Combined effects of climate change and extreme events on plants, arthropods and their interactions

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Lilac-breasted Roller (*Coracias caudatus*) in the Etosha National Park (Namibia)

“For the best is only bought at the cost of great pain… Or so says the legend”

The Thorn Birds by Colleen McCullough

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Ehrenwörtliche Erklärung

Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Dissertation mit dem Titel „*Combined effects of climate change and extreme events on plants, arthropods and their interactions*“ selbständig, am Lehrstuhl für Tierökologie und Tropenbiologie (Zoologie III) der Julius-Maximilians-Universität Würzburg, unter der Anleitung und Betreuung durch Herrn PD Dr. Jochen Krauss und Herrn Prof. Dr. Ingolf Steffan-Dewenter angefertigt habe und dabei keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet habe. Ich erkläre außerdem, dass die vorliegende Dissertation weder in gleicher, noch in ähnlicher Form bereits in einem Prüfungsverfahren vorgelegen hat. Des Weiteren habe ich außer den mit dem Zulassungsantrag urkundlich vorgelegten Graden keine weiteren akademischen Grade erworben oder zu erwerben versucht.

Würzburg, 10.07.2013 Annette Leingärtner

Curriculum vitae

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Publication list

Leingärtner, A., Krauss, J., Steffan-Dewenter, I. (subm.) Changes in the composition of butterfly assemblages and life-history traits along an altitudinal gradient.

Leingärtner, A., Hoiss, B., Krauss, J., Steffan-Dewenter, I. (subm.) Comined effects of extreme events and elevation on nutritional quality and herbivory rates of alpine plants.

Leingärtner, A., Krauss, J., Steffan-Dewenter, I. (subm.) Elevation and experimental snowmelt manipulation affect emergence phenology and abundance of soil-hibernating arthropods.

Hoiss, B., Gaviria, J., **Leingärtner, A.**, Krauss, J., Steffan-Dewenter, I. (2013) Combined effects of climate and management on plant diversity and pollination type in alpine grasslands. *Diversity and Distributions* 19, 386 – 395.

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Witte, V., **Leingärtner, A.**, Sabas, L., Hashim, R., Foitzik, S. (2008) “Symbiont microcosm in an ant society and the diversity of interspecific interactions”. *Animal Behaviour* 76: 1477 - 1486.

Summary (English)

I. Global climate change directly and indirectly influences biotic and abiotic components of ecosystems. Changes in abiotic ecosystem components caused by climate change comprise temperature increases, precipitation changes and more frequently occurring extreme events. Mediated by these abiotic changes, biotic ecosystem components including all living organisms will also change. Expected changes of plants and animals are advanced phenologies and range shifts towards higher latitudes and altitudes which presumably induce changes in species interactions and composition. Altitudinal gradients provide an optimal opportunity for climate change studies, because they serve as natural experiments due to fast changing climatic conditions within short distances. In this dissertation two different approaches were conducted to reveal species and community responses to climate change. First, species richness and community trait analyses along an altitudinal gradient in the Bavarian Alps (chapters II, III) and second, climate change manipulation experiments under different climatic contexts (chapters IV, V, IV).

II. We performed biodiversity surveys of butterfly and diurnal moth species on 34 grassland sites along an altitudinal gradient in the National Park Berchtesgaden. Additionally, we analysed the dominance structure of life-history traits in butterfly assemblages along altitude. Species richness of butterflies and diurnal moths decreased with increasing altitude. The dominance of certain life-history-traits changed along the altitudinal gradient with a higher proportion of larger-winged species and species with higher egg numbers towards higher altitudes. However, the mean egg maturation time, population density and geographic distribution within butterfly assemblages decreased with increasing altitude. Our results indicate that butterfly assemblages were mainly shaped by environmental filtering. We conclude that butterfly assemblages at higher altitudes will presumably lack adaptive capacity to future climatic conditions, because of specific trait combinations.

III. In addition to butterfly and diurnal moth species richness we also studied plant species richness in combination with pollination type analyses along the altitudinal gradient. The management type of the alpine grasslands was also integrated in the analyses to detect combined effects of climate and management on plant diversity and pollination type. Plant species richness was highest at intermediate altitudes, whereby the

management type influenced the plant diversity with more plant species at grazed compared to mown or non-managed grasslands. The pollination type was affected by both the changing climate along the gradient and the management type. These results suggest that extensive grazing can maintain high plant diversity along the whole altitudinal gradient. With ongoing climate change the diversity peak of plants may shift upwards, which can cause a decrease in biodiversity due to reduced grassland area but also changes in species composition and adaptive potential of pollination types.

IV. We set up manipulation experiments on 15 grassland sites along the altitudinal gradient in order to determine the combined effects of extreme climatic events (extreme drought, advanced and delayed snowmelt) and elevation on the nutritional quality and herbivory rates of alpine plants. The leaf CN (carbon to nitrogen) ratio and the plant damage through herbivores were not significantly affected by the simulated extreme events. However, elevation influenced the CN ratios and herbivory rates of alpine plants with contrasting responses between plant guilds. Furthermore, we found differences in nitrogen concentrations and herbivory rates between grasses, legumes and forbs, whereas legumes had the highest nitrogen concentrations and were damaged most. Additionally, CN ratios and herbivory rates increased during the growing season, indicating a decrease of food plant quality during the growing season. Contrasting altitudinal responses of grasses, legumes and forbs presumably can change the dominance structure among these plant guilds with ongoing climate change.

V. In this study we analysed the phenological responses of grassland species to an extreme drought event, advanced and delayed snowmelt along the altitudinal gradient. Advanced snowmelt caused an advanced beginning of flowering, whereas this effect was more pronounced at higher than at lower altitudes. Extreme drought and delayed snowmelt had rather low effects on the flower phenology and the responses did not differ between higher and lower sites. The strongest effect influencing flower phenology was altitude, with a declining effect through the season. The length of flowering duration was not significantly influenced by treatments. Our data suggest that plant species at higher altitudes may be more affected by changes in snowmelt timing in contrast to lowland species, as at higher altitudes more severe changes are expected. However, the risk of extreme drought events on flowering phenology seems to be low.

VI. We established soil-emergence traps on the advanced snowmelt and control treatment plots in order to detect possible changes in abundances and emergence phenologies of

five arthropod orders due to elevation and treatment. Additionally, we analysed the responses of Coleoptera species richness to elevation and treatment. We found that the abundance and species richness of Coleoptera increased with elevation as well as the abundance of Diptera. However, the abundance of Hemiptera decreased with elevation and the abundances of Araneae and Hymenoptera showed no elevational patterns. The advanced snowmelt treatment increased the abundances of Araneae and Hymenoptera. The emergence of soil-hibernating arthropods was delayed up to seven weeks at higher elevations, whereas advanced snowmelt did not influence the emergence phenology of arthropods immediately after snowmelt. With climate change earlier snowmelt will occur more often, which especially will affect soil-hibernating arthropods in alpine regions and may cause desynchronisations between species interactions.

VII. In conclusion, we showed that alpine ecosystems are sensitive towards changing climate conditions and extreme events and that many alpine species in the Bavarian Alps are endangered. Many alpine species could exist under warmer climatic conditions, however they are expected to be outcompeted by more competitive lowland species. Furthermore, host-parasite or predator-prey interactions can be disrupted due to different responses of certain guilds to climate change. Understanding and predicting the complex dynamics and potential risks of future climate change remains a great challenge and therefore further studies analysing species and community responses to climate change are needed.

Zusammenfassung (German)

I. Der globale Klimawandel beeinflusst direkt und indirekt biotische und abiotische Komponenten der Ökosysteme. Durch Klimawandel verursachte Veränderungen in den abiotischen Komponenten der Ökosysteme umfassen Temperaturanstiege, Veränderungen im Niederschlag und häufiger auftretende Extremereignisse. Als Folge dieser abiotischen Veränderungen, werden sich auch die biotischen Komponenten der Ökosysteme, die alle lebenden Organismen einschließen, verändern. Voraussichtliche Veränderungen bei Pflanzen und Tieren sind vorverlegte Phänologien und Verbreitungsverschiebungen in Richtung höherer Breitengrade und Höhenlagen, was möglicherweise Veränderungen von Interaktionen zwischen Arten und in der Artzusammensetzung verursacht. Höhengradienten bieten durch sich schnell verändernde klimatische Bedingungen innerhalb kurzer Distanzen eine optimale Möglichkeit für Klimawandelstudien im Freiland. In dieser Dissertation wurden zwei unterschiedliche Versuchsansätze genutzt, um die Reaktionen von Arten und Artengemeinschaften auf den Klimawandel zu untersuchen: erstens Analysen zum Artenreichtum und zu Merkmalen innerhalb von Artengemeinschaften entlang eines Höhengradienten in den Bayerischen Alpen (Kapitel II, III) und zweitens Manipulationsexperimente zur Simulation von Klimawandel bei unterschiedlichen klimatischen Bedingungen (Kapitel IV, V, VI).

