Altitude, land cover and climate change: mechanisms of adaptation in insects

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Altitude, land cover and climate change: mechanisms of adaptation in insects

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CHAPTER 1

Summary

1.1 Summary

Climate and land cover change are both major threats for biodiversity and can interrupt species composition and ecosystem functioning. To cope with these environmental changes species need to adapt. Although species response to climate warming has become an attractive field of research in the last decade, yet very little data are available regarding climate change in terms of the synchronisation of trophic interactions, neither on the combination with land cover change, nor on life history traits outside the laboratory. In order to disentangle how insects adapt to modified environmental conditions this thesis explores the effects of climate change / modified climatic conditions on insects with a focus on three mean issues: (1) the synchronization of phenology of interacting species, (2) butterfly diversity and historical land cover change along an altitudinal climatic gradient and (3) climate-driven changes in the life history traits of the model species *Araschnia levana* in a low mountain region.

This thesis reveals that a surprisingly low number of studies consider responses to climate warming at different trophic levels in parallel (Chapter 3). In most examined systems insects shifted in phenology towards the start of the year. But the advanced phenology of short-lived insects was often not synchronized with other trophic levels (almost 75% of interactions). Insects reacted rapidly to climate warming, whereas their long-lived counterparts like plants or birds often lag behind. As shorter life cycles implicate more generations per year and thus increase the probability of adaptation to a fast changing environment, the trophic rank seems to be less important than differences in longevity. The examined ambiguous shifts between trophic levels emphasise the need for additional studies on different functional groups.

Species richness-altitude relationships can be explained by different theories. This thesis documented highest species richness of butterflies at mid elevations in a low mountain region and is therefore in line with the mid-domain-effect theory (Chapter 4). Within the last 40-60 years about one third of the examined open habitats in the Fichtelgebirge were lost. In higher altitudes land cover change was strongest. Interestingly, species richness of butterflies was not reflected by historical loss of open habitats and did not depend on current open habitats but increased with patch size. These findings apply for open land specialized butterflies as well as for generalist and forest species. But due to the decreasing amount of open habitats with increasing altitude, rising temperatures, reforestations and intensive land use, butterfly species, which are at their thermal distribution limits, are endangered. Habitats of open habitat specialists might be decimate, hence it is on high priority to protect open habitats at high elevations.

Finally, adaptive responses to changing environmental factors can be genetically fixed or plastic and are determined by physiological thresholds. In order to determine whether life history traits of the European Map butterfly (*Araschnia levana*) differ along an altitudinal gradient, field experiments with the stinging nettle (*Urtica dioica*), the larval host plant of *A. levana*, were performed (Chapter 5). Larvae showed slower larval development rates and lower larval weight at higher altitudes and lower temperatures than at lower altitudes and higher temperatures. No differences could be recorded on pupation, adult-life-span and mortality in relation to altitude or temperature. None of the larvae was parasitized. Occurring sex differences in larval weight, pupal and adult life span might be the consequence of protandry and the adaptation to different temperatures can be explained as a result of phenotypic plasticity.

1.2 Zusammenfassung

Der Klimawandel und Landnutzungsänderungen stellen eine große Bedrohung für die Biodiversität dar und können die Artenzusammensetzung und die Funktionsweise von Ökosystemen stören. Diese Umweltveränderungen erfordern eine Anpassung der Arten. Obwohl die Reaktion verschiedener Arten auf die Klimaerwärmung im letzten Jahrzehnt ein attraktives Forschungsfeld geworden ist, sind bisher nur wenige Daten verfügbar, die die Auswirkungen des Klimawandels auf die Synchronisation von trophischen Interaktionen untersuchen. Ebenso fehlen Daten zu den Folgen des Klimawandels in Kombination mit Landnutzungsänderungen und Life-History-Merkmalen (ökologische Merkmale) in Freilanduntersuchungen. Um herauszufinden wie sich Insekten an veränderte Umweltbedingungen anpassen, wurden in dieser Dissertation die Effekte vom Klimawandel / von modifizierten klimatischen Bedingungen auf Insekten innerhalb von drei thematischen Bereichen untersucht: (1) der phänologischen Synchronität mit interagierenden trophischen Partnern, (2) der Diversität von Tagfaltern als Reaktion auf historische Landnutzungsänderungen entlang eines Höhengradienten und (3) den Änderungen in den Life-History-Merkmalen des Modelorganismus *Araschnia levana* in einem Mittelgebirge.

Die vorliegende Dissertation zeigt, dass sich erstaunlich wenige Studien dem Thema der Klimaerwärmung widmen und dabei verschiedene trophische Ebenen parallel untersuchen (Kapitel 3). Die meisten Studien zeigen, dass sich die Phänologie von Insekten in Richtung des Jahresbeginns verschiebt. Die fortgeschrittene Phänologie der kurzlebigen Insekten war in vielen Fällen nicht synchronisiert mit anderen trophischen Ebenen (fast 75% der Interaktionen). Insekten reagierten schnell auf die Klimaerwärmung, während ihre langlebigen Gegenspieler, wie Pflanzen oder Vögel, oftmals langsamere Reaktionen zeigten. Da kurze Lebenszyklen mehrere Generationen pro Jahr zur Folge haben, erhöhen sie so die Anpassungsfähigkeit an die sich schnell verändernden Umweltbedingungen. Der trophische Rang scheint hierfür weniger wichtig zu sein als die unterschiedliche Lebensdauer der Arten. Um die bisher nicht eindeutigen phänologischen Veränderungen innerhalb der trophischen Ebenen besser zu verstehen, sind weitere Studien zu unterschiedlichen funktionellen Gruppen nötig.

Verschiedene Theorien erläutern das Verhältnis zwischen Artenreichtum und Höhenlage. Die vorliegende Dissertation zeigt, dass im untersuchten Mittelgebirge die

Artenvielfalt von Tagfaltern in mittleren Höhenlagen am höchsten war. Dies ist im Einklang mit der Mid-Domain-Effect-Theorie (Kapitel 4). Innerhalb der letzten 40 bis 60 Jahre ging etwa ein Drittel der offenen Habitate im Fichtelgebirge verloren. In höheren Lagen waren die Landnutzungsänderungen am stärksten. Interessanterweise war der Artenreichtum von Tagfaltern unabhängig von dem historischen Verlust offener Habitate und von heutigen offenen Habitaten. Jedoch nahm die Artenanzahl mit zunehmender Größe der Untersuchungsflächen zu. Dies galt für Tagfalter, die auf offene Habitate spezialisiert sind sowie für Generalisten und waldbewohnende Arten. Aufgrund der abnehmenden Anzahl offener Habitate mit zunehmender Höhenlage, zunehmender Temperatur, Aufforstung und intensiver Flächennutzung sind Schmetterlingsarten, die bereits an ihren temperaturbedingten Verbreitungsgrenzen leben, besonders gefährdet. Genauso verringert sich auf diese Weise der Anteil an Lebensräumen von Tagfaltern, die auf offene Habitate spezialisiert sind. Daher kommt dem Schutz offener Habitate in höheren Lagen eine hohe Priorität zu.

Anpassung an veränderte Umweltbedingungen kann genetisch oder plastisch bedingt sein und wird durch physiologische Schwellenwerte bestimmt. Um zu bestimmen in wie weit die Life-History-Merkmale des Landkärtchens (*Araschnia levana*) entlang eines Höhengradienten variieren, wurde ein Feldexperiment mit der Großen Brennnessel (*Urtica dioica*), der Raupenfutterpflanze von *A. levana*, durchgeführt (Kapitel 5). Die Raupen entwickelten sich in höheren Lagen und bei niedriger Temperatur langsamer und waren leichter als in niedrigeren Höhenlagen mit höheren Temperaturen. Es konnten keine Unterschiede bezüglich der Verpuppung, der Lebenserwartung der adulten Tiere und der Mortalität in Abhängigkeit zu Höhe oder Temperatur festgestellt werden. Keine der Larven war parasitiert. Die nachgewiesenen geschlechtsspezifischen Unterschiede bei dem Gewicht der Raupen, der Dauer des Puppenstadiums und der Lebensdauer der adulten Tiere, sind wahrscheinlich die Folge von Protandrie. Die Anpassungsfähigkeit an die unterschiedlichen Temperaturen ist vermutlich die Folge von phänotypischer Plastizität.

CHAPTER 2

Synopsis

2.1 Introduction

2.1.1 Adaptation to environmental changes – state of art

With increasing human impact the environment changes and species have to adapt to land cover and climate change, otherwise survival is endangered (Thomas *et al.* 2004a, Franco *et al.* 2006, Thuiller 2007). Recent studies document changes in abundance and distribution (Lawson *et al.* 2012, Blois *et al.* 2013). Long-time evolved life history traits facilitate local adaptations and determine species competition and interactions with other trophic ranks (Thrall *et al.* 2007, Reiss *et al.* 2009). Due to environmental changes, species interactions can be disrupted and can lead to pest outbreaks and extinctions (Péré *et al.* 2013, Nooten *et al.* 2014). Changes in host use or a complete switch from host to host might be the consequence (Pateman *et al.* 2012). Furthermore, species adapt to environmental changes by adjusting their phenotypic values (Karl & Fischer 2008). These adaptations can be short-term (plastic adaptations) or long-term adaptations (genetic differentiation) (Berg *et al.* 2010).

Insects are assumed to be particularly vulnerable to environmental changes because of their short life-cycles, often low dispersal ability and narrow ecological niches (Bourn & Thomas 2002, Thomas *et al.* 2004b, Morris *et al.* 2008). As butterflies are well examined species, they present an ideal group for studies on biodiversity, climate change and life history traits (Hunter *et al.* 2014, van Swaay *et al.* 2006).

Climate change

Temperature is a determining factor in ectotherms physiology, development and distribution (Bale *et al.* 2002). Beside the previously specified long-term evolved processes of adaptation, climate change became a key element for species organization at temporal and spatial scales (Lurgi *et al.* 2012, Audusseau *et al.* 2013). Thus species have to adapt to new climatic conditions and shift in phenology and distribution to maintain their thermal optimum (Bale *et al.* 2002, Jeffs & Lewis 2013). The response of higher trophic levels to climate change is generally assumed to be of particular importance as higher trophic levels, like parasitoids, have to adapt to their host and to climate change in parallel (Jepsen *et al.* 2009, Thackeray *et al.* 2010). Pest outbreaks or extinctions might be the consequence if adaptation fails. Therefore biodiversity and ecosystem services are endangered, but so far only few studies focus on the response of higher trophic levels (Delava *et al.* 2014).

Land cover change

Habitat loss and fragmentation are undoubtedly major threats for biodiversity (Travis 2003, Tscharntke *et al.* 2005). Habitat loss reduces potential habitats for butterflies and leads to less connected habitats and reduced species richness (Öckinger & Smith 2006). Fragmentation, habitat loss and increasing land use intensity can change butterfly community composition and life history traits (Öckinger *et al.* 2010, Börschig *et al.* 2013). As a result of land cover change habitat area and species richness decrease (Rosenzweig 1995, Steffan-Dewenter & Tscharntke 2000). The historical loss of habitats can lead to extinctions in the next years (Bommarco *et al.* 2014). Of particular importance is the surrounding landscape for species living in fragmented habitats as larger habitats and more connected habitats in the surrounding enable colonization and provide additional resources (Öckinger *et al.* 2012, Rösch *et al.* 2013).

Not all species of a community react on landscape composition and climate change in the same way (Ewers & Didham 2006). Species with different degrees of specialisation on specific habitat characteristics and species with distinct dispersal abilities react differently to environmental changes (Warren *et al.* 2001, Crozier 2004, Weiner *et al.* 2014). Studies with focus on climate change evidence rapid range shifts and highlight the requirement on studies which account for species traits and external drivers like land cover change (Chen *et al.* 2011, Jamieson *et al.* 2012). However, case studies testing different ecological traits in relation to climate and land cover changes in parallel are still rare; only few studies were conducted outside the laboratory even though the results of studies with the same species can deviate according to the conditions in the laboratory respectively in the field (Barton *et al.* 2014). Especially specialists` response to land cover change is hardly to predict, as specialists have to adapt to land cover change, host plant occurrence and climatic factors (Menendez *et al.* 2007).

Altitudinal gradients

Mountains are diverse and rich ecosystems, but habitats in high elevations are also assumed to be more sensitive to environmental changes than lowlands (Beniston 2003, Diaz *et al.* 2003). In mountainous regions insect have to adapt to fragmented habitats and harsh environmental conditions (Hodkinson 2005). Recent studies document changes in species morphology and fitness according to altitude and temperature (Hodkinson 2005, Karl & Fischer 2008, Leingärtner *et al.* 2014).

Species richness-altitude relationships in insects mostly show two patterns: Decreasing species richness with increasing altitude, which is explained by combinations of geomorphology, climate and water-energy limitations (Clarke & Gaston 2006, Mihoci *et al.* 2011). Otherwise, species richness peaks at mid elevations and is either caused by the mid-domain-effect or by a combination of temperature and productivity effects on competition, metabolism and speciation (Colwell *et al.* 2004, Stegen *et al.* 2009, Stefanescu *et al.* 2011). Because long-time data are often not available for predictions on climate change, recent studies used altitudinal gradients as analogues (Péré *et al.* 2013, Rasmann *et al.* 2014), but so far most altitudinal studies focus on alpine gradients and there is a lack of studies on low mountain ranges (e.g. Dirnbock *et al.* 2011, Viterbi *et al.* 2013, Leingärtner *et al.* 2014).

2.1.2 Objective and key elements of this thesis

The objective of this thesis is to clarify species adaptation to modified environmental conditions such as climate and historical land cover change. As understanding of insects' adaptation to climate warming is crucial for consequences of biodiversity, species composition and ecosystem functioning, **Chapter 3** of this thesis reviews the effects of climate warming on insects and their biotic interactions. The review investigates recent literature in terms of synchronization of phenology on insects and their biotic interactions (birds and plants) in terrestrial habitats. In the review two predictions were developed and tested: 1) higher trophic levels are assumed to be slower in phenological adaptation than lower trophic levels, and 2) the degree of phenological adaptation is linked on the duration of species life time. Chapter 3 aims to increase our understanding of biotic interactions in a changing world and to reveal gaps in current research.

Whereas Chapter 3 gives an overview about recent studies, **Chapter 4** delves deeper into the effects of altitude and historical land cover change. Chapter 4 explores butterfly diversity and land cover change in a field study along an altitudinal gradient in wetland habitats in the Fichtelgebirge. Butterfly species richness is hypothesized to depend on altitude, patch size and landscape context and is assumed to be affected by historical loss of open habitats. Open land specialized butterfly species are assumed to be more sensitive to land cover changes than forest species and habitat generalist species. Chapter 4 aims to increase our ability to understand the impact of climate and land cover change on butterfly biodiversity in low mountain habitats.

Finally **Chapter 5** investigates in more detail the effects of altitude in a field experiment with the European Map butterfly (*Araschnia levana*) as model organism and its larval host plant the stinging nettle (*Urtica dioica*). Butterfly development rates and rates of parasitism were hypothesized to depend on altitude. The Chapter aims to clarify the impact of altitude on life history traits and the ability of adaptation to climatic gradients.

2.2 Materials and Methods

2.2.1 Study area

Field work for this thesis took place in the nature park Fichtelgebirge a low-mountain region in northern Bavaria (Germany) close to the border with the Czech Republic east of the German town Bayreuth. The nature park extends over an area of more than 1000 square kilometres. The region is characterized by contiguous forest and the altitude ranges up to 1051 m a.s.l. (Figure 2.1).

Figure 2.1 Landscape Fichtelgebirge

2.2.2 Trophic interactions and climate change in scientific literature (Chapter 3)

Intensive literature research was conducted in the ISI Web of Science database (1945 - 2014-10-08) to detect studies focusing on trophic interactions, insects and climate warming (search terms: “climate change”, phenolog* and “trophic interaction*”; “climate change”, phenolog* and pollination*”; “climate change”, phenolog* and herbivory”; “climate change”, phenolog* and parasitoid* and/or parasitism*”; “climate change”, phenolog* and predation*). A surprisingly low number of 25 studies concerning phenology and climate change with focus on insects and their interacting trophic levels was found. We tested the predictions on these studies concerning at least two trophic levels in parallel and added additional studies for further explanations.

