined by temperature rather than host plant distribution (Virtanen & Neuvonen 1999; Mattila et al 2011). This means that populations at their northern range margins are likely to face climatic conditions that are more restrictive for their growth and development than conditions in more central populations of their distribution range. Accordingly, populations close to range margins are often genetically and ecologically divergent from central populations, and may therefore be valuable for sustaining evolutionary potential of species (Lesica & Allendorf 1995; Cassel-Lundhagen et al 2009; Hill et al 2011; Moritz et al 2012; Osborne et al 2012; Krehenwinkel & Tautz 2013; Bridle et al 2014; Therry et al 2014). Higher specificity in host use towards species distribution margins is one example of how peripheral populations have been proposed to differ from core populations (e.g. Martin & Pullins 2004; Schmidt & Hughes 2006).

Insects are expected to suffer severely under the ongoing crisis of biodiversity (e.g. New 1995; Schultz & Chang 1998; Pimm & Raven 2000; van Swaay et al 2012; Fox et al 2014; Ollerton et al 2014; Woodcock et al 2016). Indeed, catastrophic losses in insect abundances have even been documented in well protected areas (Hallmann et al 2017). Moreover, considering that less than one million insect species have been described out of 5 million estimated to exist (e.g. Gaston 1991; Stork et al 2015), it is more than likely that many species go extinct without ever being even named or described (Samways 2007). The situation is most unfortunate as insects play fundamental role in ecosystems and provide essential ecological services, such as pollination (e.g. Öckinger & Smith 2007; Ollerton et al 2011), wildlife nutrition (e.g. Losey & Vaughan 2006), herbivory and detritivory (e.g. Belovsky & Slade 2000; Macadam & Stockan 2015), nutrient cycling (e.g. Yang & Gratton 2014) and pest control (e.g. Ridsdill-Smith & Matthiessen 1988) from which other organisms, humans included, are vitally dependent on. Preserving insect abundance and diversity thus should be a prime conservation priority.

Among insects, butterflies (Lepidoptera, Papilionoidea) are the most thoroughly studied taxonomic group (e.g. Boggs et al 2003; Bonebrake et al 2010). Indeed, for more than a century, research on butterflies has immensely contributed to development of biogeography (e.g. Wallace 1865), ecology (e.g. Fisher et al 1943; Hanski & Thomas 1994; Gotthard 2000), evolution (e.g. Singer 1983; Janz et al 1994; Pierce et al 2002), conservation (e.g. Maes & Van Dyck 2005; Thomas 2005; Thomas et al 2009), climate change (e.g. DeVictor et al 2012) and other disciplines (e.g. Als et al 2004; Nishikawa et al 2013; Guerra et al 2014; Siddique et al 2017). Nevertheless, even for butterflies, available data are geographically highly unevenly distributed (e.g. Bonebrake et al 2010; Winfree et al 2011; Fardila et al 2017) and notable gaps in our understanding concerning their life-histories, ecology, and conservation still exist (e.g. Pierce

et al 2002; Bonebrake et al 2010; Kodandaramaiah 2011; Merrill et al 2011; Seymoure 2018).

In fact, butterflies, as insects in general, appear to suffer substantially from adverse effects of environmental changes (e.g. Thomas 1991; Thomas et al 2004; Dunn 2005; van Swaay et al 2006; Fox et al 2010). In particular, due to their short life span, high sensitivity to environmental conditions, and often specific habitat requirements, butterflies react to changes in habitat quality and climate more rapidly than e.g. plants or vertebrates (Erhardt & Thomas 1991; Thomas et al 2004; DeVictor et al 2012; Rowe et al 2015). Moreover, a high share of butterflies is associated with semi-natural open landscapes (Wikström et al 2009; van Swaay & Warren 2006), habitats that have experienced vast declines in distribution and area in recent history (e.g. Pullin 1995; van Swaay & Warren 1999; Poschold et al 2005; Helm et al 2006; Brereton et al 2008; Kadlec et al 2010). Consequently, as much as one third of European butterfly species have been assessed to be currently declining (Van Swaay et al 2010).

Lycaenidae is the second-largest family of butterflies, constituting about one third of their overall diversity (de Jong et al 1996; Ackery et al 1999). Despite being the subject of wide scientific attention due to their conservation status (e.g. Thomas et al 2009), but also for their striking behavioural and ecological diversity, detailed life histories are available for less than a quarter of lycaenid species (Pierce et al 2002). However, as much as 75% of all lycaenids with sufficiently known life histories are myrmecophilous (i.e. associate with ants) at least in the larval stage – a phenomenon that among lepidopterans is almost exclusively restricted to the representatives of this family (Fiedler 1991a; Pierce et al 2002). The degree of myrmecophily in Lycaenidae ranges from loose facultative interactions in which larvae are occasionally tended by ants to complex obligate associations in which ant attendance is crucial for the butterflies' survival (Ballmer & Pratt 1992; Fiedler 1991a; Pierce et al 2002; Fiedler 2006). The fundamental nature of these associations is that caterpillars provide ants with sugar-rich secretions in exchange for vital protection against predators and parasitoids (Cotrell 1984; Pierce et al 1987; Jordano et al 1992; Thomas et al 1999). Most species of myrmecophilous lycaenids are generalist herbivores, but may also be related in facultative associations with ants throughout their larval and pupal period (e.g. Atsatt 1981; Fiedler 1991b). There also exist examples of generalist herbivores that are in obligate mutualistic relationships with specific host ants (e.g. species belonging to the genus *Plebejus*). However, a small number of lycaenids, such as species belonging to the genus *Phengaris*, are mono- or oligophagous herbivores in the early larval life, but become obligatory parasites or predators of specific host ants in late larval instars (e.g. Thomas et al 1989; Fiedler 1991a, 2006). Specific interactions with ants are a key factor to consider for successful conservation of obligately myrmecophilous species and their populations (Elmes et al 1998; Als et al 2004, Thomas et al 2009; Filz & Schmitt 2015). Furthermore, such ecological diversity and uniqueness makes lycaenids particularly amenable for comparative studies of life history evolution (Pierce et al 2002).

The present thesis examines biotic interactions and habitat requirements in two genera of obligately myrmecophilous Palearctic lycaenid butterflies – *Phengaris* Doherty 1891 (I, II, III) and *Plebejus* Kluk 1780 (IV). The thesis expands the knowledge of geographic variation in habitat requirements and habitat use in highly vulnerable parasitic *Phengaris* butterflies to the populations at (*P. alcon*) or close (*P. arion*) to the northern distribution margin of these species. Special attention is given to the composition of regional *Myrmica* fauna and host ant use. The thesis also aims to concurrently assess the distribution patterns in two species of *Plebejus* butterflies (*P. argus* and *P. idas*), the obligate mutualists of ants. In this case, the focus is on ascertaining the possible role of ant-mediated interactions in driving distribution patterns in these obligately myrmecophilous butterflies.

The dissertation is based on four empirical studies that can be divided into three distinct parts:

(1) Habitat occupancy and host ant use in *Phengaris arion* (I). Patch occupancy in *P. arion* was investigated in relation to a number of biotic and abiotic environmental characteristics. As a novel aspect for this type of studies, the effect of dragonfly predation (Odonata, Anisoptera), a factor that has recently been shown to have a strong impact on patch occupancy patterns of various butterflies, was assessed (Sang & Teder 2011; Tiitsaar et al 2013). The local *Myrmica* fauna and host ant use of *P. arion* were described for the first time in the region. The study was conducted in seminatural calcareous grasslands in Saaremaa and Muhu, two Baltic Sea islands that host some of the relatively few viable *P. arion* populations in the region.

(2) Host ant use and oviposition patterns in *Phengaris alcon* (II, III). Host ant specificity of *P. alcon* as well as the diversity and abundance of local *Myrmica* species were addressed (II). As a novel aspect, potential effect of non-host ant species (*Lasius* spp. in particular), sharing the habitat with *Myrmica*, on host ant availability in *P. alcon* was examined (II). To ascertain the main drivers of host plant use for oviposition in *P. alcon* populations, the relative importance of various host plant related factors potentially affecting butterfly's selection of particular oviposition sites were evaluated (III). Studies were conducted in Northern Estonia, the northernmost populations known for this endangered species (II, III).

(3) Habitat use and distribution in *Plebejus argus* and *P. idas* (IV). Distribution patterns and habitat use of *P. argus* and *P. idas* in their North European populations were investigated. The primary goal of the study was to assess the extent these closely related butterflies, associated with different host ant species, share their habitat and whether their relative occurrence patterns could be explained by habitat use of their ant mutualists.

2. MATERIALS AND METHODS

2.1. Study species and background

2.1.1. *Phengaris* species

Myrmecophilous butterflies from the Palearctic genus *Phengaris* (senior synonym of *Maculinea* Van Eecke 1915; Fric et al 2007; Fig. 1, 2) represent an extreme example of diet specialization as they require two resources to be present simultaneously: (1) a specific larval food plant (Fig. 1b, 2b), and (2) a suitable host ant (e.g. Clarke et al 1998; Meyer-Hozak 2000; Fig. 1d, 2d). In particular, the first three larval instars are (functionally) mono- or oligophagous developing on flowers and seeds of their host plant. In their fourth (final) instar (Fig. 1c), however, larvae are “adopted” and carried by the worker ants from the genus *Myrmica* Latreille 1804 to their nests, where for the next 10 or 22 months (in the case of biennial development; Thomas et al 1998; Schönrogge et al 2000) the caterpillars continue to live as obligate parasites (Thomas et al 1989; Elmes et al 2001). While the caterpillars of some species (e.g. *P. alcon*; Fig. 2) are directly fed by the worker ants with their regurgitations, trophic eggs and dead prey, others (e.g. *P. arion*; Fig. 1) predate on ant brood (Thomas & Wardlaw 1992). The adoption rate of *Phengaris* larvae by worker ants has not been shown to notably differ between *Myrmica* species (Elmes et al 1991; Thomas 2002; Schönrogge et al 2004). However, the survival of caterpillars inside the nests of different ant species has been considered to differ to the extent where each *Phengaris* species has been considered to have only one or a few suitable *Myrmica* hosts (Thomas et al 1989; Elmes et al 1991; Akino et al 1999; Elmes et al 2004, but see Pech et al 2007).



Fig. 1. *Phengaris arion*. A) an adult female on *Origanum vulgare*, B) a female ovipositing on *Thymus serpyllum*, C) a prepupal caterpillar (4th instar), D) a *Myrmica lonae* worker tending a *P. arion* caterpillar. © Margus Vilbas.



Fig. 2. *Phengaris alcon*. A) an adult female, B) a female ovipositing on flowers of *Gentiana cruciata*, C) eggs on *G. cruciata* leaves, D) a *Myrmica schencki* worker tending for *P. alcon* pupae. © Margus Vilbas.

