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The effects of predation risk and habitat history on butterfly communities

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

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

I. **Sang*, A.** & Teder, T. (2011) Dragonflies cause spatial and temporal heterogeneity in habitat quality for butterflies. *Insect Conservation and Diversity*, **4**, 257–264.

II. **Tiitsaar, A.**, Teder, T. & Kaasik, A. Phenology-based effects of dragonfly predation on butterfly community structure. *Manuscript.*

III. **Sang*, A.**, Teder, T., Helm, A. & Pärtel, M. (2010) Indirect evidence for an extinction debt of grassland butterflies half century after habitat loss. *Biological Conservation*, **143**, 1405–1413.

IV. Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen K.M., **Sang*, A.**, Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters*, **13**, 597–605.

* – Sang is the previous name of the author

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

1. INTRODUCTION

Revealing major biotic and abiotic gradients along which species are spatially distributed is one of the major goals in ecology. The theories of island biogeography (MacArthur & Wilson, 1967) and metapopulation dynamics (Levins, 1969; Hanski, 1999) have provided a coherent conceptual framework for describing species occurrence and persistence with regard to habitat size and its proximity to other habitat patches. At the metacommunity level, these complementary theories predict that species diversity would decline with decreasing area and increasing isolation of habitat fragments. Numerous empirical studies have confirmed these predictions (Holt et al., 1999; Lomolino, 2000). However, describing the whole essence of the habitat is a much more complex challenge, and would unlikely be captured by just habitat area and proximity of habitat patches. This insufficiency is now widely recognized, but going beyond these two variables is often not an easy task to accomplish, primarily due to difficulties in acquiring relevant data. Failure to consider heterogeneity in less obvious habitat variables can seriously impede our understanding of what constitutes a suitable habitat for a species, and may also hinder practical conservation work. In this thesis, population- and community-level consequences of two further habitat characteristics – predation risk and past habitat loss are assessed in butterflies. In spite of the growing awareness of the importance of these parameters in different ecosystems, community-level responses along these gradients, at least in the case of insects, have rarely been addressed in empirical studies and conservation practice.

The poor knowledge of among-habitat variation in natural enemy caused mortality risk is at least partly due to the difficulties of recording and quantifying mortality in natural environments. This is particularly evident in the case of adult predation. The most reliable method – direct observations – is often extremely time-consuming in small mobile organisms. For example, to record an average daily predation rate of 0.2 in a solitary insect, individuals should be tracked for an average of 5 days to observe just a single predation event. On the other hand, the interpretation of various indirect approaches used to quantify mortality is often not straightforward. For example, the frequency of predator-inflicted wing damage used to quantify bird predation (e.g. Brower, 1988; Ide, 2006) is indicative of successful escape from a predator, but cannot be applied to determine actual population loss due to predation (Brakefield et al., 1992). Another frequently used indirect way to draw inferences about adult mortality rates in the field, the mark–recapture method, fails to identify the cause of deaths, and could not satisfactorily distinguish between mortality and emigration.

It is therefore not surprising that practical assessments of habitat quality for herbivorous insects are often based on vegetation cover of the patch, and most importantly, the presence of host plants (Dennis, 2003). However, even though one cannot deny the importance of bottom-up regulation, populations of herbivorous insects are probably even more often regulated by natural enemies, such as predators and parasitoids (Cornell & Hawkins, 1995; Cornell et al., 1998). Natural enemies, being able to cause substantial losses to prey populations (Cornell & Hawkins, 1995; Cornell et al., 1998), have been shown to generate source–sink dynamics (Rosenheim, 2001), and at the extreme, to drive their prey to local extinction (Gibbs, 1998). Despite their pervasive effects on the numbers of herbivorous insects, demonstrations of the predators' impact beyond the population level – species composition and richness of prey communities – are rare (see Parmenter & MacMahon, 1988; Joern, 1992; Östman et al., 2007, for a few exceptions).

Nevertheless, mortality caused by any single type of predator is rarely uniform throughout the season. For example, Remmel et al. (2009; see also Teder et al., 2010) showed that, in boreal forests, bird predation on larvae of folivorous insects in June, during the nestling period of most insectivorous birds is several times higher than e.g. in August. As most predators of insects tend to attack only certain developmental stages of their prey, the period of vulnerability of a single prey species to a particular species or type of predator is typically relatively short. Thus, the impact of a predator on individual prey species will critically depend on the phenological match of the two. In a multispecies prey assemblage, the variability in phenological match of the predator with different prey species provides an opportunity to generate and test qualitative theoretical predictions about predators' impact on community structure.