II. Wir haben Biodiversitätsaufnahmen von Schmetterlings- und tagaktiven Nachtfalterarten entlang eines Höhengradienten im Nationalpark Berchtesgaden durchgeführt. Zusätzlich haben wir die Dominanzstruktur von Life-History-Merkmalen in Schmetterlingsgesellschaften entlang des Höhengradienten analysiert. Der Artenreichtum von Schmetterlingen und tagaktiven Nachtfaltern nahm mit zunehmender Höhe ab. Die Dominanz von bestimmten Life-History-Merkmalen veränderte sich entlang des Höhengradienten. Zum Beispiel fanden wir einen höheren Anteil an Arten mit größeren Flügeln und eine größere Anzahl an Eiern in höheren Lagen. Die mittlere Eireifezeit, Populationsdichte und geographische Verbreitung von Schmetterlingsgesellschaften nahm mit steigender Höhe ab. Unsere Ergebnisse deuten darauf hin, dass Schmetterlingsgesellschaften hauptsächlich durch den Filtereffekt der Umwelt geformt werden. Wir schlussfolgern, dass sich bestimmte Merkmalskombinationen von

Schmetterlingsgesellschaften in höheren Lagen möglicherweise ungünstig auf die Anpassungskapazität an zukünftige klimatische Veränderungen auswirken.

III. Zusätzlich zum Artenreichtum von Schmetterlingen und tagaktiven Nachtfaltern haben wir auch den Artenreichtum von Pflanzen in Kombination mit Analysen zu Bestäubungstypen entlang des Höhengradienten untersucht. Die Bewirtschaftungsform der alpinen Grasländer wurde in die Analysen integriert, um kombinierte Auswirkungen von Klima und Bewirtschaftungsform auf die Pflanzendiversität und den Bestäubungstyp zu erfassen. Der Artenreichtum von Pflanzen war auf mittleren Höhen am größten, wobei die Bewirtschaftungsform die Pflanzendiversität beeinflusste. Es kamen mehr Pflanzenarten auf beweideten im Vergleich zu gemähten oder nicht bewirtschafteten Wiesen vor. Der Bestäubungstyp wurde sowohl durch das sich verändernde Klima entlang des Gradienten als auch durch die Bewirtschaftungsform beeinflusst. Unsere Ergebnisse lassen vermuten, dass extensive Beweidung eine hohe Pflanzendiversität entlang des gesamten Höhengradienten erhalten kann. Mit fortschreitendem Klimawandel könnte sich der Bereich mit höchster Pflanzendiversität nach oben verschieben, was zu einem Biodiversitätsverlust durch eine Abnahme an Grasflächen führen könnte, aber auch zu Veränderungen in der Artenzusammensetzung und dem Anpassungspotential von Bestäubungstypen.

IV. Wir simulierten Extremereignisse (extreme Dürre, frühere und spätere Schneeschmelze) auf 15 Grasflächen entlang des Höhengradienten, um kombinierte Effekte von extremen klimatischen Ereignissen und Höhenlage auf die Futterqualität und den Blattfraß von alpinen Pflanzen zu untersuchen. Das Verhältnis von Kohlenstoff zu Stickstoff (CN) in Blättern und die Fraßschäden durch Pflanzenfresser wurden durch die simulierten Extremereignisse nicht signifikant beeinflusst. Dagegen beeinflusste die Höhenlage das CN-Verhältnis und die Herbivorieraten von alpinen Pflanzen mit entgegengesetzten Reaktionen unter den Pflanzengruppen. Des Weiteren haben wir Unterschiede in den Stickstoffkonzentrationen und Herbivorieraten zwischen Gräsern, Leguminosen und krautigen Pflanzen gefunden, wobei die Leguminosen die höchsten Stickstoffkonzentrationen aufwiesen und am stärksten angefressen waren. Zusätzlich stiegen die CN-Verhältnisse und die Fraßschäden während der Vegetationsperiode an, was auf eine Abnahme der Futterqualität im Verlauf der Vegetationsperiode hindeutet. Entgegengesetzte Muster von Gräsern, Leguminosen und krautigen Pflanzen über die

Höhe können möglicherweise die Dominanzstruktur zwischen diesen Pflanzengruppen mit fortschreitendem Klimawandel verändern.

V. In dieser Studie haben wir die phänologischen Reaktionen von Graslandarten auf ein extremes Dürreereignis, eine frühere und eine spätere Schneeschmelze entlang des Höhengradienten, analysiert. Die frühere Schneeschmelze bewirkte einen früheren Blühbeginn, wobei dieser Effekt auf höheren Lagen ausgeprägter war als auf tieferen Lagen. Extreme Dürre und spätere Schneeschmelze hatten eher geringe Auswirkungen auf die Blühphänologie und die Auswirkungen unterschieden sich nicht zwischen höher und tiefer gelegenen Flächen. Am stärksten würde die Blühphänologie von der Höhenlage beeinflusst wobei sich der Effekt im Verlauf der Vegetationsperiode verringerte. Die Länge der Blühdauer wurde durch die Simulationen nicht signifikant beeinflusst. Unsere Ergebnisse deuten darauf hin, dass Pflanzenarten in höheren Lagen stärker durch Veränderungen des Zeitpunktes der Schneeschmelze beeinflusst werden als Tieflandarten, weil in höheren Lagen stärkere Veränderungen erwartet werden. Das Risiko von extremer Dürre für die Blühphänologie scheint aber gering zu sein.

VI. Wir untersuchten Effekte der Höhenlage und früherer Schneeschmelze auf Häufigkeiten und Schlupfphänologien fünf verschiedener Arthropodenordnungen. Dazu installierten wir Bodenphotoeklektoren auf Flächen mit früherer Schneeschmelze und Kontrollflächen. Außerdem analysierten wir die Auswirkungen der Höhenlage und der früheren Schneeschmelze auf den Artenreichtum von Coleoptera. Wir stellten fest, dass die Abundanz und der Artenreichtum von Coleoptera sowie die Abundanz der Diptera mit steigender Höhenlage zunahmen, während die Abundanz der Hemiptera mit steigender Höhe abnahm. Araneae und Hymenoptera zeigten keine Abundanzmuster entlang des Höhengradienten. Eine simulierte frühere Schneeschmelze ließ die Abundanz der Araneae und Hymenoptera ansteigen. Arthropoden, die im Boden überwinterten, schlüpften in höheren Lagen bis zu sieben Wochen später. Eine frühere Schneeschmelze beeinflusste die Schlupfphänologie der Arthropoden unmittelbar nach der Schneeschmelze jedoch nicht. Aufgrund des Klimawandels wird eine frühere Schneeschmelze häufiger auftreten, was vor allem Auswirkungen auf bodenüberwinternde Arthropoden in der Alpenregion haben kann und zu Desynchronisationen mit interagierenden Arten führen kann.

VII. Abschließend lässt sich sagen, dass alpine Ökosysteme sensibel auf klimatische Veränderungen und Extremereignisse reagieren und dass viele alpine Arten in den

Bayerischen Alpen gefährdet sind. Viele alpine Arten könnten unter wärmeren klimatischen Bedingungen existieren, aber vermutlich werden sie von konkurrenzstärkeren Tieflandarten verdrängt. Des Weiteren können Wirt-Parasit oder Räuber-Beute Interaktionen durch unterschiedliche Reaktionen von bestimmten Gruppen auf Klimawandel gestört werden. Es bleibt eine große Herausforderung die komplexen Dynamiken und möglichen Gefahren des zukünftigen Klimawandels zu verstehen und vorherzusagen. Wir empfehlen weitere Studien, die die Auswirkungen des Klimawandels auf Arten und Artengesellschaften untersuchen.

I. General Introduction

Climate change

The global climate is changing and impacts of anthropogenic climate change are observable at all levels of ecological organization around the globe (Rosenzweig & Neofotis, 2013). The major driver of climate change is the human-influenced increasing concentration of greenhouse gases in the atmosphere (IPCC, 2007). Particularly carbon dioxide (CO_2), but also methane (CH_4) and nitrous oxide (N_2O) contribute to global warming by absorption and re-radiation of thermal radiation (Montzka *et al.*, 2011). From 1975 to 2005 global surface temperature has increased about 0.6°C (Hansen *et al.*, 2006b) and contrary to popular perceptions the global warming trend of about 0.2°C per decade is still continuing (Hansen *et al.*, 2010).

