

The range expansion of the European map butterfly in Finland

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Academic dissertation

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ABSTRACT

Climate change will influence the living conditions of all life on Earth. For some species the change in the environmental conditions that has occurred so far has already increased the risk of extinction, and the extinction risk is predicted to increase for large numbers of species in the future. Some species may have time to adapt to the changing environmental conditions, but the rate and magnitude of the change are too great to allow many species to survive via evolutionary changes.

Species' responses to climate change have been documented for some decades. Some groups of species, like many insects, respond readily to changes in temperature conditions and have shifted their distributions northwards to new climatically suitable regions. Such range shifts have been well documented especially in temperate zones. In this context, butterflies have been studied more than any other group of species, partly for the reason that their past geographical ranges are well documented, which facilitates species-climate modelling and other analyses. The aim of the modelling studies is to examine to what extent shifts in species distributions can be explained by climatic and other factors. Models can also be used to predict the future distributions of species.

In this thesis, I have studied the response to climate change of one species of butterfly within one geographically restricted area. The study species, the European map butterfly (*Araschnia levana*), has expanded rapidly northwards in Finland during the last two decades. I used statistical and dynamic modelling approaches in combination with field studies to analyse the effects of climate warming and landscape structure on the expansion. I studied possible role of molecular variation in

phosphoglucose isomerase (PGI), a glycolytic enzyme affecting flight metabolism and thereby flight performance, in the observed expansion of the map butterfly at two separate expansion fronts in Finland.

The expansion rate of the map butterfly was shown to be correlated with the frequency of warmer than average summers during the study period. The result is in line with the greater probability of occurrence of the second generation during warm summers and previous results on this species showing greater mobility of the second than first generation individuals. The results of a field study in this thesis indicated low mobility of the first generation butterflies. Climatic variables alone were not sufficient to explain the observed expansion in Finland. There are also problems in transferring the climate model to new regions from the ones from which data were available to construct the model. The climate model predicted a wider distribution in the south-western part of Finland than what has been observed. Dynamic modelling of the expansion in response to landscape structure suggested that habitat and landscape structure influence the rate of expansion. In southern Finland the landscape structure may have slowed down the expansion rate. The results on PGI suggested that allelic variation in this enzyme may influence flight performance and thereby the rate of expansion. Genetic differences of the populations at the two expansion fronts may explain at least partly the observed differences in the rate of expansion. Individuals with the genotype associated with high flight metabolic rate were most frequent in eastern Finland, where the rate of range expansion has been highest.

SUMMARY

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1. Introduction

The spatial distributions of species are determined by the interplay of various abiotic and biotic factors, mechanisms of population dynamics, and species' life history traits, which themselves are the result of adaptive evolution (Gaston 2003). Changes in these factors may contribute to processes that lead to changes in species' distributions at different spatial scales, including the scale of geographical ranges, via colonization and establishment of new populations beyond the existing distribution as well as extinctions of populations within the current distribution.

Changes in climate have been among the most powerful factors shaping the distributions of species and composition of communities from pre-historical times to the present (Bush & Hooghiemstra 2005; Huntley 2005). Climate and especially the prevailing temperature regime are considered to limit distributions through species' physiological requirements and constraints (Gaston 2003 and references therein). Many climatic variables are however correlated, and the causal factor limiting the range of a particular species may not be easily identified. Moreover, the climate effects are often indirect. Climate may influence other factors such as the distribution of resources or competing species, which may be the true causal factors limiting the distributions of the focal species. The Earth is now experiencing what is believed to be one of the fastest changes in climate for a very long time. The ongoing climate change has induced changes in the biota that have already been detected in all biogeographic regions of the Earth, but which are presently most evident and also best studied in the arctic, boreal and temperate regions, and which are predicted to increase in the number and intensity with irrevocable impacts on ecosystems (Hughes 2000; Thomas *et al.* 2004; Parmesan 2006; IPCC 2007).

Range shifts

Distributional shifts of European butterflies, birds and plants towards northern latitudes and higher elevations on mountains have been detected since the last decades of the 20th century (Marttila *et al.*

1990; Thomas & Lennon 1999; Walther *et al.* 2002; Parmesan 2003; 2006; Parmesan & Yohe 2003; Brommer 2004; Hannah *et al.* 2005; Lenoir *et al.* 2008). Similar changes are apparent in temperate regions in North America (Parmesan 2003; Crozier 2004; Zuckenberg *et al.* 2009). In northern Europe the rate of northward expansion of butterflies has been a striking phenomenon. In Finland, many new butterfly species from central Europe have colonized the country since the late 20th century and their northward expansion continues with rates highest ever reported for butterflies (Pöyry *et al.* 2009). One of these rapidly expanding species in Finland is the European map butterfly (*Araschnia levana*), the focal species of this thesis.

Expansion at the northern range boundary and extinctions at the southern edge of the distribution, causing retraction of the southern range boundary, are referred to as a *range shift*. Expansions without simultaneous retraction of the southern distribution are often called range shifts as well, though the term (northward) expansion might be more appropriate in this case. The length of time in a range shift to include both expansion and retraction may be rather long, and the expansion and retraction do not need to occur concurrently (Thomas *et al.* 2006). The specific climatic factors inducing species' expansion and retraction are diverse, and the climatic conditions at the northern and southern range boundaries of a species may not change in a coherent manner or at similar rates. Extinctions have been best documented at the lower elevational limits in montane regions. An example is the Edith's checkerspot butterfly (*Euphydryas editha*) in western North America, with >40% of populations at 0-2400 m elevations having gone extinct (Parmesan 1996). At the southern range limits, the last surviving populations of the Edith's checkerspot occur at highest elevations, where the climate has not yet become too warm for the species. In Europe, population extinctions at lower elevations and colonisations at higher elevations have been reported for butterflies and amphibians (Konvicka *et al.* 2003; Thomas *et al.* 2006).

Other responses to climate change

In addition to distributional changes, climate change may lead to plastic physiological and phenological changes (Hughes 2000). Such changes have been detected in several groups of species and in many biomes. Well-documented phenological changes include advanced or delayed flowering of plants (Menzel & Fabian 1999; Cleland *et al.* 2006), advanced arrival of migratory birds (Ahola *et al.* 2004), and the first appearance of butterflies in the spring (Roy & Sparks 2000; Stefanescu *et al.* 2003).

Another possible response to climate change is genetic adaptation. Again studies on butterflies provide some of the best examples. Thomas *et al.* (2001) reported a change of host plant preference in the brown argus butterfly (*Aricia agestis*) expanding its range in the U.K. In the northern parts of its range, *A. agestis* was previously restricted to only one host plant species, *Helianthemum chamaecistus*, growing in chalk and limestone grasslands, but at the southern parts of its range it used more frequently *Geranium* and *Erodium* species, which are more widespread and occupy a wider range of habitat types than *H. chamaecistus*. Between the two study periods 1970-1982 and 1995-1999, the brown argus butterfly had expanded northwards and the females at the northern expansion front had changed their preference and started to lay eggs on *Geranium* (specifically *G. molle*). The host plant choice was confirmed to be genetically determined by comparing the preference of butterflies of different origin in common garden experiments. The change in host plant preference is considered to be a consequence of increasing temperatures. The previously preferred host *H. chamaecistus* grows on sheltered and warm southerly-facing hillsides, but with increasing temperatures at the northern range boundary, *A. agestis* is no longer restricted to only these habitats and it has been able to switch to use the more common species, *G. molle*, in other habitats.