In addition to present-day habitat variables, historical characteristics of the habitat can influence current species composition. This is because the response of species to habitat change is typically not instant, but rather involves a time lag (called relaxation time; Diamond, 1972). Even if conditions for long-term persistence of a species are not satisfied, local extinctions are generally preceded by a period of decline in population sizes (Hanski & Ovaskainen, 2002). The delayed extinction of species is captured by the concept of extinction debt (Tilman et al., 1994; Hanski & Ovaskainen, 2002; Malanson, 2008; Kuussaari et al., 2009). Rapid changes in human-dominated landscapes and habitats suggest that the presence of extinction debts could be widespread.

Accumulating evidence, indeed, shows that the present-day patterns of species diversity do not necessarily depend on habitat parameters characterizing its current state but may also depend on habitat parameters prior to change (e.g. Cowlishaw, 1999; Lindborg & Eriksson, 2004; Berglund & Jonsson, 2005; Helm et al., 2006; Vellend et al., 2006; Ellis & Coppins, 2007; Gustavsson et al., 2007, Ranius et al., 2008). Although the importance of past habitat availability to current species composition is now widely recognised, supporting empirical evidence is still mostly limited to long-living organisms, vascular plants in particular (see e.g. Cowlishaw, 1999; Lammertink, 2003; Bulman et al., 2007, for a few exceptions). However, time lags to extinction following habitat change are not expected to be uniform among taxa, habitats and landscapes. Species with long lifespan are expected to have a higher probability of showing time-delayed extinctions compared to species with short lifespan (Morris et al., 2008). Species with short generation time and high turnover rate, and those that are highly specialized have been suggested to be most sensitive to environmental changes, and thus have shortest relaxation times (Ovaskainen & Hanski, 2002; Kuussaari et al., 2009). Yet these expectations remain largely unconfirmed by empirical data.

In my thesis, I focused on the role of above indicated aspects in structuring butterfly communities. Butterflies have proved to be a useful model system for various types of ecological and evolutionary research (Watt & Boggs, 2003), and they are without doubt the most important conservation target among insects (New et al., 1995; Dennis, 2010). Although various vertebrate and invertebrate predators are known to kill adult butterflies (e.g. birds, rodents, lizards, wasps, dragonflies, spiders; Brakefield et al., 1992; van Nouhuys & Hanski, 2004; Wiklund et al., 2008 and references therein), spatial and seasonal variation of their impact on butterfly populations in natural environments, and thus their role in determining habitat quality appears to be virtually unknown (Dennis, 2010). The focus here was on predation by dragonflies which, besides birds, are the perhaps most commonly reported predators of adult butterflies (e.g. Larsen, 1981; Alonso-Mejía & Marquez, 1994; Sprandel, 2001; van Nouhuys & Hanski, 2004), but there appears to be no study attempting to assess the spatiotemporal variation in dragonfly predation, and its population- and community-level consequences in butterflies.

As the study system, seminatural calcareous grasslands in Estonia were used for most of the substudies of this thesis. For butterflies, calcareous grasslands rank as the most species-rich habitat in Europe: almost half of all European butterflies have been reported to occur in calcareous grasslands (van Swaay, 2002). However, like in most parts of Europe, calcareous grasslands in Estonia have suffered a rapid decline in area during the last century. Historically large and continuous areas have lost approximately two thirds of their original extent due to changes in agricultural practice (Pärtel et al., 1999). The known extent of historical landscape structure and rapid loss of habitat area during the last 75 years enabled to test if butterflies are showing signs of delayed response to habitat loss. The response of butterfly communities to habitat change was analysed at the regional level (using a network of alvars in Estonia) and the pan-European level.

The objectives of my thesis were to examine the effects of dragonfly predation (**I**, **II**) and habitat history (**III**, **IV**) on butterfly community structure. More specifically, I investigated the spatial and seasonal heterogeneity in dragonfly predation on adult butterflies in natural habitats (**I**), and analysed the patterns of patch occupancy of individual butterfly species with regard to dragonfly abundance in space and time (**II**). The dependence of butterfly species richness on past and current habitat characteristics was explored at a regional and pan-European level (**III**, **IV**).

2. MATERIALS AND METHODS

2.1. Study system

Factors determining species richness of grassland butterflies were examined in Western Estonia – Saaremaa and Muhu islands, and coastal area of the mainland Estonia (c. 58^o N, 22–23' E, **I–IV**). In terms of vegetation, the study area belongs to the boreo-nemoral zone (Sjörs, 1965; Pärtel et al., 1999). The landscape of the two islands is a mosaic, dominated by forests (53% of the total area), while arable lands occupy 10% of the area, and various types of seminatural grassland 18% (Kään, 2002).