Consequences of global warming are increases in sea level, changes in precipitation regimes and a higher frequency and intensity of extreme events (IPCC, 2012). Climate change driven temperature rises differ between regions. Global surface temperatures increased by about 0.74°C in the last century (Trenberth *et al.*, 2007), whereas temperatures in alpine regions raised three times higher during the same period (Beniston, 2012). In addition to temperature changes, precipitation events are proposed to shift from summer towards winter months (Laghari *et al.*, 2012). An increase in winter precipitation will result in higher snow amounts and a longer lasting snow cover at higher altitudes (Stewart, 2009), but will also cause advanced snowmelt due to a higher fraction of liquid precipitation at lower altitudes (Räisänen & Eklund, 2012). In contrast, summer precipitation will decline with ongoing anthropogenic warming and that may lead to more severe drought events in the future (Rowell, 2009).

Changing abiotic conditions like temperature changes and shifts in precipitation regimes, are supposed to entail also severe changes in the biotic components of the ecosystem. Possible responses of plant and animal species to recent climate change are shifts in phenology and distribution ranges (Rosenzweig *et al.*, 2007). There is evidence for northward and upward range shifts of many species (Parmesan & Yohe, 2003), but not all species can keep up with northward temperature shifts and therefore lag behind climate change (Devictor *et al.*, 2012). Future climate change scenarios predict further shifts in species distributions, leading to extinctions of species who are unable to track climate change or adapt to new climate conditions (Thomas *et al.*, 2004a).

Altitudinal gradients

This dissertation was part of the joint research centre FORKAST, a Bavarian Research Cooperation on “Impact of climate change on ecosystems and climatic adaptation strategies” with the aim to improve the understanding of ecosystems concerning resilience and capacity under changing environmental conditions. FORKAST incorporated 17 projects investigating how extreme climatic conditions like extreme drought and torrential rains affect the characteristics of different ecological systems ranging from forests to grasslands and lakes. The focus of this project lay on grassland ecosystems along an altitudinal gradient in the Bavarian Alps and their changes with climate change regarding community structure and interactions between animals and plants.

The study area was located in the National Park Berchtesgaden in the southeast part of Germany near the border to Austria. The National Park Berchtesgaden is the only national park in Germany located in the Alps and is characterised by a large altitudinal gradient ranging from 603 m.a.s.l. (Königssee) to 2713 m.a.s.l. (Watzmann) (Fig. I.1) with strong temperature and precipitation differences (StMUG, 2001). A high climatic variability along the gradient leads to distinct altitudinal ranges supporting different animal and plant species.

In the face of climate change, studies analysing species richness patterns along climatic gradients are of crucial importance for the understanding of macroecological mechanisms and to predict future scenarios. Altitudinal gradients offer the opportunity for climate change studies, because with changing climatic conditions, species are supposed to follow these changes over time in the same way that ecosystems now vary along altitude (Dunne *et al.*, 2004). There are

Fig. I.1 Königssee with Watzmann

several hypotheses explaining the mechanisms shaping altitudinal biodiversity patterns. The species-energy hypothesis suggests a linear decline in species richness towards higher altitudes, because of less available energy towards mountain tops (Chown *et al.*, 2012). Another hypothesis explaining linear decreasing biodiversity with increasing elevation is the species-area relationship (Lomolino, 2000). The available area along altitudinal gradients shrinks towards the summit, because of the conical shape of mountains and therefore the number of species will decline (Jones *et al.*, 2003). However, species richness patterns along altitudinal gradients are not necessarily linear, but can form a hump-shaped relationship. A hypothesis explaining a biodiversity peak at mid-elevation is the mid-domain effect. Given that species' ranges are randomly distributed, species' ranges stochastically overlap more towards the centre within a bounded geographical domain and create a species richness peak (Colwell *et al.*, 2004).

Life-history traits and study organisms

Species richness gradients exist since millions of years and are formed by long-term processes of speciation, dispersal and extinction (Mittelbach *et al.*, 2007). However, present-day demographic processes reshape species richness gradients and adaptive traits strongly influence these processes (Carnicer *et al.*, 2012). Dominant traits within communities presumably shift with changing environmental conditions due to species turnover and intraspecific variation (Cornwell & Ackerly, 2009). Cool-adapted species shifted their distribution ranges towards higher latitudes and altitudes in order to escape rising temperatures (Parmesan, 2006). Furthermore, species restricted to mountain areas showed larger upward shifts in the optimum elevation than species not restricted to mountain areas (Lenoir *et al.*, 2008). Therefore, identifying adaptive traits that are sensitive to changing climate conditions contributes to the understanding of species' responses to climate change (Diamond *et al.*, 2011).

Insects comprise with about 950,000 described species more than half of all known species in the world (Groombridge, 1992), however comparatively little is known about responses of insects to climate change. The best studied insect group are butterflies (Fig. I.2), because they are easy to monitor and popular among the general public (Thomas, 2005). Additionally, high quality monitoring data are available from more than ten European countries (van Swaay *et al.*, 2008), which makes it possible to estimate biodiversity trends for Europe (de Heer *et al.*, 2005). Even more importantly, butterflies represent adequate indicators of environmental and climate changes (Thomas, 2005), as they react more sensitive and decline more rapidly than birds and plants (Thomas *et al.*, 2004b). Besides butterflies, vascular plants belong to the best studied organisms, whereas both groups hold key functions in grassland ecosystems (e.g. primary production, herbivory, pollination) and strongly interact.

Fig. I.2 Two day-active Lepidoptera species. (a) The butterfly *Vanessa cardui* and (b) the diurnal moth *Zygaena loti*.

The relationship between butterflies and their host plants is highly coevolved (Ehrlich & Raven, 1964) and represents a perfect plant-herbivore system to study the almost unknown impacts of global environmental change on species interactions (Tylianakis *et al.*, 2008). Former studies on ecological responses to recent climate change mostly focused on the effects on individual species and hardly addressed dynamic aspects and complex interactions (Walther, 2010). However, altering climate conditions are supposed to change plant-insect interactions with tremendous effects on ecosystems (DeLucia *et al.*, 2012). With increasing temperatures plant phenology presumably shifts with different intensity than insect phenology, thereby causing mismatches between herbivorous insects and their host plants (van Asch & Visser, 2007). Furthermore, climatic warming facilitates some insects to have more generations per year, thus increasing plant damage (Altermatt, 2010). Plant palatability is also modified by climate change through elevated CO_2, which increases plant growth and consequently reduces the nitrogen concentration in plant tissues (DeLucia *et al.*, 2012). A higher CN ratio in host plants forces herbivorous insects to feed more to compensate the low-quality food (Cornelissen, 2011).

In general, there are two different approaches for analysing responses of plant-herbivore interactions to climate change: (1) Studies along climatic gradients (Garibaldi *et al.*, 2011) and (2) manipulation experiments (Beier *et al.*, 2012). Both approaches have advantages, but also contain spatial and temporal limitations, which presumably limit general predictions regarding climate change (Dunne *et al.*, 2004). Combining studies along climatic gradients with experimental methods can reduce spatial and temporal limitations and enable further insights into the responses of plant-herbivore interactions to climate change. In this dissertation both approaches were combined by simulating extreme climatic events (extreme drought, advanced and delayed snowmelt) along an elevational gradient in the National Park Berchtesgaden.

Study design and chapter outline

In 2009 34 selected grassland sites along an altitudinal gradient in the National Park Berchtesgaden were used for species richness analyses of butterflies and moths (Fig. I.3). Biodiversity surveys along a climatic gradient enable predictions of possible impacts of changing climatic conditions on biodiversity patterns. These predictions are based on the space-for-time substitution approach, which assumes that climatic conditions along gradients change in the same way as climate changes in time (Dunne *et al.*, 2004). Additionally to the species richness analyses, life-history traits of butterfly species were examined to detect changes in butterfly assemblages along the elevational gradient (chapter II).