2.2.3 Sampling of butterflies/burnet moths in wetlands and landscape analysis from aerial photographs (Chapter 4)

In 2008, 27 wetland sites along an altitudinal gradient in the Fichtelgebirge (340 - 750 m a.s.l.) were selected, differing in altitude, patch size (area of the surveyed wetland study sites), current open habitats (area of non-forest habitats in the surrounding landscape in a 750 m radius around the centre of each study site) and in historical land cover change (Figure 2.2). Butterflies (Lepidoptera) and burnet moths (Lepidoptera: Zygaenidae) were sampled by visual counts along seven randomized transect walks through each wetland site according to the German butterfly monitoring scheme (for more details see http://www.tagfalter-monitoring.de and Pollard 1977) (Figure 2.3). For five of these sites historical records exist and were used for comparison of current and historic species occurrences. The amount of open habitats and forest cover were quantified within a 750 m radius around the centre of each study site by using historical (40-60 years old) and current (from 2008) aerial photographs. Total species richness and estimated species richness of butterfly specialists for open habitats (wetland and grassland species), generalist and forest species were analysed as a function of (1) altitude, (2) squared altitude, (3) current open habitats, (4) per cent of historical loss of open habitats and (5) patch size (log10-transformed) using general linear models with Type I SS, linear regressions and Pearson correlations with R Statistical Software 2.14.2.

Figure 2.2 Study site: wetland Röslau

Figure 2.3 *Boloria aquilonaris* in a wetland

2.2.4 Experimental analysis of life history traits according to altitude (Chapter 5)

In 2008 eighteen sites were selected along the whole altitudinal gradient (350 - 1100 m) of the study region. Next to forest margins and shrubs, where *Araschnia levana* populations naturally occurred, 1 m^2 patches were established with the main larval food plant of *A. levana*, the stinging nettle *Urtica dioica* (Figure 2.5). The patches were located next to natural *U. dioica* patches. Temperature at the patches was measured (06 June - 08 July 2009) using iButtons dataloggers (Maxim Integrated Products Inc., Sunnyvale, CA, USA). In March 2009 15 individuals of *A. levana* were caught near the study region and kept in a climate chamber for reproduction (Figure 2.4). 30 first and second instar larvae of the caught butterflies were randomly distributed at each of the 18 patches (09 - 10 June 2009). After three weeks, when the larvae were in the fourth to fifth instar and could have been attacked by parasitoids, they were collected and transferred in the laboratory in individual boxes (Figure 2.5). For all larvae the following seven response variables were recorded: (1) larval weight, (2) pupal weight, (3) larval development time from collecting to pupation, (4) duration of pupation, (5) adult lifespan (6) percentage larval mortality in the field and (7) percentage larval mortality in the laboratory. Statistical analyses (linear mixed effect models) were conducted in R Statistical Software 2.10.1 with a maximum likelihood method with the fixed effects sex at first position and either temperature or altitude at the second position plus the interaction between sex × altitude or sex × temperature.

Percentage larval mortality for each site was arcsinsqrt transformed. Simple regressions with altitude and temperature were calculated.

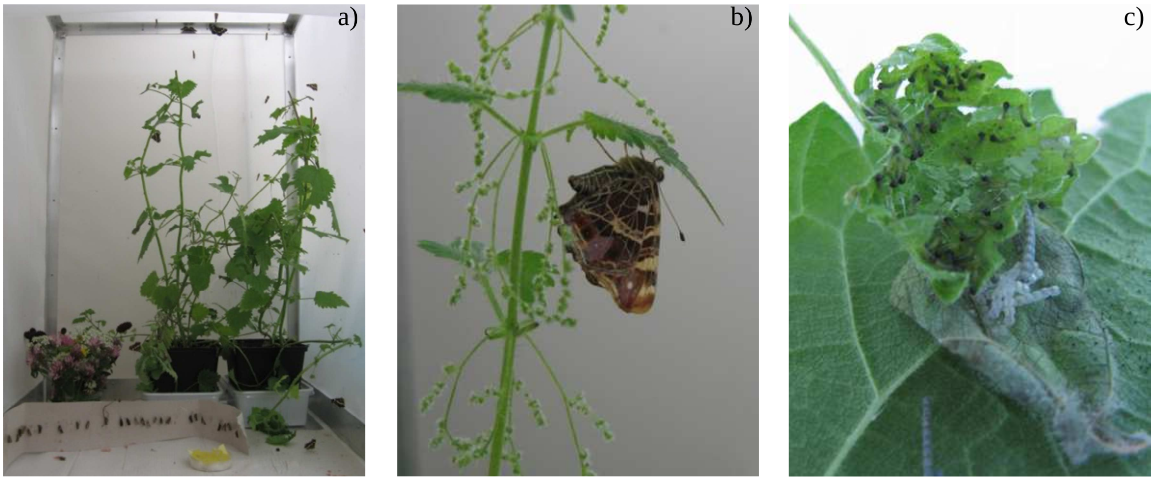

Figure 2.4 Rearing of *Araschnia levana* in the climate chamber before distribution on the experimental nettle patches in the Fichtelgebirge, a) cage for rearing, b) *Araschnia levana* female is laying eggs on nettles, c) first instar larvae.

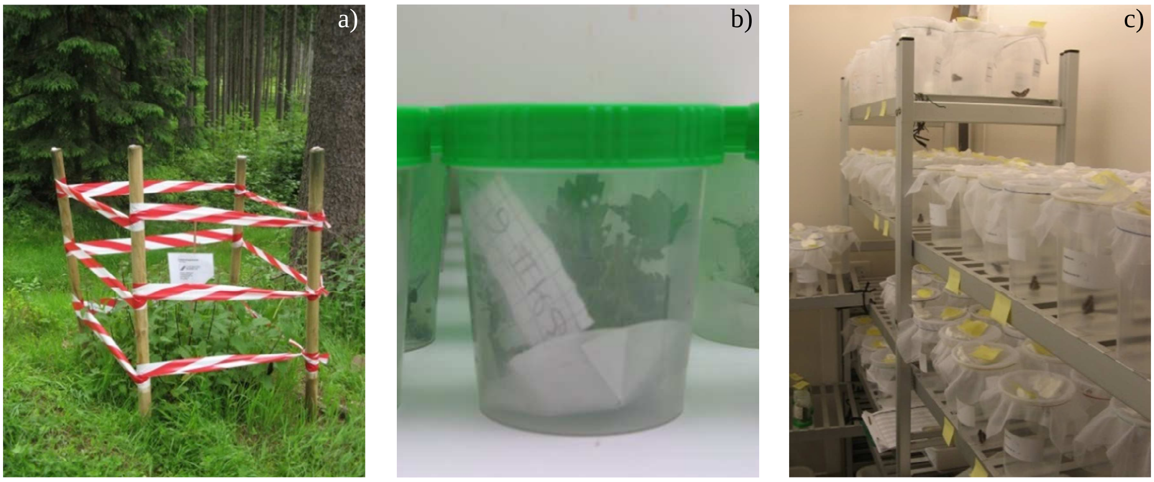

Figure 2.5 a) 1 m^2 patch of cultivated *Urtica dioica*, protected for large herbivores with barrier tape, b) larvae after collection from the field separated in boxes, c) butterflies emerged from pupae after collection from the field.

2.3 Results and discussion

2.3.1 How does climate warming affect phenology shifts of interacting species in terrestrial habitats? (Chapter 3)

Climate warming can disrupt long-evolved trophic interactions and can result in asynchronous phenological shifts (Walther 2010). Many studies concern shifts in phenology and numerous studies deal with trophic interactions, but in many cases only the phenology of one trophic level is examined and the phenology of the counterpart is experimentally modified (e.g. Yang & Rudolf 2010, Forrest & Thomson 2011, Rafferty & Ives 2012). Intensive literature study revealed that only a low number of 25 studies concerning phenology and climate change with focus on insects and their interacting trophic levels in parallel has been published (Table 2.1).

Table 2.1 Phenological studies with focus on climate change. Number of published articles according to ISI Web of Science (1945 - 2014-10-08; search terms: “climate change”, phenolog* and “trophic interaction*”; “climate change”, phenolog* and pollination*”; “climate change”, phenolog* and herbivory”; “climate change”, phenolog* and parasitoid* and/or parasitism*”; “climate change”, phenolog* and predation*) examining at least two trophic levels in parallel.

Phenological studies with focus on climate change	**Published articles**	**Published studies examining two or more trophic levels**
Trophic interactions	68	
Pollination	88	
Plant-pollinator interactions		7
Herbivory	38	
Plant-herbivore interactions		11
Parasitoids/Parasitism	22	
Herbivore-parasitoid interactions		2
Predation	85	
Herbivore-predator interactions		4

In most cases insects shifted in phenology towards the start of the year, whereas their counterparts often lagged behind. Seven studies examined different pollinator species and their pollinated plants in parallel (Gordo & Sanz 2005, Bartomeus *et al.* 2013, Burkle *et al.* 2013, Iler *et al.* 2013, Kudo & Ida 2013, Kudo 2014). In only two of these studies phenology advanced in synchrony (Bartomeus *et al.* 2013, Burkle *et al.* 2013). The other studies highlighted increasing phenological mismatches. In two of these studies plants showed increasing shifts in phenology to the start of the year, whereas insects lagged behind (Iler *et al.* 2013, Kudo & Ida 2013). In the other studies the opposite pattern was documented. None of the predictions were confirmed in plant-pollinator systems. Neither the trophic rank nor longevity seems to play a decisive role. However, additional cues like timing of snow melt, precipitation and soil temperature appear to be crucial.

In nine of eleven studies insect herbivores reacted faster to climate warming than plants (Hill & Hodkinson 1992, Strathdee *et al.* 1993, Buse & Good 1996, Sparks & Yates 1997, Harrington *et al.* 1999, Visser & Holleman 2001, Gordo & Sanz 2005, Sparks *et al.* 2005, de Vries *et al.* 2011, Liu *et al.* 2011, Schwartzberg *et al.* 2014). This was in contrast with the first prediction. However longevity might account for the advanced phenological shifts in insects. Higher temperatures enhanced survival rates of herbivores and enabled them to switch their host plants.

Two studies compared the phenology of herbivores and their parasitoids (Klapwijk *et al.* 2010, Evans *et al.* 2013). In both cases parasitoids did not change in phenology, whereas herbivores shifted in phenology and might create predator free space. Studies on herbivore-predator interactions, examining two trophic levels in parallel, exclusively examined predator prey interactions whereas interactions with invertebrate predators are lacking. In the presented studies the relationship between the phenology of caterpillar biomass peak and bird phenology was investigated (Visser *et al.* 1998, Both & Visser 2001, Cresswell & McCleery 2003, Nussey *et al.* 2005, Visser & Both 2005, Hegyi *et al.* 2013). In line with the predictions the caterpillar prey reacted faster to climate change than their predators. Differences in shifts were probably caused by differences in phenotypic plasticity and birds’ response to photoperiod (Visser & Both 2005). Only one study compared the phenology of four-trophic levels in parallel (Both *et al.* 2009). In line with prediction caterpillars adapted rapidly to climate warming and their interacting levels (plant, bird and top predator) lagged behind.

If phenological adaptation is genetically fixed or plastic was only in some of the studies examined, nevertheless additional studies emphasized the importance of phenotypic plasticity in the context of phenology (Forrest & Thomson 2011, Charmantier & Gienapp 2014, Pitts-Singer *et al.* 2014). If phenotypic plasticity is sufficient for adaptation to climate change remains unclear and further studies are necessary to understand future phenology of interacting trophic systems.

2.3.2 Butterfly diversity and historical land cover change along an altitudinal gradient (Chapter 4)

Land cover change can implicate decreased habitat area and reduced species richness, resulting in extinctions in the following years (Rosenzweig 1995, Steffan-Dewenter & Tscharntke 2000, Bommarco *et al.* 2014). The quantification of historical and current aerial photographs of the study site documented drastic shifts in landscape composition. On average one-third of the current open habitats within the 750 m radius around the centre of the study site was transformed. The historical loss of open habitats increased with increasing altitude and current open habitats decreased with increasing altitude. Especially in higher altitudes forest area increased and minimized the number of potential habitats for open habitat butterfly specialists.

According to the hypotheses, species richness of butterflies depends on altitude and was highest at mid-elevations probably due to the mid domain effect. This complies with other butterfly studies (e.g. Wilson *et al.* 2007). Species richness did not depend on historical loss of open habitats nor on current open habitats, but historical surveys document butterfly species in wetlands, which went extinct throughout the study region. With increasing wetland patch size species richness increased and emphasizes the importance of the conservation and recovery of large wetland sites in high altitudes. The results suggest that the effects of land cover and climate change should not be considered separately, because species responses can overlap and are hard to disentangle. Since higher altitudes are refuges of cold adapted species, increasing land cover change might reduce suitable habitats and tree line expansions in higher regions increases the probability of extinctions (Dirnbock *et al.* 2011).

Contrary to the expectations, open land specialists did not show more sensitive response to decreasing habitat area and to historical loss of open habitats than generalist and forest species. Butterfly species seems to respond independent to their restriction of specific host plants, but the response of open land specialists might also be hidden by an adaptation of the community to land cover change from specialist to generalist traits characteristics (Börschig *et al.* 2013).

2.3.3 Changes in the life history traits of the European Map butterfly, Araschnia levana (Lepidoptera: Nymphalidae) with increase in altitude (Chapter 5)

As higher altitudes are characterized by harsher environment, limited resources and lower pressure of parasites (Pyrcz *et al.* 2009) higher mortality rates were assumed with increasing altitude and decreasing temperature (Figure 2.6). But contrary to the expectations the average percentage mortality per larvae per site of 65% (after collection from the field) did not depend on altitude or temperature. Based on the same requirements decreasing rates of parasitism with increasing altitude and decreasing temperature were expected (Figure 2.6). However none of the collected larvae was parasitized and suggest that top-down control did not occur.

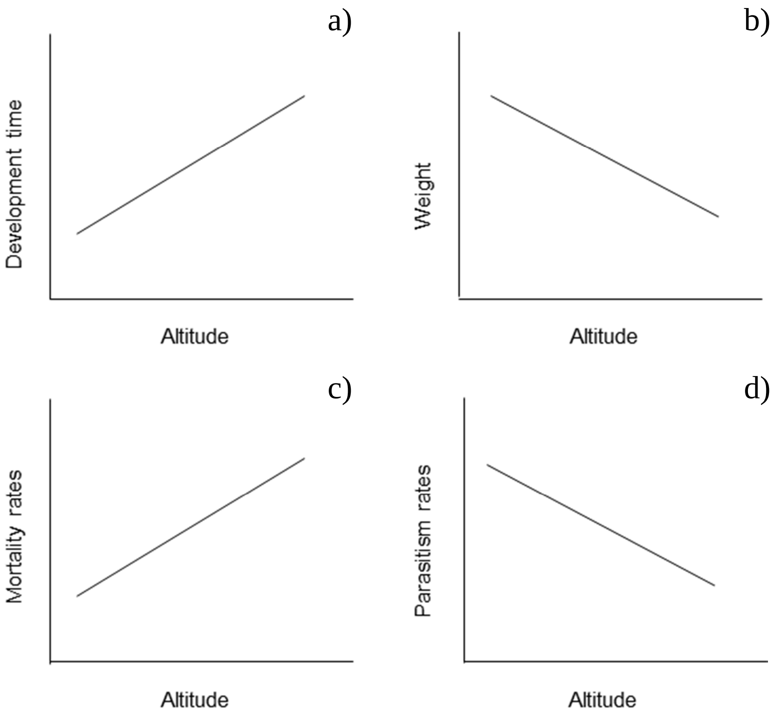

Figure 2.6 Hypotheses for butterflies reared at different altitudes a) butterflies reared at higher altitudes take longer to develop and b) are lower in weight; c) fewer butterfly larvae survive in higher than in lower altitudes and d) fewer butterfly larvae are parasitized in higher than in lower altitudes.

As hypothesized, larval development was slower at higher altitudes and lower temperatures than at lower altitudes and higher temperatures (Figure 2.6). Larval weight decreased with increasing altitude and decreasing temperature. Both responses seem to be the result of high plasticity (e.g. Alonso 1999), as the surveyed larvae were originally from sites at a low altitude and are in line with other altitudinal studies (e.g. Karl *et al.* 2008).

No significant differences in pupation, adult life span and percentage mortality could be found in relation to altitude or temperature. Male and female butterflies reacted similarly to altitude and temperature (no significant interactions) but females took longer to complete their larval and pupal development and lived longer than males probably caused by protandry (Bauerfeind *et al.* 2009).

In line with other studies, which show that species traits can be important predictors for species response to climate change (Bale *et al.* 2002, Diamond *et al.* 2011), this experiment demonstrates that altitudinal and temperature gradients affect the life history traits of the European Map Butterfly (*Araschnia levana*) and suggests that climate change might alter butterflies altitudinal requirements. Altered life history traits might enhance species colonization of higher altitudes due to the fact that higher altitudes become more attractive by increasing development rates and the possibility of having more instars per season.

2.4 Conclusions

This thesis shows that insects are sensitive bioindicators of environmental change. In most examined literature short-lived insects shifted in phenology towards the start of the year in response to climate change. However shifts were often not synchronized with other trophic levels like long-lived plants or birds, indicating a possible disruption of trophic interactions in the future. The absence of parasitoids in the model organism, the European Map butterfly (*Araschnia levana*) might indicate that this kind of disruption has occurred or that top-down control is less important in *A. levana* populations.