The focus of the current study was primarily on alvar grasslands (**I–IV**) – a type of seminatural calcareous grassland characterised by thin soil layer on limestone bedrock (see Pärtel et al., 1999, for detailed habitat description). Dragonfly predation on adult butterflies was examined in 29 grasslands within 2 km from the coastline (**I**, **II**). The grasslands were chosen along the coastline to minimise patch differences in terms of vegetation cover and abiotic conditions. The effect of historical habitat area to current species composition and richness was studied in a set of 36 alvar grasslands scattered over the two islands, and covering a patch area gradient in the study region (**III**, **IV**). The effect of historical habitat area to current butterfly species richness was further analysed on a broader scale, using 147 semi-natural grasslands in five European countries (**IV**; the type of grassland being the same within each country but differing among countries).

2.2. Habitat data

Data on *current areas* of focal grasslands were obtained from a recent inventory of Estonian seminatural communities (2004) and upgraded using orthorectified aerial photographs of the study area (**I–IV**). For the pan-European study, aerial photographs taken between 1999–2007 were used depending on availability at different countries (**IV**). *Current connectivity* of the habitat patches was quantified as the area covered by the same grassland type within a 2 km buffer, including the study patch. The radius of 2 km was chosen for delimiting focal areas, as this corresponds to realistic values of mean lifetime dispersal distances reported for butterflies (e.g. Hanski et al., 2000, 2006). To control for any sea proximity effects (climatic, vegetational, etc.), patch *distance from the sea* was determined (**II**, **III**).

To analyse the response of butterflies to habitat loss, *past area* and *past connectivity* of the studied grasslands were determined on the basis of detailed maps of Estonian vegetation cover in the 1930s (Laasimer, 1965; **III**). The distribution of alvar grasslands at that time corresponded to their distribution and proportion in the landscape that had persisted for centuries (Helm et al., 2006). To quantify past habitat variables in the pan-European study, historical aerial photographs mainly from the 1950s to 1960s were used for all countries (**IV**).

2.3. Biodiversity data

Repeated surveys using standardised transect counts (Pollard & Yates, 1993) were conducted to determine species abundance, composition, and richness of butterflies (**I–IV**; also including burnet moths in **III**, **IV**) and dragonfly abundance (**I**, **II**) in the focal grasslands. Along with recording dragonflies and butterflies during the transect walks, all dragonfly attacks on butterflies were recorded (**I**). For each attack, its outcome (butterfly captured / butterfly escaped), and the species involved were documented. Transect walks were conducted during the active foraging time of the insects. Sites were visited several times over the season so that flight time of most butterfly species was covered (4–5 visits per site per season II–III; 3–7 visits in different countries in the pan-European study – **IV**).

Biodiversity data were collected over three years (2007–2009; in the pan-European study one year per country between 2000–2007). The effect of dragonfly predation was assessed in 2008–2009 (**I**, **II**), and the effect of past habitat variables in 2007–2008 (**III**).

2.4. Focal species

The population-level response of a butterfly species to habitat variables is likely to depend on its habitat breadth. To take this meaningfully into account, butterfly species were classified into subsets of species according to their habitat preference (**II–IV**). Expert opinion and literature were used for this purpose. Three subsets of butterflies were distinguished: (1) *strict specialist species*, i.e. a species depending on the focal grassland type in the study region; (2) *other grassland species*, i.e. all grassland species that are not confined to alvar grasslands; and (3) *other species*, i.e. those not restricted to grasslands, such as habitat generalists, woodland species and migrants. The focus of the Estonian studies was on the first two groups of the species (**II**, **III**). To analyse the effect of predation to butterfly species composition, group (1) and (2) were pooled (**II**). In the pan-European study, the classification followed a somewhat different approach: the focus was on a subset of species dependent (i.e. *strict specialist species* in the previous classification) or clearly favouring the focal grassland type (a subset of the species falling to the group of *other grassland species*).

2.5. Data analyses

Transect data were used to calculate butterfly mortality rate at different dragonfly densities (**I**). As counting butterflies and dragonflies and recording dragonfly attacks on butterflies were made in the same spatiotemporal window, we could calculate comparable estimates of butterfly and dragonfly densities and link them with dragonfly-induced mortality (**I**). Moreover, for each butterfly species, an index describing its phenological match with seasonal variation in dragonfly abundance was calculated. Furthermore, quantifying the spatiotemporal variation in dragonfly predation and life expectancies in butterflies at different dragonfly densities enabled to predict and test the impact of dragonfly predation on butterfly community structure (**II**).