Adaptation may help some species to adjust to climate change, but in general the rate of climate change is so high and the changes are so great that it is doubtful whether many species are able to adapt fast enough (Visser 2008). Adaptation would require microevolutionary changes in the reaction norms, because the past environmental cues for reaction norms controlling phenotypic plasticity may no longer function under altered climatic conditions. Visser (2008) uses an example of optimal egg laying date, for which spring temperatures may be used as a proximate cue determining the peak in food abundance. The cue is not useful if the correlation between it and the environmental variable that

determines selection no longer holds. In these cases the cue can no longer predict the future. Climate change may reduce the correlations between the cue and the relevant environmental factors. Thus, when a certain spring temperature previously predicted a food peak in 30 days, the food peak may now occur in 20 days. Another consideration about the possibility of adaptive evolution is the reduced genetic diversity in a broad range of species that have been adversely affected by human land use and other factors. Other things being equal, reduced genetic diversity means reduced opportunities for evolutionary change.

Many studies on the biological consequences of climate change are focused on responses to temperature. Although temperature is often used as an explanatory variable in modelling studies and many species indeed respond to changes in temperature, it should be kept in mind that temperature is not the driving factor in all climate-induced responses. The factor actually causing the response may be correlated with temperature, which may lead to a positive association between temperature and the response variable, which is often just the occurrence of the species in modelling studies. Another possible complication is that other climatic variables may induce a response that is opposite to what is expected in response to elevated temperature. This kind of situation was observed in a study of the responses of grassland plant species to climate change, where atmospheric CO₂ and N delayed flowering, whereas an advance in flowering would have been expected based on the change in temperature alone (Cleland *et al.* 2006). In many cases the responses of plants to climate change determine the occurrence and distribution of the herbivores dependent on them. For instance, a change in rainfall causing deterioration or withering of a host plant may cause the regional extinction of a butterfly species specialized to use it. To return back to temperature, changes in the average temperature, which is the usual climatic variable in species-climate models, is often not likely to be the causal factor. Responses occur when temperature thresholds in particular life history stages that are critical to development or survival are exceeded or when the required temperature level is not reached. Changes in temperature may also occur in relation to seasonality. An example that is particularly relevant for this thesis concerns larval development times in butterflies and in insects in general. Development times are reduced with increasing temperature, and thereby with increasing temperature there may be time for two generations to develop during one summer. It has been suggested that such bivoltinism will extend further north in response to climate change (Bryant *et al.* 2002).

Another important issue is the spatial scale of the environmental change. The temperatures experienced by individuals in local populations may vary greatly from population to population and be weakly correlated with changes in regional average temperatures. Furthermore, there may be substantial variation in the temperatures experienced by individuals in the same population but occurring in different microhabitats. A study about the larval microhabitat selection in the butterfly *Parnassius apollo* in the mountains of Sierra de Guadarrama, central Spain, showed that the association of larvae with a certain type of microhabitat was dependent on elevation (Ashton *et al.* 2009). At higher elevations, the larvae were found to favour warmer microhabitats such as bare ground or dead vegetation, while at lower elevations they favoured cooler microhabitats with higher vegetation. The choice of microhabitat was used as a means of thermoregulation. The host plant availability in Sierra de Guadarrama varies in different elevations and the larvae may use different species of *Sedum* spp. in different microhabitats. The authors concluded that the importance of thermoregulation via microhabitat selection may become more important with climate change, and that habitat heterogeneity may buffer populations against climate change induced changes in host plant availability.

Other environmental changes may counteract the consequences of climate change and modify environmental conditions in different microhabitats. Wallisdevries and Van Swaay (2006) studied the decline in widespread European butterfly species with the hypothesis that the decline would be caused by cooling of microhabitats. Such cooling was expected to happen in the spring due to advanced plant growth in response to climate change, with increased nitrogen deposition further boosting plant growth. Microhabitats with high vegetation are cooler than those with short vegetation. Wallisdevries and Van Swaay (2006) analysed data for 79 butterfly species and found that nitrogen deposition, average temperature and the stage of hibernation of the species contributed to the statistical model explaining the observed decline in the species. The observed decline has been greater in species that overwinter at the egg or larval stages and are therefore dependent on warm microclimates in the spring for larval development.

Responses are species specific

As the examples above have demonstrated, the responses to climate change are often likely to be species specific. Here I will discuss two particular

traits of species, the degree of habitat specialization and mobility, which have been shown to have a substantial influence on species' responses to climate change. Human land use and other activities have caused widespread habitat fragmentation and deterioration that poses a threat to very large numbers of species. Climate change together with habitat destruction is expected to increase the extinction rate in many taxa during this century (Thomas *et al.* 2004; Hannah *et al.* 2005; Hanski 2005). Species that are under the greatest pressure due to the interaction of these two factors are the ones that are already rare or endangered as a result of habitat fragmentation (Warren *et al.* 2001). Thus species specialized to use very restricted habitat types, or a single host plant as is often the case in butterflies, are unable to move to new climatically suitable areas beyond their current range if the distribution of the habitat or host plant is highly fragmented. This is likely to be case for large numbers of species, as the vast majority of species especially in the urbanized temperate regions suffer from habitat fragmentation (Hanski 2005). Generalist species have a wider choice of habitats and they are expected to be better able to track the changing climate. However, even generalist species depend on their ability to move to new areas. Therefore the dispersal range of a species is a key characteristic in the context of range expansion in response to climate change and other environmental changes. Unsuitable habitat, such as large water bodies, may constitute a dispersal barrier preventing expansion. In butterflies, habitat specialists with poor dispersal capacity are the ones that are most vulnerable to climate change and simultaneous habitat fragmentation (Hill *et al.* 1999b; Warren *et al.* 2001; Pöyry *et al.* 2009).