The thesis demonstrates that even low altitudinal/temperature gradients affect butterfly species richness and life history traits and emphasizes the importance of low mountain gradients for predictions on climate change. In *A. levana* phenotypic plasticity has enabled it to adapt its larval development time to altitude and temperature and indicates that the degree of plasticity might be a crucial factor for insects’ adaptation to climate change. In accordance with the mid-domain-effect butterfly species richness in the field study was highest at mid-elevations.

Although effects of land cover change on species richness could not be found, historical surveys document extinct butterfly species throughout the study region. These extinctions might be a result of historical land cover change, as land cover change can act on other time scales than those examined in the study. Moreover, the relevance of patch size for species richness emphasizes the protection of large habitats in high altitudes and highlights the importance of management schemes to obtain future refuges for butterflies at their distribution limits.

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CHAPTER 3

How does climate warming affect phenology shifts of interacting species in terrestrial habitats?

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3.1 Abstract

Climate warming is one of the major threats for biodiversity. However, the consequences of enhanced temperature for biotic interactions are little understood, even though long-term coevolutionary processes between species can be disrupted by asynchronous shifts in phenology, potentially leading to species extinctions, pest outbreaks and reduced ecosystem services. This review focuses on the effects of climate warming on insects and their trophic interactions with plants and antagonists, in terms of synchronisation of phenology in terrestrial habitats. In theory, lower trophic levels and short-lived species should react faster to climate warming than their counterparts. The few existing studies provide evidence for advanced phenology of short-lived insects, compared to less pronounced responses of long-lived plants and birds. Differences in shifts between trophic levels were ambiguous, highlighting the need for additional case studies considering life history trait variation within functional groups. We conclude that rapid phenological shifts of short-lived insects due to climate warming might result in unpredictable cascading effects in natural food webs.

Key-Words

climate change, global change, biotic interactions, phenological synchronisation, trophic cascades, insect timing

3.2 Introduction

Global climate change, including changes in temperature, shifts in precipitation, increasing atmospheric carbon dioxide and higher frequencies of extreme weather events, has the potential to profoundly alter biotic interactions in terrestrial ecosystems (Walther *et al.* 2002, Barton *et al.* 2009, Jentsch *et al.* 2009). Climate change is considered one of the major biodiversity threats as it is expected that many species will fail to adapt to rapidly changing habitat conditions (Thomas *et al.* 2004, Thuiller 2007). Global warming trends are predicted to continue for at least another 100 years (IPCC 2007a). During the last 100 years the Earth's climate has warmed by 0.6°C and current climatic models predict an average increase of 1.8°C to 4°C until 2100 (IPCC 2007a). Due to these rising temperatures the distribution and the phenology of plant and animal species are subject to considerable change (Pounds *et al.* 1999, Walther *et al.* 2002, Root *et al.* 2003, Parmesan 2005, Primack *et al.* 2009, Thackeray *et al.* 2010, Mortensen *et al.* 2014). Changes in species composition of communities and alteration of life history traits of plant and animal species have been observed in a variety of ecosystems (Biesmeijer *et al.* 2006, Newton *et al.* 2007, Burkle *et al.* 2013).

In particular, not only single species but also biotic interactions between species might be affected by climate change (Sutherst *et al.* 1995, Tylianakis *et al.* 2008). Antagonistic and mutualistic biotic interactions such as competition, herbivory, predation and pollination are the result of long-term coevolutionary processes (Thrall *et al.* 2007) and play an important ecological role for the maintenance of biodiversity and ecosystem functioning (Reiss *et al.* 2009). Climate warming may disrupt these interactions by asynchronous shifts in phenology (Hughes 2000, Stenseth & Mysterud 2002). Asynchronous shifts in species phenology could lead to the release from antagonist top-down control, which might have negative consequences like pest outbreaks, or the loss of mutualists like pollinators with potential negative consequences for plant reproduction (Hegland *et al.* 2009). On the other hand, phenology shifts might create new trophic interactions (Hodkinson 1997, Hodar & Zamora 2004, Andrew & Hughes 2007, Jepsen *et al.* 2009). Furthermore native species compete with invasive species which might be better adapted to new climatic conditions and related phenology shifts (Mooney & Cleland 2001, Yang *et al.* 2013).

Species phenology depends on several climatic parameters like cold and warm periods in previous years, seasonal changes and the timing and duration of frost (Roy & Sparks 2000, Visser & Holleman 2001). Changes in phenology might be the result of an adaptive response, genetically fixed or an adjustment of the genotype to environmental conditions (phenotypic plasticity) (Hodgson *et al.* 2011, Donnelly *et al.* 2012, Merila & Hendry 2014).

Higher rates of phenological shifts have been shown in ectotherms than in endotherms and especially insects are assumed to be particularly affected by environmental changes due to their short life cycles and partly low dispersal ability (e.g. Bourn & Thomas 2002, Thackeray *et al.* 2010). Increasing temperature can cause physiological changes in insects, like deviations in diapauses and dormancy. Therefore divergences between thermal preferences of host and natural antagonist species can lead to disruptions in synchronisation (Harrington *et al.* 1999).

Numerous studies highlight the impact of climate warming on the phenology of insect species (e.g. Sparks & Yates 1997, Menzel *et al.* 2006, Parmesan 2007, Chen *et al.* 2011) and on trophic interactions between these species (e.g. Thackeray *et al.* 2010, Rafferty & Ives 2011, Gillespie *et al.* 2013, Welch & Harwood 2014). Nevertheless, few studies focus on the timing of live history events of two interacting trophic levels in parallel, while several warming experiments manipulate the phenology of one trophic level (e.g. Yang & Rudolf 2010, Forrest & Thomson 2011).

As far as we know this is the first review, which addresses coupled phenology shifts of at least two trophic levels with a focus on insects. On the basis of general predictions for trophic interactions, this review analyses if basic principles for different taxa according to their life history traits exist. The aim of our study is (1) to review the effects of climate warming on insects and their biotic interactions in terrestrial habitats, (2) to identify possible cascading effects in phenology across trophic levels and (3) to analyse the role of trophic position and longevity to climate warming.

Predictions for different trophic systems and taxa were kept simple to ensure the detection of common principles according to their functional groups. We developed two predictions for the response of species with different life history traits to climate warming.

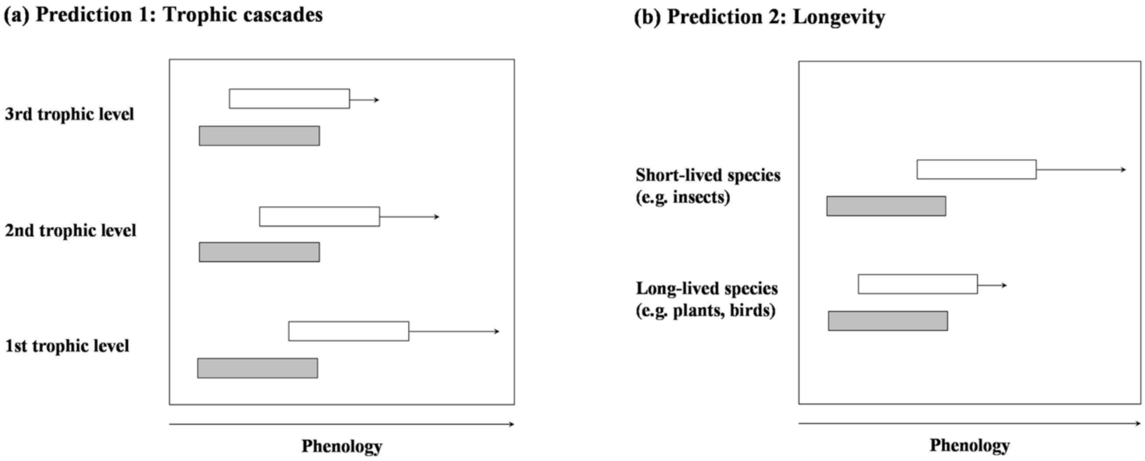

Figure 3.1 Theoretical changes in species responses due to climate warming. Before climate warming species are expected to be in synchrony (grey bars) and climate warming causes different magnitudes of phenological shifts (a) due to trophic level: lower trophic levels are assumed to shift more in phenology than higher trophic levels, resulting in asynchronous phenological shifts; (b) due to longevity: short-lived species are assumed to shift more rapidly in phenology than long-lived species, which also results in asynchrony. Grey bars indicate species phenology before climate warming and white bars expected species phenology after climate warming. Arrows symbolize the expected magnitude of shifts.

Prediction 1

Higher trophic levels are more negatively affected by climate change than lower trophic levels, as species of high trophic levels have to adapt to both shifts in climatic conditions and new types of host dynamics, like changes in phenology, physiology and ecology caused by rising temperatures (Hance *et al.* 2007, Both *et al.* 2009). Therefore, we assume that higher trophic levels follow shifts of lower trophic levels with a time lag depending on their adaptation capacity (Figure 3.1a).

Prediction 2

Longevity of species can determine the time frame for species adaptation to new environmental conditions (Kuussaari *et al.* 2009, Krauss *et al.* 2010). Short-lived species should change their phenology faster than long-lived species as they have more generations per year (plastic response) and thereby higher capability for rapid adaptation (Morris *et al.* 2008, Donnelly *et al.* 2012). (Figure 3.1b).

3.3 Trophic interactions and climate change in scientific literature

Climate change is a contemporary issue. From the enormous number of publications on climate change (> 92000 articles published according to ISI Web of Science, 1945 - 2014-10-08; search terms: “climate change”), we focused our review on studies of climate warming dealing with phenological (temporal scale) match or mismatch based on at least two trophic levels (including insects as one trophic level). Apart from the 265 articles addressing biotic interactions (ISI Web of Knowledge, Web of Science, 1945 - 2014-10-08; search terms: “climate change”, phenolog* and “trophic interaction*”; “climate change”, phenolog* and pollination*”; “climate change”, phenolog* and herbivory”; “climate change”, phenolog* and parasitoid* and/or parasitism*”; “climate change”, phenolog* and predation*), we considered a large number of additional publications focusing on trophic interactions, insects and climate warming, based on intensive literature research.

A perfect synchronisation of interacting species is difficult to expect as trophic interactions are modulated by complex evolutionary and ecological mechanisms (Parmesan 2007, Singer & Parmesan 2010). In this study we compared the phenology of interacting species in 1.) experimental studies for which the phenological starting point of measurement in all interacting partners is known 2.) long-term studies for which the phenological time frame on the beginning and on the end of the study is known. Nonetheless a surprisingly low number of 25 phenological studies could be considered to test our two predictions (see below), as only these 25 studies provided data with at least two trophic levels in parallel.

Table 3.1 Empirical studies on shifts in phenology of interacting species at different trophic levels. Legend: big arrow: essential shift; small arrow: minor shift; circle: no shift. Different responses of interaction partners indicate desynchronisation. We distinguish between long-term field studies (including monitoring-data) and (mostly short-term) warming experiments.

Phenology of trophic interactions		**Study design**	**References**
Plant-pollinator interactions			
↑ *Prunus dulcis, P. armeniaca, P. avium, P. domestica, P. persica, Pyrus communis, Malus domestica, Cydonia oblonga* average flowering date	⇧ Honeybee (*Apis mellifera*) first appearance	Long-term field study	Gordo & Sanz 2005
↑ *Prunus dulcis, P. Armeniaca, P. avium, P. domestica, P. persica, Pyrus communis, Malus domestica, Cydonia oblonga* average flowering date	⇧ Small white butterfly (*Pieris rapae*) first appearance	Long-term field study	Gordo & Sanz 2005
⇧ Apple (*Malus domestica* Borkh.) flowering peak	⇧ Bee pollinator community first appearance	Field study historical data	Bartomeus *et al.* 2013
⇧ Spring blooming forest forbs flowering peak	⇧ Bee pollinator community activity peak	Long-term field study	Burkle *et al.* 2013
⇧ *Achillea millefolium, Androsace septentrionalis, Erigon speciosus Linum lewisii, Ligusticum porteri sPotentilla gracilis, Sedum rosaea Taraxacum officinale, Valeriana capitata* flowering period	↑ Syrphid fly community (Surphidae) activity period	Long-term field study	Iler *et al.* 2013
⇧ *Corydalis ambigua* first flowering	○ Bumble bees first appearance	Long-term field study	Kudo & Ida 2013
↑ Herbs and dwarf shrubs first flowering	Bumble bees (*Bombus* ssp.) first appearance ⇧ Queen bees ⇩ Worker bees	Field study warm spring	Kudo 2014
Plant-herbivore interactions			
○ Potato (*Solanum tuberosum*) sowing	⇧ Potato beetle (*Leptinotarsa decemlineata*) first appearance	Long-term field study	Gordo & Sanz 2005
↑ Olive tree (*Olea europaea*) flowering	⇧ Olive fruit fly (*Bactrocera oleae*) interval of appearance	Long-term field study	Gordo & Sanz 2005
⇧ White dryas (*Dryas octopetala*) development time of buds	⇧ Arctic aphid (*Acyrthosiphon svalbardicum*) development time	Warming experiment	Strathdee *et al.* 1993
○ Dwarf willow (*Salix lapponum*) development time of catkins	⇧ Jumping plant lice (*Cacopsylla palmeni, C .brunneipennis*) development time	Warming experiment	Hill & Hodkinson 1992
↑ Oak (*Quercus robur*) timing of bud burst	⇧ Winter moth (*Operophtera brumata*) egg hatching	Warming experiment	Visser & Holleman 2001

⇧ Oak (*Quercus robur*) timing of bud burst	⇧ Winter moth (*Operophtera brumata*) egg hatching	Warming experiment	Buse and Good 1996, Buse *et al.* 1999
⇧ Gentian (*Gentiana formosa*) flowering peak Anemone (*Anemone trullifolia* var. *Linearis*) vegetative phenology	⇩ Broom moth (*Melanchra pisi*) larvae emergence	Warming experiment	Liu *et al.* 2011
⇧ Aspen (*Populus tremuloides*), Birch (*Betula papyrifera*) timing of budbreak	⇧ Forest tent caterpillar moth (*Malacosoma disstria*) egg-hatching	Warming experiment	Schwartzberg *et al.* 2014
⇧ Garlic mustard (*Alliaria petiolata*) first flowering	⇧ Orange tip butterfly (*Anthocaris cardamines*) first appearance	Long-term field study	Sparks & Yates 1997, Harrington *et al.* 1999
○ Stinging nettle (*Urtica dioica*) first flowering	⇧ Red admiral (*Vanessa atalanta*) first appearance (return date)	Long-term field study	Sparks *et al.* 2005, Visser & Both 2005
⇧ Blackthorn (*Prunus spinosa*) timing of bud burst	⇧ Brown hairstreak (*Thecla betulae*) egg hatching	Field study, warming experiment	de Vries *et al.* 2011

Herbivore-parasitoid interactions			
⇧ Marsh fritillary butterfly (*Euphydryas aurinia*) development time	○ Braconid wasp (*Cotesia bignellii*) development time	Field study, warming experiment	Klapwijk *et al.* 2010
⇩ Cereal leaf beetle (*Oulema melanoposus*) larval occurrence	○ Parasitoid wasp (*Tetrastichus julis*) parasitism rates	Long-term field study, warm spring	Evans *et al.* 2013

Herbivore-predator interactions			
⇧ Caterpillar biomass peak	⇧ Great tit (*Parus major*) egg laying	Long-term field study	Visser *et al.* 1998, Nussey *et al.* 2005, Husby *et al.* 2009
⇧ Caterpillar biomass peak	⇧ Great tit (*Parus major*) egg hatching	Long-term field study	Cresswell & McCleery 2003
⇧ Caterpillar biomass peak	Pied flycatcher (*Ficedula hypoleuca*) ⇧ egg laying ○ bird migration	Long-term field study	Both & Visser 2001, Visser & Both 2005
⇧ Caterpillar biomass peak	⇧ Collared flycatcher (*Ficedula albicollis*) egg-hatching	Long-term field study	Hegyi *et al.* 2013

Multitrophic interactions					
⇧ Oak (*Quercus robur*) timing of budburst	⇧ Caterpillar biomass peak	⇧ Passerine species egg-hatching	○ Sparrow-hawk (*Accipiter nisus)* egg-hatching	Long-term field study	Both *et al.* 2009

3.4 Testing predictions for different functional groups

Plant-pollinator interactions

Global warming is a possible factor for pollinator decline (Memmott *et al.* 2007). On average, vascular plants flower one to three days per decade earlier in the northern hemisphere, which significantly affects the start and duration of the pollination season (IPCC 2007b). Shifts in phenology due to rising temperatures may reduce the floral resources for pollinators as suggested in a simulation experiment (Memmott *et al.* 2007).