General linear models and Akaike information criteria were used to evaluate the relative contribution of past and current habitat variables to current species richness (**III**, **IV**). To reveal the effect of past and current habitat area on patch occupancy of individual species, species-level logistic regressions were conducted for habitat specialists (**III**). Spatial autocorrelation term was included into the analyses where relevant (**II**, **III**).

3. RESULTS

3.1. Predation risk

Nine transect counts were conducted in 29 focal grasslands over two years to quantify the magnitude and spatio-temporal variation of dragonfly predation risk on adult butterflies and the effect of dragonfly-induced mortality on butterfly populations and community structure (**I**, **II**). Dragonfly densities appeared to be extremely variable spatially. During a single sampling period, dragonfly density could differ two orders of magnitude between different grasslands. Moreover, there was also a high seasonal variation in abundance of these predators: they reached peak densities in June, and then gradually declined towards the end of the season. This seasonal variation in dragonfly abundance largely followed the flight period of the most abundant dragonfly species, *Orthetrum cancellatum* (**I**). Despite the high variation in absolute densities during the season, relative differences in dragonfly density between the sites remained fairly persistent throughout the season within years as well as between the years (**I**).

Over the two field seasons, a total of 86 dragonfly attacks on 14 different butterfly species were observed (**I**). Of these 15% ended with a capture of the butterfly. When dragonfly involved in the attack could be identified (50% of the cases), it was always the most common dragonfly species in our study area, *O. cancellatum*. The average attack rate across the nine sampling rounds over the two field seasons was 1.9 (95% confidence interval: 1.2–3.0) attacks per hour per butterfly, and the average capture rate 0.27 (95% CI: 0.10–0.47) captures per hour per butterfly. This value of capture rate corresponds to an average life expectancy of 3.7 h (CI: 2.1–10.0) during the butterflies' active foraging time. Butterfly attack and capture rate increased with increasing dragonfly density. At dragonfly densities of less than 10 individuals ha^{-1}, no attacks were observed in spite of high sampling effort. At dragonfly densities between 10 and 24.9 individuals ha^{-1}, a butterfly received on average one attack per two hours, which corresponds to a life expectancy estimate of 13 hours during active foraging time. At dragonfly densities above 200 individuals ha^{-1} each butterfly was attacked about 17 times per hour on average, corresponding to an estimated life expectancy of less than an hour (**I**).

Where statistically feasible, logistic regression was conducted to analyse the association between patch occupancy of individual specialist butterfly species and site-specific dragonfly abundance (**II**). In most of the tested species, the probability of a species to be absent in a patch tended to increase with increasing dragonfly abundance (**II**). The parameter estimates of site-specific dragonfly abundance obtained from logistic regression analyses for individual butterfly species were further used as a dependent variable in a weighted least squares regression to examine if they depend on phenological predation risk of butterflies. A significant negative effect suggests that patch occupancy in butterfly species flying at the time of higher overall dragonfly abundance is more sensitive to site differences in dragonfly abundance than patch occupancy in species with less phenological overlap with dragonflies. As a logical follow-up, butterfly communities in dragonfly-rich sites tended to yield fewer species and contain more species flying during off-peak dragonfly abundance (**II**).

3.2. Extinction debt

To evaluate the response of individual butterfly species and butterfly species richness to habitat loss, a series of transect counts were conducted in 36 alvar grassland patches over two years. A total of 68 species of butterflies (approximately 2/3 of the butterfly species recorded in Estonia) and five burnet moth species were recorded in the surveyed grasslands. Twelve of the recorded species (10 butterflies and two burnet moths) were classified as strict habitat specialists, and a further 30 species (28 butterflies and two burnet moths) as other grassland species (**III**).

Current species richness of strict habitat specialists was best explained by the model containing both current and past habitat area as explanatory variables. The models including either past or current area only were less supported. Both variables had a positive effect on current species richness. The lack of correlation between current and past area of surveyed grasslands implies that the effect of the two variables was independent. The sums of Akaike weights across models suggest that the relative importance of current area, past area and patch distance from the sea in explaining current species richness of strict habitat specialists was nearly equal (**III**).

By contrast, no single model received overwhelming support for species richness of other grassland species. Based on model averaging, patch distance from the sea was the most important predictor of species richness of this group. The relative importance of other variables remained substantially lower. The qualitative results of the full general linear models were consistent with the results based on model selection (**III**).

The response of individual species (strict habitat specialists were considered here) to past and current habitat characteristics was not uniform. However, a distinct pattern emerges when classifying species by their habitat area requirements. In particular, six of the twelve strict habitat specialists, showing a tendency to be present in historically larger habitat patches, were those that also require larger habitat patches. The same six species had also a tendency to occur at currently larger habitat patches. No other single functional trait could be used to distinguish species showing signs of extinction debt from other strict habitat specialists (**III**).