Since mid-twentieth century the abundance of all *Phengaris* species has significantly declined throughout Europe (Wynhoff 1998). These butterflies have even disappeared from many habitats seemingly suitable for them (Clarke et al 1997). Inadequate understanding of the causes of these declines made the early conservation attempts of *Phengaris* species unsuccessful (Thomas et al 2009). A strong population decline followed by the extinction of *P. arion* in England launched extensive studies on the species (Thomas et al 2009). However, it also brought wide scientific attention to other representatives of the genus (e.g. Thomas et al 1989; Steiner et al 2003; Nowicki et al 2005; Tartally et al 2014). As a result, *Phengaris* species are some of the most thoroughly studied butterflies, and have become ‘flagships’ of European biodiversity conservation (Thomas & Settele 2004). Nevertheless, despite a high concern, numerous populations all over Europe have experienced severe declines, especially in the northern part of the species range (Wynhoff 1998). As a response, the European status of *P. arion* has been changed from ‘near threatened’ to ‘endangered’ (Van Swaay & Warren 1999; Van Swaay et al 2010). Other European species are either ‘near threatened’ (*P. alcon*, *P. nausithous*) or ‘vulnerable’ (*P. teleius*) (Van Swaay et al 2010). *P. arion* is also included in the Annex II of the Habitats Directive of the European Union (Council Directive 92/43/EEC, 1992).

Recent studies conducted in Central (e.g. Steiner et al 2003, 2006; Sielezniew et al 2010a, 2010b, 2010c; Tartally et al 2014) and Southern Europe (e.g. Casacci et al 2011; Patricelli et al 2011) have significantly expanded and partly altered the early understanding of habitat use and host ant preference in *Phengaris* butterflies derived from Western Europe (e.g. Thomas et al 1989). In particular, host plant and host ant use have both been found to be much more diverse than initially thought. For example, it has been shown in Poland that *P. arion* may successfully develop on as many as seven different *Myrmica* species, and thus does not depend solely on *M. sabuleti*, the primary host ant in Western Europe (Sielezniew & Stankiewicz 2008; Sielezniew et al 2010a, 2010b, 2010c). Similarly, in earlier studies on host specificity of *P. alcon*, its

hygrophilous (*P. alcon* s. str.; see Pech et al 2004; Bereczki et al 2005, 2006; Steiner et al 2006) and xerophilous ecotype (*P. rebeli* auct. Nec Hirschke; *P. alcon* X hereafter; see Als et al 2004; Pecsénye et al 2007; Tartally et al 2014) have been shown to specialize on *Myrmica ruginodis* and *M. schencki*, respectively (Thomas et al 1989). More recent studies, however, have changed this view showing that both ecotypes can successfully exploit quite a number of different *Myrmica* species (e.g. Elmes et al 1998; Meyer-Hozak 2000; Steiner et al 2003; Arnaldo et al 2011; Casacci et al 2011; Czokes et al 2014).

Nevertheless, findings of multiple host ant use are predominantly confined to Central Europe (e.g. Tartally et al 2008; Witek et al 2008; Sielezniew et al 2010c; Tartally et al 2017). In different parts of the range (particularly in periphery), *Phengaris* butterflies display narrower host specialization, involving specific physiological adaptations to different hosts (e.g. Thomas et al 2013). As ecological requirements of different plant and ant species vary to a considerable extent (Thomas et al 1998; Sielezniew et al 2010c; Casacci et al 2011; Patricelli et al 2011), this necessarily also entails differences in other aspects of habitat use in *Phengaris* butterflies. Creating successful conservation of the species in a particular region thus cannot be based solely on the species' life history and habitat preference data obtained from geographically distant populations.

In Estonia, two species of *Phengaris* are known to be present – *P. arion* (Fig. 1) and *P. alcon* X (Fig. 2). Both butterflies occur on nutrient-poor xerothermic and calcareous grasslands. *P. arion* exploits predominantly *Thymus serpyllum* (Fig. 1b) as the larval host plant, however, in some areas, *Origanum vulgare* is also used (pers. obs.). *P. alcon* X is known to oviposit exclusively on *Gentiana cruciata* (Fig. 2b, 2c). The butterflies pupate in June and emerge in the beginning of July. While *P. arion* can be found in a few locations across the country, the occurrence of newly discovered (in 2012) *P. alcon* X appears to be confined to a small area in Central and Northern Estonia (Fig. 3). The butterfly has probably expanded to its current northern range margin relatively recently. However, a further northward shift as shown for numerous other European butterflies (e.g. DeVicтор et al 2012), is unlikely as its sole larval food plant in the region, *G. cruciata* also reaches its northern distribution margin in Estonia (Kukk & Kull 2005; GBIF Backbone Taxonomy 2016). In the upcoming update of the Estonian Red Data Book (unpublished), the status of *P. arion* will be kept as 'endangered', while *P. alcon* will be listed as the only 'critically endangered' butterfly species in Estonia.

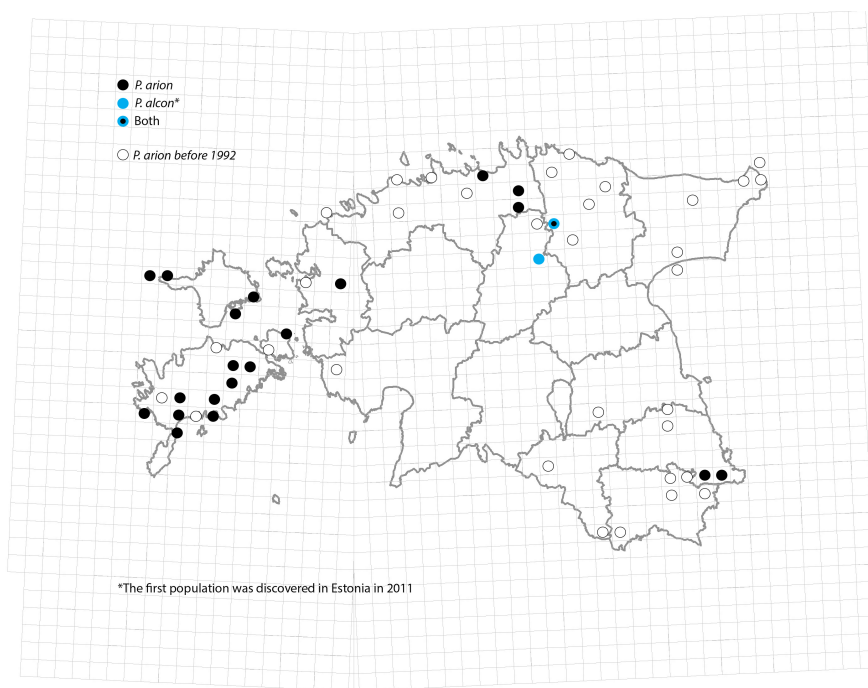


Fig. 3. The distribution of *Phengaris arion* and *P. alcon* in Estonia, Northern Europe.

2.1.2. *Plebejus* species

Plebejus is a species-rich genus of myrmecophilous butterflies. The closely related *Plebejus argus* L. and *P. idas* L. (Fig. 4a, 4b) are only butterflies that are known to be engaged in obligate mutualistic relationships with ants in Europe (Fiedler 2006; Fig. 4c). The habitat of these butterflies, as in *Phengaris* and other obligate myrmecophiles, is primarily determined by two resources that should be spatially overlapping for successful larval development. In particular, polyphagous caterpillars of both species, depending on locality, feed on various plants of Ericaceae, Fabaceae and Cistaceae (Fiedler 1991b; Thomas et al 1999; Jordano & Thomas 1992; Péténian & Nève 2003) whereas they are tended by worker ants of specific ant genera. The caterpillars of *P. argus* are reported to exclusively associate with *Lasius* spp. (e.g. Thomas 1985a, 1985b; Ravenscroft 1990; Levington 1991; Jordano et al 1992; Thomas et al 1999; Davis et al 2011) while *P. idas* shows high specificity for *Formica* spp. (e.g. Malicky 1969; Fiedler 1991b; Fig. 4c). Both partners benefit from the interaction – the caterpillars provide nutritious secretions for ants and receive protection against predators and parasitoids in return. *P. argus* and *P. idas* are still widespread in most of Europe and Asia (Thomas & Harrison 1992; Kudrna 2002). However, many populations in Central and Northern Europe are isolated and patchily distributed, and have shown notable declines (Asher et al 2001; Beneš et al 2002; Dennis 2004).



Fig. 4. *Plebejus argus* and *P. idas*. A) *P. argus* adult male, B) adults of *P. argus* and *P. idas* feeding on *Vicia cracca*, C) *Formica* sp. milking the DNO (Dorsal Nectary Organ) of a caterpillar of *P. idas*. © Margus Vilbas.

In Estonia, *P. argus* and *P. idas* are univoltine and inhabit open landscapes across the country (Fig. 5). Females lay eggs singly close to the ground on leaf litter or the stems of larval food plants (Ravenscroft & Warren 1996). The butterflies overwinter as eggs and complete their development in the following spring. Larvae feed on the buds, flowers, and young shoots of various host plants such as common heather (*Calluna vulgaris*), bog blueberry (*Vaccinium uliginosum*), various vetches (*Vicia* spp.; Fig. 4b) and clovers (*Trifolium* spp.) (Õunap & Tartes 2014). The caterpillars pupate for three weeks before emerging as adults in June or July. The flight period of *P. idas* starts in late June and lasts until mid-August. *P. argus* emerges approximately ten days later (Õunap & Tartes 2014).

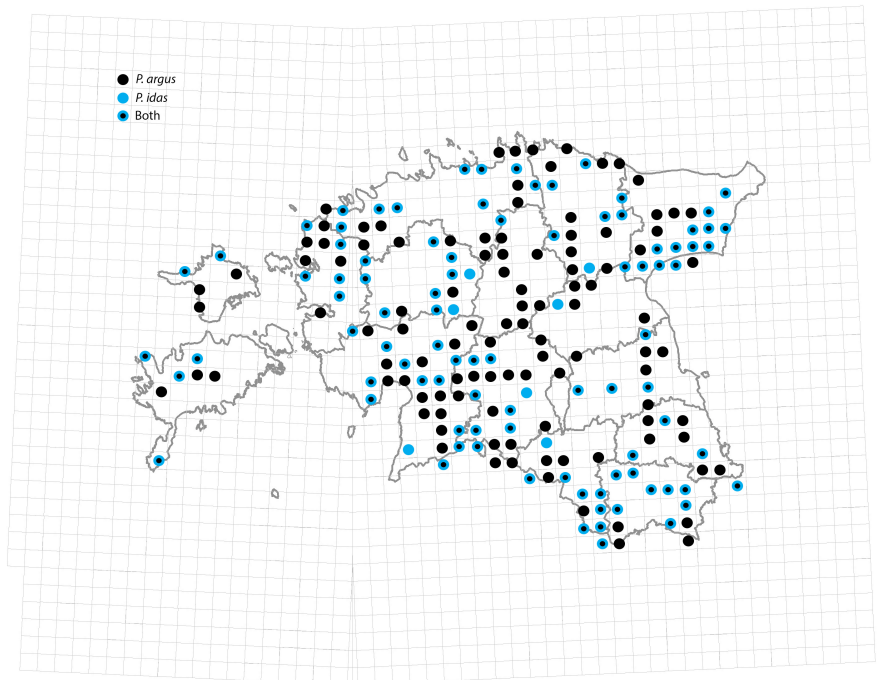


Fig. 5. The distribution of *Plebejus argus* and *P. idas* in Estonia, Northern Europe.