The documented plant-pollinator studies, examining both levels in parallel, are long-term field studies, comparing current with historic data or base on examinations in warm springs. Evidence for a potential phenological mismatch (decreasing magnitude of overlapping phenology) between plants and pollinators was detected for honey bees (*Apis mellifera*) and a butterfly species (*Pieris rapae*) and their associated plant species (Gordo & Sanz 2005) (Table 3.1). Another plant-pollinator study shows that high levels of biodiversity stabilize the system over time and increase the synchrony between apple peak bloom and an apple bee community (Bartomeus *et al.* 2013) (Table 3.1). However, this synchrony exists only on the community-level, as some bee species of the community fly earlier and some later.

In another long-term study, spring blooming forbs and bee species shifted in phenology towards the start of the year (Burkle *et al.* 2013) (Table 3.1). Just as the previous study some species shifted more than others. The study observed 120 years of plant-pollinator interactions and highlights extinctions, mismatches, shifts in network structure and an alarming amount of only 24% of interactions which are still intact (Burkle *et al.* 2013). Although this study includes a period of time before temperatures increases on a larger scale, the study indicates that bee species are most affected by temperature and forest forbs by different cues. That interacting taxa can response to different phenological cues was also documented in a syrphid fly-plant system (Iler *et al.* 2013) (Table 3.1). Flowering advanced faster than syrphids activity period but the synchrony was still intact as syrphids generally emerged after the start of flowering (Iler *et al.* 2013). For both, the start of the season depended on snow melt (Iler *et al.* 2013). On the contrary, the end of the season was determined by a combination of snow melt, temperature and precipitation (Iler *et al.* 2013).

Two bumble bee studies show different results compared to the previous studies. Earlier spring caused a mismatch in a spring ephemeral herb (*Corydalis ambigua*) and its bumble bee queen pollinators (Kudo & Ida 2013) (Table 3.1). *C. ambigua* generally flowers briefly after snowmelt and predominantly depends on overwintered bumble bee queens (Kudo & Ida 2013). However, first flowering has advanced, probably caused by warm spring temperatures and late soil thawing, whereas bumble bees first appearance did not change, resulting in lower seed production (Kudo & Ida 2013).

In a year with an unusual warm spring the first appearance of bumble bees and the first flowering of herbs and shrubs revealed a phenological mismatch in an alpine region due to soil thawing and warming (Kudo 2014) (Table 3.1). First, flowering was earlier but queen bees` emergence was even ten days ahead of flowering, resulting in slower colony development and delayed worker bee emergence (Kudo 2014). Due to earlier snow-melt, flowering finished two weeks earlier (Kudo 2014). Though, an alpine bumble bee species (*Bombus hypocrita sapporoensis*) responded more flexible and was still in synchrony contrary to the other examined species of the study, which also occur in lower altitudes (Kudo 2014).

The seven studies do not indicate a clear pattern. Neither the trophic rank nor longevity seems to play a decisive role. On the contrary, different cues like temperature, timing of snow melt, precipitation and soil temperature appear to be crucial. Another important factor for pollinators' phenological response is the development stage. When overwintering temperatures were experimentally changed, adults showed different phenological responses than pre-imaginal stages (Fründ *et al.* 2013).

If climatic response is exclusively caused by phenotypic plasticity remains unclear. Though, in a solitary bee species (*Osmia lignaria*) climatic response was demonstrated to be mostly heritable with some acclimatory plasticity (Pitts-Singer *et al.* 2014). On the contrary, in an altitudinal reciprocal transplant experiment, pollinators did not show local adaptation in timing of emergence, suggesting that phenological changes are probably caused by phenotypic plasticity (Forrest & Thomson 2011).

On the one hand, pollinators seems to be extremely vulnerable to climate warming, as high extinction rates were observed and more specialized pollinator species were more affected (Burkle *et al.* 2013). On the other hand, it could be shown that pollinators are less sensitive to climate change, as they can flexible choice their interacting partners and can buffer the plant-pollinator-system to ensure high pollination service (Hegland *et al.* 2009, Willmer 2012, Benadi *et al.* 2014). However, experiments with manipulated flowering phenology revealed reduced visitation rates, when plants flowered earlier (Parsche *et al.* 2011, Rafferty & Ives 2012). This resulted in reduced pollination success compared to plants where phenology was not manipulated (Parsche *et al.* 2011, Rafferty & Ives 2012). Thus, further studies on the species-level, including specialist species, are necessary for better understanding of future phenological responses of plant-pollinator-systems and the underlying mechanisms of plant and insect timing.

Plant-herbivore interactions

Herbivores are restricted to their host plants in terms of diet, distribution and phenology. Therefore they depend on the specific climatic and habitat requirements of their host plants (Villalpando *et al.* 2009). Phenological mismatches of plants and herbivores might have serious consequences in agricultural systems (Gordo & Sanz 2009, Thomson *et al.* 2010). Two agricultural studies reveal an increasing mismatch due to managed agriculture and environmental conditions. For the potato beetle (*Leptinotarsa decemlineata*), shifts in phenology towards the start of the year have been observed, whereas potato sowing by farmers has remained unchanged (Gordo & Sanz 2005) (Table 3.1). Thus potato beetles can cause more economical damage by completing more generations within the growing season. The olive fruit fly (*Bactrocera oleae*) also shifts in phenology towards the beginning of the year, whereas its host plant, the olive tree, shifts at a lower rate (Gordo & Sanz 2005) (Table 3.1).

For plant-phloem feeders inconsistent shifts in phenology patterns were documented. In a manipulation experiment an increase in temperature over one summer season advanced the phenology of an aphid species (*Acyrthosiphon svalbardicum*) and its host plant in parallel (Strathdee *et al.* 1993) (Table 3.1). Thus enhanced temperatures of 2.8°C resulted in higher survival rates of the aphid and in an eleven-fold increased number of overwintering eggs (Strathdee *et al.* 1993). In contrast, another study indicated that under elevated temperatures the phenological synchrony of the development time of the jumping plant lice (*Cacopsylla palmeni, Cacopsylla brunneipennis*) and their host plant dwarf willow (*Salix lapponum*) decreased (Hill & Hodkinson 1992) (Table 3.1). The lice species had lower thermal requirements than catkins of the dwarf willow (Hill & Hodkinson 1992). Interestingly, the three examined lice species of the study showed local adaptation to temperatures: species of higher altitudes had lower thermal requirements than species of lower altitudes (Hill & Hodkinson 1992).

A well-investigated system is the relationship between the winter moth (*Operophtera brumata*) and its host the English oak (*Quercus robur*). Larval development of the winter moth strongly depends on the bud burst of the oak. Asynchrony in egg hatching and bud burst leads to higher mortality rates in caterpillars or to reduced nutritional intake (Visser & Holleman 2001). In a greenhouse experiment increased temperature did not affect the synchronisation between hatching of winter moth and budburst of oak (Buse & Good 1996) (Table 3.1). In contrast poor synchrony has been found in warm springs for the same species under field conditions, as the winter moth eggs hatched before bud burst (Visser & Holleman 2001) (Table 3.1). An explanation for the different results might be that the phenological shift is not related to average temperature, but to days in winter without frost (Visser & Holleman 2001).

Two warming experiments with other moth species reveal a different phenological pattern. The phenology of plants advanced, whereas the forest tent caterpillar moth (*Malacosoma disstria*) advanced less and the broom moth (*Melanchra pisi*) showed delayed larvae emergence (Liu *et al.* 2011, Schwartzberg *et al.* 2014) (Table 3.1). The causes of these trends are unclear but might also be due to experimental conditions. Contrary to the other warming experiments on moth-plant interactions, in the open-top chamber experiment broom moth eggs were not introduced from natural sites (Liu *et al.* 2011). Adult moths were able to fly from chamber to chamber and to natural resources to lay eggs on gentian and anemone plants, even though larvae emergence was delayed (Liu *et al.* 2011). Warming increased larval density 10-fold compared with unwarmed chambers (Liu *et al.* 2011). The experiment reveals a change in host plant preferences and indicates that climate change can result in host plant switching (Liu *et al.* 2011). Larvae normally feed on anemone leaves and gentian usually flowers after peak larvae density, but due to higher experimental temperature larvae caused high damage on the gentian (Liu *et al.* 2011).

In butterfly-plant interactions synchronous as well as asynchronous shifts towards the start of the year were detected. Females of the orange tip butterfly (*Anthocharis cardamines*) preferably lay eggs on the flower of its host plant the garlic mustard (*Alliaria petiolata*) and larvae feed on flowers and siliques. Thus, to match with flowering synchrony is of decisive importance. A long-term study provides evidence that the synchrony of garlic mustard and orange tip butterfly is maintained; however the study was performed before temperature increased dramatically (Sparks & Yates 1997, Harrington *et al.* 1999, Visser & Both 2005). (Table 3.1). In contrast, the highly mobile red admiral butterfly (*Vanessa atalanta*) showed an advanced return date to Britain, while flowering phenology of its host plant has not changed (Sparks *et al.* 2005, Visser & Both 2005) (Table 3.1). In a warming experiment with the brown hairstreak (*Thecla betulae*) and its main larval food plant the blackthorn (*Prunus spinosa*) increasing temperatures of 5°C in the climate chamber did not affect synchrony (de Vries *et al.* 2011) (Table 3.1). However, in one year with an extremely long and cold period, additional field data documented a delay in egg-hatching compared to the timing of budburst (de Vries *et al.* 2011). Days with frost seemed to have more negative effects on butterfly's phenology than climate warming (de Vries *et al.* 2011).

Contrary to our first prediction most examined herbivore species shifted in phenology towards the beginning of the year. For their plant partners this was less frequently the case. One conclusion might be that the trophic rank is less important than differences in longevity within and between trophic levels, but additional studies are necessary to verify the relevance of local adaptation and phenotypic plasticity in plant-herbivore interactions.

Herbivore-parasitoid interactions

The vulnerability of a host to its parasitoid mainly depends on the development time of the larvae, as juvenile stages are most prone to parasitoid attacks (Hicks *et al.* 2007, Desneux *et al.* 2009). Inconsistent results on changes in rates of parasitism with increasing temperature were reported, showing higher (Virtanen & Neuvonen 1999, van Nouhuys & Lei 2004) or lower rates of parasitism in caterpillars (Stireman III *et al.* 2005). But in most studies it remains unclear if phenology is also affected.

Especially in agroecosystems pest management is of particular importance but the phenology of species interactions has been rarely studied and is poorly understood (Welch & Harwood 2014). A ten-year study examined the phenological relationship of the cereal leaf beetle (*Oulema melanopus*), an agricultural pest and its principal enemy, the parasitoid wasp (*Tetrastichus julis*) in warm springs (Evans *et al.* 2013) (Table 3.1). Larvae of the beetle feed on different type of grains and the wasp was introduced in the study region in the late 1980s for biological control (Evans *et al.* 2013). Generally, first hatched larvae of the cereal leaf beetle showed higher parasitism rates (Evans *et al.* 2013). However, in warm springs the beetle revealed delayed larval phenology, whereas the wasp did not shift in phenology, resulting in decreasing rates of synchrony and decreasing rates of parasitism (Evans *et al.* 2013). The phenological shift was probably due to later terminated diapause in beetle adults (Evans *et al.* 2013). A growing risk of pest outbreaks was the result.

In another experimental study higher temperatures led to increased development rates in the butterfly *Euphydryas aurinia*. Butterfly larvae grew more rapidly and showed higher masses at pupation, whereas its parasitic wasp (*Cotesia bignelii*) was not affected (Klapwijk *et al.* 2010) (Table 3.1). Long-term population dynamics have shown that these effects were not sufficient for phenological mismatches in the last 20 years and projected warming does not support future mismatches as there was no correlation between butterfly fluctuations and thermal and sunshine conditions (Klapwijk *et al.* 2010).

According to these two studies, it is difficult to confirm or to reject our predictions but the two studies document that herbivores shifted in phenology in response to increasing temperatures, whereas parasitoids as higher trophic levels did not. It is still unclear whether other cues are crucial for herbivore-parasitoid-synchrony. Another study also documents the impact of temperature and shading: Larvae of the butterfly *Melitaea cinxia* increase their body temperature at earlier spring temperatures due to their dark colour, whereas the development of the white immobile cocoons of their parasitic wasp (*Cotesia melitaearum*) lags behind (van Nouhuys & Lei 2004). In warm springs the generation overlap of both species is more synchronised, the wasps hatch in time to parasitize the host larvae leading to higher mortality rates of larval stages (van Nouhuys & Lei 2004).

Distributional shifts in parasitoids were documented to be not necessarily limited by host availability (Delava *et al.* 2014), which might also apply to phenological shifts. Further studies should investigate, whether host-parasitoid-systems generally show similar phenological shifts as the presented studies or if they shift idiosyncratically (Jeffs & Lewis 2013). Differential responses of host and antagonist species due to climate warming will presumably lead either to pest outbreaks in case of reduced top down control, or alternatively to diminished local populations if top down control is increased.

Herbivore-predator interactions

Predator-prey interactions have been examined in detail for birds and their caterpillar prey. Breeding birds must match their egg-laying with the time when most food can be found, in order for sufficient amounts of insects to be available for the nestlings (Both *et al.* 2009). If birds fail to match egg-laying and hatching with the food supply, they face low prey densities and show decreased fitness (Thomas *et al.* 2001).

Different adaptation strategies were found to compensate for phenological shifts in great tits (*Parus major*). An increasing mismatch in caterpillar biomass peak and egg-laying was detected (Visser *et al.* 1998). Caterpillars shifted in phenology towards the start of the year, while egg-laying of birds did not change accordingly (see also Nussey *et al.* 2005, Husby *et al.* 2009) (Table 3.1). Breeding success was linked with caterpillar abundance, as females' ability to produce a second clutch depends on timing of their first clutch to caterpillar peak abundance (Husby *et al.* 2009). In another study the period between first egg date and food peak also increased, but great tits maintained synchronisation by increasing their incubation period after clutch completion (Cresswell & McCleery 2003) (Table 3.1).

Timing of bird migration is also crucial to maintain synchrony. Birds have to adapt to prey phenology in their breeding grounds as well as to prey phenology in their colder stop-over habitats (Strode 2003). North American wood warblers (Parulidae) did not advance in migration phenology. Synchronisation is further complicated as, based on a thermal model, their main prey, the eastern spruce budworm (*Choristoneura fumiferana*), advanced in phenology on its breeding ground but not in the birds´ colder stop-over habitats (Strode 2003). In the pied flycatcher (*Ficedula hypoleuca*) related pattern was found, with caterpillar phenology shifting to the start of the year, whereas flycatcher arrival did not (Both & Visser 2001). However, the birds' egg-laying dates advanced, although insufficiently to match caterpillar peak abundance (Both & Visser 2001) (Table 3.1).

In a combined long-term field study and manipulation experiment the nestling rearing period was delayed as the caterpillar biomass peak advanced more than egg-hatching date of the collared flycatcher (*Ficedula albicollis*) (Hegyi *et al.* 2013) (Table 3.1). The peak of caterpillar biomass was a response to winter temperatures and the phenological adjustment of the long-distance migratory bird was not sufficient (Hegyi *et al.* 2013). In experimentally mistimed broods the collared flycatcher showed reduced compensatory growth due to phenotypic plasticity (Hegyi *et al.* 2013). Existing studies on birds also document that adaptation to climate change is plastic and not evolutionary, although individual variation in plasticity is heritable and selection can privilege high plastic individuals (Nussey *et al.* 2005, Charmantier & Gienapp 2014).

Different phenological shifts of insects and birds are probably caused by differences in phenotypic plasticity or reflect the responses to different cues (Visser & Both 2005, Donnelly *et al.* 2012, Charmantier & Gienapp 2014). Mismatches might be the consequence of birds' adaptation to photoperiod, while insects might be more affected by temperature (Visser & Both 2005). Furthermore, adaptation to prey phenology can be sex specific, as bird males used experience in caterpillar prey phenology and actual plant phenology for breeding settlement, whereas females did not (Husek *et al.* 2014).

Bird-insect systems provide a good example for predator-prey interactions which are highly sensitive to seasonal changes caused by climate warming. As hypothesised in the trophic cascade and longevity predictions, in most studies the caterpillar prey react faster to rising temperature than their predators. These shifts towards the beginning of the year can lead to mismatches in the following years and might be a critical factor for prey availability (Pearce-Higgins 2011). However there is a lack of studies with other predator species. Invertebrate predators for example were observed to be more available in warmer, lower altitudes and climate warming might increase their level of interaction (Straw *et al.* 2009).