Considering those species that are able to keep up with the rate of climate change, enhanced dispersal at the expanding range margin may be selected for, because the most dispersive individuals are most likely to establish new populations beyond the current range boundary. In this case, the dispersal capacity of individuals at the range margin will become greater than that of individuals in populations at the core of the range, which may further accelerate the expansion. A few studies have reported results that indicate such changes (Hill *et al.* 1999a; Hughes *et al.* 2003; Simmons & Thomas 2004; Phillips *et al.* 2006). In the speckled wood butterfly (*Pararge aegeria*), studies have demonstrated differences in the morphology of individuals between the populations in the range margin and in the core areas of the distribution, and these morphological differences are assumed to be associated with differences in dispersal rate (Hill *et al.* 1999a; Hughes *et al.* 2003). However, empirical results concerning

the relationship between morphology and flight performance are often indirect. Part of the difficulty of relating morphology to flight performance and dispersal capacity results from the fact that flight in butterflies has many different functions (Van Dyck & Matthysen 1999; Watt 2003). For instance, wing morphology may allow high flight performance in terms of acceleration capacity, which is critical for males chasing females. Measurements of the flight acceleration capacity in *Pararge aegeria* suggest that in this species flight morphology is of importance for mate-locating behaviour (Berwaerts *et al.* 2002). A morphometric measure called the aspect ratio (related to wing shape) was found to correlate with the acceleration capacity only in males. Males had higher aspect ratios than females. High aspect ratio corresponds to longer and more slender forewings which improve the flight performance in terms of higher acceleration capacity. On the other hand, low aspect ratio may be connected to slow agile flight (Hill *et al.* 1999a and references therein). Berwaerts *et al.* (2002) studied also another morphometric trait, the wing loading ratio (total body mass/forewing area), expecting a positive relationship with flight performance, again in terms of acceleration capacity, and a stronger relationship in males than females. This hypothesis was supported. The relationships between flight morphology and other aspects of flight, such as flight endurance or flight speed, have been more difficult to establish. They are affected by various factors such as the different ecological role and behaviour of the sexes or the type of mate locating behaviour in males (Berwaerts *et al.* 2002; Van Dyck 2003). Female flight for instance is affected by the abdomen mass, which in turn depends on the egg load and varies through the lifespan of the female as a result of egg laying (Berwaerts *et al.* 2002 and references therein). In *P. aegeria* females are considered to be the dispersive sex (Merckx & Van Dyck 2006). The morphological differences in the individuals between the populations at the core and the margin of the range demonstrated by Hill *et al.* (1999a) were more evident in females.

Measuring long-distance dispersal in butterflies is difficult and the results of mark-release-recapture studies often underestimate the dispersal distances because of small spatial scale in the study (Schneider 2003). Studying dispersal is also complicated by the fact that dispersal is often not only dependent on capacity in terms of flight ability but also on behaviour, which may be influenced by sex, as discussed above, but also by landscape. Merckx and Van Dyck (2007) tested the orientation ability of *P. aegeria* originating from different habitats. They collected males from fragmented agricultural habitat

and continuous woodland habitat and released them from distances of 25 to 200 meters to forested habitat in an open agricultural landscape in the field. They predicted the butterflies from fragmented habitats to have better orientation ability. Forest is the primary habitat of the speckled wood butterfly and in the fragmented habitats better orientation ability may be selected for, as it will reduce the time the individuals spend in the matrix. The results were in line with the hypothesis; the individuals from fragmented agricultural habitat were better able to orient to forested habitat at greater distance than the butterflies from continuous woodland habitat. Merckx and Van Dyck (2007) suggest a more complete experimental set-up to confirm the interpretations. An earlier study by Merckx *et al.* (2003) compared the behaviour at boundaries in speckled wood butterfly originating from woodland and agricultural habitats. In this experiment the behaviour of laboratory-reared individuals was studied in outdoor cages containing both shaded and open habitat. The butterflies of woodland origin were found to cross the open-shade boundaries more often than the butterflies originating from agricultural habitat. The results suggest that flight behaviour in *P. aegeria* has a heritable component which is affected by the landscape of origin (Merckx *et al.* 2003). However, Merckx *et al.* (2003) emphasize that a straightforward connection between behaviour at boundaries and dispersal capacity has yet not been established. The behaviour at boundaries is related to dispersal propensity, but not necessarily to the dispersal distances covered by the species. Apart from morphology and behaviour discussed above, flight and dispersal in butterflies are related also to other factors, such as flight metabolism (Niitepõld *et al.* 2009).

One of the projects in this thesis examined variation in the metabolic enzyme phosphoglucose isomerase (PGI) in different populations and in relation to flight metabolism. The pioneering studies by Ward Watt (Watt 1983; Watt *et al.* 1983; 1985; 1996) established a relationship between molecular variation in *Pgi* and flight performance in *Colias* butterflies. More recently, comparable results have been found for another butterfly species, the Glanville fritillary butterfly (*Melitaea cinxia*) (Haag *et al.* 2005; Hanski & Saccheri 2006; Saastamoinen & Hanski 2008; Niitepõld *et al.* 2009). The PGI enzyme is involved in energy metabolism and the gene *Pgi* encoding for the enzyme is therefore a good candidate for a gene with great functional significance for flight performance. PGI is an enzyme of the glycolytic pathway catalyzing the conversion of glucose-6-phosphate to fructose-6-phosphate and vice versa. In glycolysis, ATP, the energy source needed for

flight and other functions, is produced. Watt *et al.* (1983) have shown for *Colias* that different *Pgi* genotypes have different metabolic characteristics, and butterflies with different *Pgi* genotypes show variation in their flight performance and fitness that is considered to be related to the differential functioning of the different isoforms of the PGI enzyme. In particular, Watt *et al.* (1983) have found that the kinetically fastest PGI isoforms are superior in their capacity to sustain flight in temperatures below the optimal body temperature. The results on *Melitaea cinxia* additionally link molecular variation in the *Pgi* gene to flight metabolic rate (Haag *et al.* 2005) and to dispersal capacity in the field (Niitepöld *et al.* 2009). Moreover, in the large metapopulation of *M. cinxia* in the Åland Islands in Finland individuals originating from newly-established populations were found to have higher flight metabolic rate than individuals originating from old populations, and the kinetically superior *Pgi* genotype (called *Pgi-f*) was more common in the newly-established populations. Saastamoinen (2007) and Saastamoinen and Hanski (2008) have demonstrated a connection between the *Pgi* genotype and fitness in *M. cinxia*. Females with the *Pgi-f* genotype produced larger egg-clutches than the other females, at least partly because the *Pgi-f* females were able to initiate egg-laying in lower ambient temperatures, earlier in the day, than the other females.

Studying range shifts in butterflies

In this introduction, I have discussed some responses of species to climate change and especially those factors that influence a particular response, range shift, in butterflies. What is the motivation to study range shifts in response to climate change in general and in butterflies in particular? The above examples provide partial answers, but in conclusion I add some further arguments. First of all, studying range shifts in butterflies is easier than in many other taxa, because butterflies comprise a well-known group and generally their responses to climate are detected without long time lags. Distributional changes are easy to detect in species that are clearly visible, readily identified, and carefully monitored. Butterflies fulfil all these requirements, and have consequently been widely used in studies of distributional shifts in response to climate change. Owing to their fast life cycle and often multiple generations per year, the responses of butterflies are rapid in comparison with many other well-known groups of animals, such as mammals and birds. Being poikilothermic organisms butterflies are sensitive to changes in temperature, and hence a correlative approach to study the relationships with

climatic variables can be expected to be successful (Parmesan 2003). An additional advantage of butterflies is that in general they are rather easy to rear, which facilitates experimental studies.

Studies on butterfly range shifts will provide (and have already provided) information on the direction and magnitude of the kind of changes that can be expected to occur in other species as well. Research results on butterflies have been among the first ones to inform the general public and policy makers on what kind of changes climate change is likely to induce. Studies on butterfly range shifts have helped in developing modelling methods and in recognizing deficiencies in the existing methods. These studies have also revealed how other factors apart from the climate may influence range shifts. Understanding of range shifts based on studies of butterflies can be applied while designing networks of protected areas.