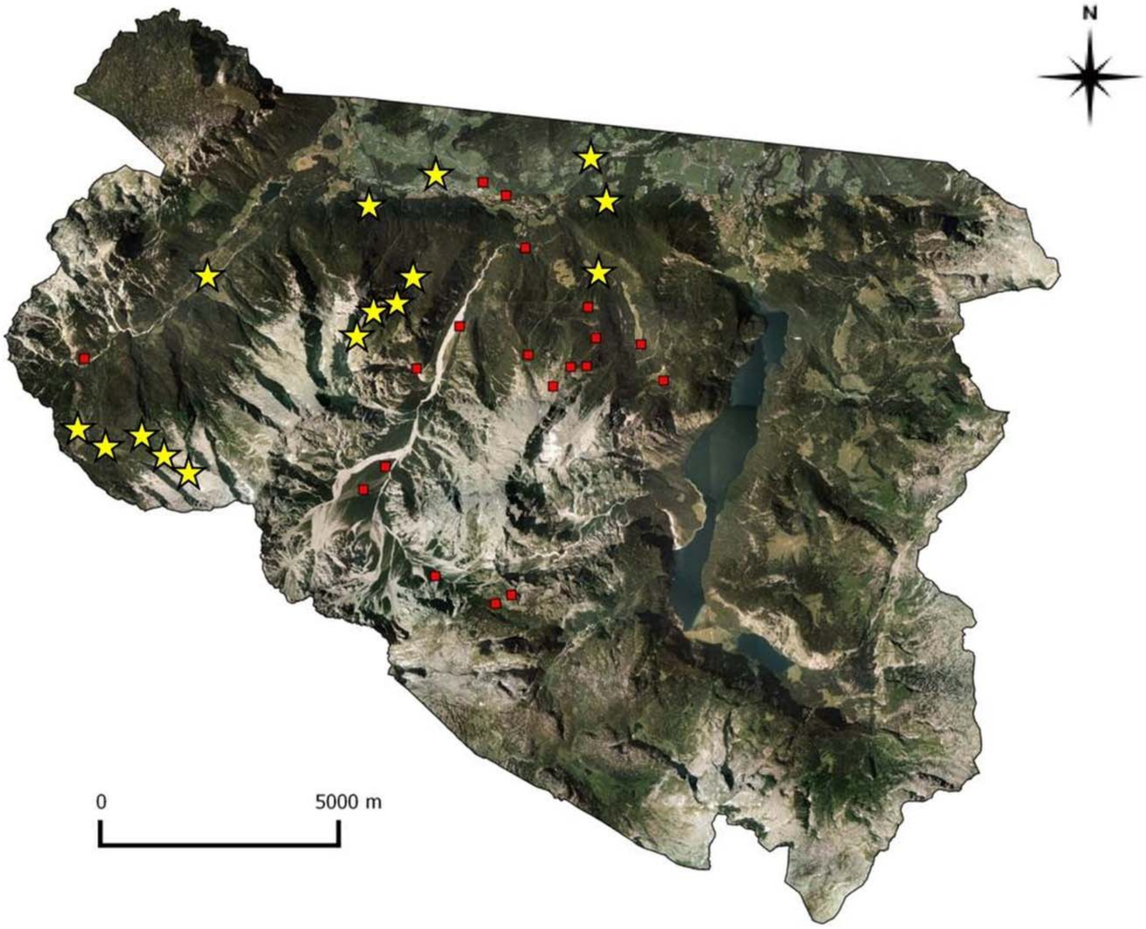


Fig. I.3 34 grassland sites in the National Park Berchtesgaden. Sites that were only used in 2009 are marked with red squares. 15 sites that were used in 2009 and for the experiments in 2010 are marked with yellow stars.

As butterfly species strongly rely on plant species as food and nectar source, plant species richness was also analysed at the 34 grassland sites along the altitudinal gradient. Furthermore, different management types (grazed, mown, abandoned) were integrated in the analyses to study combined effects of climate and management on plant diversity, since land use intensity is besides climate change one of the main drivers shaping biodiversity patterns (Tscharntke *et al.*, 2005). Additionally the pollination types of the plant species were analysed to study the ecological importance of pollination types for the adaptation of plant communities along a climatic gradient (chapter III).

In 2010 a climate experiment simulating extreme drought, advanced and delayed snowmelt was conducted at 15 grassland sites along an elevational gradient (Fig. I.3). The aim of this study was to analyse combined effects of extreme climatic events and elevation on the nutritional quality of plant species and plant damage through herbivores. Extreme climatic events are supposed to influence plant-herbivore interactions (Walter *et* *al.*, 2012), however experiments simulating climate change were mostly conducted at single locations (Bütof *et al.*, 2012). We simulated an extreme drought at 15 grassland sites with 4 x 4 m rain-out shelters (Fig. I.4). Advanced and delayed snowmelt was simulated by shovelling snow from one plot (advanced) to an adjacent plot (delayed) in early spring (Fig. I.5) (chapter IV).

Fig. I.4 Rain-out shelter to simulate an extreme drought event.

Additionally to the effects of extreme climatic events on the nutritional quality and herbivory rates of alpine plants, phenological responses of the plant species were also analysed. Phenological shifts due to warmer temperatures have been determined in many European countries (Menzel *et al.*, 2006), however effects of snowmelt changes and long lasting drought periods within varying climatic conditions on plant phenology are almost unknown. Many alpine species highly depend on the timing of snowmelt (Inouye, 2008) and climate change induced changes in snowmelt can have severe fitness consequences for several plant species. Extreme drought events can shift flower phenology (Jentsch *et al.*, 2009), but whether theses shifts are congruent between lower and higher altitudes is hardly known (chapter V).

Fig. I.5 Shovelling snow to simulate an advanced and delayed snowmelt.

Fig. I.6 Soil-emergence trap

Not only plant species are supposed to response with phenology shifts to advanced snowmelt, but also arthropods may shift their phenologies. However, little is known about the factors that trigger arthropod emergence and synchronise it with environmental conditions (Hodkinson, 2005). An advanced snowmelt can accelerate arthropod emergence, but in combination with freezing temperatures declines of arthropod abundances can be expected (Bale & Hayward, 2010). The altitudinal distribution of five arthropod orders was recorded by weekly surveys at 15 grassland sites with soil emergence traps (Fig. I.6). Furthermore, soil emergence traps were also placed at the plots where snow was removed in spring, to analyse the effects of advanced snowmelt on arthropod abundances and possible emergence phenology shifts (chapter VI).

II. Changes in the composition of butterfly assemblages and life-history traits along an altitudinal gradient

Abstract

Species richness patterns along altitudinal gradients can serve as model system to understand climatic drivers of biodiversity and to predict consequences of climate change. We studied diversity patterns of butterfly and diurnal moth species along an altitudinal gradient in the National Park Berchtesgaden (Germany). Furthermore, we analysed the changes of life-history traits of butterfly assemblages concerning dispersal capacity, reproductive strategies and developmental time from lowland to highland. We found a linear decrease of species richness of both butterfly and diurnal moth species with altitude and significant changes in the dominance of life-history traits of the butterfly assemblages with altitude. The proportion of larger-winged species and species with a higher egg number increased with altitude. In contrast, egg maturation time decreased in the butterfly assemblages along the altitudinal gradient. Further, with increasing altitude butterfly assemblages contained more species with a lower population density and were increasingly dominated by less widespread species. Our results suggest that environmental filtering is the dominant effect shaping life-history patterns along altitudinal gradients. Trade-offs among species characteristics result in specific trait combinations of butterfly assemblages at higher altitudes, presumably hampering their adaptive capacity to ongoing global warming.

Keywords

alpine ecosystems; biodiversity; environmental filtering; global change; Lepidoptera

Introduction

Altitudinal gradients provide an optimal possibility for studying future responses of species and species assemblages to climate change (Hodkinson, 2005). Environmental conditions will change with global warming and particularly in alpine regions climate change will have strong effects on species assemblages, because the Alps represent an endemism hotspot with many cold-adapted specialists. There are two main patterns of biodiversity distributions along altitudinal gradients (i) the unimodal distribution with a mid-elevational peak and (ii) the linear decline of biodiversity with altitude (Rahbek, 2005). Various hypotheses for different regions and different species groups exist to explain species richness-altitude patterns (Nogues-Bravo *et al.*, 2008; Beck *et al.*, 2010; Gutierrez Illan *et al.*, 2010; Obertegger *et al.*, 2010; Hoiss *et al.*, 2012, 2013). However, the mechanisms determining species richness along altitudinal gradients are poorly understood (Hodkinson, 2005).