Multitrophic interactions

Complex trophic interactions are suspected to be particularly sensitive to climate warming (Chapin III *et al.* 1997, Tylianakis *et al.* 2008). Changed phenology of the higher trophic level may alter the selection pressure on its prey (Both *et al.* 2009). One study concerns a four-trophic level interaction, combining budburst and caterpillar phenology as first and second trophic level, as well as passerine hatching date and sparrow hawk (*Accipiter nisus*) phenology as third and fourth trophic level (Both *et al.* 2009) (Table 3.1). In accordance with prediction two, short-lived caterpillars adapted rapidly to climate warming, whereas passerines, as the higher trophic level, had lower ability to respond and their predators even less so. This leads to fitness deficits in higher trophic levels (Brook 2009).

A tritrophic study examined rates of parasitism and hyperparasitism in aphids. Even though phenology was not examined, the study highlights the effect of increased temperatures (Romo & Tylianakis 2013). Either higher temperatures or drought had negative top-down effects on aphids. Parasitism rates were higher under warmer conditions, however hyperparasitism were only marginally related to temperature (Romo & Tylianakis 2013). Other multitrophic studies also documented shifts in phenology of one trophic level and increasing density of their interacting insect partners in higher temperatures, but if phenology was also affected, remains unclear (Dong *et al.* 2013, Gillespie *et al.* 2013). Therefore, further studies on complex trophic interactions are needed.

3.5 Conclusion

In this review we show that insects are sensitive bioindicators of climate warming (see also Gordo & Sanz, 2006). In most examined systems insects shifted in phenology towards the start of the year, but shifts were often not synchronised with other trophic levels (almost 75% of interactions). Short-lived insects reacted rapidly to environmental changes, whereas long-lived species like plants and birds lagged behind in about half of the cases. Our prediction that higher trophic level species are more negatively affected by climate warming than lower trophic level species could only be partly confirmed. Most adaptations to climate warming are probably caused by phenotypic plasticity. However, it remains unclear if phenotypic plasticity is sufficient for adaptation to rising temperatures and the assumed increasing interannual variability of future climate (IPCC 2013). The high complexity of adaptations between trophic levels with different life history traits makes generalisations difficult (Dunn *et al.* 2009). Asynchronous shifts might also negatively affect important ecosystem services such as pest control. Our review reveals that a surprisingly low number of studies consider responses at different trophic levels and shifts in biotic interactions in parallel. Therefore, the lack of studies represents an important gap in current knowledge (1) on potential feedbacks of disrupted biotic interactions on distribution range shifts, (2) on the predictive power of life history traits to generalise findings, and (3) on combined effects with other global change drivers.

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CHAPTER 4

Butterfly diversity and historical land cover change along an altitudinal gradient

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4.1 Abstract

Land cover and climate change are both major threats for biodiversity. In mountain ecosystems species have to adapt to fragmented habitats and harsh environmental conditions but so far, altitudinal effects in combination with land cover change have been rarely studied. The objective of this study was to determine the effects of altitude and historical land cover change on butterfly diversity. We studied species richness patterns of butterflies occuring in wetlands and other open habitats along an altitudinal gradient in a low mountain region (340-750 m a.s.l., Bavaria, Germany) with drastic loss of open habitats within the last 40-60 years. We recorded in 27 sites a total of 4,523 individuals of 49 butterfly species and five species of burnet moths. Species richness peaked at mid elevation and increased with patch size. Land cover change was most pronounced at high altitudes, but neither current open habitats, nor the historical loss of open habitats affected the species richness of butterflies. Neither open land specialized butterflies nor generalist and forest species were significantly affected by the loss of open habitats. However, increasing forest area in high altitudes reduces possible refuge open habitats for butterflies at their thermal distribution limits. This could lead to extinction of such butterfly species when temperatures further rise due to global warming.

Keywords

Global change, elevational gradients, landscape structure, species-area relationships

4.2 Introduction

Altitudinal gradients and land cover play an important role in species composition and ecosystem functioning (Ewers & Didham 2006, Körner 2007, Hoiss *et al.* 2012). In mountainous regions insects often have to adapt to fragmented habitats and harsh environmental conditions (Hodkinson 2005, Hoiss *et al.* 2012). As their range margins are determined by environmental and climatic conditions many species fail to adapt to rapidly changing habitat conditions caused by climate and land cover change (Thomas *et al.* 2004, Franco *et al.* 2006, Thuiller 2007).

Altitudinal gradients and land cover change are both important predictors driving biodiversity in patchy habitats (Körner 2007). However most studies focus either on the effect of land cover change or of altitude, while little is known how both effects in parallel affect diversity and resulting extinction risks (Forister *et al.* 2010). As altitudinal gradients are also temperature gradients, species richness-altitude relationships can be explained with two main hypotheses. First, decreasing species richness with increasing altitude is explained by combinations of specific geomorphology, climate and by water-energy limitations along temperature gradients (Clarke & Gaston 2006, Mihoci *et al.* 2011). Second, maximal species richness in mid-elevation occurs due to the mid-domain effect or a combination of temperature effects on competition, metabolism and speciation (Colwell *et al.* 2004, Stegen *et al.* 2009, Stefanescu *et al.* 2011). Additionally, human land cover change might impact elevational species richness gradients (Nogues-Bravo *et al.* 2008).

Habitat loss, land cover change and agricultural intensification led in the past to the decline of insect populations and species richness (Tscharntke *et al.* 2005). Above all habitat loss results in decreasing habitat area and reduced species richness (Rosenzweig 1995, Steffan-Dewenter & Tscharntke 2000). However, in many cases the composition of the surrounding landscape is also crucial for the distribution of species in fragmented habitats by providing additional resources or modifying dispersal (Fahrig *et al.* 2011, Leidner & Haddad 2011, Öckinger *et al.* 2012).

The historical loss of natural or seminatural habitats in the context of land use intensification is a significant cause of biodiversity loss and might lead to delayed extinctions in the future (Kuussaari *et al.* 2009, Krauss *et al.* 2010). So far the impact of land cover change under different climatic conditions has not yet been assessed. Not all species in a community react to climate change and landscape composition in the same way, thus life history traits can facilitate or impede species dispersal and sensitivity to environmental change (Berner *et al.* 2004). Species with narrow feeding niches like habitat specialists are often stronger affected by habitat loss, isolation and land cover changes than generalist species (Tscharntke *et al.* 2012).

Wetlands are species rich habitats for butterflies and have disappeared from many regions in central Europe due to drainage and agricultural improvements (BUWAL 1990, van Swaay *et al.* 2006, Cozzi *et al.* 2008). As wetlands are also vulnerable to climate change (Erwin 2009, Lütolf *et al.* 2009) we studied the effect of altitude and land cover change on butterfly species richness in wetland habitats with focus on species living in open habitats to evaluate the following hypotheses:

(1) Species richness of butterflies and burnet moths depends on altitude, patch size and landscape context.

(2) The historical loss of open habitats leads to lower local species richness.

(3) Effects of land cover change are stronger at high compared to low altitudes.

(4) Open land specialists are more sensitive to decreasing patch size and historical loss of open habitats than generalist and forest species.

4.3 Materials and methods

Study region and sampling sites

The study region is located in the Fichtelgebirge, a low mountain region in northern Bavaria (Germany) close to the border to the Czech Republic and east of the town Bayreuth. The highest peak in the region is 1,051 m a.s.l. We selected 27 wetland sites along an altitudinal gradient (340-750 m a.s.l.), differing in altitude, patch size (area of the surveyed wetland study sites), current open habitats (area of non-forest habitats in the surrounding landscape in a 750 m radius around the centre of each study site) and in historical land cover change (Table S 4.4). We measured at all study sites the temperature (11 June-10 August 2008) with iButtons dataloggers (Maxim Integrated

Products Inc., Sunnyvale, CA, USA) suspended on trees. The average vertical temperature gradient was about 0.7°C/100 m resulting in a climatic range of 2.9°C that represents the expected increase in mean temperature during the next 50-100 years (IPCC 2007).

Study species

Butterflies (Lepidoptera) and burnet moths (Lepidoptera: Zyaenidae) were recorded from April to August 2008. We performed variable visual transect walks per study site to achieve reliable butterfly occurrence data with a minimized influence of seasonal fluctuations (Krauss *et al.* 2003, Westphal *et al.* 2008). All study sites were sampled approximately every second to third week (25 April-22 August 2008), adding up to seven surveys per study site. To ensure a high detectability of species we performed the transects under sunny conditions with temperatures above 13 °C and low wind speed between 10.00 and 17.00 o'clock within a 5 m corridor according to the German butterfly monitoring scheme (for more details see http://www.tagfalter-monitoring.de and Pollard 1977). The transect length of each walk was 800 m and the transect time was 40 min. We measured length and time with a GPS (eTrex Vista; Garmin, München, Germany) and divided the butterfly transects in 50 m sub-transects to calculate species richness estimators.

Identification and nomenclature followed for burnet moths Ebert and Rennwald (1994) and Naumann *et al.* (1999) and for butterflies Settele *et al.* (2005). Most species could be identified in the field, but some species groups had to be collected for genitalization. We did not distinguish between *Colias alfacariensis* and *Colias hyale* or between *Leptidea reali* and *Leptidea sinapis*. With regard to habitat requirements all detected species were grouped according to their habitat specialisation either as wetland specialists, grassland specialists, forest specialists or generalist (Krauss *et al.* 2003, van Swaay *et al.* 2006) (Table S 4.1). As wetland and grassland species are specialists for open habitats, we combined them as open land specialists for further analyses. We also combined generalists and forest species and call them generalist and forest species, because both groups do not only rely on wetland or grassland habitats. Finally the analyses showed no different responses of the species group (see below). In the following the term butterflies includes burnet moths when not stated otherwise.

Five wetland sites were intensively surveyed for butterfly species (except burnet moths) between 1920 and 1979 by several butterfly collectors. These five sites belong to the 27 surveyed sites. The data of the historical records were allocated by the departed butterfly collector Vollrath and digitalized by a local conservation agency GEYER and DOLEK (http://www.geyer-und-dolek.de). We used these historical data of detected species per site for comparison of current and historic species occurrence but not for statistical analyses as butterfly collectors only noted occurrence data and did not perform transects.

Landscape data

Historical and current aerial photographs were used to quantify the amount of open habitats and forest cover within a 750 m radius around the centre of each study site. Current aerial photographs were taken 2008, historical photographs were taken 1945-1966 (40-60 years old). Current digital aerial photographs and historical photographs were bought from ‘‘Bayerische Vermessungsverwaltung’’ (http://www.geodaten.bayern.de/). Historical analog photographs were scanned, orthorectified and transferred to a Geographical Information System (GIS) by the company Gisat (http://www.gisat.cz), while current aerial photographs were available in a GIS compatible form. We used the software ArcView GIS 3.2 (ESRI 1995) to quantify land cover and land cover change.

Statistical analysis

Statistical analyses were made in R 2.14.2 (R Development Core Team 2012). General linear models with Type I SS, linear regressions and Pearson correlations were calculated. We did not simplify our statistical models with a selection procedure, but present the full models (Crawley 2007). Models were checked with plot diagnostics. We could not correct for spatial autocorrelation, as lower sites are closer to each other than higher altitude sites. Therefore the spatial autocorrelation is covered by the altitude. The explanatory variables entered the models in the following sequence (1) altitude, (2) squared altitude, (3) current open habitats, (4) per cent of historical loss of open habitats and (5) patch size (log10-transformed). Although some explanatory variables were correlated we present one general linear model in the results because other analyses showed the same tendencies (Table S 4.3). The response variables were total species richness, estimated total species richness, generalist and forest species richness and open land specialist species richness. Species richness estimators were calculated using the software EstimateS 8.20 (Colwell 2009). We used the species estimator ACE (with 16 transect intervals; one interval per 50 m transect length).

4.4 Results

In total we identified 49 butterfly species and five species of burnet moths on the 27 wetland sites with a total of 4,523 individuals. On average 19.1 ± 1.0 butterfly species (range: 9-31) were found on each of our sites with 46% open land specialists and 54% generalist and forest species. *Aphantopus hyperantus* (23.7%), *Maniola jurtina* (13.7%) and *Melanargia galathea* (8.6%) were the most abundant species (% of all recorded individuals).

Table 4.1 Pearson correlations between the four explanatory variables altitude, current open habitats, historical loss of open habitats and patch size (Significance levels: **** P < 0.0001; *** P < 0.001; n.s. not significant).

	Altitude	Current open habitats	Historical loss of open habitats
Patch size (log10-transformed)	<-0.001 n.s.	-0.171 n.s.	0.076 n.s.
Altitude		-0.624***	0.642***
Current open habitats			-0.827****

Table 4.2 Pearson correlations between the four response variables open land specialists, generalist and forest species, total species richness and estimated total species richness (Significance levels: **** P < 0.0001; *** P < 0.001; ** P < 0.01).

	Generalist and forest species	Total species richness	Estimated total species richness
Open land specialists	0.563**	0.938****	0.847****
Generalist and forest species		0.815***	0.615***
Total species richness			0.852****

Between 1920 and 1979 altogether 60 butterfly species (excluding burnet moths) were recorded in five of our wetlands, whereas we recorded 37 species on these sites. 28 species were not detected in 2008 and could be extinct whereas five species were newly detected. 58% of open land specialists were not detected in 2008 (for not-detected species see Table S 4.1, 4.5).

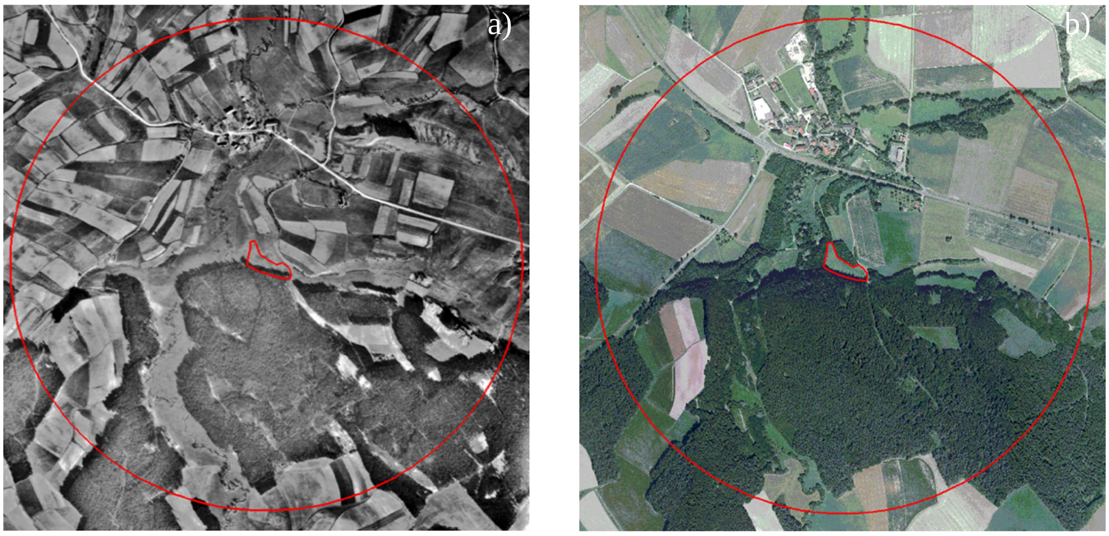

Figure 4.1 Land cover change of one region (750 m radius) with a) wetland study site in the centre (outlined red), aerial photograph: ‘‘Bayerische Vermessungsverwaltung’’, Germany a) in 1945, b) in 2008.

Table 4.3 General linear model, degrees of freedom and P-values for the dependence of species richness of open land specialists with patch size (log10 transformed), altitude and altitude², current open habitats and historical loss of open habitats (significant P-values are presented in bold).

	df	F-value	P-value
Species richness of open land specialists			
Patch size (log10-transformed)	1,21	8.20	**0.009**
Altitude	1,21	0.23	0.638
Altitude^2	1,21	5.36	**0.030**
Current open habitats	1,21	3.27	0.085
Historical loss of open habitats	1,21	1.85	0.188

Land cover change and altitude

The studied wetland sites faced a drastic shift in the surrounding landscape composition during the last 40-60 years. On average one-third (34.1%) of current open habitats within the 750 m radius around the centre of the study sites was transformed and the average gain of forest area compared to earlier forest area was 21.3% (see Figure 4.1 for an example). The current open habitats decreases with increasing altitude and the historical loss of open habitats increased with altitude (Figure 4.2). Thus, land cover change was more pronounced at high compared to low altitudes and in 2008 higher altitudes in the study region were more dominated by forest than 40-60 years ago (Figures. 4.1, 4.2; Table 4.1).