The development of geographic information systems (GIS) has enabled modelling studies based on the use of spatially referenced data (Kivinen 2007, and references therein). At the same time, the statistical methods of relating species occurrence to environmental variables in the spatial context have advanced greatly and become widely used in studies predicting the species distributions based on environmental surrogates. These modelling methods are widely used especially in studies concerning the influence of environmental change on species distributions and in conservation applications, e.g. in reserve selection (Guisan & Zimmermann 2000). Correlative statistical methods like Generalized Linear Models (GLMs), Generalized Additive Models (GAMs), Classification Tree Analysis (CTA), Artificial Neural Networks (ANN), and some specific software like CLIMEX, BIOCLIM, and GARP are tools for making predictions about species' distributions (Elith *et al.* 2006; Heikkinen *et al.* 2006; Vanhanen *et al.* 2007). Using the predictions of climate models one can extend the predictions about species' occurrence in relation to climate to the future.

Species-climate models, which are also referred to as climate envelope models, have been criticised for producing overly optimistic predictions about the occurrence of species (Pearson & Dawson 2004). This is likely to be often true, because these models do not take into account many of the other factors influencing the distribution of species and their opportunities to disperse to new areas. Therefore, to gain better understanding of the process of range expansion, other than static modelling approaches are also needed. Dynamic simulation methods can be used to model population dynamics in a spatially explicit context (see e.g. Hill *et al.* 2001). In the past,

the correlative modelling methods such as climate-envelope models and simulation models have been applied to different spatial scales. There is now a need to develop large-scale simulation models that are nonetheless based on individual-level processes. Even then, there are other factors that may often influence range expansion but are difficult to incorporate in models. For instance, interspecific interactions may hinder range expansion, and changes in habitat quality may either facilitate or hinder expansion. Land cover variables have been used in some models with climatic variables (see e.g. Kivinen 2007), but often the climatic variables and the land cover variables influence at different scales, and the model predictions are improved only when using scales that are relevant for both types of variables (Heikkinen *et al.* 2006; Luoto *et al.* 2007). Predictions made with different modelling approaches vary often greatly (Lawler *et al.* 2006), and it is important to remember that the model predictions can only be as reliable as the data used to build the models (Lobo 2008). The modelling results are naturally dependent on the explanatory variables, and the various methods of variable selection are one source of uncertainty for model predictions (Heikkinen *et al.* 2006 and references therein). An issue related to model accuracy is that the performance of the models may be evaluated too high because of the problems of model validation. In most cases there is no independent data available and the model validation is done with approaches like resubstitution and data splitting, where the same data is used for both model calibrating and model evaluation (Araújo *et al.* 2005).

It would probably be an overly challenging task to identify all the factors and processes influencing the distribution of even one particular species and to evaluate the role and importance of each of them individually. In this study, I use the European map butterfly (*Araschnia levana*) as a model species of butterfly expansion in response to climate change in the northern temperate region. My aim is to study some of the factors that are often assumed to influence the distributional changes of species within a restricted region (Finland) during a 30-year period, to build better understanding of the roles of selected key factors in a climate-driven range expansion.

2. Specific aims of this thesis

The specific aims of this project are:

1. To analyse the roles of the likely key factors, climate and spatial configuration of habitat, in the observed range expansion of the map butterfly in Finland.
2. To identify possible additional factors, especially genetic variation in the metabolic enzyme PGI and its influence on flight performance, which may also affect range expansion.
3. To apply Generalized Additive Models (GAMs) to study the effects of climate and habitat on species distributions and to apply a spatially explicit simulation model to study the effect of landscape structure on the expansion.

The individual projects in this thesis were conducted on spatial scales that were considered appropriate for the particular factors. Thus the climate-model predictions (I) were made at the scale of Europe and Finland, molecular variation in the *Pgi* gene (II) was studied in two regions in Finland and compared with results for a study area in Estonia, whereas habitat preference (III) and the effect of landscape structure on the expansion (IV) were examined at local and regional scales (Fig. 1). Field experiments (III) were conducted to gain information about the biology of the species, habitat selection and spatial population structure at local scale.

3. Material and methods

The European map butterfly

The European map butterfly (*Araschnia levana*) was selected as the focal species for this project based on its observed rapid northwards expansion in Finland and for several other characteristics of the species that make it a convenient study object. Shapiro (1976) noted a long time ago the potential of the map butterfly as a study organism, and proposed that this species would be used to study the relationships between physiology, environment, genetics, and natural selection. Indeed, the map butterfly is an interesting species for several reasons, and it turned out to be a good choice for this project. Here I shortly introduce the species and discuss the reasons for selecting it for this study.

The European map butterfly has expanded its range in Europe rapidly since the late 20th century. According to Kudrna (2002), its distribution in Europe encompasses the central and western European countries excluding the U.K. In southern Europe the species is found in northern Spain as well as in northern Greece. The eastern European distribution in Kudrna's butterfly atlas (2002) has



Fig. 1. An illustration of the spatial scales at which individual studies (I to IV) in this thesis were conducted. (a) The species-climate model (I) was calibrated at the European scale (0.5° N x 1.0° E) and the prediction was transferred to Finland (10×10 km squares). The figure also illustrates the distribution of the map butterfly in Europe during the period 1950-1995. (b) The distribution of the map butterfly in Finland in 2008 and the simulation study (IV) areas of 160×160 km and 160×80 km at the eastern and southern expansion fronts, respectively. (c) The mark-release-recapture study (III) was conducted in the Kiteenlahti (3×5 km) region at the scale of 0.2×0.2 km grid cells.

gaps in data (based on information from other sources, mentioned in Chapter I and in the Section *Distributional data* below), but the atlas shows that the distribution extends to areas further east in Russia (Fig. 1). According to Reinhardt (1972), the geographical distribution of the genus *Araschnia* with seven species extends to Russian Far East and Japan in the east. During the last few decades the European map butterfly has expanded towards west and north in Europe (Radigue 1994; Parmesan 2001; Bolotov & Shutova 2006; Öckinger *et al.* 2006). Information about possible expansion in the other parts of the species' wide geographical range was not searched as this study is focused on the expansion in northern Europe.

Parmesan (2003) considers the European map butterfly to be an example of somewhat controversial species in terms of whether the expansion is only driven by climate change. She suggests that the observed rapid expansion at the northern range boundary of the species is climate-driven, but the map butterfly has also expanded towards south in the

Pyrenees in Spain, which is probably caused by other factors than climate.

The map butterfly is a well-studied species, but the previous studies have been mostly concerned with seasonal polyphenism and colour polymorphism and their regulation (Reinhardt 1972; Koch & Bückmann 1987; Windig & Lammar 1999). In most parts of its range, there are two generations per year, and the spring and summer generations have strikingly different appearances. The spring generation butterflies are orange with black markings, whereas the second generation butterflies, flying in late summer, are black with white stripes on the upper wings, resembling the White admiral (*Limenitis camilla*) (Fig. 2). Polyphenism is controlled by day length and temperature (Windig & Lammar 1999; Gilbert 2001). In central Europe, a third generation is common, and it closely resembles the second generation in appearance. The European map butterfly has been named based on the map-like patterns on the undersides of its wings (Fig. 3).