Species along altitudinal gradients have specific life-history traits, which allow them to occupy different niches. Changes in life-histories along environmental gradients can be studied on three levels: (i) an intraspecific, (ii) an interspecific and (iii) a community assemblage level (Gaston *et al.*, 2008). Intraspecific studies show shifts in life-history traits within individual species (Berner *et al.*, 2004; Karl *et al.*, 2008; Wagner *et al.*, 2011), whereas studies on an interspecific level analyse life-history trait variations between species (Hawkins & DeVries, 1996). The community assemblage level, in contrast to the interspecific level, does not use each species as a response, but calculates mean values of community assemblages along an environmental gradient (Chown & Klok, 2003; Hoiss *et al.*, 2012). Community assemblage studies can be used to detect changes in the community composition due to climate change. One example to measure changes in the community composition along a climate gradient is the community temperature index (CTI) based on the average of each species temperature index (STI) indicating the average temperature of the species range (Devictor *et al.*, 2008). This approach, which was originally applied for birds, was extended to butterfly communities, as it was shown to be a good indicator for climate change effects (Devictor *et al.*, 2012), but has not yet been expanded to other life-history traits.

Community life-history traits, which presumably change along altitudinal gradients can be dispersal capacity, reproductive strategies and developmental time, but it is unknown how these traits change with altitude and which trade-offs between different traits exist. Therefore, analysing multiple traits of community assemblages along altitudinal gradients is crucial to predict changes in community composition due to future climate change (Diamond *et al.*, 2011).

One important life-history trait is the body size and its variation through time and space (Chown & Gaston, 2010). The wing length as a measure of body size often increases with altitude for endothermic and ectothermic animals (Atkinson, 1994; Meiri & Dayan, 2003; Hodkinson, 2005). This is in line with the Bergmann's rule describing increased body size with latitude for endothermic animals (Meiri & Dayan, 2003). Bergmann's rule was extended to ectotherms by the temperature-size rule indicating increases in body size for species developing at lower temperatures (Atkinson, 1994). Body size and the often linked dispersal ability play a crucial role for (i) regional shifts in species distribution ranges as a consequence of climate warming and for (ii) the response of species to annual variation in weather conditions (Stevens *et al.*, 2010).

Reproduction at high altitudes is a challenge for ectothermic animals, because of a shorter reproductive season, which has to be compensated with special reproduction strategies. For example the investment in fewer, but larger eggs has been shown for single bird and butterfly species at high altitudes (Fischer & Fiedler, 2001; Bears *et al.*, 2009). Similarly to reproduction, the developmental time can change with altitude. Low temperatures at high altitudes can prolong developmental time, increase mortality of species before they reproduce (Norry *et al.*, 2001; Hu *et al.*, 2011), and might lead to low population densities. The density of populations is often connected with the species distribution according to the density-distribution relationship, indicating that locally rare species are less widespread than species that are locally common (Cowley *et al.*, 2001).

In this study, we tested how altitude affects butterfly and diurnal moth species richness on alpine meadows and which traits prevail in butterfly assemblages at different altitudes. We tested the following predictions:

1) Species richness is highest in lowlands and decreases with altitude.
2) Traits in butterfly assemblages change along the altitudinal gradient.
3) Butterfly assemblages at higher altitudes contain a higher proportion of species and individuals with low population densities and narrow distribution ranges than butterfly assemblages at lower altitudes.

Methods

Study sites

The study was carried out in the National Park Berchtesgaden and its surroundings, located in the "Berchtesgadener Alps", a part of the northern limestone alps in the southeast of Germany. The national park is characterised by alpine meadows and high mountains with an altitudinal gradient from 600 to 2700 m.a.s.l.. Alpine pastoral systems have an over 1000 year old tradition in the National Park Berchtesgaden, but today only few alpine meadows are still traditionally managed while the others are abandoned. The annual mean temperature varies between + 7°C and -2°C and the annual mean precipitation varies between 1500 and 2600 mm depending on the altitude.

We selected 34 grasslands with an altitudinal range from ca. 641 to ca. 1984 m.a.s.l (mean latitude/longitude of all grasslands: N47°6', E12°9'), located along two valleys with smooth slopes and two mountainsides with steep slopes. We did not use sites higher than 2000 m.a.s.l., because only bare rocks and coarse gravel could be found. A total of 29 grasslands were located inside the national park and five in the close vicinity. We selected five grasslands outside the national park to cover a larger altitude gradient, because within the park we did not find suitable grasslands between 600 and 800 m.a.s.l.. Almost all grasslands below the timberline were surrounded by coniferous forests. The selection criteria for the 34 grasslands were: (i) location along an altitudinal gradient with about 250 m altitude difference between the grasslands; (ii) extensively used or not used; (iii) permission of the farmers.

Data collection

Butterflies (Lepidoptera: Hesperioidea and Papilionoidea) and diurnal moths (Lepidoptera: Bombycoidea, Geometroidea, Lasiocampoidea, Noctuoidea and Zygaenoidea) were recorded from 8 May to 10 September in 2009. We sampled Lepidoptera six times on study sites below 1200 m.a.s.l., because of a longer snow free season and five times above this altitude. There were no differences between the mean species saturation of five and six transect walks, therefore we pooled the data (for calculation and statistics see statistical analyses). Butterflies and diurnal moths were caught with a sweep net, determined and released immediately after determination. Only some of the diurnal moths and *Erebia* species were collected for determination and genitalization by external experts. We did not distinguish between *Leptidea reali* and *Leptidea sinapis* and between *Colias alfacariensis* and *Colias hyale*.

All 34 study sites had a size of 60 x 60 m where we recorded all Lepidoptera within a 5 m corridor in randomised transect walks (Krauss *et al.*, 2003). Transect walks on each grassland were subdivided into eight 4 min sections to calculate species saturation. We sampled between 10 a.m. and 5 p.m. on sunny days or when temperature was above 17°C on cloudy days. We did not sample when temperature was below 13°C or on rainy days. All grasslands were visited in regular time spans over the sampling period in a random sequence. To analyse the effect of flower cover on Lepidoptera occurrence, we estimated the cover of all flowering plant species as a percentage of the whole study site (60 x 60 m) after each transect walk. We used the mean value of the flower cover over all transect walks per study site for statistical analysis.

For life-history trait analyses of butterfly species we used published literature data concerning the following six trait values: wing length, dispersal capacity, egg number, the way of egg deposition, egg maturation time and the number of generations per year (Table II.S1). In contrast to intraspecific studies with traits of a single species, it was impossible for us to measure the traits of all sampled species for our community assemblage analyses. We only performed life-history trait analyses for butterfly species, as trait data availability for diurnal moth species is very limited. We used the average wing length of the forewing of male butterfly species as proxy for butterfly body size (Higgins & Riley, 1971), because male and female wing length is strongly positively correlated (Komonen *et al.*, 2004). The dispersal capacity of butterfly species was classified into migration categories, where each butterfly species was assigned to one migration category ranging from 1 = sedentary to 9 = migratory (Settele *et al.*, 1999). The egg number per species represents the total number of eggs potentially laid per individual (Settele *et al.*, 1999; Sonderegger, 2005). The mode of egg deposition was divided in eggs, which were singly laid and in eggs laid as egg packages (clutches) (Schweizerischer Bund für Naturschutz, 1994; Weidemann, 1995; Sonderegger, 2005). The egg maturation time was stated in the literature as days from hatch of the adult female until the first egg deposition (Settele *et al.*, 1999; Sonderegger, 2005). For data analyses of the egg maturation time we only used records without hibernation and aestivation to have comparable data sets. The two butterfly species *Gonepteryx rhamni* and *Nymphalis antiopa* always hibernate before they lay their eggs, therefore we excluded these two species from the analyses of egg maturation time. We used the number of generations per year in the literature to calculate the proportion of multivoltine species per study site, which also included bivoltine species (Settele *et al.*, 1999; Stettmer *et al.*, 2007).

For the analysis of population density we used literature data provided for each species as individuals per area in nine population density classes ranging from an extreme high density of 1000 individuals per hectare to an extreme low density of 2 individuals per km^2 (Settele *et al.*, 1999). To calculate the geographical distribution of butterfly assemblages we took a distribution index from literature indicating "the size of the species' European range in relation to the size of the area of Europe" (Kudrna *et al.*, 2011). In few cases data on specialised alpine butterfly species were missing so we included external expert opinion and used estimated data from closely related species (Table II.S1).

Statistical analyses

Statistical analyses were performed with the software R 2.15.1 for Windows (R Core Team, 2012). We used general linear models with Type III sums of squares with the explanatory variables altitude and flower cover. The predictors altitude and flower cover showed no significant correlation (r = - 0.3) and thus could be included in one model. We removed one study site from the species richness and abundance analysis, as flower cover at this study site was identified as outlier with high influence. Model simplification was performed with likelihood ratio tests by removing non-significant terms from the model. The residuals of the models were normally distributed and met the assumptions of variance homogeneity.