An analysis of the response of butterfly species richness to past and current habitat characteristics at pan-European level did not show signs of delayed response over a time frame of 36–49 years of rapid habitat loss. The current patch area was the best predictor of current species richness. Current patch area occurred in the eight best ranked AIC_c models. Past explanatory variables and current landscape area were much less important and showed no relationship with butterfly species richness after considering the effects of all other explanatory variables. Testing each country separately confirmed that current patch area predicts current butterfly species richness best in four of five countries. In case of Estonia none of the explanatory variables could explain a significant proportion of the variation in the species richness of butterflies. By contrast, in four other countries, where the habitat remnants studied were much smaller than in Estonia, current habitat parameters tended to predict current butterfly species richness better than past habitat variables (**IV**).

4. DISCUSSION

The natural enemy induced variation in mortality risk and habitat history have been virtually neglected in explaining butterfly community structure. This thesis shows that the gradients of predation risk and past habitat characteristics can explain a significant amount of variation in patch occupancy patterns of butterflies. Nevertheless, the effect of these variables to different butterfly species and species groups is not uniform, and as such, they act as ecological filters for the butterfly community composition.

The results of this thesis emphasise the importance of considering predation as a component of habitat quality that may strongly affect butterfly populations and shape butterfly communities. Depending on their density, dragonflies can exert a high predation pressure on butterfly populations. In many focal grasslands, adult butterfly life-expectancy was estimated to not exceed a day. The very low life expectancy of adult butterflies at high dragonfly densities, together with a typically several day long maturation time (Scott, 1973; Scott, 1974; Boggs & Freeman, 2005) implies that many individuals die without leaving any offspring. The persistent relative differences in dragonfly abundance between habitat patches suggest that the detrimental impact of dragonfly predation on local butterfly populations is unlikely to be a short-term one in the study area (**I**, **II**). Dragonflies can thus have a profound effect on long-term spatial structure of butterfly populations (and communities), and a potential to form a classic source–sink habitat structure for butterflies (Pulliam, 1988), where populations in sink habitats cannot persist without immigration from source habitats. As the sites in the study region had been selected randomly without prior knowledge of dragonfly densities, high dragonfly predation of adult butterflies is unlikely to be rare in open habitats near water bodies suitable for dragonfly breeding, either in Estonia or elsewhere (*O. cancellatum* is one of the commonest species in most of Europe, breeding in different water bodies; Askew, 2004).

Still, due to a high amplitude seasonal variation in dragonfly abundance, not all butterfly species experience similarly high risk of dragonfly predation. The adult period of most temperate butterflies, i.e. the time when they are vulnerable to dragonfly predation usually has a rather distinct peak of just a couple of weeks. Even though dragonflies were present throughout the sampling season (more than two months) in the study area, their density showed a clear peak in June and subsequent decrease to the beginning of August (**I**). In good correspondence with a priori expectations, the impact of dragonfly predation on the spatial structure of individual butterfly species was seasonally variable and depended on phenological overlap of the predator and the prey. As predicted, spatial patterns of patch occupancy in butterflies flying during peak dragonfly abundance were more affected by dragonfly predation than in species with their adult period having less overlap with dragonfly phenology. As an expected consequence, butterfly species composition in habitat patches with high dragonfly densities tended to show a shift towards a greater proportion of species flying at the time when overall predation pressure exerted by dragonflies was lower (**II**).

The concordance of the observed patterns of patch occupancy of individual butterfly species with the predicted impact of dragonfly predation suggests that the negative correlation between butterfly species richness and site-specific dragonfly abundance reflects a causal association rather than spatial covariation of the two variables with some unmeasured confounding factors. The problems related to inferring causal relationships from observational data were further mitigated by taking into account habitat size and connectivity in the analyses, which have often been shown to affect butterfly species richness (e.g. Öckinger & Smith, 2006; Brückmann et al., 2010). The negative sign of the relationship between dragonfly abundance and butterfly species richness is well consistent with what theory predicts when predation intensity is high and predators nonselective (Hixon, 1986) as was the case in the study area (**I**).

It has been increasingly recognised that, besides current habitat characteristics, the presence of a species in a habitat patch may also depend on its characteristics in the past and the degree of its change. The results of this thesis suggest that the response of butterflies to habitat changes depends on their habitat preference. In particular, the species richness of strict habitat specialist butterflies was best explained by a model containing both current and past area of habitat patches. The independent effect of past habitat area on current species richness of strict specialists is likely to indicate the presence of extinction debt in the surveyed range of grassland sizes. The significant effect of current habitat area, however, indicates a partly paid extinction debt in this group. In contrast to strict habitat specialists, the species richness of other grassland species was related neither to current nor to past area of the alvar grasslands (**III**). The lack of correlation with either current or past habitat parameters implies that the habitat change has not been severe enough to become affecting species richness of this group.