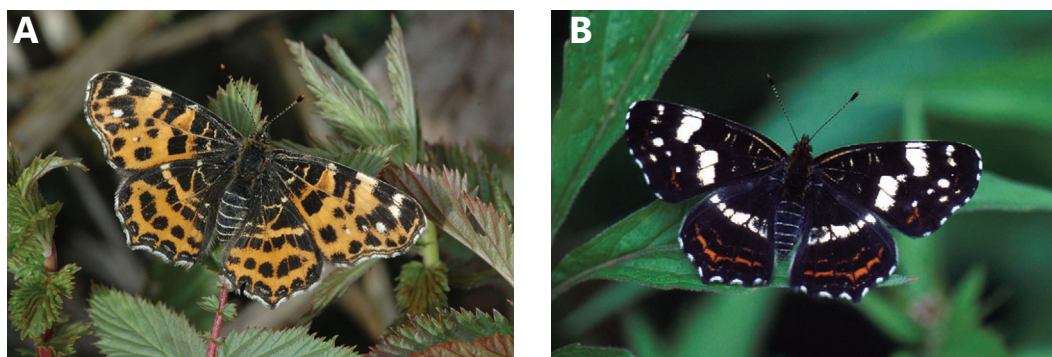


Fig. 2. The two generations of the European map butterfly have very different phenotypes in terms of wing colouration. Panel (a) shows the first (spring) generation butterfly (female) and (b) the second (summer) generation butterfly (female). Photos by Juha Sormunen and Tari Haahtela, respectively.

In Finland, the spring generation occurs from the end of April until the end of June depending on the region, while the second generation ecloses from the beginning of July onwards and occurs until the end of August. The over-wintering stage is the pupa. The host plant is the common nettle (*Urtica dioica*), which is distributed throughout Finland in appropriate habitats. It has been suggested that the map butterfly may use also *Urtica urens* and *Humulus lupulus* as larval host plants (Reinhardt 1972), but there are no such observations from Finland. Females lay eggs in clusters that are actually turrets or chains of eggs one on top of each other, typically including about 20 eggs each. The egg chains are laid on the underside of nettle leaves and they resemble the nettle inflorescences. This form of egg clusters is unique to the genus *Araschnia* (Ruf 2002). The larvae live gregariously through three instars. The 4th instar groups are smaller than the groups of smaller larvae, and the 5th instar larvae develop individually before they pupate to a nettle branch (Ruf 2002). The map butterfly larvae can be identified from other butterfly larvae living on nettles based on the conspicuous horns that they have in the head capsule (Fig. 4). The pupal development time is about one week between the spring and the summer generations. The second generation pupae enter winter diapause. A part of the first generation offspring reared in captivity during this project entered diapause and successfully eclosed in the following spring. The Finnish populations have a single generation, partial second generation or two generations depending on the region and time period.

The preferred habitats of the map butterfly are forest edges adjoining meadows and openings in mixed and deciduous forests, edges of pastures and other half-open habitats often situated close to a body of water, e.g. banks of rivers with lush vegetation. Trees

and forest edges are probably important because the butterflies often fly into the canopy. Males typically perch on nectar plants near nettle plants and take off to chase passing females.

Distributional data

The distributional data at the European scale in Chapter I was extracted from Kudrna (2002), supplemented for eastern Europe with data from other sources (Keskula 1992; Ivanov 1999; Dovgailo *et al.* 2003; Popov 2005; and pers. comm. with Gorbach, Humala and Tammaru 2005). The spatial resolution of the data is 0.5° N x 1° E (Fig. 1). Records made since 1950 were included in the analysis.

The Finnish distribution of the map butterfly was reconstructed based on the records of the National



Fig. 3. The European map butterfly has been named based on the map-like patterns of the underside of the wing. Photo by Juha Sormunen.



Fig. 4. A larva of the map butterfly on the common nettle. The larva can be distinguished from other caterpillars using nettle based on the horns in the head capsule.

Butterfly Recording Scheme (NAFI), available from 1991 onwards. The NAFI data are recorded in 10 x 10 km grid cells, they are collected every year from the voluntary lepidopterists, and they include information on recording intensity (the number of times each grid cell was visited; Saarinen 2003). The NAFI data comprise altogether 1931 10 x 10 km grid cells in the period 1991-2008. The average annual numbers of recording forms returned, recording days, grid cells visited, and species and butterfly individuals are 659, 5764, 461, 99.5 and 189803, respectively (Anon 2009). The NAFI data were supplemented with pre-1991 records collected by the Finnish Lepidopterological Society and additional records received from individual voluntary amateur and professional lepidopterists. The combination of all these data were used in the climate-envelope modelling in Chapter I and more generally to describe the expansion history (IV).

Field studies

Empirical studies were conducted in the field (mark-release-recapture study) and in semi-natural conditions in a large population cage. In these studies, I obtained data on the life history, habitat selection and flight behaviour of the map butterfly. Additional field work included collection of material (larvae and adult butterflies) for the population cage experiment and for laboratory analyses described in the next section.

The mark-release-recapture (MRR) study was conducted during the flight season of the spring generation in 2004, in the Kiteenlahti region in eastern Finland, about 100 km southwest from the site where the expansion to Finland started in 1983 (Fig. 1). The MRR study was carried out to gain information on habitat selection and dispersal distances in the field, to be used in the modelling

studies (III, IV). Additionally, this study provided general information on the biology of the species, such as the egg-laying behaviour of females.

The population cage experiments were conducted at the Tvärminne Zoological Station in southwestern Finland in 2004 and 2005 to collect data on the movement behaviour and reproduction of the second-generation map butterflies. The population cage (30 x 26 x 2 m) is covered with a mesh that allows natural environmental conditions inside the cage and represents natural habitat for the map butterfly, with the exception that there were no trees (for a description of the cage see (for a description of the cage see Hanski *et al.* 2006). The cage had planted nettles as oviposition host plants for females. To obtain butterflies for the experiments, first-generation progeny were collected in the field as larvae from several localities in Finland in 2004 and from several localities in Finland and Estonia in 2005. Following the eclosion of the butterflies in July-August they were marked and released into the cage. Systematic transect lines were walked along three times per day to record the activity of butterflies and to locate matings and ovipositions. In 2005, mated females were transferred individually into small cylinder cages with a host plant to facilitate recording of egg-laying. The small cages were kept inside the population cage under the natural environmental conditions.

Though the population cage allowed the study of movement behaviour and reproduction, there were logistical problems in conducting the experiments and the results were less complete than intended. Therefore the results are referred to only briefly in this thesis.

PGI genotype and flight metabolism

Molecular variation in the glycolytic enzyme phosphoglucose isomerase (PGI) was studied in populations from eastern and southern Finland and from Estonia (II). In a laboratory experiment, I examined possible variation in flight metabolic rate between the different PGI genotypes. For this purpose, first-generation adult map butterflies and larvae were collected in 2005 from several populations in eastern and southern Finland and Estonia. The larvae were reared into adults, which were marked and released into the population cage, where they spent several days before being captured for the measurement of flight metabolic rate and subsequent PGI genotyping. Samples of adult butterflies collected in the field and a part of the butterflies reared from the larvae were frozen in -80°C to be later genotyped for PGI.