We calculated species richness estimators using the software EstimateS (Version 8.2, R. K. Colwell, http://purl.oclc.org/estimates) to verify that sampling effort on the study sites was sufficient. We used the eight 4 min sections (sub-samplings) per transect walk as replicates for species richness estimation. We divided the recorded species richness by the estimator ACE (Abundance-based Coverage Estimator of species richness) to obtain species saturation per study site. Species saturation was high and similar between the study sites for butterfly species (mean: 83 %, range 60 - 100 %). Moth species saturation was lower (mean: 72 %, range 18 - 100 %). We used a Two Sample t-test to compare the mean species saturation of five transect walks with the mean species saturation of six transect walks (butterfly species saturation: t_{32} = 0.21, p = 0.84, five walks mean: 83 %, six walks mean: 82 %; moth species saturation: t_{31} = 1.40, p = 0.17, five walks mean: 77 %, six walks mean: 66 %). The variances of the five and six walks mean for both butterfly and moth species were equal. To test for spatial autocorrelation we calculated Moran's I with the *correlog* function of the R package *ncf* (Kissling & Carl, 2008).

For community traits we calculated species- and abundance-based means for wing length, migration categories, egg number, egg maturation time, population density and distribution per site. Additionally, we used the ratio of egg number to wing length of each butterfly assemblage to correct for the effect that larger butterfly species lay more eggs. Furthermore, we calculated the proportion of egg deposition in clutches and the proportion of multivoltine species per butterfly assemblage. Species life-history trait values were averaged, when ranges were presented in the literature. Thus, our community-based trait analyses do not take into account intraspecific trait variation along the elevational gradient. We used regression analyses with species-based and abundance-weighted trait values as response variables and altitude as explanatory variable to test the shifts of life-history traits along the altitudinal gradient. For the population density and the distribution of the butterfly assemblages we performed regressions with the species-based and abundance-based means per study site as response variables and altitude as predictor. Relationships between the response variables were analysed with Pearson's correlations.

Life-history traits among phylogenetically more closely related species can be more highly correlated compared to distantly related species. We prepared polytomous, ultrametric trees with the taxonomy of the butterfly species to analyse the phylogenetic relatedness within the studied butterfly assemblages at the study sites along the altitudinal gradient. Phylogenetic analyses were performed similar to a method used by (Hoiss *et al.*, 2012). We used the R package *ape* (Paradis *et al.*, 2004) to calculate branch lengths of the taxonomic tree with a method provided by (Grafen, 1989). The phylogenetic relatedness within butterfly assemblages was estimated with the net relatedness index (NRI) (Webb *et al.*, 2002). Species assemblages with a higher NRI are closer related than species with a lower NRI.

Results

Species richness and abundance

Altogether we recorded 67 butterfly species with 4691 individuals and 43 diurnal moth species with 698 individuals on the 34 grassland study sites. Fourteen of the sampled butterfly species are restricted to alpine regions including eleven species of the genus *Erebia*. Five butterfly species were only found above 1500 m.a.s.l. (*Aricia artaxerxes*, *Boloria pales*, *Erebia epiphron*, *Erebia gorge*, *Erebia pandrose*) (Table II.S1). The number of butterfly and moth species linearly declined with increasing altitude (Fig. II.1). Flower cover had no significant influence on the number of moth species and was positively correlated with butterfly richness (Table II.1). At 2000 m.a.s.l. we recorded on average half of the butterfly species and 40 % of the moth species compared to the species richness found at 600 m.a.s.l.. Butterfly and moth abundance were not significantly related to altitude and flower cover (Table II.1). Further, Moran's Index was not significantly different from zero for the tested distance classes 1 – 5 km with intervals of 1 km, indicating that our dataset was not spatially autocorrelated.

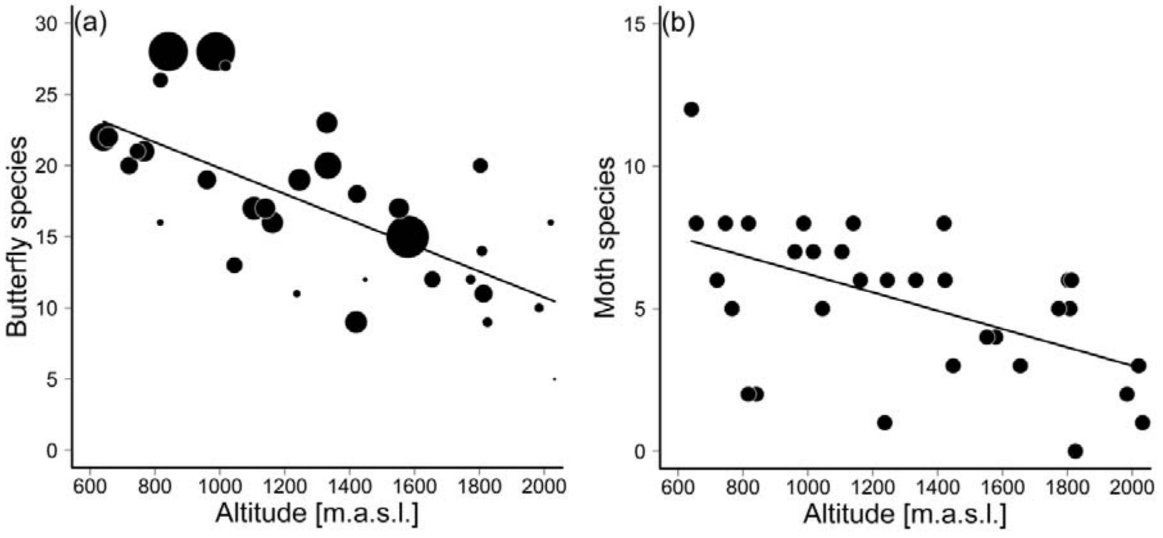


Fig. II.1 Species richness of (a) butterfly species ($y = 28.9 - 0.009\ x$) and (b) moth species ($y = 9.4 - 0.003\ x$) decreases with altitude (n = 33 study sites). The size of the points in the butterfly graphic corresponds with flower cover (min = 0.41 %, max = 4.39 %). See Table II.1 for statistical details.

Table II.1 General linear models output (Type III sums of squares) with species richness and abundance of butterflies and moths as response variables and flower cover and altitude as explanatory variables. See Fig. II.1.

response	predictor	d.f.	*F*	*P*
butterfly richness	flower cover	1, 30	5.65	0.02
	altitude	1, 30	18.01	< 0.001
moth richness	flower cover	1, 30	2.06	0.16
	altitude	1, 30	7.80	0.009
butterfly abundance	flower cover	1, 30	3.93	0.06
	altitude	1, 30	1.76	0.19
moth abundance	flower cover	1, 30	1.85	0.18
	altitude	1, 30	0.93	0.34

Life-history traits

In the next step we analysed whether life-history traits related to mobility, reproduction and development changed along the altitudinal gradient. We observed significant shifts in species- and abundance-based means of several life-history traits (Table II.2). Butterfly assemblages at higher altitudes contained relatively more larger-winged species and individuals than butterfly assemblages at lower altitudes (Fig. II.2a). Further, butterfly assemblages at higher altitudes consisted of relatively more individuals with higher migration categories than butterfly assemblages at lower altitudes (Fig. II.2b). The mean number of eggs produced per individual as measure of reproductive investment increased for species- and abundance-based assemblage means with increasing altitude (Fig. II.2c). The relationship with altitude was still significant after correction for wing length (F = 20.82, $R^2 = 0.39$, $p < 0.001$; y = 3.0 + 0.001 x). The mode of egg deposition, i.e. single eggs versus egg clutches did not significantly change with altitude (Fig. II.2d). The species-based mean developmental time of eggs from the hatch of the female until the first egg was laid of butterfly assemblages was longer at lower altitudes than at higher altitudes (Fig. II.2e). In contrast to expectations the proportion of multivoltine species and individuals did not significantly change along the altitudinal gradient (Fig. II.2f).