Previous studies have largely focused on only one of these two *Plebejus* species. In particular, while *P. argus* has been used as a model species in numerous ecological studies across Europe (e.g. Thomas 1985a, 1985b; Jordano & Thomas 1992; Thomas & Hanski 1997; Thomas et al 1999; Seymour et al 2003; Dennis 2004; Sielezniew et al 2011), its congeneric, *P. idas*, has received little scientific attention. Accordingly, there are no published studies focusing on distribution patterns and ecology of both *Plebejus* species at the same time. Concurrent comparative studies, however, would be insightful to understand the factors shaping habitat use in these closely related butterflies.

2.2. Methodology

2.2.1. Habitat occupancy and host ant use in *Phengaris arion* (I)

The study was conducted on two large Baltic Sea islands in Western Estonia – Saaremaa and Muhu, where local populations of *P. arion* are confined to small patches of calcareous grasslands in a landscape dominated by forests (50% of the islands; Kään 2002). Due to cessation of traditional management practices the area of calcareous grasslands has declined more than threefold in the past 70 years (Helm et al 2006). The majority of grasslands are currently not managed.

The field works were conducted in a total of 37 calcareous grasslands where the primary host plant of the butterfly (*T. serpyllum*) was known to be present. Timed surveys (see Kadlec et al 2012) were conducted in 2007–2013 to establish presence/absence of *P. arion* in focal grasslands. All patches were visited at least once a year for three to seven years (altogether 6 visits per grassland as a minimum). Surveys were conducted in July, the peak flight period of *P. arion* in Estonia. Each grassland was inspected for 15 minutes up to 4 hours (depending on patch area) during the active flight time of the butterfly (between 10 AM and 6 PM) under suitable weather conditions (>18°C, sunny, weak wind).

Four parameters that have been suggested to affect habitat quality for *P. arion* in particular, and for butterflies in general were estimated for each grassland: (1) turf height, (2) bush coverage (mainly *Juniperus communis*), (3) coverage of larval host plant (*T. serpyllum*), and (4) abundance of dragonflies (Anisoptera spp.). In addition, grassland areas and their distances to the sea were measured using high resolution orthophotos of the Estonian Land Board (<http://www.maaamet.ee>). Due to strong correlation between turf height and coverage of larval food plant (Pearson $r = -0.67$), the first principal component (PC1) of these variables was calculated. Another principal component (PC2) was calculated for the correlated (Pearson $r = -0.44$) dragonfly abundance and distance to the sea.

Turf height and bush coverage were primarily considered because of their potential impact to abundance and community composition of *Myrmica* ants

(Thomas et al 2009), as well as their effect on larval food plant abundance. Both dragonfly abundance and distance to the sea were considered as proxies of dragonfly predation. First, dragonfly abundance has been shown to strongly correlate with dragonfly-induced predation on adult butterflies in the study area (e.g. Sang & Teder 2011; Tiitsaar et al 2013). Second, the dominant dragonfly species in the region, such as *Orthetrum cancellatum* (Sang & Teder 2011), breed in brackish water (Lindberg 1948; Kalkman et al 2002), suggesting distance to the sea to be a suitable surrogate for dragonfly abundance.

Host ant use in *P. arion* was approached from two complementary perspectives. Firstly, overall species composition of *Myrmica* ants in the study area was assessed. For this purpose, six random 1 m² plots in each of 37 grasslands were sampled for *Myrmica* ants. For the purpose of determining the possible association between *Myrmica* ants and the butterfly's larval food plant, three of the six plots were chosen with host plant present and another three without the plant in the plot or its close vicinity. The ants were identified using the key of Radchenko & Elmes (2010). Secondly, to directly establish host ant use of local *P. arion* populations, *Myrmica* colonies in altogether 527 randomly chosen 1 m² plots in confirmed *P. arion* habitats were systematically inspected for *P. arion* caterpillars and pupae. Sampling was conducted before the flight period of the butterfly (i.e. in late May and early June). Ant colonies were localized by partial removal of the vegetation. All colonies were carefully opened and examined for the presence of *P. arion* juveniles. If the presence of the butterfly was established in upper chambers of nests, no further disturbance was undertaken. The ground and vegetation were restored as close as possible to pre-excavation conditions after inspection. Samples of 5–10 workers from each examined ant colony were preserved in 75% alcohol for further identification. Negative effects of this methodology to ant colonies and populations have been considered to be insignificant (e.g. Sielezniew et al 2010a).

2.2.2. Host ant use and oviposition patterns in *Phengaris alcon* X (II, III)

The study was conducted in two populations, about 6.5 km apart, in the Pandivere Upland, Northern Estonia. Host ant data from both populations were pooled as the data derived from the smaller one were insufficient for separate statistical analyses (II). Oviposition preference was investigated only in the larger of the two populations (III) which inhabits a 13.2 ha grassland. With an estimated 400 *G. cruciata* plants, this grassland harbours one of the largest *G. cruciata* populations in the region. Neither of the studied grasslands are actively managed and have therefore started to show signs of overgrowing.

Host ant use was examined in May 2014, well before the flight period of the butterfly. *Myrmica* colonies around randomly chosen host plants were examined for butterfly larvae and pupae in 29 plots of 2x2 m. Excavations were conducted as described above for *P. arion*. As ground-dwelling ant communities are strongly structured by interspecific competition (e.g. Savolainen & Vepsäläinen

1988; Hölldobler & Wilson 1990), *Lasius* spp. nests were also counted in all sample plots. For each *Myrmica* nest, its distance to the nearest host plant was measured and colony size was estimated using the methodology described by Skórka et al (2006). Examining ant colonies in well-defined plots allowed to evaluate their density in the study area.

Field examination of oviposition patterns was conducted in the beginning of September 2014, shortly after the flight period of the butterfly. The distinctive and resilient egg shells of the butterfly are firmly attached to the host plants (Thomas et al 1991), facilitating detailed field studies of host plant use for oviposition even after eggs have hatched. Data were obtained by counting all eggs and egg shells on each host plant within a sampling area of 300×150 m (i.e. 4.5 ha, Fig. 1 in II). For each host plant individual, the following data were recorded: (a) number of shoots, (b) average height of the shoots, (c) average height of the vegetation surrounding the host plant (see Stewart et al 2001, for methods), (d) presence/absence of flowers, and (e) host plant patchiness (number of *G. cruciata* shoots within a one metre radius around the focal plant). Besides these parameters, host plant apparency for ovipositing butterflies was quantified for each host plant individual by calculating the difference between the height of its tallest shoot and average height of the surrounding vegetation. Finally, damage caused by wild mammal herbivores to individual shoots (shoot damaged/undamaged) was recorded.

2.2.3. Habitat use and distribution in *Plebejus argus* and *P. idas* (IV)

The patch occupancy patterns of *P. argus* and *P. idas* were investigated in 227 10×10 km Universal Transverse Mercator (UTM) squares distributed across the country (Fig. 5). Altogether 881 different habitat units were preselected, so that 2–4 sites per UTM square were surveyed. More precisely, at least one grassland and one forest clear-cut were designated to each UTM square whereas a peat bog was included if present. Additionally, linear landscape elements such as waysides were included in every other UTM square. Across all sites, 40% of the surveys were conducted in grasslands, 38% in forest clear-cuts, 16% along waysides and 6% in peat bogs. Particular habitat units were selected using high-resolution orthophotos provided by the Estonian Land Board (<http://geoportaal.maaamet.ee>). Field works were conducted as an integral part of the Estonian butterfly mapping project (led by Anu Tiitsaar) in the summer of 2016. More than 40 researchers and field assistants were engaged in monitoring and sample collection. All sites were visited three times in the periods: I) from the end of May to the beginning of June; II) from the end of June to mid-July; and III) from the end of July to mid-August. Timed counts (see Kadlec et al 2012) were conducted to record butterflies. All visits were conducted during the active flight time of butterflies (between 9 AM and 6 PM) under suitable weather conditions (≥ 18 °C, no rain, weak to moderate wind). Butterflies were recorded during a 30 minute transect walk (non-fixed in case of areal sites). As

P. argus and *P. idas* are difficult to distinguish in the field, up to 10 specimens were collected for subsequent microscopic identification from each site to assess the presence of the target species.

Various soil related characteristics have been shown to be significant drivers of habitat use in numerous ant species, *Lasius* and *Formica* included (e.g. Vasconcelos et al 2003; Boulton et al 2005; Deblauwe & Dekoninck 2007). Therefore, soil type was determined for each investigated site. The data were acquired using a digital soil map of Estonia provided by the Estonian Land Board. In addition, a number of other factors were estimated: (1) habitat wetness (wet, partially wet, dry), (2) presence of drainage ditches, (3) presence of roads and pathways, and (4) habitat patch area. The area of each site (except for linear landscape elements) was measured using high-resolution orthophotos of the Estonian Land Board.

For each forest clear-cut, a number of additional parameters were obtained: (1) age of the clear-cut; (2) soil pH level; (3) soil humidity level. The latter two parameters were derived from the ordination scheme of forest site types by Lõhmus (2004). Data on the time of logging and forest site types were obtained from the Estonian Forest Registry (<http://register.metsad.ee/avalik/>). Soil pH and humidity, again, were considered because of their potentially high impact on plant and ant communities.

2.3. Data analyses

Generalized linear model (GLM) with binomial errors (logistic regression) were built to determine the factors (and possible interactions between them) affecting patch occupancy (presence-absence) of *P. arion* (I), *P. argus* and *P. idas* (IV), and the presence of eggs and egg shells of *P. alcon* X (III). In the quantitative analyses of *P. alcon* oviposition patterns (III), only the subset of plants with eggs present was included, number of eggs on a plant was treated as a dependent variable and a GLM model with a Poisson error structure was applied. Additional analyses were carried out to assess potential effects of mammalian herbivore browsing on oviposition patterns (III). The data for *P. argus* and *P. idas* were analysed at two levels: (1) across all habitat types, and (2) across the subset of forest clear-cuts (IV). Further analyses were performed to compare differences in habitat use of *P. argus* and *P. idas* (IV). More precisely, the model prediction approach was opted to visually interpret the modelling results and compare the effects between the species (see IV for reasoning).

All the variables were standardised to a mean of zero and a standard deviation of one to improve convergence and eliminate possible effects of the scale of measurement (I). Continuous independent variables were normalized by subtracting the mean and dividing by the standard deviation (III, IV). The data on patch area and distance to the sea were natural logarithm transformed to reduce variance heterogeneity (I). To test for the goodness of fit of the models, the Hosmer-Lemeshow (H-L) test was performed (Hosmer & Lemeshow 2000;

IV). Area under the receiver-operating characteristic curve data (AUC) was used to assess the predictive accuracy of models (IV). The data were checked for nonlinearity and interactions (I–IV). Best models were visually inspected to assess spatial autocorrelation in the model residuals (I, III). As no obvious spatial autocorrelation in the residuals of any of the best models were detected in either study, non-spatial models were used (I, III).

Information-theoretic approaches were employed for model selection and multimodel inference (I, III, IV). Competing models were ranked using Akaike's Information Criterion corrected for small sample size (AIC_C). For each particular model, the difference between its AIC_C value and AIC_C value of the best model was calculated (ΔAIC_C), ΔAIC_C of the best model being zero. The models with $\Delta AIC_C \leq 2$ were considered to be close to the best model (Burnham & Anderson 2002). The ΔAIC_C values were used to calculate Akaike weights for each model. To infer the relative importance of predictor variables, model averaging was conducted across models with all possible combinations of variables. The relative importance for each variable was calculated by summing Akaike weights across all the models containing that particular variable – the larger the sum for a particular variable, the more important it was considered relative to other variables (Burnham & Anderson 2002).