PGI genotypes were characterized by enzyme electrophoresis, in which the different isomorphs of the enzyme are separated by mobility based on their charge and scored by the distances moved on the gel. I used cellulose acetate electrophoresis (Hebert & Beaton 1993), using the head of the butterfly homogenized in water as the sample. The same method was used to score two other allozymes to be used as reference loci: aspartate aminotransferase (AAT) and phosphoglucosmutase (PGM). Unfortunately, there were problems in scoring the different isomorphs of PGM and there was very little variation in AAT, and hence these loci did not provide helpful information for this study.

The flight metabolic rate was measured using the standard respirometry technique described by Lighton (1991). Butterflies were caught from the population cage for several hours prior to the measurement to allow them to adjust to the room temperature. The measurements were conducted in the average temperature of 32.8°C. The purpose of the measurement was to measure the rate of CO₂ production by a continuously flying butterfly. The butterfly was placed in a plastic 1-liter jar through which CO₂-free air was pumped at a constant rate. Continuous flight by the butterfly was stimulated by tapping the jar if the butterfly stopped flying. The measurement continued for 15 min and the baseline CO₂ production was measured afterwards while the butterfly was at rest (the jar was covered with a black cloth). Nineteen females and 21 males were measured. Two different measures, the peak flight metabolic rate and the integrated CO₂ emission during the experiment were calculated as explained by Lighton (1991) and Haag *et al.* (2005).

The dry weight and the wing length of butterflies were measured for samples collected from eastern and southern Finland and from Estonia using a balance (0.1 mg precision) and a digital camera for photographing the detached wings. An image analysis programme ImageJ 1.37 by W. Rasband was used to take measurements on digital photographs.

Modelling methods

I used Generalized Additive Models (GAMs) to relate the climatic (I) and habitat (III) variables to species occurrence data and to predict the species occurrence based on the statistical relationship produced by the model. A spatially explicit simulation model was used to predict the range expansion in eastern and southern Finland (IV).

The data used in GAMs are spatially referenced at the selected spatial resolution. ArcGIS was used to prepare the land cover data used in the habitat model

(III) and in the simulation model (IV). Climate data for Europe used in (I) was interpolated from the original resolution to the spatial resolution used in this study. Two of the three climatic variables used, the degree-days above 5°C (GDD) and water balance (WB), were calculated from the original climate variables following Luoto *et al.* (2004), Hodridge (1967), and Skov and Svenning (2004).

To study the effect of landscape structure on range expansion, I used a dynamic simulation model, the grid-based incidence function model (GIFM) (Moilanen 1999; Gu *et al.* 2002) at the spatial resolution of 0.2 x 0.2 km (Fig. 1). The model requires a measure of habitat suitability for each grid cell. Habitat quality was predicted by the habitat model (III), as the predicted probability of occurrence in the particular grid cell. The GIFM calculates grid occupancy at each time step based on a metapopulation model, which specifies metapopulation dynamics in terms of the extinction probability of occupied cells and the colonization probability of unoccupied cells (Gu *et al.* 2002). The details are described in Chapter IV. The methods and data used in the chapters of this thesis are summarised in Fig. 5.

4. Results and discussion

The expansion history of the map butterfly in Finland

The expansion of the map butterfly in Finland started from eastern Finland, where the first population was observed in 1983. The very first observation was made in south-eastern Finland in 1973, but as the species was not recorded at this locality during the subsequent years, this record apparently represented a single vagrant individual. The first observation on the south coast was made in 1992, but there were only very few scattered records during the subsequent years. In 1999, a large colonization event took place in July, clearly aided by warm south-easterly winds and most likely originating from the Baltic countries, across the Gulf of Finland (Mikkola 2000; Mitikka *et al.* 2008). This singular event represents the colonization of south Finland, which has been followed by subsequent range expansion. The eastern and southern expansion fronts have remained separate. There are observations made in recent years in one 10 x 10 km grid cell in southeast Finland located between the two expansion fronts, but as this square is situated near the Russian border it is likely that the butterflies have dispersed from Russia.

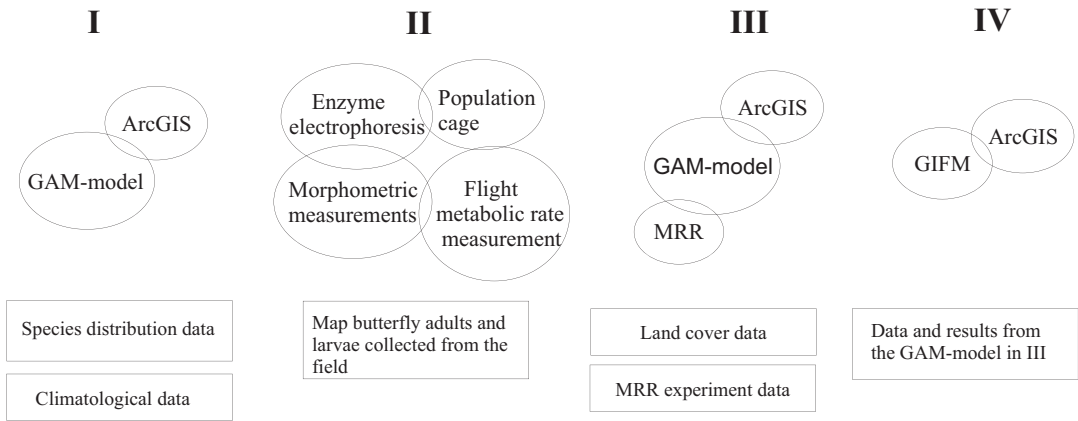


Fig. 5. A schematic illustration of the study methods and material used in this thesis. Methods are in circles, and data are in boxes.

During the past 10 years the expansion on the eastern front has been faster than on the southern front (I). A visual examination of the results shows that the rate of expansion has accelerated in the past 10 years at the scale of the whole country (see Fig. 6 below, and Fig. 2 in Chapter I). The expansion rate was measured as the square root of the occupied area (km^2) (following Hill *et al.* 2003), calculated separately for three time periods. The first time period 1983-1991 (a) represents the first years of expansion in Finland, when the species was present only in the eastern part of the country. The second time period (b) starts from 1992, when the first observation on the south coast was made, and the third (c) period starts from 1999, the year of the big invasion on the south coast (note that in Fig. 2 in Chapter I the dots for the years 1998, 1999 and 2000 are incorrect, and have been corrected in Fig. 6 in this summary). The corrected rate of expansion is 5.2 for the period 1999-2004. Figure 6 is based on the

updated data, including data obtained since making Fig. 2 in Chapter I, and the new revised values for the rate of expansion are 1.4, 1.4 and 4.0 for the three time periods mentioned above.