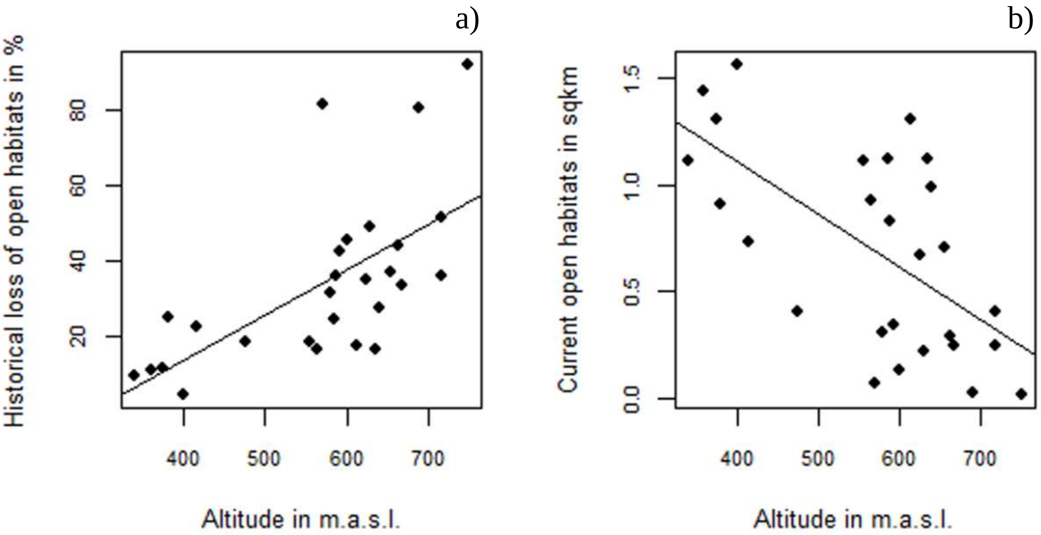

Figure 4.2 Linear regressions. a) Historical loss of open habitats during the past 40-60 years for a landscape radius of 750 m around the wetland study sites increases with increasing altitude ($y = 0.12x - 34.19$; $R^2 = 0.412$; $P < 0.001$, n = 27 sites) and b) current open habitats decrease with increasing altitude ($y = -0.002x + 2.10$; $R^2 = 0.390$; $P < 0.001$, n = 27 sites).

Species richness of butterflies

The results showed that patch size and the squared altitude are significant predictors for species richness of open land specialists, while current open habitats and historical loss of open habitats showed no significant relations with species richness (Table 4.3, Table S 4.2). Species richness increased with increasing patch size. However the significant effect is mainly caused by the largest site in our region (Figure 4.3; Table 4.3). Excluding this site from the analyses would result in a relationship above the significance level (P = 0.057). As altitude and land cover change were correlated we also conducted two separate models, which show the overall same significances (Table S 4.3). Species richness of open land specialists correlated strongly with total species richness, estimated total species richness and species richness of generalist and forest species (Table 4.2). Therefore the results for the different species groups are essentially identical to the species richness of open land specialists (Table 4.3, Table S 4.2 and S 4.3). Graphs are only shown for open land specialists.

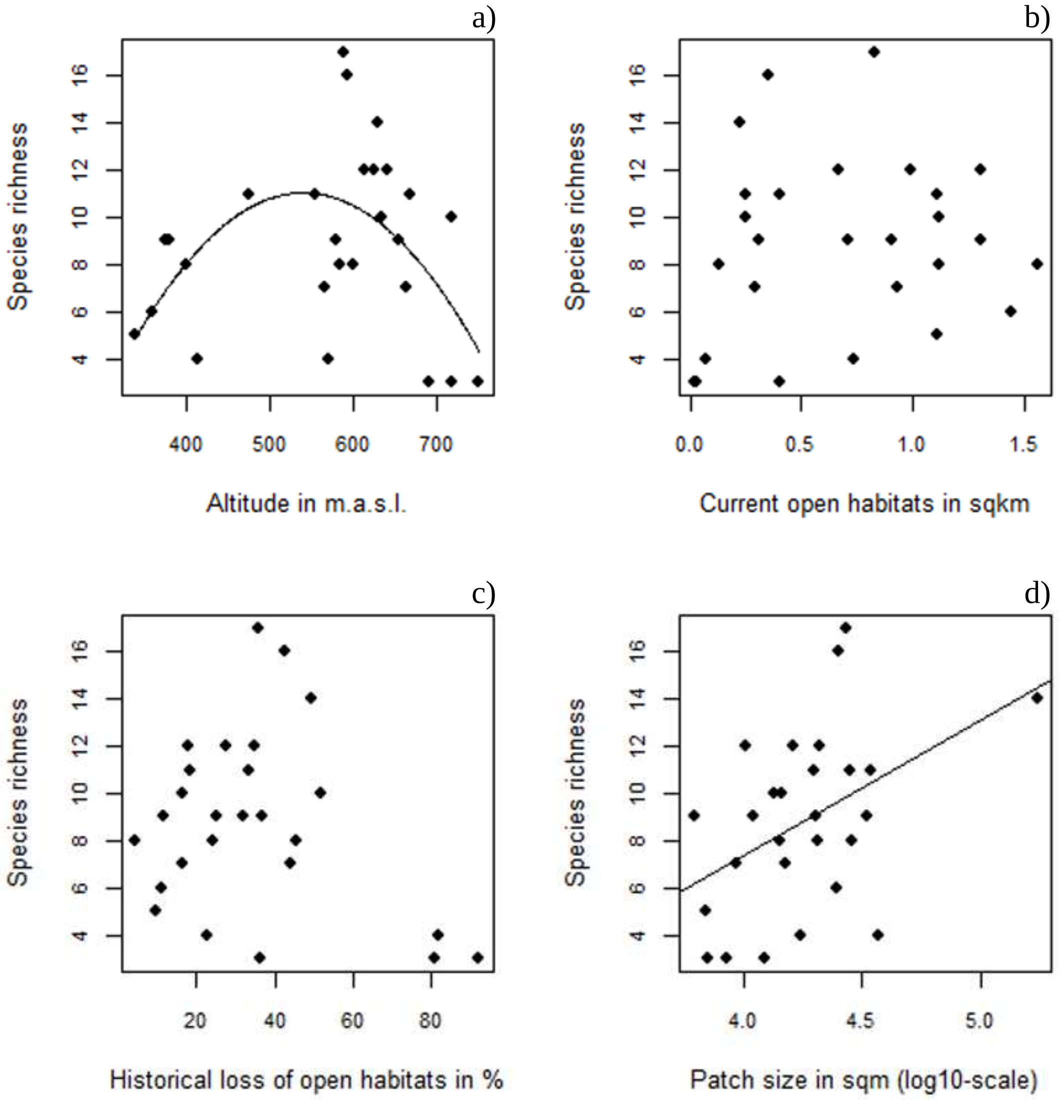

Figure 4.3 Linear regressions. Species richness of open land specialists a) peaks at mid elevation ($y = (-1.53 \times 10^{-4})\ x^2 + 1.66 \times 10^{-1}\ x - 3.38 \times 10^{1}$; $R^2 = 0.283$; P = 0.019, n = 27 sites), but is not related to b) current open habitats in a 750 m radius or c) the loss of open habitats within the last 40-60 years on a 750 m radius scale. However species richness d) increases with patch size ($y = 5.81\ x - 15.89$; $R^2 = 0.206$; P = 0.018; n = 27 sites).

4.5 Discussion

Altitudinal gradient

In our study species richness was highest at mid-elevations, which might be explained by the mid-domain effect and is assumed for landmass boundaries, where restricted species ranges overlap and create a maximum of species richness (Colwell & Lees 2000). Species richness in higher altitudes could be limited by the increasing forest area and reduced metabolic rates of species due to decreasing temperatures. In lower altitudes species richness is assumed to be more strongly affected by habitat destruction and land use change as human agriculture causes less connected and fragmented patches resulting in mosaic habitats which come along with local adaptation strategies of insect-plant interactions (Inouye *et al.* 2000, Nogues-Bravo *et al.* 2008, Scriber 2010).

Accordingly, the amount of open habitats in our study was highest in low altitudes. However, historical land cover change was most pronounced at high altitudes due to the abandonment of extensive agriculture and reforestation resulting in a significant reduction of wetlands and other open habitats that might play an important role as climatic refuges in the future for butterfly species at their upper thermal distribution limits. Other studies already show an up-hill shift of species due to rising temperatures and increasing habitat availability in high mountain ranges (e.g. Fleishman *et al.* 2000, Wilson *et al.* 2007, Franzen & Öckinger 2012). Even in low mountain regions rising temperatures can disturb butterfly species habitats. Especially wetlands as open habitats are extremely vulnerable to changes in water supply and rising temperatures can modify the quantity of moisture of these species rich habitats (Erwin 2009). Accordingly increasing temperatures can reduce habitat quality and species shifting from lower to upper habitats due to changing temperatures might come across unsuitable habitats with changing mountain flora. Environmental adaptation might therefore depend on thermal sensitivity of life history traits of interacting trophic groups (Berg *et al.* 2010).

Hence we showed that altitude is a useful predictor for species richness in low-mountain regions. As climate determines species range margins, rising temperatures can change species distribution and thermal adaptation can lead to shifts in species range margins to higher altitudes and can modify the observed humped-shaped relationship of diversity patterns (Walther *et al.* 2002, Konvicka *et al.* 2003, Franzen & Öckinger 2012).

Landscape context

Land cover change and habitat loss are main drivers for the extinction of species (Krauss *et al.* 2010, Tscharntke *et al.* 2012). In fragmented habitats open habitats facilitate butterfly species dispersal, whereas forests can act as dispersal barriers (Matter *et al.* 2004, Cant *et al.* 2005). Therefore we expected lower species richness in sites with a higher proportion of forest habitat in the landscapes and more severe historical loss of open habitats. Contrary to our hypothesis, species richness did neither increase with increasing current open habitat area nor decrease with increasing historical loss of open habitats.

In our study region, the surrounding of sites at high altitudes was dominated by forest and the amount of current open habitats decreased with increasing altitude. The historical loss of open habitats in the last 40-60 years was also highest at high altitudes. However increasing historical loss of open habitats did not affect butterfly species richness in our study. Whether forest is a barrier for butterflies has been questioned, because forest dominated landscapes are regularly in heterogeneous landscapes with interspersed suitable habitats for butterflies, which might be suitable corridors for species dispersal (Cozzi *et al.* 2008, Öckinger *et al.* 2012, Schultz *et al.* 2012).

Our data provide no direct evidence that land cover change had negative effects on species richness patterns in our study region. However the time periods of responses to land cover change are little known (Kuussaari *et al.* 2009) but a recent study suggests that butterflies rapidly respond to habitat loss and do not face a long extinction debt (Krauss *et al.* 2010). The interpretation that extinctions related to historical land cover change already took place in our study system is supported by the high rates of not detected open land specialists in 2008 compared with historical surveys. Red list species for example *Plebejus optilete* and *Colias palaeno* which occurred in marshes in the past are now extinct throughout the study region.

The positive relationship between species richness and patch size, that was detected for butterflies in previous studies (Peintinger *et al.* 2003, Brückmann *et al.* 2010), was affirmed by our study. Hence patch size is more important than the surrounding landscape. Therefore the conservation of large wetlands should be given priority in our study region.

Specialist, generalist and forest species

Specialized and sedentary butterfly species are less capable to adapt to changing environments (Warren *et al.* 2001). Therefore we assumed that open land specialists are more sensitive to decreasing habitat area and to historical loss of open habitats than generalist and forest species. In our study the species richness of generalist and forest species was strongly correlated with the number of open land specialists and did not show different responses. This is in contrast with other butterfly studies, where specialized and generalized butterflies reacted differently (Forister *et al.* 2010, Stefanescu *et al.* 2011). In our low-mountain study butterfly species respond to changes in patch size independent of their restriction to specific host plants. But under future scenarios the loss of open habitats in combination with increasing temperatures due to climate change can have deviating effects for species communities (Hoiss *et al.* 2012).

4.6 Conclusion

In conclusion, our data emphasize the importance of altitude for butterfly diversity. Species richness was highest at mid-elevations, perhaps explained by the mid domain effect. Contrary to the expectations species richness did not dependent on current open habitats or on the historical loss of open habitats and did not differ for open land specialists or generalist and forest species. But effects of land cover change might act at shorter or longer time periods (Krauss *et al.* 2010). Patch size played an important role for species richness of butterflies and burnet moths which highlights the importance of the protection of large habitats. Importantly, in the context of climate change, the abandonment of extensive land use and reforestation particularly at high altitudes threatens potential future refuge habitats for open habitat specialists and butterfly species at their thermal distribution limits. Regional environmental management schemes should therefore aim to protect first open habitats at high elevations.

4.7 Acknowledgements

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4.9 Supplementary Tables

Table S 4.1 Butterfly species recorded in the 27 study sites classified as generalists, forest, grassland and wetland specialists and our classification as generalist and forest species and open land specialists. Species detected in historical records in the region, but not in 2008 are highlighted with “x”, species not recorded at the same sites, but still in the study region in 2008 are highlighted with “(x)”.

Butterfly species	**Generalist**	**Forest Specialist**	**Grassland specialist**	**Wetland specialist**	**Combined: Generalist and forest species (GF), Open land specialist (O)**	**Not detected species in 2008**
Adscita statices			x		O	
Anthocharis cardamines	x				GF	
Apaturia iris		x			GF	x
Aphantopus hyperantus			x		O	
Aporia crataegi	x				GF	
Araschnia levana	x				GF	
Argynnis adippe			x		O	x
Argynnis aglaja			x		O	
Argynnis paphia		x			GF	
Boloria aquilonaris				x	O	(x)
Boloria dia			x		O	x
Boloria eunomia				x	O	
Boloria euphrosyne			x		O	(x)
Boloria selene				x	O	
Brenthis ino				x	O	
Callophrys rubi	x				GF	x
Caterocephalus palaemon	x				GF	
Celastrina argiolus	x				GF	
Coenonympha glycerion			x		O	
Coenonympha pamphilus	x				GF	
Coenonympha tullia				x	O	x
Colias crocea	x				GF	
Colias hyale/alfacariensis			x		O	
Colias palaeno				x	O	x
Cupido argiades			x		O	x
Euphydryas aurinia			x		O	x
Erebia ligea		x			GF	x
Erebia medusa			x		O	
Erynnis tages			x		O	x
Glaucopsyche alexis			x		O	x
Gonepteryx rhamni	x				GF	
Hesperia comma			x		O	x
Issoria lathonia	x				GF	x
Lasiommata maera	x				GF	
Lasiommata megera			x		O	
Leptidea sinapis/reali			x		O	
Limenitis populi		x			GF	x
Lycaena alciphron				x	O	
Lycaena hippothoe				x	O	
Lycaena phlaeas			x		O	
Lycaena tityrus			x		O	(x)
Lycaena virgaureae				x	O	(x)
Maniola jurtina	x				GF	
Melanargia galathea			x		O	
Melitaea athalia				x	O	
Melitaea diamina				x	O	
Melitaea cinxia			x		O	x
Nymphalis antiopa		x			GF	
Nymphalis c-album	x				GF	
Nymphalis io	x				GF	
Nymphalis urticae	x				GF	x
Ochlodes sylvanus	x				GF	
Papilio machaon			x		O	(x)
Pararge aegeria		x			GF	

Butterfly species	**Generalist**	**Forest Specialist**	**Grassland specialist**	**Wetland specialist**	**Combined: Generalist and forest species (GF), Open land specialist (O)**	**Not detected species in 2008**
Pieris brassicae	x				GF	
Pieris napi	x				GF	
Pieris rapae	x				GF	
Polyommatus amandus			x		O	(x)
Polyommatus eumedon			x		O	
Polyommatus icarus	x				GF	
Polyommatus semiargus	x				GF	x
Polyommatus thersites			x		O	
Plebeius argus			x		O	x
Plebeius optilete				x	O	x
Pyrgus alveus			x		O	x
Pyrgus malvae	x				GF	x
Satyrium w-album		x			GF	
Thymelicus lineola			x		O	
Thymelicus sylvestris	x				GF	
Vanessa atalanta	x				GF	
Vanessa cardui	x				GF	(x)
Zygaena filipendulae	x				GF	
Zygaena lonicerae			x		O	
Zygaena trifolii				x	O	
Zygaena viciae			x		O	

Table S 4.2 General linear models for a) total species richness, b) species richness of generalist and forest species and c) estimated total species richness in relation to patch size (log10 transformed), altitude and altitude², current open habitats and historical loss of open habitats (significant P-values are presented in bold).

	df	F-value	P-value
(a) Total species richness			
Patch size (log10-transformed)	1,21	10.33	**0.004**
Altitude	1,21	0.16	0.691
Altitude^2	1,21	9.00	**0.007**
Current open habitats	1,21	0.67	0.423
Historical loss of open habitats	1,21	1.87	0.186
(b) Species richness of generalist and forest species			
Patch size (log10-transformed)	1,21	7.34	**0.013**
Altitude	1,21	3.24	0.086
Altitude^2	1,21	9.94	**0.005**
Current open habitats	1,21	1.43	0.245
Historical loss of open habitats	1,21	0.82	0.375
(c) Estimated total species richness			
Patch size (log10-transformed)	1,21	7.71	**0.011**
Altitude	1,21	0.05	0.825
Altitude^2	1,21	5.99	**0.023**
Current open habitats	1,21	2.62	0.120
Historical loss of open habitats	1,21	0.56	0.462

Table S 4.3 General linear models for a) species richness of open land specialists, b) total species richness c) species richness of generalist and forest species and d) estimated total species richness in relation to patch size (log10 transformed), altitude and altitude² and with patch size, current open habitats and historical loss of open habitats (significant P-values are presented in bold).

	df	F-value	P-value
(a) **Species richness of open land specialists**			
(Model 1)			
Patch size (log10-transformed)	1,23	7.22	**0.013**
Altitude	1,23	0.20	0.658
Altitude^2	1,23	4.72	**0.040**
(Model 2)			
Patch size (log10-transformed)	1,23	6.75	**0.016**
Current open habitats	1,23	1.66	0.211
Historical loss of open habitats	1,23	1.43	0.244
(b) **Total species richness**			
(Model 1)			
Patch size (log10-transformed)	1,23	10.10	**0.004**
Altitude	1,23	0.16	0.694
Altitude^2	1,23	8.80	**0.007**
(Model 2)			
Patch size (log10-transformed)	1,23	8.71	**0.007**
Current open habitats	1,23	1.49	0.235
Historical loss of open habitats	1,23	3.07	0.093
(c) **Species richness of generalist and forest species**			
(Model 1)			
Patch size (log10-transformed)	1,23	7.26	**0.013**
Altitude	1,23	3.21	0.087
Altitude^2	1,23	9.84	**0.005**
(Model 2)			
Patch size (log10-transformed)	1,23	5.49	**0.028**
Current open habitats	1,23	0.38	0.545
Historical loss of open habitats	1,23	3.88	0.061
(d) **Estimated total species richness**			
(Model 1)			
Patch size (log10-transformed)	1,23	7.34	**0.013**
Altitude	1,23	0.05	0.829
Altitude^2	1,23	5.70	**0.026**
(Model 2)			
Patch size (log10-transformed)	1,23	6.50	**0.018**
Current open habitats	1,23	1.79	0.195
Historical loss of open habitats	1,23	0.67	0.422

Table S 4.4 Geographic coordinates in decimal degrees of the 27 wetland sites along an altitudinal gradient (340 m - 750 m a.s.l., mean values) in the Fichtelgebirge, a low mountain region in northern Bavaria (Germany) close to the border to the Czech Republic and east of the town Bayreuth.