To test for host ant specificity, a contingency table (with each *Myrmica* species treated separately) was used to calculate the chi-squared statistic (I, II), the significance of which was tested by Monte Carlo simulation procedure. The presence-absence data of *P. alcon* X larvae in host ant colonies were further analysed using logistic regression with Firth's correction for separation (Firth 1993; II). Colony distance from the host plant and colony size entered the model as continuous independent variables.

All the analyses were performed in R versions 2.15.1–3.2.2 (R Development Core Team, 2011–2015), using the *logistf* (logistic regression; Heinze et al 2013; I, II), *MuMIn* (model selection and model averaging; the effects of covariates on detection probabilities; Bartoń 2018; I, III, IV), *Ape* (assessing spatial autocorrelation; Paradis et al 2004; III), *lme4* (Poisson mixed models; Bates et al 2018; IV), *AUC* (predictive accuracy; Ballings & Van den Poel 2015; IV), *ResourceSelection* (resource selection functions for use-availability data; Lele et al 2017; IV) packages.

3. RESULTS

3.1. Habitat occupancy and host ant use in *Phengaris arion* (I)

P. arion was found to be present in almost one-third of the surveyed grasslands (11 out of 37). The model including PC1 (i.e. the principal component of host plant coverage and turf height), PC2 (principal component of dragonfly abundance and distance to the sea) and patch area as predictor variables had the highest rank. Based on model averaging, PC1 and PC2 were the most important predictors of patch occupancy. Accordingly, the butterfly was more likely to occupy grasslands with higher host plant coverage, lower turf height, lower dragonfly abundance and longer distance to the sea (for quantitative data see I, Table 3). Indeed, host plant coverage in habitats occupied by *P. arion*, being consistently higher than 30% of the open area, was, on average, about 2.5 times higher than in unoccupied patches. Turf height was roughly 60% lower in patches occupied by *P. arion*. Also, there was on average about a two-fold difference in dragonfly abundance and three-fold difference in distance to the sea between the occupied and unoccupied patches. Additionally, there was some tendency for the butterfly to occur more frequently in patches with fewer bushes (I, Table 3).

A total of 188 *Myrmica* ant colonies were excavated and examined at these 11 patches where *P. arion* was present. Altogether 8 *Myrmica* species were recorded: *M. schencki* (57 colonies), *M. lonae* (41), *M. scabrinodis* (26), *M. rubra* (17), *M. sabuleti* (15), *M. ruginodis* (12), *M. lobicornis* (11) and *M. rugulosa* (9). Three nests of *M. lonae* (1.6% of all *Myrmica* nests, 7.3% of *M. lonae* nests), were infested by a single full grown *P. arion* caterpillar (see Fig. 1d). Host ant use was significantly influenced by the host species (Barnard's exact test: *M. lonae* vs. all other *Myrmica* species; $p = 0.041$). Additionally, there was a tendency (though marginally non-significant) for the density of *M. lonae* colonies to show some local-scale association with *Thymus* presence. In particular, there was about two-fold difference in colony densities between squares with and without *Thymus* plants (404 vs. 180 colonies per ha respectively).

3.2. Host ant use in *Phengaris alcon* X (II)

A total of 56 *Myrmica* colonies in 29 plots (116 m²) were excavated and examined for *P. alcon* X larvae and pupae. Altogether 5 *Myrmica* species were recorded: *M. schencki* (18 colonies), *M. sabuleti* (13), *M. scabrinodis* (9), *M. rugulosa* (8) and *M. rubra* (8). Four *M. schencki* colonies that were found in the vicinity of four different *G. cruciata* plants were infested by a total of 17 *P. alcon* X individuals (11 larvae and 6 pupae; see Fig. 2d). Host ant use in

P. alcon X was not random ($p = 0.044$; Monte Carlo contingency table test with 10,000 replicates).

Distance of the colonies to the nearest *G. cruciata* plant had a significant negative effect on their probability of being parasitised (logistic regression: $X^2 = 7.05$; $p = 0.008$). There was also more than two-fold difference in average number of worker ants between infested and uninfested *M. schencki* colonies (1504 vs 632, respectively). However, probably due to a small sample size and relatively high variation in worker numbers, this difference remained marginally non-significant (logistic regression; $X^2 = 1.67$; $p = 0.096$). The overall density of *M. schencki* colonies across the study area was estimated to be about 1550 colonies/ha.

Besides *Myrmica* colonies, the study sites harboured very high densities of *Lasius* spp colonies (particularly *L. niger*), potentially strong competitors of *Myrmica* ants (Binz et al 2014). *Lasius* colonies recorded in sampling plots corresponded to an estimate of 10 000 colonies per ha. There was a strong and highly significant negative correlation between colony densities of *Myrmica* spp. and *Lasius* spp. across sample plots (Spearman rank correlation: $r_s = -0.76$, $N = 29$, $p < 0.0001$). Statistically significant negative association was also found between the colony densities of *Lasius* and *M. schencki*, the local host ant of *P. alcon* X (Spearman rank correlation: $r_s = -0.56$, $N = 29$, $p = 0.002$).

3.3. Oviposition site use in *Phengaris alcon* X (III)

Altogether 295 *G. cruciata* plants (66 plants per hectare) with 918 shoots were examined for *P. alcon* X eggs. In total, 2733 eggs on 192 plant individuals (65% of all plants) were found (see Fig. 2c). Based on the eggs counted, the size of the local population was estimated to be about 50–70 individuals (see details in III).

Presence-absence of *P. alcon* X eggs on individual plants was best explained by a model that contained host plant apparency and host plant patchiness as predictor variables. Based on model averaging, host plant apparency was the predictor with the highest relative importance (RI=1) followed by host plant patchiness (RI=0.59). Accordingly, *P. alcon* X was more likely to oviposit on host plants that were protruding from the surrounding vegetation, and those being spatially less clumped / more isolated.

Number of eggs laid on individual host plants was best explained by two models that contained host plant apparency, host plant patchiness, number of shoots and presence of flowers as predictor variables (the second best model also included turf height). Accordingly, all these variables achieved very high relative importance values from model averaging (RI = 1). The females were more likely to deposit greater number of eggs on prominent host plant individuals protruding from the surrounding vegetation, and that were growing further away from their conspecifics (were more isolated). Specifically, *G. cruciata* plants with no conspecifics within 3 m radius carried almost twice as

many eggs as those with at least one other host plant individual within 3 m radius (15.6 vs. 8.7 eggs, on average, respectively). Also, the number of eggs was higher on larger host plant individuals (with greater number of shoots) and those boring flowers.

Wild herbivore browsing was recorded in 81 shoots of 41 plants (8.8% and 13% of all shoots and plants, respectively) that had their upper parts (mainly flowers) missing. Significant differences between damaged and undamaged shoots were detected both at the qualitative (presence-absence of eggs) and quantitative (number of eggs) scale. In particular, damaged shoots had significantly lower probability of carrying butterfly eggs (Fisher's exact test: $p < 0.0001$). More specifically, they bore on average 3.5 times less eggs than undamaged ones (Welch's two-tailed t-test: $t = 4.36$, $df = 6.3$, $p = 0.004$). Interestingly, herbivore browsing was more severe in *G. cruciata* plants that had fewer conspecifics around (2.2 shoots within 1 m radius, on average, around damaged plants and 4.5 shoots around undamaged plants: $F_{1,293} = 8.5$, $p = 0.004$).

3.4. Habitat use and distribution in *Plebejus argus* and *P. idas* (IV)

Out of 881 sites surveyed, *P. argus* and *P. idas* were found to be present in 318 (36%; Fig. 5). *P. argus* was exclusively found in 196 (62%) and *P. idas* in 15 (5%) of the sites. The species co-occurred in 107 patches (33% of the cases). The occurrence probability of *P. argus* was consistently higher, regardless of habitat type or habitat characteristic investigated.

In analyses across all habitat types no single patch occupancy model received overwhelming support in either of the butterflies. Nevertheless, based on model averaging, two variables – habitat type and soil type – received maximum relative importance (RI=1) for both *P. argus* and *P. idas*. Accordingly, the occurrence of both butterflies was highest in bogs, followed by forest clear-cuts and linear landscape elements. The preferred habitats were predominantly located on soils characterized by higher acidity, such as podzols, haplic albeluvisols, histosols and gleysols. The patches inhabited by *P. argus* were also characterized by higher wetness.

In the analysis focusing on forest clear-cuts, again, no single model solely explained patch occupancy in either of the two butterflies. In case of *P. argus*, soil pH was the only predictor variable receiving maximum relative importance (RI=1). It was followed by soil humidity (RI=0.88), the interaction term of soil pH and soil humidity (RI=0.77) and the quadratic term of humidity (RI=0.71). The significant interaction term indicates that *P. argus* showed a decrease in occurrence probability with rising humidity at lower pH levels while the pattern tended to be the opposite in case of high values of pH. In *P. idas*, soil pH was the only predictor variable that received maximum relative importance, followed by soil humidity (RI=0.77). Consequently, both butterflies were more

likely to occur in patches characterized by lower pH and lower humidity levels. *P. argus* also showed tendency for higher occurrence probability at high humidity levels, however the relationship turned out to be marginally non-significant ($p = 0.07$).

Visual comparison of the occurrence probabilities of the two *Plebejus* species largely supported previously described findings (see Fig. 5 in IV). Indeed, both species were more likely to occur in forest clear-cuts characterized by lower pH and lower humidity levels. Moreover, the occurrence probability of *P. argus* was seen to be invariably higher than that of *P. idas*. *P. argus* also showed an increase in occurrence probability in highly humid clear-cuts, a pattern that could not be seen in *P. idas*. Additionally, the shapes of the curves describing the decline of occurrence probabilities with increasing pH slightly differed between the species. Namely in *P. argus*, the decline was slower than in *P. idas* at low pH values, but more rapid at higher pH values.

4. DISCUSSION

4.1. Habitat occupancy and host ant use in *Phengaris arion* (I)

The results from near the northern range margin of *P. arion* explicitly complement the emerging evidence of regional diversity of host ant use in this myrmecophilous butterfly. Accordingly, this thesis is the first to record *M. lonae* as the primary host ant of *P. arion*. The same ant species has been suggested (although never demonstrated) to be the host ant of *P. arion* in Finland as well (Saaristo 1995; Kolev 1998). Therefore, the host ant use of *P. arion* in North European populations seems to be notably different from that in the Western Europe where *M. sabuleti* has been often shown as the sole host ant of this butterfly (e.g. Thomas et al 1989). Multiple host ant use in our study area cannot be fully excluded as the local *Myrmica* fauna includes several species that are exploited by the butterfly in Central Europe (Sielezniew et al 2010b).

Besides ascertaining the host ant use of *P. arion*, several factors were found to significantly affect the patch occupancy of the butterfly. More precisely, the butterfly was more likely to occur in grasslands characterized by higher host plant coverage, lower turf height, lower dragonfly abundance and shorter distance to the sea.