The differential response of habitat specialists and other grassland species to habitat change was in line with the theoretical predictions. Indeed, the group of other grassland species consists of species which are not confined to the focal type of grassland, and is therefore presumably less sensitive to habitat changes than the group of habitat specialists (With & Crist, 1995; Tscharntke et al., 2002; Kuussaari et al., 2009). This differing pattern (**III**) also helps to explain why, in the pan-European study, none of the explanatory variables could explain a significant proportion of the variation in the species richness of butterflies in the Estonian case (**IV**). In particular, besides strict habitat specialists, the focal species group used in the pan-European study included also many species from the group of other grassland species (see above) used in the regional study. By contrast, in four other countries, where the habitat remnants studied were much smaller than in Estonia, current habitat parameters tended to predict current butterfly species richness better than past habitat variables (**IV**). It is plausible that, within the range of grassland areas studied in these countries, relaxation of the butterfly species richness towards a new equilibrium has already occurred.

The patch occupancy patterns of individual species are unavoidably more prone to contain random noise than species richness patterns. Nevertheless, species-specific analyses help to shed light on mechanisms governing the variation in species richness. The data available suggest that, among the group of strict specialist butterflies, species demonstrating signs of extinction debt tend to require larger habitat patches, on average, than do other habitat specialists (**III**). It appears that no other single functional trait could be used to distinguish species showing signs of delayed response to habitat loss from other habitat specialists. Indeed, the species in either group represent a rather broad range of different body sizes, dispersal abilities and population densities (**III**). Neither could the distinction be easily made at the level of larval host plant use, as all strict habitat specialists have rather narrow host range (**III**).

The knowledge gained in this thesis would be useful from the perspective of practical conservation biology. Biodiversity in seminatural grasslands continues to decline in response to habitat loss and degradation. The results of the thesis show that relying on just habitat area and connectivity is necessarily incomplete for doing research with conservation purposes in mind. As this thesis demonstrates, areas otherwise meeting the habitat requirements of a butterfly may appear to be sink habitats when accompanied with high abundance of predators. Obtaining prior knowledge of where and when predators are abundant, and avoiding such sites for butterfly conservation, could sometimes substantially improve the efficiency of butterfly conservation practices. Furthermore, relying only on current habitat parameters is not sufficient to understand species diversity patterns in dynamic, human-affected landscapes. Relaxation to a new equilibrium in species richness may occur after a remarkably long time period even in organisms which are predicted to respond to habitat changes quickly. The reported data on butterflies imply that special attention should here be given to habitat specialists and species with large habitat area requirements, as these are likely to be affected most from habitat loss. On the other hand, long time lags to extinction suggest that early detection of extinction debt may allow sufficient time to facilitate the recovery of such species.

SUMMARY

Revealing major biotic and abiotic gradients along which species are spatially distributed is one of the major goals in ecology. The theories of island biogeography and metapopulation dynamics have provided a coherent conceptual framework for describing species occurrence and persistence with regard to habitat size and its proximity to other habitat patches. However, describing the whole essence of the habitat where a species actually occurs is a much more complex challenge, and would unlikely be captured by just habitat area and proximity of habitat patches. Going beyond these two variables, however, is often not an easy task to accomplish due to difficulties in acquiring relevant data. In this thesis, population- and community-level consequences of two further habitat characteristics – predation risk and past habitat loss are assessed in butterflies. In spite of the growing awareness of the importance of these parameters in different ecosystems, community-level responses along these gradients, at least in the case of insects, have rarely been addressed in empirical studies and conservation practice.

The objectives of my thesis were to examine the effects of dragonfly predation (**I**, **II**) and habitat history (**III**, **IV**) on butterfly community structure. More specifically, I investigated the spatial and seasonal heterogeneity in dragonfly predation on adult butterflies in natural habitats (**I**), and analysed the patterns of patch occupancy of individual butterfly species with regard to dragonfly abundance in space and time (**II**). The known extent of historical landscape structure and rapid loss of habitat area since 1930s enabled to examine the response of butterflies to habitat loss (**III**). These questions were addressed using seminatural calcareous grasslands (alvars) as the study system. Factors determining species richness and composition of grassland butterflies were examined in Western Estonia – Saaremaa and Muhu islands, and coastal area of the mainland Estonia. Like in most parts of Europe, calcareous grasslands in Estonia have suffered a rapid decline in area during the last century. The dependence of butterfly species richness on past and current habitat characteristics was further explored at the pan-European level (**IV**). Repeated surveys using standardised transect counts were conducted to determine species abundance, composition, and richness of butterflies (**I–IV**) and dragonfly abundance (**I**, **II**) in the focal grasslands.