The influence of climate change on the expansion

The climate model (I) predicted the observed northern limit of the geographical range of the map butterfly in Finland quite accurately for the period 2000-2004, but the model overestimated the occurrence in the south-western part of Finland and underestimated the occurrence in eastern Finland. The discrepancy between the prediction and the actual distribution may be at least partly a consequence of a bias in the data, due to the deficiency of calibration data (butterfly records) for north-eastern Europe. The model may also have failed because it does not take into account geographical barriers for dispersal

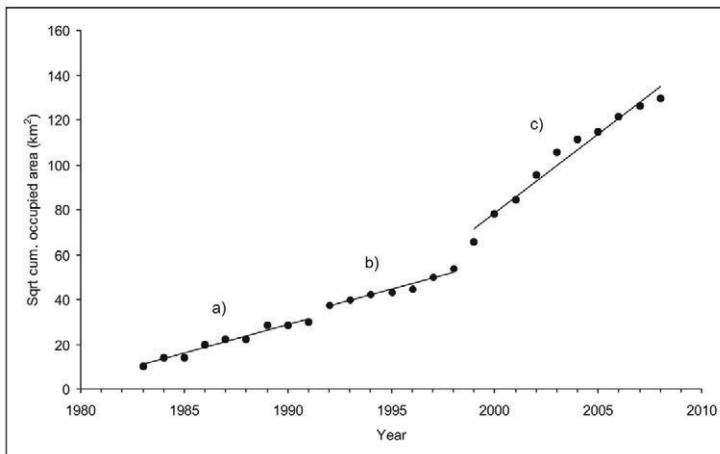


Fig. 6. The rate of expansion of the map butterfly in Finland, shown as the square root of the area (km^2) occupied per year, in three periods during 1983-2008: (a) the period of expansion starting at the eastern distribution front, (b) expansion after 1992, when the first observation on the south coast was made, and (c) expansion since the 1999 invasion of the south coast. (This figure is an updated version of Fig. 2 in Chapter I.)

(the sea) or the prevailing wind direction in south-western Finland (from the west), which influence the expansion. Furthermore, the change of spatial scale from the calibration data at the European scale (0.5° N x 1° E) to 10 x 10 km grid resolution for the prediction made for Finland may have reduced the model performance (I). In general, one could expect that there are problems in transferring a model from one spatial scale to another (Araújo *et al.* 2005).

There are also other possible reasons for the failure of the model to predict correctly the distribution of the map butterfly in south-western Finland. One possible reason is the spatial configuration of habitat, which can only be examined by analysing the small-scale structure of the landscape. This was done in the modelling study in Chapter IV (below). The expansion was simulated with a dynamic model for eastern and southern Finland separately using a resolution of 0.2 x 0.2 km grid cells for which the landscape structure was described. The spatial pattern of the expansion in eastern Finland was predicted well by the simulation model. For southern Finland the simulation model predicted a slower than observed rate of expansion. The results support the hypothesis that the landscape structure in southern Finland would be less favourable than the landscape in eastern Finland for the expansion.

The range expansion of butterflies and other taxa due to climate change is affected directly by particular climatic factors or, alternatively, the range expansion is due to other environmental factors correlated with climate change. The importance of summer temperatures for butterfly range expansions has been demonstrated in several studies (Pollard 1988; Pollard & Yates 1993; Parmesan 2006). In the present study, I showed that the late summer temperatures (July-August) correlated positively with the yearly dispersal distances (I). This may be related to the occurrence of the second generation primarily in warm summers and the difference in the dispersal rate of butterflies in the two generations. The first-generation butterflies move only short distances, which was observed also in the present project (III). In contrast, the summer-generation butterflies are more mobile (Fric & Konvi ka 2000). The accelerated expansion during the latest time period, 1999-2004, examined in chapter I coincided with years of warm summer temperatures, as discussed above (Fig. 6). Therefore, environmental conditions prevailing in late summer, during the flight season of the second generation, may be particularly important for range expansion, as well as the conditions that determine the occurrence of the second generation in the first place.

The modelling study in Chapter I is representative of many other climate-envelope models that have been constructed to predict the response of species to warming climate e.g. (Berry *et al.* 2002; Hill 2002; Hill *et al.* 2003; Harrison *et al.* 2006; Huntley *et al.* 2008; Settele *et al.* 2008; Virkkala *et al.* 2008). These models have been criticized for lacking several important factors that are likely to influence range expansion (Hampe 2004; Pearson & Dawson 2004) and which have been referred to above. The other chapters in this thesis address some of these additional factors.

Phenotypic and genotypic composition of expanding populations

I compared the PGI genotypic composition of populations that are situated close to the expanding range boundary with those located in more central parts of the range. Three allozyme alleles, PGI-1, PGI-2 and PGI-3 (in the kinetic order from the fastest to the slowest), were detected in the samples from eastern and southern Finland and Estonia. PGI-3 was very rare and was not considered in the analyses. The frequencies of the three genotypes PGI-1/1, PGI-1/2, and PGI-2/2 were in the Hardy-Weinberg equilibrium in all the study regions, in eastern and southern Finland and in Estonia. In eastern Finland, the frequency of the PGI-1 allele was significantly higher than in southern Finland and in Estonia, but there was no significant difference in the allele or genotype frequencies between southern Finland and Estonia.

The result for eastern Finland is consistent with the hypothesis that butterflies with the PGI-1 allele are superior in dispersal, and that range expansion has selected for these butterflies. This is consistent with the results for *Colias* butterflies (Watt *et al.* 1983; Watt *et al.* 1985; Watt *et al.* 1996) and the Glanville fritillary (Haag *et al.* 2005; Hanski & Saccheri 2006), in which individuals with the kinetically fastest PGI allele, or heterozygous individuals, are superior fliers and dispersers. This conclusion is also supported by the distribution of the alleles among local populations in eastern Finland. Samples were obtained from both newly-established (<4 years old) and old populations (11-22 years old). If the PGI-1 allele is associated with high dispersal rate, one could expect that, among the populations in eastern Finland, the frequency of PGI-1 is higher in the newly-established than old populations. Such a difference was indeed found in a comparison involving the first-generation butterflies, for which the sample size was reasonably large. This result supports the hypothesis that PGI-1

is indeed associated with mobility and that the more mobile butterflies are more likely to establish new populations beyond the range boundary than the less mobile butterflies.

The samples included both first-generation and second-generation butterflies. In the pooled material for eastern and southern Finland, there was a significant difference between the generations due to higher frequency of the PGI-1 allele in the first-generation butterflies. A possible explanation of this result relates to the greater mobility of the second-generation than first-generation butterflies (Fric and Konvi ka (2000). If the butterflies with the PGI-1/1 genotype, PGI-1/2 genotype, or both, are particularly mobile, and if high mobility increases the fitness of the second-generation map butterflies, one could expect that the frequency of the PGI-1 allele increases from the second to the first generation. Selection may then reverse in the first generation. The results for southern Finland do not indicate an excess of the PGI-1 allele in comparison with the Estonian population, which at first appears to refute the above hypothesis and interpretation of the results for eastern Finland. However, this apparent discrepancy in the results may be due to the difference in the expansion processes at the eastern and southern expansion fronts in Finland. In eastern Finland, the expansion has occurred gradually since 1983 and is likely to be a continuation of a similar gradual expansion previously in Russian Karelia. In contrast, the colonization of the south coast is due to the invasion of 1999, when large numbers of butterflies crossed the Gulf of Finland from Estonia with the help of favourable winds. In such migration, the PGI genotype may not make a difference, unlike in gradual expansion due to normal flight of butterflies. Thus I suggest that gradual expansion is a mechanism that leads to natural selection for increased mobility and, in this case, increased frequency of the PGI-1 allele.