Based on a spatial simulation model, Griebeler & Seitz (2002) have proposed that minimum requirements for viable *P. arion* populations are 5% of host plant cover and host ant density of at least 500 colonies per ha. The observed values in our study area differed substantially from the minimum parameter values inferred from this model. In particular, for *P. arion* to be present, host plant had to cover at least 30% of the open area. On the other hand, the average density of host ant colonies across patches occupied by *P. arion* was lower than the proposed minimum value. There are several possible ways to explain this discrepancy in the habitat requirements proposed by the model (Griebeler & Seitz 2002) and those observed in our study area. First, different host plant (*T. serpyllum* in our study area, *T. pulegioides* in the model) and host ant (*M. sabuleti* vs *M. lonae*) species were involved. Second, the within-habitat distributions of host ants and larval food plants can be coupled (see also Casacci et al 2011). Indeed, the average density of *M. lonae* colonies estimated in plots with *T. serpyllum* was about three times higher than in plots without the host plant. Such a local-scale coupling of food plant and host ant is likely to have a substantial impact on their minimum values required for viable populations of the butterfly. Third, the oviposition selectivity of *P. arion* could be higher than was considered in the model. Indeed, Patricelli et al (2011) have demonstrated that *P. arion* females prefer to lay their eggs on host plants growing in close vicinity of *Myrmica* ant nests. Selective oviposition is likely to lower the minimal host ant density required to ensure a reasonable rate of caterpillar adoption by ants, and maintain viable populations of *P. arion*.

The habitat patches occupied by *P. arion* were characterized by notably lower turf height. Low turf height *per se* can be an important determinant of habitat occupancy of *P. arion* as it creates suitable microclimatic conditions for particular host ants (Thomas et al 1989; Elmes et al 1998; Thomas et al 2009). However, given the strong correlation between turf height and host plant coverage, the effect of turf height on patch occupancy of the butterfly is likely mediated through its effect on host plant coverage. In particular, *T. serpyllum* successfully grows on thin, low-fertility soil not suitable for high productivity plants, whereas on high fertility soil, it gets outcompeted. Moreover, the average turf height in *T. serpyllum* habitats is inevitably lower as the plant itself is a low subshrub not growing more than 4 cm tall (Ložienė 2009). Therefore, higher *T. serpyllum* coverage negatively affects turf height and therefore generates or at least strengthens the association between turf height and patch occupancy in *P. arion*. Consistently, average turf height is notably higher in Central Estonian *P. arion* populations (localities described in III) where *T. serpyllum* is missing and thus the butterfly most likely feeds exclusively on *Origanum vulgare*, a perennial herb growing up to 80 cm (Zobel et al 2005).

The results indicate that top-down effects such as dragonfly predation could also be essential drivers of patch occupancy in *Phengaris* butterflies. Indeed, PC2, the principal component of dragonfly abundance and distance to the sea (which we used as a proxy for potential dragonfly predation pressure; see Sang & Teder 2011, Tiitsaar et al 2013 for reasoning) was present in all top ranked models, and was the second best predictor variable according to model averaging. Consistently, rare small-sized flying insects such as *P. arion* have been suggested to be particularly vulnerable to generalist predators such as dragonflies (Spiller & Schoener 1998; Tiitsaar et al 2013). To my knowledge, this is the first time to demonstrate that predators can affect patch occupancy patterns in *Phengaris* butterflies. Distance to the sea *per se*, being inherently correlated with abundance of dragonflies, is likely to have no direct significant effect on patch occupancy of *P. arion*. In particular, majority of dragonfly species in the region, local dominant *O. cancellatum* included, inhabit brackish reed vegetation along the coast of the Baltic Sea (Kalkman et al 2002).

4.2. Host ant use in *Phengaris alcon* X (II)

The data indicate that, at its northern distribution margin, the xerophilous ecotype of *P. alcon* is primarily parasitizing a single host ant species. In particular, all documented *P. alcon* X juveniles (altogether 17 caterpillars and pupae) were limited to the colonies of *M. schencki* (II). As with *P. arion* in Saaremaa and Muhu (I), we did not find any other ant species to serve as hosts. Nevertheless, three other *Myrmica* species previously documented as host ants of the butterfly elsewhere (i.e. *M. sabuleti*, *M. scabrinodis*, *M. rubra*) were relatively abundant. The results are in line with previous studies that have shown *P. alcon* X to occur as two ecologically distinct forms that exploit two different host ants

across their European range. More precisely, while the form occurring mainly in Central Europe (e.g. in Austria, Poland, Romania, Ukraine) has been shown to parasitize on *M. sabuleti* (Steiner et al 2003; Sielezniew & Stankiewicz 2007; Tartally et al 2008; Witek et al 2008), the form dominating peripheral areas (e.g. Estonia, Lithuania, Spain) appears to exploit *M. schencki* (this study; Stankiewicz et al 2004; Thomas et al 2013). In addition, the findings are consistent with the idea of higher host specificity near species range margins (Martin & Pullins 2004; Schmidt & Hughes 2006).

The data presented in this thesis indicate that numerous host ant related factors could have a notable effect on the adoption probability and survival of *P. alcon* X larvae. Indeed, host colony size, its distance to the initial host plant as well as the presence of interspecific competitors of *Myrmica* could affect the viability of *P. alcon* X juveniles.

M. schencki colonies infested by *P. alcon* X larvae were twice the size of uninfested colonies (i.e., contained twice as many workers, on average; II). Although the difference remained marginally non-significant (probably because of a small sample size), such a relationship may exist for several reasons. First, the larvae of *Phengaris* butterflies have higher probability of being adopted to larger colonies because they contain more foraging workers (e.g. Herbers & Choiniere 1996; Palmer 2004). Second, infestation by *Phengaris* larvae (or any other detrimental event) is less likely to cause larger colonies to collapse or abandon the nest site (Thomas & Wardlaw 1992; Elmes et al 1998). Third, higher polygyny typical for larger colonies (Elmes & Keller 1993; Sundström 1995) may reduce worker aggressiveness towards intruding caterpillars (Fürst et al 2012) and facilitate their chemical infiltration into the colonies (Nash & Boomsma 2008).

There was a strong negative correlation between colony densities of *M. schencki* and *Lasius* spp. (II). Although other causal factors cannot be excluded, these results suggest that competition between these ants may have a substantial influence on the viability of *Phengaris* populations. Indeed, interspecific competition is known to be one of the major factors shaping species composition and spatial distribution patterns in ant communities (e.g. Savolainen & Vepsäläinen 1988; Hölldobler & Wilson 1990; Andersen & Patel 1994; Ślipiński et al 2014). However, previous studies investigating host ant availability in *Phengaris* butterflies have largely overlooked the possible effect of competitive interactions between *Myrmica* spp. and ants from other genera. In particular, *Myrmica* species are among the most subordinate ones in the ant competition hierarchy (e.g. Seifert 2007; Vepsäläinen & Czechowski 2014) and hence their population performance may substantially be affected by other ant genera. Moreover, *Phengaris* parasitism by itself could have substantial impact on both the number and size of host ant colonies (Hochberg et al 1994), deepening their competitive disadvantage even further.

4.3. Oviposition site use in *Phengaris alcon* X (III)

Factors driving female oviposition site selection largely determine the environment in which the progeny will grow (e.g. Bergström 2005; Küer & Fartmann 2005; Doak et al 2006). Quite naturally, offspring growth and survival are primarily determined by host plant presence. However, numerous other factors such as plant size (e.g. Wiklund 1984; Heisswolf et al 2005; Valdés & Ehrlén 2017), its nutritional quality (e.g. Baylis & Pierce 1991) and apparency (e.g. Chew & Courtney 1991), microclimatic conditions around the plant (e.g. Shreeve 1986) as well as the presence of natural enemies (e.g. Wiklund & Friberg 2008) and mutualists (e.g. Pierce & Elgar 1985) could further affect the availability and suitability of a particular plant individual. As a consequence, a considerable proportion of potentially suitable host plants may remain unused by ovipositing butterflies.

In the population examined, more than one-third of all investigated *G. cruciata* plant individuals did not receive even a single egg, whereas 10% of most egg-loaded plants carried about half of all eggs (III). These data indicate that selection of individual host plants in *P. alcon* X is strongly influenced by plant characteristics and environmental context. The use of particular host plants as oviposition substrate was most strongly associated with host plant apparency (III).

The data indicate that host plant height compared to the surrounding vegetation rather than plant height *per se* is the main factor that determines if a particular host plant is used or not for oviposition. In fact, all plant individuals used for oviposition were taller than the surrounding vegetation. Above all, such prominent plants are visually easier to detect for the ovipositing butterflies. In addition, relatively tall host plants protruding above surrounding vegetation are likely more suitable for larval development as they have been suggested to provide more protection (isolation) from predators such as orb-weaving spiders (Küer & Fartmann 2005). Consistently, oviposition on tall, visually conspicuous plants is a pattern, documented also in several other butterfly species (e.g. Courtney 1982; Porter 1992; Nowicki et al 2005; Árnýas et al 2006; Wynhoff et al 2015).

An alternative explanation could be related to more favourable microclimatic conditions that such plants might provide. Indeed, plants protruding above surrounding vegetation receive more solar radiation that might be beneficial for developing eggs and larvae (Thomas 1991; Küer & Fartmann 2005). If this were the case, we might expect to see the females from northern populations to lay proportionally more eggs on upper surfaces of the leaves to compensate for lower solar radiation. Also, host plant apparency should become an increasingly important driver of oviposition behaviour towards northern range margin of the species. However, data available from previous studies and the data presented in this thesis do not provide evidence for such latitudinal variation. In fact, relative amounts of eggs laid on the upper and lower surfaces of the leaves (55–60% on the upper surface, 10–14% on the lower surface) are almost identical in various

regions spanning over 1500 km (Estonia: this study; Lithuania: Oškinis 2012; Hungary: Árnayas et al 2006). Moreover, host plant apparency has been shown to have an equally significant effect on oviposition site use of *P. alcon* X in most of its European range (Germany: Dolek et al 1998; Hungary: Árnayas et al 2006; Lithuania: Oškinis 2012; Romania: Osváth-Ferencz et al 2016). Microclimatic factors thus appear to have a marginal effect on oviposition patterns in *P. alcon* X.

In the quantitative analyses of oviposition site use, a few other variables such as host plant patchiness, number of shoots and presence of flowers received high relative importance in predicting the number of eggs laid on particular host plants (III). While the effect of flowers on the number of eggs is self-explanatory for a species that is florivorous in the first larval instars, the causality of host plant patchiness is less straightforward. Indeed, plants that had fewer conspecifics in the vicinity received notably higher numbers of eggs than more clustered host plants. In part, this pattern could be related to the high time stress *P. alcon* X is suffering from (Kőrösi et al 2008). Indeed, according to Van Dyck & Regniers (2010), the females of *P. alcon* demonstrate highly stereotypic oviposition behaviour which encompasses repetitive climbing and descending down the plant to distribute eggs on neighbouring shoots. Therefore, in case of clustered plants, the ovipositing females are likely to distribute their eggs between numerous host plants resulting in fewer eggs per plant on average (Capman et al 1990). The above described behaviour could also explain the relationship between number of shoots and egg-load on respective host plants (i.e. the egg load per shoot was higher in plants with fewer shoots).