This thesis shows that the gradients of predation risk and past habitat characteristics can explain a significant amount of variation in patch occupancy patterns of butterflies. Nevertheless, the effect of these variables to different butterfly species and species groups is not uniform, and as such, they act as ecological filters for the butterfly community composition. In many focal grasslands, adult butterfly life-expectancy was estimated to not exceed a day. Relatively persistent site differences in dragonfly predation imply that dragonflies may have a profound effect on spatial structure of butterfly populations (and communities; **I**). This suggests that dragonflies can generate substantial

spatiotemporal heterogeneity in habitat quality for butterflies in terms of survival. Indeed, the seasonal and spatial variation in predator density had a measurable effect on butterfly communities. Butterfly communities at predator rich sites were biased toward species flying during off peak dragonfly abundance. As a logical follow-up, butterfly species richness in dragonfly-rich habitat patches was generally lower than in dragonfly-poor patches (**II**).

It has been increasingly recognised that, besides current habitat characteristics, the presence of a species in a habitat patch may also depend on its characteristics in the past and the degree of its change. The results of this thesis suggest that the response of butterflies to habitat changes depends on their habitat preference. The species richness of strict habitat specialist butterflies was best explained by a model containing both current and past area of habitat patches. The independent effect of past and current habitat area on current species richness of strict specialists is likely to indicate the presence of partly paid extinction debt. In contrast to strict habitat specialists, the species richness of other grassland butterflies was related neither to current nor to past area of the alvar grasslands (**III**), indicating that the habitat change has not been severe enough to become affecting species richness of this group. In the pan-European study, in four out of five countries, where the remnants of habitat patches were much smaller than in Estonia, current habitat parameters predicted current butterfly species richness better than past habitat variables (**IV**). It is plausible that, within the range of grassland areas studied in these countries, relaxation of the butterfly species richness towards a new equilibrium has already occurred.

The knowledge gained in this thesis would be useful from the perspective of practical conservation biology. The results of the thesis show that relying on just habitat area and connectivity is necessarily incomplete for doing research with conservation purposes in mind. As this thesis demonstrates, areas otherwise meeting the habitat requirements of a butterfly may appear to be sink habitats when accompanied with high abundance of predators. Obtaining prior knowledge of where and when predators are abundant, and avoiding such sites for butterfly conservation, could sometimes substantially improve the efficiency of butterfly conservation practices. Furthermore, relying only on current habitat parameters is not sufficient to understand species diversity patterns in dynamic, human-affected landscapes. Relaxation to a new equilibrium in species richness may occur after a remarkably long time period even in organisms, which are predicted to respond to habitat changes quickly.

SUMMARY IN ESTONIAN

Kisklusrisk ja elupaiga ajalugu päevaliblikate koosluste mõjutajatena

Ökoloogia üks keskseid ülesandeid on kirjeldada ja seletada liigirikkuse varieeruvuse mustreid. Saarte biogeograafia ja metapopulatsiooniteooria ennustavad, et liigirikkus on seda suurem, mida suuremad on elupaigalaigud ja mida lähemal need asuvad üksteisele. Elupaiga pindala ja sidususega saame kirjeldada siiski vaid osa liigirikkuse varieeruvusest. Liigirikkuse mustrite täpsemaks kirjeldamiseks on vaja arvestada ka teisi elupaiga parameetreid. Lisaparameetrite kaasamine pole sageli aga lihtne ning nõuab spetsiifiliste andmete kogumist või olemasolu. Käesolevas doktoritöös uurisin kahe, sageli raskesti hinnatava elupaigaparameetri, kiskluse (**I**, **II**) ning elupaikade hävimise määra (**III**, **IV**), mõju päevaliblikate populatsioonidele ja kooslustele. Vaatamata sellele, et nende faktorite mõju peetakse liigirikkuse mustrite kujunemisel oluliseks, on vähemasti putukate kohta empiirilist infot looduslikes kooslustes minimaalselt.

Töös keskendusin päevaliblikate liigilise koosseisu ja liigirikkuse mustritele Lääne-Eesti mandriosa ning Saare- ja Muhumaa loopealsetel. Ajalooliselt on need elupaigad püsinud päevaliblikatele sobivaina karjatamise abil, kuid traditsioonilise põllupidamise vähenemise tõttu on nende pindala alates 1930. aastatest võsastumise tõttu kahanenud umbes kolm korda. Konkreetsemalt küsisin, kuivõrd mõjutavad kiilid kui kiskjad päevaliblikate liigirikkuse mustreid (**I**, **II**) ning kas päevaliblikate liigirikkuse tänapäevane muster korreleerub pigem elupaiga tänapäevase või ajaloolise pindalaga (**III**, **IV**). Loopealsete liigilise koosseisu ning liigirikkuse määramiseks kasutasin standardseid päevaliblikate jaoks välja töötatud transektloenduse meetodeid.