Turning to the measurements of the flight metabolic rate, there were no significant differences between the PGI genotypes in the peak flight metabolic rate and in the total CO₂ produced during the 15 min experiment. There was, however, a significant difference in the peak flight metabolic rate between the PGI genotypes when the total CO₂ production was used as a covariate. The rationale for this analysis is that the total CO₂ production reflects differences among individuals in their general physiological condition, while the peak flight metabolic rate reflects differences in flight metabolic capacity. In this analysis, the PGI-1/2 heterozygotes had the highest level of flight metabolism, PGI-1/1 the second highest and PGI-

2/2 the lowest flight metabolism. A closer analysis showed that the genotypic effect was present in females but not in males. Taking into account that the PGI-1 allele in the map butterfly is likely to be functionally analogous to the kinetically fast *Pgi-f* allele in the Glanville fritillary, the present results and the results for the Glanville fritillary (Haag *et al.* 2005) are strikingly similar.

There were no morphometric differences among butterflies originating from southern and eastern Finland and from Estonia in individual traits, but the scaling of the wing length by body size showed significant differences among the regions. The measurements were taken on second-generation butterflies, which are more dispersive than the first-generation butterflies (Fric and Konvi ka (2000). These results are not in line with the hypothesis of wider wing span and higher wing loading ratios contributing to better flight capacity (Hill *et al.* 1999a; Hughes *et al.* 2003). As a matter of fact, in the present study the wing loading ratio in the populations at the expanding range margin in eastern Finland was smaller, on average, than in butterflies from the stable populations in Estonia. On the other hand, these results are comparable with those for the Glanville fritillary in the Åland Islands, where there is a difference in the mobility of butterflies from newly-established (more mobile) versus old populations (Ovaskainen *et al.* 2008), but no corresponding differences in any morphological traits (Hanski *et al.* 2002; Hanski *et al.* 2004).

In summary, the present results support the hypothesis that molecular variation in the *Pgi* gene is associated with mobility in the map butterfly as it is in the Glanville fritillary butterfly (Haag *et al.* 2005; Hanski & Saccheri 2006) and in *Colias* butterflies (Watt *et al.* 1996). Map butterflies with the PGI-1 allozyme allele, and thus, the kinetically fastest type of the enzyme, are suggested to be more dispersive than butterflies that lack this allele. Whether there is a difference between the PGI-1/1 homozygotes and PGI-1/2 heterozygotes is not clear based on the present results.

Habitat selection and the effect of landscape structure on range expansion

As discussed in Introduction, the lack of suitable habitat prevents the expansion of the specialist species, but the amount of preferred habitat type may influence the expansion of the generalist species as well. Landscape structure has been shown to influence the expansion rate of the speckled wood butterfly, (*Pararge aegeria*), the expansion rate being slower in areas where the cover of the preferred

habitat, woodlands, is reduced (Hill *et al.* 2001). I studied the habitat preference and the effect of landscape structure on the pattern of expansion of the map butterfly in chapters III and IV.

The results of the habitat model constructed in Chapter (III) confirmed the field observations on habitat use by the map butterfly. The land cover classes and the variables derived from them that were selected in final model and that explained the largest amount of deviance were the edge between fields and forests, pasture, the matrix consisting of habitat entirely unsuitable for the map butterfly, and population dynamic connectivity. Connectivity explained most of the deviance, suggesting that the map butterfly has an aggregated spatial distribution that cannot be entirely attributed to habitat quality. The first two variables had a positive effect on the occurrence of the map butterfly, whereas the matrix had a negative effect, as expected.

The results of the simulation model (IV) supported the expectation that the effect of landscape structure on the pattern of range expansion is detected at the fine spatial scale. The simulation results for the eastern expansion front were in close agreement with the observed expansion, though in this case the data used to test model predictions were not entirely independent of the data used for estimating parameter values. On the other hand, the model-predicted expansion on the south coast was slower than observed for the period 1999-2008, suggesting a less favourable landscape composition for the map butterfly. Secondly, the simulations confirmed the importance of long-distance dispersal events for the observed range expansion (I, II). Taking into account that the second-generation butterflies are more dispersive than the first-generation butterflies this result points to the importance of the second generation for range expansion. The regular occurrence of the second generation has been reported in Finland since 1999, which is also the year when the south coast was colonized and the expansion of southern Finland began. The occurrence of the second generation from the beginning of the expansion in southern Finland may have enhanced the expansion rate in comparison with the model prediction. In eastern Finland, the simulation model predicted a little slower expansion in the beginning of the expansion period (until 1997) but relatively faster expansion in subsequent years in relation to the observed expansion. As the 160 x 160 km study area for which the simulation was run is smaller than the actual distribution of the map butterfly in 2008, it is not possible to assess to what extent the model would predict the very long-distance colonization events that have been observed in the past 10 years.

5. Conclusions

A climate-envelope model (I) was used to predict the potential distribution of the map butterfly in Finland. The model predicted correctly the northern distribution limit, but it clearly overestimated the distribution of the map butterfly in western Finland. This failure of the model may at least partly be explained by technical reasons, but it is also possible that the difference between the predicted and observed distribution is due to fragmented landscape structure that would hinder the expansion of the species. This hypothesis was tested via a simulation study (IV). The results are consistent with the hypothesis that landscape structure has hindered expansion, more in southern than in eastern Finland.

A habitat model constructed with mark-release-recapture data quantifies the habitat requirements of the map butterfly and confirms that the preferred habitat is forest edges and comparable habitats (III). The results indicated that the map butterfly has a strongly aggregated spatial distribution that is partly independent of habitat quality. The first-generation butterflies have very limited mobility and thus, the second generation is seen more important for dispersal. These results and the results of a simulation model (IV) predicting slower than observed rate of expansion in southern Finland suggest that occasional long-distance dispersal events by second-generation butterflies are necessary for tracking suitable climate. A clear example of this is the colonization of South Finland across the Gulf of Finland in 1999.

This study supports the hypothesis that molecular variation in the glycolytic enzyme phosphoglucose isomerase is associated with flight metabolic rate and range expansion in eastern Finland. The PGI-1 allele has a higher frequency at the expanding range margin in eastern Finland than in populations in Estonia, and within eastern Finland the frequency of PGI-1 is higher in newly-established (age around 4 years) than in older local populations (11 to 22 years). The frequency of PGI-1 is not higher in southern Finland than in Estonia, probably because the colonization of southern Finland from Estonia occurred during a singular migration event of large numbers of butterflies in 1999 rather than as a gradual process like in eastern Finland.

The results of this thesis support the findings of previous studies suggesting that distributional changes in response to climate change are also affected by other factors. It is therefore preferable to use several research approaches to build a comprehensive understanding of the process of range expansion.

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