The data indicate, that if not addressed properly, herbivore grazing could inflict substantial damage to the populations of *P. alcon* X and its larval food plant (III). In particular, a substantial amount of all investigated *G. cruciata* individuals were damaged, with their uppermost organs torn off. The most likely cause of such damage is herbivory by wild mammals such as European roe deer (*Capreolus capreolus*), a species often observed in the study area. Herbivore grazing appeared to have a notable damage on the progeny of *P. alcon* X – more than one-tenth (13%) of all plant individuals had signs of herbivore feeding, while these damaged plants carried less than 0.5% of all eggs (III). Interestingly, herbivore damage was particularly prevalent among isolated (less clumped) host plants which, when undamaged, received higher number of eggs than more aggregated plants. Detrimental effects of herbivore grazing are likely to be expressed in two ways: a) directly, as large herbivores eat the eggs inadvertently together with plant organs; b) indirectly as damage through grazing turns the plant less detectable or less attractive to ovipositing butterflies (shorter shoots with less flowers and buds). Consistently, damaged shoots were, on average, 3.5 cm shorter and bore 3 times less flowers than undamaged shoots.

The results of this thesis suggest that *P. alcon* X populations at the northern range margin are primarily limited by the host plant availability. In particular, the sole larval food plant of the species, *Gentiana cruciata* also reaches its northern distribution limit in Estonia (Kukk & Kull 2005, GBIF Backbone

Taxonomy 2016), whereas a northward shift of the plant is not expected as the potential habitats (seminatural calcareous grasslands) are lacking at higher latitudes. Moreover, the northern populations of *G. cruciata* tend to be sparse even in suitable habitats. Indeed, the density of the plant in the study area was less than 50 plants/ha (II) which is far lower than the suggested optimum for sustainable *P. alcon* X populations (1500 *G. cruciata* plants/ha; Clarke et al 1998). A relatively high average egg load on individual plants (9.2 eggs per shoot; III), potentially leading to intraspecific competition between *Phengaris* juveniles (see discussion of study III for reasoning), also indicates the important role the host plant is likely to play. By contrast, host ant densities in the study area (average *M. schencki* colony density: 1550 colonies/ha, average overall *Myrmica* density: 4900 colonies/ha; II) were considerably higher than required for long-term population persistence suggested by population viability analysis (PVA) for predatory *Phengaris* species (e.g. Griebeler & Seitz 2002; see above). Optimal densities for *P. alcon* are probably even lower as the carrying capacity of *Myrmica* colonies for cuckoo-type feeders is generally higher (Thomas & Wardlaw 1992; Thomas & Elmes 1998). Nevertheless, the high host ant (*M. schencki*) density may to some extent compensate for the food plant deficiency by ensuring higher proportion of *G. cruciata* plants to be within the foraging range of potential host ants.

4.4. Habitat use and distribution in *Plebejus argus* and *P. idas* (IV)

P. argus and *P. idas* were found to follow rather similar patterns of patch occupancy throughout the study area – the butterflies were found to be sharing habitats in more than 30% of the surveyed sites inhabited by either or both of the butterflies (Fig. 3, 5). Both species were more likely to occur in habitats characterized by wet acidic soils, peat bogs in particular. Nevertheless, habitat wetness appeared to have a stronger effect on *P. argus*. Both species showed higher occurrence probability in forest clear-cuts characterized by highly acidic but drier soils. The occurrence probability of *P. argus* tended to have another peak at high levels of soil humidity.

Despite similarities in their general habitat use, the occurrence probability of *P. argus* was consistently higher than that of *P. idas*. The observed patterns are likely to be related to substantially wider niche breadth of the ant associates of *P. argus* (Seifert 2017). In particular, with a few exceptions (e.g. *F. picea* and *F. lemni* inhabiting humid bogs; Mabelis & Korczynska 2012), majority of *Formica* are associated with dry, warm (e.g. *F. sanguinea*, *F. pratensis*, *F. rufibarbis*, *F. exceta*), often sandy (*F. truncorum*, *F. cinerea*), sparsely forested areas (mainly coniferous forests; e.g. Seifert 1996; Czechowski et al 2002; Markó & Czechowski 2004; Jurgensen et al 2005; Mabelis & Chardon 2006; Robinson et al 2008; Seppä et al 2009; Trigos Peral et al 2016; Seifert et al

2017) or forest ecotones (e.g. Czechowski et al 2002; Vepsäläinen et al 2007; Goryunov 2015). Some species are highly susceptible to clear-cutting (e.g. *F. lugubris*; Puntila et al 1991) and disturbance (e.g. trampling and mowing; *F. rufibarbis* and *F. cunicularia*; Pontin 1996; Mabelis & Korczynska 2012). *Lasius* species, in contrast, inhabit a much broader variety of biotopes from dry sandy dunes (e.g. *L. psammophilus*; Markó & Czechowski 2004) and deciduous forests (e.g. *L. fuliginosus*; Czechowski 2000) to semi-dry or wet grasslands (e.g. *L. niger*, *L. alienus*, *L. flavus*; Radchenko et al 1999; Lehouck et al 2004) and bogs (e.g. *L. platythorax*; Radchenko et al 1999). *Lasius* also show strong synanthropic tendencies (Radchenko et al 1999; Vepsäläinen et al 2007) and hence are highly abundant in grasslands, arable lands and in gardens (e.g. Radchenko et al 1999; Vepsäläinen et al 2007; Hertzog et al 2016). Consistently, *L. alienus* and *L. niger*, two major mutualists of *P. argus* are estimated to be the most widespread and abundant ant species in Europe (e.g. Vepsäläinen et al 2007; Seifert 2017).

Significantly wider niche breadth and higher general abundance of *Lasius* also likely enable them to successfully compete with other species in variety of habitats, especially in open grasslands (e.g. Brian et al 1965; Smallwood & Culver 1979; Holec 2006; Vepsäläinen et al 2007; Collins 2011; Binz et al 2014; Hertzog 2016). For example, *L. fuliginosus* has been demonstrated to be a dominant territorial ant species, strongly shaping local ant assemblages (e.g. Ślipiński et al 2014; Stukalyuk 2017). *L. niger* is also known to often occupy and dominate food resources and small areas within habitat patches (e.g. Vepsäläinen & Pisarski 1982; Collins 2011). Moreover, *L. niger* is particularly resilient to extreme climatic events such as flooding (Hertzog et al 2016), and, therefore, is likely to support more stable habitat for *P. argus*. Considering all above, the relative habitat availability for *Formica* appears to be notably lower than that for *Lasius*. Nevertheless, *Formica* species have been demonstrated to be dominant in some habitats such as certain forests and forest ecotones (e.g. Czechowski 2000; Vepsäläinen et al 2007; Goryunov 2015; Trigoso Peral et al 2016). Consistently, vast majority of patches inhabited by *P. idas* were located in immediate proximity of coniferous (pine) forests.

Peat bogs were found to be the most important habitat type for both species. Indeed, as slowly changing heterogeneous environments (e.g. Masing 1984), bogs are likely to provide a constant undisturbed habitat with abundance of resources for successful development for these sedentary butterflies (Hovestadt & Nieminen 2009). Accordingly, as mentioned above, *Lasius* and *Formica* both are represented in bogs (e.g. Wheeler 1915; Czechowski et al 2002; Vepsäläinen et al 2007; Vele et al 2009; Collins 2011; Mabelis & Korczynska 2012; Seifert 2017). Moreover, habitat preferences of various host plants such as *C. vulgaris*, *V. myrtillus*, and *V. uliginosum*, being adapted to moist acidic soils (i.e. histosols and gleysols) (Chapman & Bannister 1994; Jacquemart & Thompson 1996; Syrett et al 2000; Boulanger-Lapointe et al 2017; Haest et al 2017), well coincide with the revealed patterns of habitat use in *P. argus* and *P. idas*.

Forest clear-cuts proved to be the second most important habitat for the studied *Plebejus* butterflies. Both species were more likely to occur in clear-cuts characterized by lower soil pH. In contrast to the inference drawn from the cross-habitat models, butterflies were more frequent in clear-cut patches with lower soil humidity. In the case of *P. idas*, these patterns appear to follow the habitat use of their xerophilous *Formica*-hosts while the *Lasius*-hosts of *P. argus* are also abundant in such habitats. Moreover, *C. vulgaris*, the dominant host plant of *Plebejus* butterflies in bogs, is also well adapted to dry acidic soils (Chapman & Bannister 1994; Haest et al 2017) and therefore could serve as an important host plant in xerothermous landscapes as well. Additionally, *Arctostaphylos uva-ursi*, a plant adapted to dry acidic soils (Hardy BBT 1989) is also known to serve as host plant in dry sandy habitats.

In forest clear-cuts, *P. argus* tended to have another peak at higher levels of humidity. Accordingly, *L. platythorax*, a major host of *P. argus* (e.g. Péténian & Neve 2003), has been shown to have a clear preference for higher soil humidity (e.g. Radchenko et al 1999). The absence of the clear second peak in *P. idas* could be related to the *Formica* being generally more xerophilous (see above). Moreover, a few known *Formica* species adapted to humid conditions are rather confined to specific habitats such as bogs (Czechowski et al 2002; Mabelis & Korczynska 2012). Nevertheless, there is often no shortage of host plants in humid habitats as various host plants, such as *C. vulgaris* and *V. myrtillus* often colonize humid acidic soils (i.e. podzols and haplic albeluvisols; Löhmus 2004) in peat bogs or boggy forests (e.g. Chapman & Bannister 1994; Boulanger-Lapointe et al 2017). Other potential host plants such as *Trifolium* spp. and *Vicia* spp. (e.g. Korshunov & Gorbunov 1995) also occur on moist but less acidic soils (e.g. Lindström & Myllyniemi 1987; Schubert et al 1989; Jensen et al 2010).

The patch occupancy was lowest in grasslands, both in absolute and relative terms. Indeed, as few as 11% and 2% of grasslands studied (out of 348) were inhabited by *P. argus* and *P. idas* respectively. While these results could have been expected for *Formica*-related *P. idas*, it is somewhat surprising for *Lasius*-related *P. argus* (see above for reasoning). Unexpectedly low occurrence in grasslands could be related to the butterfly's narrow host preference in the region. Nevertheless, further studies are necessary to confirm this suggestion.

4.5. Conclusions and importance

The work reported in the present thesis makes a number of original contributions to the studies of myrmecophilous butterflies. Novel data derived from geographically distant and unexplored populations in Northern Europe are relevant both at local and broader geographical scales. First, this research improves the fundamental understanding of life history and ecology in myrmecophilous butterflies. Second, the collected data provide a solid framework for

developing adequate and meaningful conservation strategies for studied populations.

This thesis is the first to describe host ant specificity of endangered *Phengaris* butterflies in the region (I, II). The data, indicating that both *P. arion* and *P. alcon* X are primarily parasitizing on a single host ant species, supports the idea of higher host specificity near species' range margins (Martin & Pullins 2004; Schmidt & Hughes 2006). The present thesis is also the first to report *M. lonae* as a primary host of any *Phengaris* butterflies (I). Moreover, other host ant related factors such as the size of host colonies and their distance to the nearest larval food plant appeared to have a notable effect on the probability of adoption as well as on the survival of caterpillars (II).