No.	Site	Altitude	Latitude, Longitude
1	Zeitelmoos	630	50.053081, 11.970030
2	Ochsentränke	580	49.989392, 12.180424
3	Reuth	585	50.183349, 12.150166
4	Häuselloh	570	50.151494, 12.178454
5	Egertal	475	50.119487, 12.158898
6	Niederlamitzerhammer	600	50.166057, 11.998417
7	Hütten	718	50.005487, 11.820899
8	Torfmoorhölle	668	50.095672, 11.822779
9	Kreuzstein	750	49.965925, 11.802317
10	Wolfsbach	415	49.898546, 11.609412
11	Katzeneichen	400	50.008544, 11.642487
12	Bad Berneck	360	50.042453, 11.635518
13	Brandholz	690	50.021315, 11.746646
14	Röslau	565	50.088255, 11.988215
15	Selb Sommermühle	555	50.173796, 12.159853
16	Geiersberg	718	50.012704, 11.797574
17	Tröstau	593	50.004317, 11.944885
18	Wunsiedel	613	50.045883, 11.988260
19	Destuben	375	49.910668, 11.581672
20	Heinersgrund	340	50.009945, 11.580274
21	Lehen	380	49.907006, 11.663847
22	Neugrün	640	49.988753, 11.844254
23	Nagel	588	49.972899, 11.920034
24	Kornbach	635	50.092621, 11.798878
25	Bischofsgrün	655	50.055580, 11.814217
26	Fuchsmühlwiese	663	50.153159, 11.925028
27	Weißenstadt	625	50.084255, 11.897951

Table S 4.5 Butterfly species recorded in the 27 study sites (patches 1-27). The five grey-highlighted patches were surveyed for butterfly species between 1920 and 1979 and in 2008. Others were only surveyed in 2008. Butterflies only detected in historical records were highlighted with (○), only detected in 2008 with (●). Species detected in historical records and in 2008 were highlighted with (x).

Patch / Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Adscita statices	●	●						●									●					●	●			●	
Anthocharis cardamines	x		○		●	●		●	●	●							●	●			●	●	●			●	
Apaturia iris	○		○																								
Aphantopus hyperantus	x	●	●	x	x	●	●	●		●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Aporia crataegi	●	●	●			●	●	●	●	●		●	●	●		●	●						●		●	●	●
Araschnia levana	●	x	●	●	x	●			●					●	●	●					●		●				
Argynnis adippe		○																									
Argynnis aglaja	x	●	●		●	●	●	●					●	●	●	●	●	●			●	●	●	●	●	●	●
Argynnis paphia	●	○																			●						
Boloria aquilonaris	○		○	○		●			●																		●
Boloria dia			○		○																						
Boloria eunomia														●													●
Boloria euphrosyne																		●									
Boloria selene	x	○			○	●		●							●		●					●	●	●			●
Brenthis ino	○	●	●		●		●	●		●	●	●			●		●	●	●	●	●	●		●	●	●	●
Callophrys rubi	○			○	○																						
Caterocephalus palaemon	○		●	○	x						●				●					●							●
Celastrina argiolus		○	○	●		●																					
Coenonympha glycerion	x		●		x		●	●							●		●		●			●	●	●	●		●
Coenonympha pamphilus			●				●			●	●	●						●	●	●	●	●	●	●	●		
Coenonympha tullia	○		○																								
Colias crocea		●									●								●				●				
Colias hyale/alfacariensis												●		●					●			●	●	●	●		
Colias palaeno	○		○	○																							
Cupido argiades			○		○																						
Erebia ligea	○				○																						
Erebia medusa	x	○			○	●	●	●						●	●		●					●	●	●			●
Erynnis tages		○		○																							
Euphydryas aurinia	○				○																						
Glaucopsyche alexis		○																									
Gonepteryx rhamni	x	x		●	●	●		●		●	●	●			●	●	●	●	●	●	●	●	●	●	●	●	●
Hesperia comma			○																								
Issoria lathonia	○	○																									
Lasiommata maera	x	●		x	x	●									●	●	●									●	
Lasiommata megera	●	●	●		●										●		●	●					●			●	
Leptidea sinapis/reali	○	x		○	●						●	●					●	●	●	●	●		●				
Limenitis populi	○	○																									
Lycaena alciphron	x			○	●		●								●			●						●			●
Lycaena hippothoe	x		○	○	●		●										●	●				●	●	●			
Lycaena phlaeas				●	○		●										●					●	●		●		
Lycaena tityrus				○	○							●									●				●		

Patch **Species**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**
Lycaena virgaureae	○	○		○	○										●												
Maniola jurtina	x	●	●		●	●	●	●		●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	
Melanargia galathea	x	●	●	○	●	●		●	●	●	●	●		●	●		●	●	●	●	●		●			●	●
Melitaea athalia	x	x		x	x		●	●		●			●			●	●						●				
Melitaea cinxia			○																								
Melitaea diamina	x		●		○			●			●						●						●				
Nymphalis antiopa	x				○																			●			
Nymphalis c-album	○	○		●																							
Nymphalis io	●	x	●	●	x	●		●		●	●		●	●	●		●	●	●	●	●	●	●	●	●	●	●
Nymphalis urticae		○		○	○																						
Ochlodes sylvanus	x	●	●	x	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Papilio machaon	○																		●		●		●				
Pararge aegeria	○	○		●	x								●			●	●						●		●	●	
Pieris brassicae	○		●	○				●						●	●		●	●				●			●		
Pieris napi	x	●	●	●	x	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Pieris rapae	●				●			●	●	●	●	●			●		●	●		●	●		●		●	●	●
Plebeius argus	○			○																							
Plebeius optilete	○		○	○																							
Polyommatus amandus	○	○	○	○	○													●									
Polyommatus eumedon											●																
Polyommatus icarus	x	x	○	○		●				●		●					●	●	●	●	●				●		
Polyommatus semiargus	○	○	○		○																						
Polyommatus thersites																			●								
Pyrgus alveus	○		○																								
Pyrgus malvae	○	○			○																						
Satyrium w-album														●													
Thymelicus lineola	x	●	●	●	x	●	●	●	●		●	●			●		●	●	●	●	●	●	●	●	●	●	●
Thymelicus sylvestris	x	●	●	●	●	●	●	●		●	●	●		●	●		●	●	●	●	●	●	●	●	●	●	●
Vanessa atalanta	○	○		●				●						●							●						
Vanessa cardui	○	○		○																			●				
Zygaena filipendulae																			●						●		●
Zygaena lonicerae														●													
Zygaena trifolii	●					●											●	●				●	●		●		●
Zygaena viciae											●										●						

CHAPTER 5

Changes in the life history traits of the European Map butterfly, Araschnia levana (Lepidoptera: Nymphalidae) with increase in altitude

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5.1 Abstract

Climatic conditions can modify the life history traits, population dynamics and biotic interactions of species. Therefore, adaptations to environmental factors such as temperature are crucial for species survival at different altitudes. These adaptive responses, genetically fixed or plastic (phenotypic plasticity), can be determined by physiological thresholds and might vary between sexes. The objective of this study was to determine whether the life history traits of the European Map butterfly (*Araschnia levana*) differ at different altitudes. A field experiment was carried out along an altitudinal gradient from 350 to 1010 m a.s.l. in a low mountainous region (Bavaria, Germany). 540 butterfly larvae were placed at different altitudes in 18 planted plots of their larval host plant, the stinging nettle (*Urtica dioica*). After three weeks the larvae were collected and reared under laboratory conditions. Developmental traits of the butterflies, mortality and percentage parasitism were measured. Larval development was generally slower at higher altitudes and lower temperatures and larval weight decreased with increasing altitude and decreasing temperature. However, there were no significant differences in pupation, adult lifespan and percentage mortality at the different altitudes and temperatures. Female larvae were heavier than those of males, and the pupal and adult lifespans were longer in females than in males. However, male and female butterflies reacted similarly to altitude and temperature (no significant interactions). None of the 188 larvae collected were parasitized. In conclusion, the phenotypic plasticity of European Map butterfly has enabled it to adapt to different temperatures, but the strategies of the sexes did not differ.

Key words

Nymphalidae, *Araschnia levana*, global change, altitudinal gradients, trophic interactions, geographical synchronisation

5.2 Introduction

Environmental and climatic conditions determine the limits of the ranges of many plant and animal species (Warren *et al.* 2001, Franco *et al.* 2006, Parmesan 2006). Increasing temperatures, caused by climate warming, can modify species life history traits and may result in reduced or enhanced species survival (Bale *et al.* 2002). If species specific tolerances to temperature are exceeded, the phenology of plants and animals or their distribution will change or they will go extinct (Parmesan & Yohe 2003, Root *et al.*, 2003, Primack *et al.* 2009). Therefore, species might expand their ranges into cool regions, polewards or move to higher altitudes (Wilson *et al.* 2007, Merrill *et al.* 2008). Life history traits can facilitate or impede species migration and shifts in geographic distribution (Berner *et al.* 2004).

Insects, especially, should be affected by temperature, because of their short life cycles, ectothermic physiology and often low dispersal ability (Bourn & Thomas 2002). Increasing temperature can cause physiological changes in insects, like deviations in diapause or dormancy. In mountainous regions insects often have to adapt to fragmented habitats and harsh environmental conditions (Hodkinson 2005). Therefore rapid changes in mountain communities can be expected as the climate changes (McCarty 2001). However, there are only a few altitudinal studies on the effect of temperature on insects (e.g. Karl *et al.* 2008). Recent studies show that insects at higher altitudes adapt to lower temperatures by having fewer instars and generations per year (Hodkinson 2005). Enhanced adaptation to local climate and altitude can be facilitated by high phenotypic plasticity (Karl *et al.* 2008). Alpine species of insects, for example, are often better adapted to low temperatures than widespread species (Buse *et al.* 2001). Body size can increase with increasing altitude (Angilletta & Dunham 2003, Karl & Fischer 2008) and species fitness can decrease at low temperatures (Hodkinson 2005).

Extreme environmental conditions have different effects on different trophic levels (Schweiger *et al.* 2010). At high altitudes insects like parasitoids have to adapt to both host dynamics and to harsh environmental conditions, which might result in a decrease in the rates of parasitisation (Both *et al.* 2009, Holt & Barfield 2009). Slower development of host species in colder habitats also increases the time for which they are vulnerable and can result in an increased risk of predation and parasitism, according to the slow-growth-high-mortality hypothesis (Benrey & Denno 1997).

Most altitudinal studies on the effects of temperature are laboratory based (e.g. Karl *et al.* 2008). Field studies on the relation between altitude and life history parameters are still rare, but of particular importance since individuals live in the context of complex environmental and trophic interactions. The aim of this experimental field study is to disentangle potential effects of altitudinal gradients on the life history of *Araschnia levana* and its hostparasitoid interactions. The butterfly *A. levana* is a good model species as it extended its distribution over the last few decades (Parmesan *et al.* 1999, Parmesan 2001, Konvicka *et al.* 2003) and therefore the butterfly and interacting species might not be optimally adapted and synchronized. *A. levana* occurs naturally along the whole altitudinal gradient in the study region and because it is bivoltine it is easily reared. Developmental time, mortality and percentage parasitism of larvae placed in experiment plots along an altitudinal gradient were measured. It was hypothesized that: (1) butterflies reared at high altitudes will take longer to develop, be lower in weight and fewer will survive because of the more unsuitable climatic conditions there, compared to low altitudes and that (2) fewer of the butterfly larvae transferred to high altitude sites will be parasitized than of those transferred to low altitude sites.

5.3 Material and methods

Study region and experimental sites

The study region is located in the nature park Fichtelgebirge, a low-mountain region in northern Bavaria (Germany) close to the boarder with the Czech Republic east of the German town Bayreuth. The altitude ranges up to 1051 m a.s.l. Eighteen sites, covering the whole altitudinal gradient from about 350 up to 1010 m, were selected. The sites were located in fields next to forest and shrubs, where *A. levana* populations occurred naturally. At each of the 18 sites patches of the main larval food plant of *A. levana*, nettle *Urtica dioica*, were established.

Experimental design

In October and November 2008 1 m^2 sized patches of *U. dioica* were established at each of the 18 study sites by planting four pots of *U. dioica*. Study sites were located next to natural *U. dioica* patches. To assure that the larval food plants had the same phenological and genetic background commercially available seeds (Appels Wilde Samen, Darmstadt, Germany) were used. In contrast to vegetatively reproduced plants the seeds have the advantage that they are homogenous and allow fast and repeatable growing of one genetically homogenous cultivar. Seedlings were reared in a greenhouse and each planted in a 10 l plant pot containing potting soil with osmocote fertiliser (0.3%). After six months in the greenhouse the plants were transferred to the field. When necessary the plants at the study sites were protected from large herbivores by surrounding the patches with wire mesh fences. The nettles were initially watered. To obtain the average temperatures along the altitudinal gradient the temperature every second hour at each of the 18 nettle sites along the altitudinal gradient (06 June - 08 July 2009) was measured using iButtons dataloggers (Maxim Integrated Products Inc., Sunnyvale, CA, USA).

Study species

The European Map butterfly *Araschnia levana* (Linnaeus 1758) (Lepidoptera: Nymphalidae) is a widespread species in Europe and has recently expanded its range in all directions and colonized higher altitudes (Parmesan *et al.* 1999, Parmesan 2001, Konvicka *et al.* 2003). The species occurs naturally in the Fichtelgebirge and has two polymorphic generations per year (in the intensive surveys carried out in 2008, spring and summer generations were detected up to 800 m; Wagner unpublished data). A partial third generation is possible in warmer regions in southern Germany and is recorded only for places below 400 m a.s.l. (Ebert & Rennwald 1991). The generations of *A. levana* in spring and summer differ in wing colour (Fric & Konvicka 2002). The larval host plant of *A. levana* is the stinging nettle, *U. dioica*, but it might also feed on other Urtica species (Ebert & Rennwald 1991). The butterfly lays eggs in long strings on the underside of nettle leaves, where the larvae develop in groups of between 10-30 individuals until the last larval stage. In the field pupae are rarely found on the larval host plant, perhaps because the larvae disperse from the host plant before pupating (Ebert & Rennwald 1991). Most of the parasitoids of butterflies attack the first or second instar larvae and emerge from the fifth instar or pupae (see for example Brückmann *et al.* 2011). Parasitoids recorded from *A. levana*, are the two ichneumonids *Apechthis compunctor* and *Thyrateles camelinus*, and the tachinids *Bactromyia aurulenta*, *Compsilura concinnata*, *Phryxe nemea*, *Phryxe vulgaris* and *Sturmia bella*

(Hertin & Simmonds 1976). Other parasitoids e.g. braconids are also commonly recorded parasitizing butterflies (Hertin & Simmonds 1976).