Tulemused näitasid, et kiilid on olulised kiskjad päevaliblikatele. Kiilide kõrge arvukus loopealsel lühendas päevaliblikate keskmise oodatava eluea vähem kui ühe päevani. Kisklussurve oli varieeruv nii sesoonselt kui elupaigalaikude vahel. Kiilide arvukus oli kõrgeim juuni keskpaigas ning kahanes siis ühtlaselt augustini. Hoolimata kiilirohkuse sesoonsest varieeruvusest, olid suhtelised erinevused alade vahel üsna püsivad (**I**). Edasised analüüsid näitasid, et selline ruumiliselt ja ajaliselt varieeruv kisklussurve on piisav, et mõjutada mitte ainult päevaliblikate arvukust, vaid ka liigirikkuse mustreid. Nimelt korreleerus kiilide arvukus loopealsel päevaliblikate liigirikkusega. Seejuures puudusid kõrgema kiilide arvukusega loopealsetelt suurema tõenäosusega need päevaliblikaliigid, kelle lennuaeg kattub kiilide arvukuse tippajaga (**II**).

Analüüsimaks päevaliblikate vastust elupaiga pindala kahanemisele, jagati päevaliblikad vastavalt elupaigaeelistustele rühmadesse. Kitsaste elupaigaspetsialistide puhul leiti liigirikkuse korrelatsioon nii elupaiga ajaloolise kui ka tänapäevase pindalaga. Täpsem liigipõhine analüüs näitas, et sellise signaali andsid eelkõige liigid, kes vajavad stabiilse populatsiooni eksisteerimiseks suuremaid elupaigalaike (**III**). Laialt levinud rohumaaliikide puhul sellist seost ei tuvastatud: nende liigirikkus ei korreleerunud tänapäevaste ega ajalooliste elupaiga parameetritega (**III**). Üleeuroopalises uuringus leiti enamiku riikide puhul, et päevaliblikate liigirikkust seletavad eelkõige elupaiga tänapäevased parameetrid (**IV**). Selline seos viitab liigirikkuse kohandumisele uutele elupaigaparameetritele. See ei ole ka üllatav, kuna elupaikade jääkpindala oli neis riikides oluliselt väiksem kui Eesti alade puhul.

Käesoleva töö tulemused on kasulikud ka praktilise looduskaitse vaatenurgast. Doktoritöö tulemused näitavad, et liigile sobiva elupaiga kirjeldamisel tuleb sageli arvestada ka mitmesuguseid varjatud parameetreid. Nagu töö tulemustest nähtub, võib päevaliblikatele muude parameetrite poolest sobiv elupaik osutuda mülkaks, kui seal on kõrge kiskluse tase. Kiirete elupaiga muutuste korral on oluline arvestada väljasuremisvõlaga. Nagu doktoritöö näitab, võib elupaiga parameetrite muutus päevaliblikate liigilises koosseisus kajastuda vägagi pika aja möödudes. Teisalt jätab suhteliselt aeglane vastus elupaiga muutustele aega negatiivsetele tendentsidele reageerida: väljasuremisvõla varases faasis avastamine võimaldab kasutusele võtta meetmed, et taastada liikidele piisav elupaiga pindala nende püsimiseks pikas perspektiivis.

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***

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Sang, A., Teder, T., Helm, A., Pärtel, M. *Extinction debt evident for grassland butterflies half century after habitat loss.* Butterfly Conservation: 6th International Symposium: The 2010 target and beyond for Lepidoptera, Suurbritannia, Reading, 26.–28.03.2010.

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Allar Liiv, magistrikraad, 2011, (juh) Anu Sang, Tiit Teder, Freerk Molleman. *Parasvöötme päevaliblika kaalumuutus ning eluiga looduslikus ja labori keskkonnas.* Tartu Ülikool, Loodus- ja tehnoloogiateaduskond, Ökoloogia ja Maateaduste Instituut, Zooloogia osakond.

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

1. **Toivo Maimets**. Studies of human oncoprotein p53. Tartu, 1991, 96 p.
2. **Enn K. Seppet**. Thyroid state control over energy metabolism, ion transport and contractile functions in rat heart. Tartu, 1991, 135 p.
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