The patch occupancy of studied butterflies and their progeny was strongly dependent on environmental context (I, III, IV), with some biotic interactions largely been neglected in the context of habitat use and conservation of butterflies. In particular, the data indicate that predators such as dragonflies could significantly impact population dynamics in low-density small-sized flying species such as *Phengaris* butterflies (I; see also Sang & Teder 2011; Tiitsaar et al 2013). Moreover, this study raises the possibility of interspecific interactions between ants to be an important factor affecting habitat use in the studied butterflies (II, IV). Furthermore, substantial damage to local food plant population indicates that wild herbivore grazing could strongly affect butterfly populations, especially the ones exploiting larval food plants as rare as *G. cruciata* (III).

To my knowledge, this thesis is the first to present concurrent data on distribution patterns in *P. argus* and *P. idas* (IV). The thesis showed these two congeners to be often syntopic suggesting their ecological niches to overlap considerably. The data indicate that specialization to different interspecific associates in these butterflies may have a notable effect on their occurrence probabilities, but does not necessarily have a fundamentally divisive effect on their habitat use, at least at the level of habitat type. Accordingly, habitat heterogeneity combined with ecological and behavioural differences between *Lasius* and *Formica* enable these ants to often share the habitat without competitive exclusion (e.g. Rosengren 1986; Vepsäläinen et al 2007; Collins 2011; Kanizsai et al 2013; Seifert 2017), allowing their mutualist butterflies also to co-occur as demonstrated. The results also confirm the findings of recent studies (e.g. Viljur & Teder 2016) proposing forest clear-cuts to be an important temporary habitat for open-habitat butterflies.

For both practitioners and scientists, several guidelines and suggestions for management of *Phengaris* populations can be derived from this thesis. Most importantly, it is crucial to prevent host plants of *Phengaris* butterflies from becoming overgrown by surrounding vegetation. Indeed, tall, lush plants and bushes either by outcompeting the host plants or by reducing their apparency (detectability), may strongly affect the availability of host plants for ovipositing butterflies (I, III). Overgrown plants providing fewer resources for caterpillars may also reduce their reproductive success (III). Moreover, high vegetation

could be unsuitable for various *Myrmica* host ants as well (e.g. *M. sabuleti* in UK; see Thomas et al 2009). Indeed, *M. schencki*, the sole host ant of *P. alcon* X in our study area (II), has been considered to be one of the most xerothermophilous ant species (Elmes et al 1998). Carefully thought out grazing regime has been suggested as an effective tool to manage *Phengaris* habitats (e.g. Maes et al 2004). Nevertheless, caution must be exercised because of potential direct and indirect negative effects of grazing on the butterflies (III). As showed in our study on oviposition patterns in *P. alcon* X (III), even wild herbivores can cause substantial damage on *G. cruciata* plants. In such cases, temporal and spatial restrictions should be applied on grazing regimes. For more targeted management, mowing and small-scale sod cutting have also been proposed (WallisDeVries 2004). Our results indicate dragonfly predation to be an essential driver of patch occupancy in *Phengaris* butterflies (I). Consequently, top-down effects that have largely been neglected in butterfly conservation, may have to be taken into consideration, particularly in cases of species relocation or reintroduction. As another novel aspect, the results of this thesis suggest that interspecific competition between ants could have a strong influence on host ant availability in myrmecophilous butterflies (II). Therefore, conservation strategies for such species and their respective host ants could also incorporate respective (adverse) management strategies for non-host ant species.

4.6. Recommendations for further research

Number of recommendations for further research can be abstracted from the findings of this thesis. There are still gaps in our regional knowledge concerning ecology and conservation of myrmecophilous butterflies that would benefit from further research:

- 1) Studies to ascertain the use of secondary host ants in *P. arion* and *P. alcon* X. Given the fairly species-rich *Myrmica* fauna in the study areas of both species (which also includes several species used in other regions of Europe; I, II), multiple host ant use of the species cannot be fully excluded.
- 2) As one of the most xerothermophilous *Myrmica* species in Europe (Elmes et al 1998), *M. schencki* is typically associated with low vegetation and bare ground patches (Sielezniew et al 2010b). The results, showing this species to be abundant in relatively high and dense vegetation (II), highlight the need to review habitat requirements of *M. schencki* (and of other *Myrmica* species) in a broader geographical context.
- 3) Quantitative studies on interspecific interactions between *Phengaris*- and *Plebejus*-related ant species with other ants and their influence to butterflies. Our data suggest that competition between ant species could have a notable effect on population dynamics of the butterflies (II). Nevertheless, direct evidence for the link between competition in ants and distribution patterns of myrmecophilous butterflies remains to be found. This could be particularly

important in cases when several species of obligately myrmecophilous butterflies, each adapted to a different host, occupy the same habitat.

- 4) Further studies on top-down effects as potentially important drivers of population dynamics in butterflies. Initial qualitative studies in coastal areas on dragonflies have yielded significant results (Sang & Teder 2011; Tiitsaar et al 2013; I). Nevertheless, more quantitative studies involving inland areas are likely to provide more comprehensive (direct) perspective on this factor.
- 5) Studies on *P. arion* population exclusively exploiting *Origanum vulgare* as the host plant. First population of *P. arion* in Estonia, using *O. vulgare* as a host plant, was discovered in the course of the present studies. As notable differences in various habitat characteristics (e.g. turf height, the absence of *T. serpyllum*) and *Myrmica* fauna were observed, studies on the population that uses *O. vulgare* as a host would considerably contribute to our understanding of host specificity and local specialization in *Phengaris* butterflies.
- 6) More detailed ecological studies on *P. argus* and *P. idas*. Further studies should also provide quantitative assessment of distribution patterns in these butterflies. Additionally, local host plant use of the species needs to be reviewed (IV).
- 7) Further studies to determine the best practices for opening vegetation around butterfly's host plants are recommended. Host ants are a key factor to consider here, their abundance in relation to vegetation height and their response to opening vegetation, in particular (e.g. Thomas et al 2009). Accordingly, optimal mowing or cutting regimes for local *Phengaris* populations should be determined.

SUMMARY

In the present thesis I examined habitat use determinants and distribution patterns in four obligately myrmecophilous Palearctic butterflies – 1) *Phengaris arion* (I); 2) xerophilous ecotype of *P. alcon* (*P. alcon* X hereafter; II, III); 3) *Plebejus argus* (IV) and 4) *P. idas* (IV). A primary focus was on biotic interactions as important determinants of habitat use. The thesis expands the knowledge of geographic variation in habitat requirements in highly vulnerable *Phengaris* butterflies close to their northern distribution margin. A special attention is given to the composition of regional *Myrmica* fauna and host ant use. The thesis also aims to concurrently assess the distribution patterns in two morphologically similar yet ecologically divergent *Plebejus* butterflies.

The data from northern peripheral populations show *P. arion* and *P. alcon* X both to exploit a specific *Myrmica* ant species (I, II). More precisely, all documented *P. arion* caterpillars were limited to the colonies of *M. lonae* (I), while the caterpillars of *P. alcon* X were exclusively found in the colonies of *M. schencki* (II). The thesis is the first to record *M. lonae* as the primary host ant of *P. arion* or any other *Phengaris* butterflies (I). These results explicitly complement the emerging evidence of regional diversity in host ant use in *Phengaris* butterflies. In addition, the findings are consistent with the idea of higher host specificity near species range margins (I, II).

The data indicate that several host ant related factors could have a notable effect on the adoption probability and survival of *P. alcon* X larvae. In particular, larger *Myrmica* colonies that were closer to the host plant had higher probability of being infested (II). Moreover, competition between host and non-host ant species may have a substantial influence on *Phengaris* populations (II).

P. arion was more likely to occupy grasslands with higher host plant coverage, lower turf height and lower dragonfly abundance that were located further away from the sea (I). To my knowledge, this is the first time to demonstrate that predators can affect habitat occupancy patterns in *Phengaris* butterflies (I).

The data on *P. alcon* X indicate that host plant height compared to the surrounding vegetation (i.e. plant apparency) rather than plant height *per se* is the main factor that determines the suitability of particular host plants for oviposition (III). Moreover, more isolated plants had higher probability of being used as hosts. Additionally, the data indicate that grazing of mammalian herbivores could inflict substantial damage to the populations of *P. alcon* X and its larval food plant (III).

P. argus and *P. idas* were found to often share habitats suggesting their ecological niches to overlap considerably (IV). The butterflies were more likely to occur in habitats characterized by more acidic soils, predominantly peat bogs. In forest clear-cuts, both species showed higher occurrence probability in drier habitat patches on more acidic soils. Despite similarities in their general habitat use, the occurrence probability of *P. argus* was found to be invariably higher than that of *P. idas* regardless of habitat types or other factors investigated.

These patterns coincide with the ecological differences between the mutualist ants of *P. argus* nad *P. idas* (*Lasius* and *Formica*, respectively). Also, the data indicate that forest clear-cuts could be an important temporary habitat for myrmecophilous butterflies (IV).

To conclude, novel data derived from these previously unexplored populations in Northern Europe are relevant both at local and broader geographical scales. First, this research improves the fundamental scientific understanding of life history and ecology in myrmecophilous butterflies. Second, the collected data provide a solid framework for developing adequate and meaningful conservation strategies for studied populations.

KOKKUVÕTE

Biotiliste interaktsioonide mõju mürmekofiilsete päevaliblikate elupaigakasutusele Põhja-Euroopas

Oma väitekirjas uurisin biotiliste interaktsioonide mõju nelja obligatoorselt mürmekofiilse (assotsieeruvad mingis eluetapis alati sipelgatega) päevaliblikaliigi elupaiganõudlusele ja levikule. Uuritud liikideks olid nõmme-tähniksinitiib (I), soo-tähniksinitiib (II, III), ogasäär-sinitiib (IV) ja mesika-sinitiib (IV). Doktoritöö esimeseks eesmärgiks oli laiendada olemasolevaid teadmisi ohustatud tähniksinitiibade elupaigakasutuse geograafilise varieeruvuse osas leviku põhjapiiril või selle läheduses paiknevate populatsioonideni. Sealjuures oli peamine rõhk tähniksinitiibade peremehespetsiifilisuse välja selgitamisel. Töö teiseks eesmärgiks oli paralleelselt uurida morfoloogiliselt sarnaste, kuid ökoloogiliselt erinevate ogasäär- ja mesika-sinitiiva elupaigaeelistusi ja levikumustreid.

Kogutud andmestik nõmme- ja soo-tähniksinitiiva põhjapopulatsioonidest näitab, et kumbki liik parasiteerib siin vaid ühel rautsikuliigil (I, II). Täpsemalt dokumenteeriti kõik nõmme-tähniksinitiiva röövikud *Myrmica lonae* ja soo-tähniksinitiiva röövikud häilurautsiku (*M. schencki*) kolooniatest. Käesolev töö on esimene, kus näidatakse, et *M. lonae* võib olla nõmme-tähniksinitiiva (või mistahes tähniksinitiiva) peamiseks peremeheks (I). Tulemused kinnitavad ja täiendavad oluliselt akumuleeruvaid tõendeid tähniksinitiibade regionaalselt laiema peremehekasutuse osas. Lisaks kinnitab mõlema uuritud tähniksinitiiva peremehekasutus hüpoteesi kõrgemast peremehespetsiifilisusest liikide leviku äärealadel (I, II).