In March 2009 15 first generation individuals of *A. levana* were caught at a location about three kilometres from the nearest study site (300 m a.s.l., 49°54´N, 11°40´E). This location was chosen as the individuals there are probably similar genetically to the natural populations in the study region. To encourage the butterflies to reproduce they were kept in a climate chamber (22°C, 16L : 8D). As it was unknown whether the females had already mated in the field, both males and females were placed together in a cage (50 × 50 × 70 cm) with *U. dioica,* flowering plants, sucrose solution and water, which are the optimum conditions for reproduction. Females were allowed to deposit eggs on the nettles. To synchronize egg hatching, the eggs were collected and kept at 14°C (16L : 8D). Afterwards the eggs were kept at 22°C (16L : 8D) to induce hatching. The first and second instar larvae were randomly distributed between the experimental nettle patches at the study sites in the Fichtelgebirge (09 - 10 June 2009). 30 larvae were put on the nettles at each site. After three weeks (01 - 02 July 2009) the larvae were collected and were in the fourth to fifth instar, but had not yet pupated. Therefore, the larvae could have been attacked by parasitoids but they would not have emerged before collection (Brückmann *et al.* 2011). The larvae spent three weeks in the field and adapted to the climatic conditions at the study sites before they were collected and transferred in the laboratory. These larvae were placed individually in boxes (125 ml) with moistened filter paper and leaves of *U. dioica* (22°C, 16L : 8D). When necessary the boxes were supplied with new leaves. The weights (in mg) of the larvae (directly after collecting) and pupae (one day after pupation) and the larval development time from collection in the field to pupation in the laboratory (in days) and the time spent in the pupal stage, were recorded . The butterflies that emerged from the pupae were placed in boxes (1 l) and provided with sucrose solution and water. Adult life span was recorded (in days from emergence to natural death). Percentage mortality of the 30 larvae transferred to each site and percentage mortality which occurred after collecting the larvae and prior to adult emergence in the laboratory was calculated for each site. Sex was determined after the adults emerged from the pupae.

5.4 Statistical analyses

The statistical analyses were conducted in R (v. 2.10.1). Linear mixed effect models (library nlme; Pinheiro *et al.* 2010) with a maximum likelihood method were calculated with the fixed effects sex at first position and either temperature or altitude at the second position plus the interaction between sex × altitude or sex × temperature. As it was not possible to determine the sex of all the individuals due to mortality during development, the analyses were carried out with and without sex as a fixed factor. However, the results were consistent and only the data with sex as a cofactor is presented. The following 7 response variables were recorded: (1) larval weight, (2) pupal weight, (3) larval development time from collecting to pupation, (4) duration of pupation, (5) adult lifespan (6) percentage larval mortality in the field and (7) percentage larval mortality in the laboratory. Percentage larval mortality for each site was arcsinsqrt transformed. As the mortality rates are a single value at each site and the sex of the individuals that died was unknown, simple regressions with altitude and temperature were calculated.

5.5 Results

Temperature decreased with increase in altitude ($y = -0.0059x + 20.13$; $R^2 = 0.885$; $P < 0.001$; $N = 18$ sites), which confirms that both altitude and temperature can be used as alternative explanatory variables.

Mortality and percentage parasitism

Of the 540 larvae placed at the 18 sites along an altitudinal gradient a total of 188 larvae were found and collected from 16 sites after 3 weeks. At two of the sites no larvae were found. Thus, the average percentage mortality of larvae per site is 65%. Percentage larval mortality did not change significantly with temperature or altitude, even though there was a tendency for the percentage mortality to increase in the field with increase in temperature (Table 5.1). No parasitoids emerged from the butterfly larvae.

Table 5.1 Mean ± SE (arithmetic means and standard errors of back-transformed data), test-statistic, degrees of freedom and P-values for the life history traits of the European Map butterfly (*Araschnia levana*). The dependence on altitude and temperature is shown (significant P-values are presented in bold). Sex was used as an additional fixed factor for larval and pupal weight, larval development time, pupal and adult life span. Percentage mortality at each site was related to temperature and altitude.

	mean ± SE	test-statistic	N	P
Larval weight (mg)	72.03 ± 3.48		156	
Females	78.63 ± 5.54		76	
Males	65.76 ± 4.19		80	
Altitude				
Sex		$F_{1,140}$ = 4.20	156	**0.042**
Altitude		$F_{1,13}$ = 9.83	15	**0.008**
Temperature				
Sex		$F_{1,140}$ = 4.35	156	**0.039**
Temperature		$F_{1,13}$ = 18.96	15	**< 0.001**
Pupal weight (mg)	129.41 ± 1.31		156	
Females	140.01 ± 1.59		76	
Males	119.34 ± 1.28		80	
Altitude				
Sex		$F_{1,140}$ = 104.35	156	**< 0.001**
Altitude		$F_{1,13}$ = 3.39	15	0.089
Temperature				
Sex		$F_{1,140}$ = 106.66	156	**< 0.001**
Temperature		$F_{1,13}$ = 6.69	15	**0.023**
Larval development time (days)	7.93 ± 0.19		155	
Females	8.14 ± 0.26		76	
Males	7.72 ± 0.26		79	
Altitude				
Sex		$F_{1,139}$ = 6.88	155	**0.010**
Altitude		$F_{1,13}$ = 10.58	15	**0.006**
Temperature				
Sex		$F_{1,139}$ = 6.71	155	**0.011**
Temperature		$F_{1,13}$ = 19.27	15	**< 0.001**
Pupal life span (days)	11.26 ± 0.07		155	
Females	11.51 ± 0.09		76	
Males	11.01 ± 0.09		79	
Altitude				
Sex		$F_{1,139}$ = 13.93	155	**< 0.001**
Altitude		$F_{1,13}$ = 0.15	15	0.709
Temperature				
Sex		$F_{1,139}$ = 13.95	155	**< 0.001**
Temperature		$F_{1,13}$ = 0.37	15	0.556
Adult life span (days)	23.52 ± 0.97		156	
Females	27.32 ± 1.56		76	
Males	19.91 ± 1.03		80	
Altitude				
Sex		$F_{1,140}$ = 16.10	156	**< 0.001**
Altitude		$F_{1,13}$ < 0.01	15	0.990
Temperature				
Sex		$F_{1,140}$ = 16.10	156	**< 0.001**
Temperature		$F_{1,13}$ = 0.20	15	0.661
Mortality in the field				
Altitude		$F_{1,16}$ = 2.91	18	0.107
Temperature		$F_{1,16}$ = 4.15	18	0.059
Mortality in the laboratory				
Altitude		$F_{1,13}$ = 0.13	15	0.724
Temperature		$F_{1,13}$ = 0.10	15	0.757

Life history traits

There was a strong relationship between altitude/temperature and the weight of the butterfly larvae (Table 5.1; Figure 5.1a) and between altitude/temperature and length of larval development (Table 5.1; Figure 5.1b), whereas other life history parameters were not associated with altitude or temperature (all $P > 0.1$; Table 5.1). All the traits of the female and male larvae differed significantly. Female larvae and pupae were heavier than those of males (Table 5.1). Females lived longer than males and took longer to develop and spent longer in the pupal stage (Table 5.1). None of the interactions between sex × altitude or sex × temperature had a significant effect on the life-histories (all $P > 0.05$).

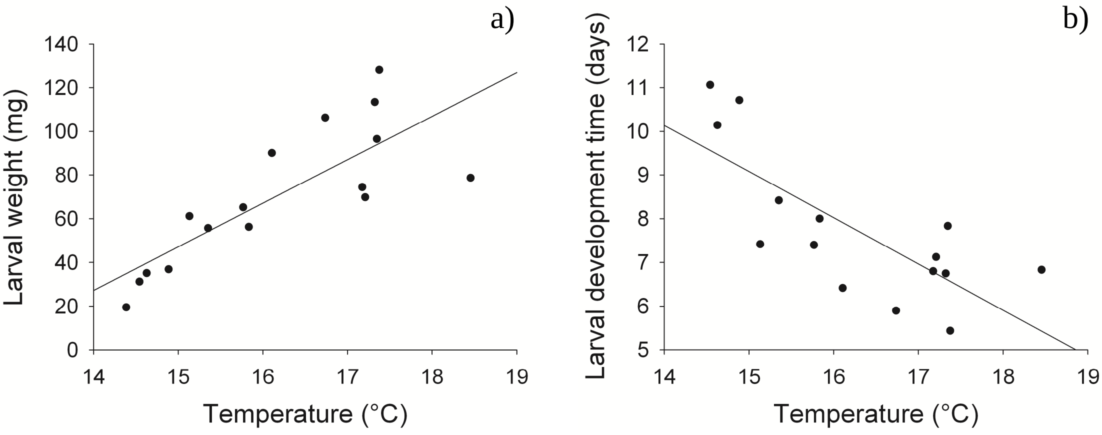

Figure 5.1 Relationship between life history traits of the European Map butterfly (*Araschnia levana*) and temperature: a) mean larval weight for each site ($y = 19.91x - 251.54$; $R^2 = 0.642$; $P < 0.001$; N = 16 sites); b) mean larval development time (from collecting to pupation) for each site ($y = -1.06x + 24.93$; $R^2 = 0.570$; $P = 0.001$; N = 15 sites).

5.6 Discussion

As cited in the literature there was a decrease of 0.6°C for every 100 m increase in altitude (e.g. Rolland 2003). As predicted, the life history traits of the European Map butterfly (*Araschnia levana*) changed with increase in altitude and decrease in temperature. Life histories of females and males differed, but did not interact with altitude or temperature. Comparison of the associations between life history traits with altitude and temperature, revealed that the association with temperature was higher than with altitude, which indicates the usefulness of measuring temperature in addition to altitude at each location.

Mortality and percentage parasitism

Species are restricted to defined climatic envelopes (Walther *et al.* 2002). If climate becomes less favourable, deviations from the optimal temperature can result in increased mortality (Alonso 1999, Karban & Strauss 2004). Therefore, an increase in mortality with increase in altitude was expected. However, there were no significant negative associations between percentage mortality and increase in altitude and decrease in temperature. This might be because the larvae collected from the field were all reared under the same temperature conditions.

As the species richness of insects generally decreases with increase in altitude and increase in harshness of the climatic conditions at high altitudes (Begon *et al.* 1996) it was assumed that percentage parasitism would be lower at the higher altitudes. However, none of the larvae collected were parasitized, even those collected at low altitudes. In theory, less favourable conditions and longer development times of the host lead to increased percentage parasitism (Benrey & Denno 1997), but at this study site only bottom-up effects controlled the system and top-down-control by parasitoids did not occur. Larval development is more strongly determined by host plant quality and abiotic environmental factors (bottom-up control) than by top down control (Hunter *et al.* 1997). The fact that the *A. levana* larvae were not parasitized might not be due to the absence of parasitoids, but due to the parasitoids being unable to detect the larvae in the newly planted experimental nettle plots. Microclimatic conditions, a too low population density of *A. levana* or possible chemical and landscape properties may have contributed to the lack of parasitoids. Nevertheless none of the 208 larvae of *A. levana* collected in an extensive survey of sites where nettles were growing naturally, in the same area as the study sites, (Fichtelgebirge) in 2009 were parasitized (Wagner unpubl. data). Also the author of an unpublished thesis from Sweden reports not finding any parasitized *A. levana* larvae, which is attributed to the relatively recent colonization of Sweden by *A. levana* (Söderlind, 2009 unpubl).

Life history traits

As the rate of development in insects strongly depends on temperature (van Doorslaer & Stoks 2005, Bernardo *et al.* 2006) it is assumed that they adapt to and have different developmental strategies at different altitudes (Karl *et al.* 2008). Laboratory studies provide evidence that an interaction between temperature and the origin of butterflies affect larval growth rates and adult fecundity (Burke *et al.* 2005, Karlsson & van Dyck 2005, Nylin 2009). In accordance with other altitudinal studies, the larvae of *A. levana* were lighter and took longer to develop at high compared to low altitudes, presumably because of the lower temperatures and high plasticity (e.g. Alonso 1999).

The comparison of insects collected from low and high altitudes has revealed that developmental rate increases with altitude (Berner *et al.* 2004). This increase in developmental rate is associated with an increase in metabolic rate (Terblanche *et al.* 2009). In the current study the individuals originally came from sites at a low altitude. Their response to high altitudes might be an adaptive response to local climate facilitated by high phenotypic plasticity (Berner *et al.* 2004). In another transplant experiment craneflies that were transferred from a high altitude to a lower altitude emerged at the same time despite the differences in temperature (Coulson *et al.* 1976). This result contrasts with those of the current study in which larvae from lower sites developed more slowly and were less fit due to the lower temperatures at the higher altitudes, probably not for genetic reasons but because of their high plasticity.

Furthermore females took longer to complete their larval and pupal development than males. This accords with other laboratory studies and might be caused by protandry (Bauerfeind *et al.* 2009), which may also account for the lower weight of male butterfly larvae and pupae (Fischer & Fiedler 2001).

5.7 Conclusion

The results indicate that altitudinal and temperature gradients affect the life history traits of the European Map butterfly (*Araschnia levana*). The assumption that butterflies at higher altitudes develop more slowly and fewer survive because of unsuitable climatic conditions could only partly be confirmed. The lower weights and slower development recorded at high altitudes compared to low altitudes, where the temperatures were higher, is probably a consequence of this species phenotypic plasticity. Sex differences in larval weight, pupal and adult lifespan might be due to protandry. The absence of parasitoids prevented a comparison of percentage parasitism at different altitudes and a test of the hypothesis that increasing temperatures might disrupt biotic interactions e. g. in the synchrony between parasitoids and hosts. However, the complete absence of natural antagonists either indicates that this kind of disruption has occurred or that top-down regulation of *A. levana* populations plays a minor role.

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Publication list

Peer-reviewed articles (published)

Wagner, K.D., Krauss, J. and Steffan-Dewenter, I. (2011). Changes in the life history traits of the European Map butterfly, *Araschnia levana* (Lepidoptera: Nymphalidae) with increase in altitude. *European Journal of Entomology* 108: 447-452.

Wagner, K.D., Krauss, J. and Steffan-Dewenter, I. (2013). Butterfly diversity and historical land cover change along an altitudinal gradient. *Journal of Insect Conservation* 17: 1039-1046.

Peer-reviewed articles (in preparation)

Wagner, K.D., Krauss, J. and Steffan-Dewenter, I. (2014). How does climate warming affect phenology shifts of interacting species in terrestrial habitats? *In preparation.*

Manuscripts in this thesis and individual contributions

The studies described in this thesis refer to the following three manuscripts. Manuscript 1 is *in preparation* (Chapter 3). Manuscript 2 is published in the *Journal of Insect Conservation* (Chapter 4). Manuscript 3 is published in the *European Journal of Entomology* (Chapter 5).

Manuscript 1 (Chapter 3)

Title:	How does climate warming affect phenology shifts of interacting species in terrestrial habitats?
Authors:	K.D. Wagner, J. Krauss, I. Steffan-Dewenter
Status:	*in preparation*

<u>Author contributions</u>

K.D. Wagner:	Design, methods, data collection, analysis, discussion, manuscript writing and editing (corresponding author)
J. Krauss:	Design, discussion, manuscript editing
I. Steffan-Dewenter:	Design, discussion, manuscript editing

Manuscript 2 (Chapter 4)

Title:	Butterfly diversity and historical land cover change along an altitudinal gradient
Authors:	K.D. Wagner, J. Krauss, I. Steffan-Dewenter
Status:	published

<u>Author contributions</u>

K.D. Wagner:	Design, methods, data collection, analysis, discussion, manuscript writing and editing (corresponding author)
J. Krauss:	Design, discussion, manuscript editing
I. Steffan-Dewenter:	Design, discussion, manuscript editing

Manuscript 3 (Chapter 5)

Title: Changes in the life history traits of the European Map butterfly, *Araschnia levana* (Lepidoptera: Nymphalidae) with increase in altitude

Authors: K.D. Wagner, J. Krauss, I. Steffan-Dewenter

Status: published

<u>Author contributions</u>

K.D. Wagner: Design, methods, data collection, analysis, discussion, manuscript writing and editing (corresponding author)

J. Krauss: Design, discussion, manuscript editing

I. Steffan-Dewenter: Design, discussion, manuscript editing

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Kathrin Wagner
Bayreuth, December 2014

(Eidesstattliche) Versicherungen und Erklärungen

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Hiermit erkläre ich, dass keine Tatsachen vorliegen, die mich nach den gesetzlichen Bestimmungen über die Führung akademischer Grade zur Führung eines Doktorgrades unwürdig erscheinen lassen.

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