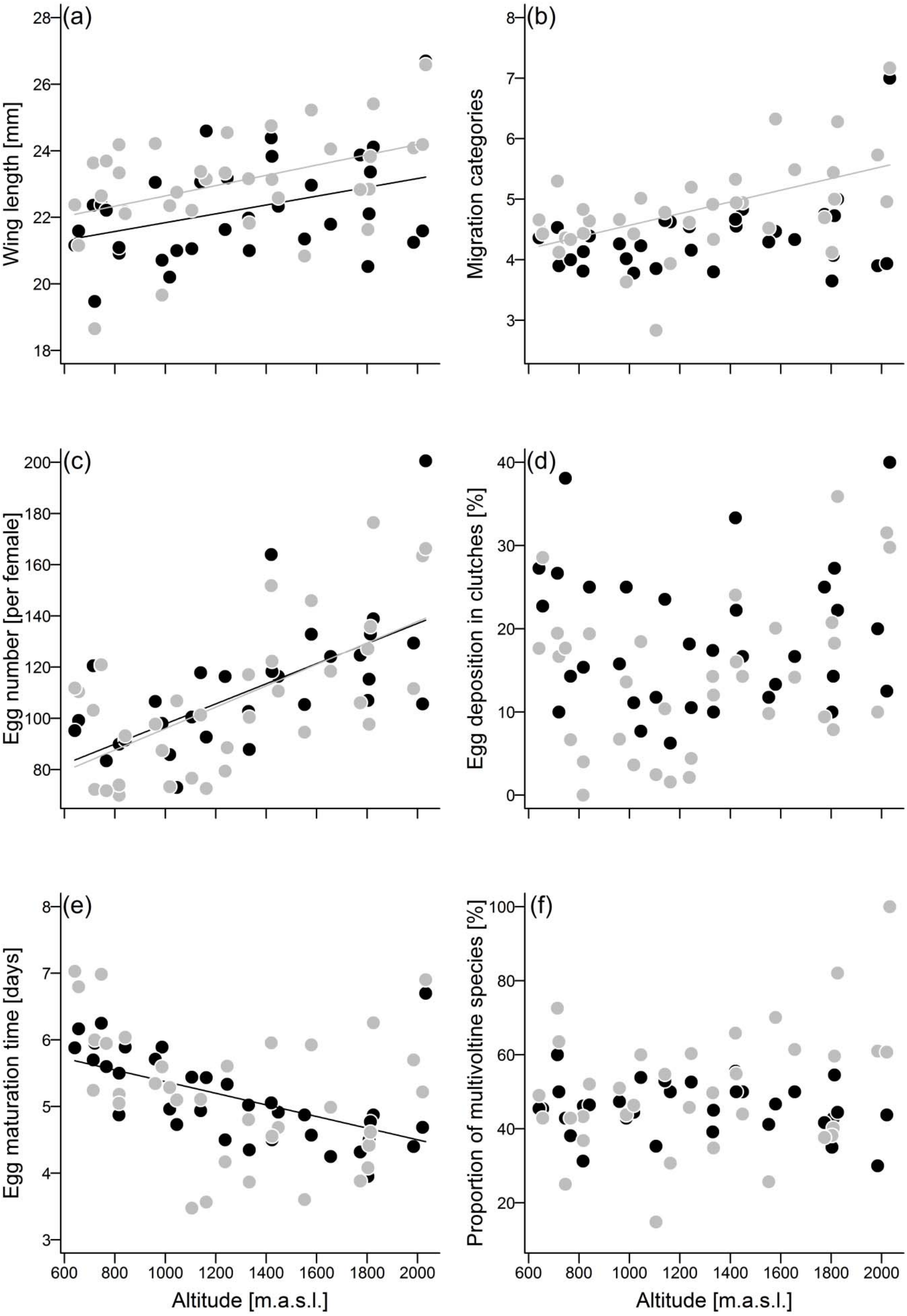

(a)
Wing length [mm]
18
20
22
24
26
28
(b)
Migration categories
3
4
5
6
7
8
(c)
Egg number [per female]
80
100
120
140
160
180
200
(d)
Egg deposition in clutches [%]
0
10
20
30
40
(e)
Egg maturation time [days]
3
4
5
6
7
8
(f)
Proportion of multivoltine species [%]
20
40
60
80
100
600
800
1000
1200
1400
1600
1800
2000
Altitude [m.a.s.l.]

Fig. II.2 Relationships between altitude and (a) wing length [mm], (b) migration categories (ranging from 1 = sedentary to 9 = migratory), (c) egg number [per female], (d) proportion of egg deposition in clutches [%], (e) egg maturation time [days] and (f) proportion of multivoltine species [%] for butterfly assemblages of 34 study sites. Black symbols show species-based life-history traits and grey symbols show abundance-based life-history traits. Proportions (d, f) or mean values (a, b, c, e) of the life-history traits per study site are shown. Lines are drawn, when the relationship was significant ($P < 0.05$). See Table II.2 for statistical details.

Table II.2 Simple regressions model output with the six life-history traits, population density and the distribution index as response variables and altitude as explanatory variable. Analyses were made for species-based and abundance-weighted means or proportions for butterfly assemblages of 34 study sites. See Fig. II.2 and Fig. II.3.

	$F_{1,32}$	r^2	P	estimates
species-based				
mean wing length [mm]	5.89	0.16	0.02	$y = 20.5 + 0.001\,x$
mean migration categories	3.32	0.09	0.08	n.s.
mean egg number [per female]	19.58	0.38	< 0.001	$y = 58.5 + 0.04\,x$
proportion of egg deposition in clutches [%]	0.20	0.006	0.66	n.s.
mean egg maturation time [days]	15.66	0.33	< 0.001	$y = 6.2 - 0.0009\,x$
proportion of multivoltine species [%]	0.84	0.03	0.37	n.s.
mean population density [individuals/ha]	22.25	0.41	< 0.001	$y = 109.6 - 0.04\,x$
mean distribution index [%]	10.59	0.25	0.003	$y = 62.3 - 0.01\,x$
abundance-weighted				
mean wing length [mm]	7.28	0.19	0.01	$y = 21.1 + 0.002\,x$
mean migration categories	12.73	0.28	0.001	$y = 3.6 + 0.001\,x$
mean egg number [per female]	21.89	0.41	< 0.001	$y = 54.2 + 0.04\,x$
proportion of egg deposition in clutches [%]	3.32	0.09	0.08	n.s.
mean egg maturation time [days]	2.81	0.08	0.1	n.s.
proportion of multivoltine species [%]	3.90	0.11	0.06	n.s.
mean population density [individuals/ha]	25.74	0.45	< 0.001	$y = 188.5 - 0.09\,x$
mean distribution index [%]	2.39	0.07	0.13	$y = 60.2 - 0.008\,x$

Species- and abundance-based analyses showed that at high altitudes species with generally low population densities and restricted geographic distribution dominate in butterfly assemblages (Fig. II.3a,b).

To test whether the expression of different life-history traits at a community assemblage level was independent, we calculated a correlation matrix for all studied trait values (Table II.3). Although only three *r*-values were above 0.8, 21 out of 28 possible trait combinations were significantly correlated, indicating that covariation or trade-offs among traits play an important role in the community-level assemblage of life-history traits. Further, we tested for potential evolutionary impacts on species composition and related life-history trait characteristics. However, the phylogenetic relatedness within butterfly assemblages did not significantly change along the altitudinal gradient ($F_{1,32}$ = 3.53, r^2 = 0.10, P = 0.07), indicating that species in butterfly assemblages at higher altitudes are not closer related than species in butterfly assemblages at lower altitudes. The net relatedness index (NRI) varied between -2.77 and 1.50 between the butterfly assemblages.

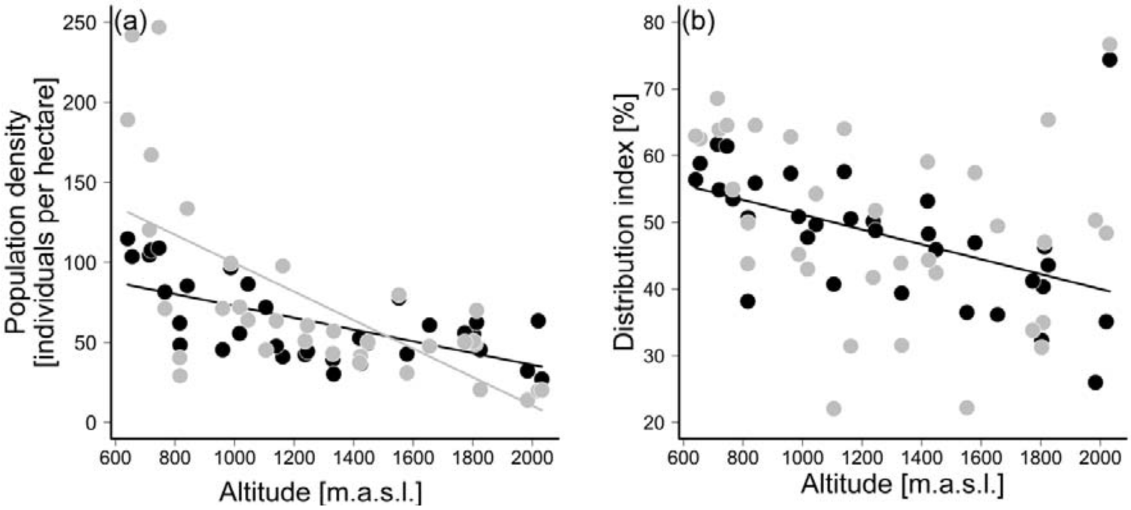


Fig. II.3 Effects of altitude on (a) population density and (b) the distribution index (relative size of the European distribution of the species). Black symbols show species-based analyses and grey symbols show abundance-based analyses. Mean values per study site are shown. Lines are drawn, when the relationship was significant ($P < 0.05$). See Table II.2 for statistical details.