Soo-tähniksinitiiva röövikute esinemistõenäosus oli märkimisväärselt kõrgem suuremates ning rööviku toidutaimede (südame-emajuur) isenditele lähemal asuvas rautsikukolooniates (II). Ilmselt on suured kolooniad püsivamad väliste mõjude (kaasaarvatud parasitism) suhtes. Lisaks tõstab suurem tööliissipelgate hulk ning toidutaimede lähedus oluliselt liblikarööviku leidmise tõenäosust. Läbi viidud uuringute tulemused soo-tähniksinitiival viitavad ka sellele, et tähniksinitiibade peremeessipelgate ja mitteperemeessipelgate omavaheline konkurents võib omada potentsiaalselt tugevat mõju tähniksinitiiva röövikute elumusele ja esinemistõenäosusele rautsikukolooniates (II).

Nõmme-tähniksinitiib esines suurema tõenäosusega toidutaimede (nõmm-liiva-tee) kõrgema katvuse, taimestiku madalama kõrguse ja kiilide (*Anisoptera* spp) madalama arvukusega merest kaugemal paiknevatel rohumaadel (I). Taimestiku kõrgus, olles negatiivselt seotud nii toidutaimede kui ka termofiilse peremeessipelga arvukusega, mõjutab seeläbi ilmselt ka liblika esinemist elupaigas. Kiilide negatiivset mõju päevaliblikate arvukusele on uuritud piirkonnas näidatud varemgi, kuid autori teada on käesolev töö esimene, kus demonstreeritakse kiskjate (kiilide) negatiivset mõju tähniksinitiibade esinemistõenäosusele.

Uuring soo-tähniksinitiiva munemispaiga eelistustest näitas, et emasliblika munemisotsuse tegemisel ei ole esmatähtis mitte toidutaimede absoluutne kõrgus,

vaid selle suhteline kõrgus võrreldes ümbritseva taimestikuga (st. taime silmapaistus) (III). Ümbritsevast taimestikust väljaulatuvad toidutaimed on ilmselt munevale liblikale lihtsamini leitavad, kuid tõenäoliselt pakuvad need ka paremat kaitset (isoleeritust) lüljalgsetest röövloomade eest. Munemiseks kasutati suurema tõenäosusega taimeisendeid, mis kasvasid liigikaaslastest kaugemal (olid rohkem isoleeritud). Nimetatud muster võib olla seotud suurest ajastressist tingitud vähese elupaigasise liikuvusega uuritud tähniksinitiival. Lisaks näitavad käesoleva töö tulemused, et taimtoidulised imetajad (näiteks metskits) võivad põhjustada olulist kahju soo-tähniksinitiiva ja tema toidutaime populatsioonidele (III).

Ogasäär- ja mesika-sinitiiva levikumustrid osutusid väga sarnasteks ning liigid jagasid tihti elupaiku. Mõlemad liblikad esinesid suurema tõenäosusega happelise pinnaga niisketel aladel, peamiselt turbarabades. Ka raiesmikele keskendunud uuringuosas leiti, et mõlemad liigid esinesid suurema tõenäosusega happelistel, kuid kuivadel raiesmikel. Vaatamata sarnasele üldisele elupaigakasutusele ja hoolimata uuritud elupaigatüübist ja keskkonnafaktoritest, osutus ogasäär-sinitiiva esinemistõenäosus võrreldes mesika-sinitiivaga märkimisväärselt kõrgemaks. Kirjeldatud muster langeb hästi kokku ogasäär- ja mesika-sinitiiva mutualistidest sipelgate (vastavalt murelased ja kuklased) ökoloogiliste erinevustega. Nimelt on kuklased seotud eelkõige soojade ning kuivade elupaikadega, peamiselt okasmetsadega, kuid laiema ökoloogilise amplituudiga murelasi leidub arvukalt nii liivikutel, niisketel rohumaadel kui ka rabades. Lisaks kinnitavad ogasäär- ja mesika-sinitiival läbiviidud töö tulemused raiesmike olulisust ajutise elupaigana ka sipelgaseoseliste päevaliblikate jaoks.

Käesoleva töö tulemused seni uurimata Põhja-Euroopa populatsioonidest on olulised nii lokaalses kui laiemas kontekstis. Esiteks parandab töö meie alusteaduslikku arusaama mürmekofiilsete päevaliblikate elukäigutunnustest ja ökoloogiast. Teiseks annab kogutud andmestik olulisi teadmisi kohalike populatsioonide kaitseks adekvaatsete looduskaitseliste strateegiate väljatöötamisel.

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PUBLICATIONS

CURRICULUM VITAE

Name: Margus Vilbas
Date of birth: 01.02.1985
Citizenship: Estonian
Current position: University of Tartu, Institute of Ecology and Earth Sciences, PhD student
Contact: Department of Zoology, Institute of Ecology and Earth Sciences, Vanemuise 46, 51014, Tartu, Estonia
E-mail margus85@ut.ee, margusvilbas@gmail.com

Education:
2012– University of Tartu, Doctoral studies in Zoology and Hydrobiology (Zoology)
2010–2012 University of Tartu, MSc Ecology and Biodiversity Conservation
2008–2010 University of Tartu, BSc Ecology and Biodiversity Conservation
2004–2007 Tartu Aviation College, Helicopter piloting (*unfinished*)
2001–2004 Rapla Co-educational Gymnasium
1993–2001 Valgu Elementary School
1992–1993 Eidapere Elementary School

Research interest: butterfly ecology and conservation, myrmecophily

Publications:

- Vilbas M**, Teder T, Tiitsaar A, Kaasik A, Tammaru T, Esperk T (2018) Two obligately myrmecophilous butterflies regularly share habitat despite different host ants. *Manuscript*
- Vilbas M**, Esperk T, Edovald T, Kaasik A & Teder T (2016) Oviposition site selection of the Alcon blue butterfly at the northern range margin. *Journal of Insect Conservation* 20:1059–1067
- Vilbas M**, Esperk T, Teder T (2016) Host ant use of the Alcon blue butterfly at the northern range margin. *Journal of Insect Conservation* 20:879–886
- Vilbas M**, Teder T, Tiitsaar A, Kaasik A & Esperk T (2015) Habitat use of the endangered parasitic butterfly *Phengaris arion* close to its northern distribution limit. *Insect Conservation and Diversity* 8:252–260

Conference presentations:

- Vilbas M**, Teder T, Tiitsaar A, Kaasik A, Tammaru T and Esperk T. Oral presentation ‘Endangered myrmecophiles at the northern range margin: the story of *Phengaris* butterflies’ The Graduate Seminar of Insect Evolutionary Ecology. Vana-Veski, Estonia, 4th to 6th May 2017.

Vilbas M, Teder T, Tiitsaar A, Kaasik A, Tammaru T and Esperk T. Poster presentation 'Habitat requirements of the endangered parasitic butterfly *Phengaris arion* close to the northern distribution limit' The 7th International Conference on the Biology of Butterflies. Turku, Finland, 11th to 14th August 2014.

Vilbas M, Teder T, Tiitsaar A, Kaasik A, Tammaru T and Esperk T. Oral presentation 'Habitat requirements of the endangered parasitic butterfly *Phengaris arion* close to the northern distribution limit' Butterfly Conservation's 7th International Symposium: The ecology and conservation of butterflies and moths. Southampton, United Kingdom, 3rd to 6th April 2014.

Vilbas M, Teder T, Tiitsaar A, Kaasik A, Tammaru T and Esperk T. Poster presentation 'The ecology of *Phengaris arion* in Estonia' Future of butterflies in Europe III. Wageningen, Netherlands, 29th to 31st March 2012.

Dissertations supervised:

Triin Edovald, Master's Degree, 2015, Margus Vilbas, Tiit Teder. Soo-tähtnik-sinitiiva (*Phengaris alcon*) (Lepidoptera: Lycaenidae) munemispäiga valik liigi levila pöhhäpiiril (*Oviposition site selection of Phengaris alcon (Lepidoptera: Lycaenidae) at the species northern range margin*). University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, Department of Zoology.

Ingrid Talgre, Bachelor's Degree, 2013, Tiit Teder, Margus Vilbas. Tähtnik-sinitiibade *Phengaris alcon* ja *P. rebeli* levik ja ököloogia – mida tuleks arvestada liigi kaitse kavandamisel (*Distribution and ecology of Phengaris alcon and P. rebeli – implications for conservation planning*). University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, Department of Zoology

ELULOOKIRJELDUS

Nimi: Margus Vilbas
Sünniaeg: 01.02.1985
Kodakondsus: Estonia
Töökoht: Tartu Ülikool, Ökoloogia ja Maateaduste Instituut, doktorant
Kontakt: Zooloogia osakond, Ökoloogia ja Maateaduste Instituut, Vanemuise 46, 51014, Tartu, Eesti
E-post: margus85@ut.ee, margusvilbas@gmail.com

Haridus:
2012– Tartu Ülikool, Zooloogia ja hüdrobioloogia (Zooloogia), doktoriõpe
2010–2012 Tartu Ülikool, MSc Ökoloogia ja elustiku kaitse
2008–2010 Tartu Ülikool, BSc Ökoloogia ja elustiku kaitse
2004–2007 Lartu Lennukolledž, helikopteri piloteerimine (*lõpetamata*)
2001–2004 Rapla Ühisgümnaasium
1993–2001 Valgu Põhikool
1992–1993 Eidapere Põhikool

Peamised uurimisvaldkonnad:
päevaliblikate ökoloogia ja kaitse, mürmekofiilia

Publikatsioonide loetelu:

- Vilbas M**, Teder T, Tiitsaar A, Kaasik A, Tammaru T, Esperk T (2018) Two obligately myrmecophilous butterflies regularly share habitat despite different host ants. *Viimistlemisjärgus käsikiri*
- Vilbas M**, Esperk T, Edovald T, Kaasik A & Teder T (2016) Oviposition site selection of the Alcon blue butterfly at the northern range margin. *Journal of Insect Conservation* 20:1059–1067
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Konverentsiettekanded:

- Vilbas M**, Teder T, Tiitsaar A, Kaasik A, Tammaru T and Esperk T. Suuline ettekanne 'Endangered myrmecophiles at the northern range margin: the story of *Phengaris* butterflies' teemakoolis The Graduate Seminar of Insect Evolutionary Ecology. Vana-Veski, Eesti, 4.–6. mai 2017.
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Juhendatud väitekirjad:

Triin Edovald, magistrikraad, 2015, Margus Vilbas, Tiit Teder. Soo-tähniksinitiiva (*Phengaris alcon*) (Lepidoptera: Lycaenidae) munemispäiga valik liigi levila põhjapiiril. Tartu Ülikool, Loodus- ja Tehnoloogia teaduskond, Ökoloogia ja Maateaduste Instituut, Zooloogia osakond.

Ingrid Talgre, bakalaureusekraad, 2013, Tiit Teder, Margus Vilbas. Tähniksinitiivade *Phengaris alcon* ja *P. rebeli* levik ja ökoloogia – mida tuleks arvestada liigi kaitse kavandamisel. Tartu Ülikool, Loodus- ja Tehnoloogia teaduskond, Ökoloogia ja Maateaduste Instituut, Zooloogia osakond.

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