Table II.3 The relationship between species-based means of six life-history traits, population density and distribution of 34 alpine butterfly communities (Pearson's correlation coefficients (*r*) are shown).

species life-history traits	migration categories	egg number	egg deposition in clutches	egg maturation time	proportion of multivoltine species	population density	distribution index
wing length	0.81***	0.73***	0.51**	0.16 n.s.	0.63***	- 0.44**	0.40*
migration categories	-	0.75***	0.63***	0.36*	0.85***	- 0.22 n.s.	0.58***
egg number	-	-	0.73***	- 0.02 n.s.	0.58***	- 0.38*	0.22 n.s.
egg deposition in clutches	-	-	-	0.44**	0.51**	0.17 n.s.	0.57***
egg maturation time	-	-	-	-	0.43*	0.51**	0.81***
proportion of multivoltine species	-	-	-	-	-	- 0.14 n.s.	0.69***
population density	-	-	-	-	-	-	0.32(*)

Significance levels are: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$, n.s. = not significant

Discussion

Elevational gradients are suitable model systems to study the impact of climatic conditions on species richness and assemblage rules. However, very few studies performed species- and abundance-based analyses of life-history traits at the community level to reveal trait combinations that promote adaption to certain climatic conditions. Our results show that species richness of butterfly and moth linearly declined with increasing altitude. Even more importantly, we find that the dominance of life-history traits in alpine butterfly assemblages is significantly influenced by altitude.

Species richness and abundance

Declining species richness has been reported for different species groups in several regions (Stevens, 1992; Hunter & Yonzon, 1993; Vazquez & Givnish, 1998), however there are also studies presenting hump-shaped relationships of species richness patterns along altitudinal gradients (Rahbek, 1995). Species richness patterns may change depending on the observed range and may shift from a hump-shaped to a monotonic relationship when the observed range was reduced by omitting the lower sites (Nogues-Bravo *et al.*, 2008). This study covered a wide altitudinal range from 600 to 2000 m.a.s.l. but excluded the lowlands, which are often the most disturbed elevational zones (Rahbek, 1995), with presumably low diversity. This fact could explain why we found a monotonic instead of a hump-shaped relationship of species richness along the altitudinal gradient. Plant diversity showed a hump-shaped altitudinal pattern in the same study region (Hoiss *et al.*, 2013). Therefore, we conclude that climatic factors were more important drivers of richness patterns than biotic interactions with plants as larval host plants or nectar sources. While species richness decreased with altitude, the abundance of butterfly and moth species was not influenced by altitude. Presumably, the lower population densities of alpine specialists at higher altitudes were compensated by some highly abundant and mobile generalist species, which dispersed to higher altitudes during the summer month.

Shifts in life-history traits along altitude

Our study addressed not only diversity patterns but also the dominance of life-history traits in butterfly communities at different altitudes. We calculated species-based and abundance-based means, assuming that species occurrence reflects long-term distribution patterns while species abundance rather reflects fitness benefits of life-history traits under current environmental conditions. We found that the proportion of butterfly species and individuals with larger wings increased in butterfly assemblages along altitude. In the few other assemblage studies no consistent patterns were found so far for butterfly and moth species (Hawkins & DeVries, 1996; Brehm & Fiedler, 2004). An increase of butterfly wing length with altitude can be explained with the lower atmospheric pressure at higher altitudes, which decreases the flight potential (Hodkinson, 2005; Dillon *et al.*, 2006). Our butterfly wing data also follow Bergmann's rule claiming that species of larger size occur in colder regions. To distinguish between these explanations a comparison of altitudinal and longitudinal gradients would be required. The butterfly assemblages with larger-winged species also contained species with better dispersal ability. However, only the proportion of individuals with high dispersal capacity increased in the butterfly assemblages with altitude, while the proportion of species with high dispersal capacity remained constant. This indicates that short-term dispersal patterns of migratory individuals but not longer-term distribution patterns caused this pattern. Other dispersal observations of alpine butterfly species detected a low mobility of endemic alpine species (Roland *et al.*, 2000; Kuras *et al.*, 2003; Junker *et al.*, 2010). Based on our findings we conclude that the composition of alpine butterfly assemblages presumably comprises both well adapted alpine species with relatively low dispersal capacity and species with larger dispersal capacity that follow seasonally abundant flower resources at high altitudes.

Interestingly, the proportion of butterfly species and individuals with a higher number of eggs per female increased in the butterfly assemblages. A higher egg number at higher altitudes can be explained by a risk spreading strategy, because more eggs increase the fecundity and might spread the risk of reproductive failure under harsh and variable environmental conditions prevailing in alpine regions. Furthermore, it was observed that females lay numerous small eggs when egg laying time is limited (Gibbs *et al.*, 2005). This concurs with the model described by (Mangel *et al.*, 1994) predicting that females should produce large clutches with small eggs when egg laying conditions are not optimal. Importantly, environmental filtering at the community level might result in other trait distribution patterns than intraspecific trait variation of individual species (Fischer & Fiedler, 2001). Additionally, we also found a significant correlation between wing length and egg number (Garcia-Barros, 2000). However, the increase of butterfly wing length with altitude could not explain the higher egg number at higher altitudes, because the increase of eggs with altitude remained significant after correction for wing length. Altitude did not significantly affect the mode of egg deposition neither with a species- nor with an abundance-weighted analysis. This implies that the way of egg deposition presumably will not change under changing climate. Furthermore, egg clustering is generally a fixed, species-specific trait and less than 7 % of butterfly species worldwide form egg clusters (García-Barros & Fartmann, 2009). Although egg clustering species do not occur more often at higher altitudes our data are in support with former findings that larger butterflies tend to lay their eggs in clutches (Garcia-Barros, 2000).

We observed a decrease in the species-based egg maturation time along the altitudinal gradient, indicating that a rapid development is important in harsh alpine environments. Although we do not have data for egg sizes, several studies suggest a conflict between egg size and egg number with shorter developmental time for smaller eggs (Garcia-Barros, 2000; Braby, 2002). Therefore we assume that the numerous eggs laid by alpine butterfly species were smaller than the eggs laid by lowland species and that this is also a consequence of a trade-off between egg size and developmental time. Additionally, adverse conditions at high altitudes may increase the mortality rate of females before any egg was laid, which may favour the occurrence of species with shorter egg maturation times. In contrast to our expectations (Nylin, 2009), the number of generations per year was not significantly influenced by altitude, perhaps due to upwards dispersal of multivoltine species later in the season (Beck *et al.*, 2010).

Our results showed a decrease of the mean population density and distribution ranges in butterfly assemblages with increasing altitude and thus supports the expectation that species with smaller distribution ranges also have smaller population densities. Other studies also indicate that rare and endemic species occur at lower densities than common, wide-spread species (Gaston, 1996). Smaller distribution ranges at higher altitudes are not surprising, because the higher altitudes in the Alps contain many endemic species (Schweizerischer Bund für Naturschutz, 1994). The fact that altitude did not influence the abundance-weighted distribution data implies that the proportion of rare alpine species increased with altitude, but that highly abundant generalist species with wider geographical distribution ranges dominated the butterfly assemblages.

Conclusions

In conclusion, our study contributes to the understanding of general patterns along altitudinal gradients by providing one of the few assemblage studies for insects in temperate regions and, even more importantly, by addressing the role of life-history strategies in explaining species richness patterns. Life-history traits concerning dispersal capacity, reproductive strategies and developmental time gave valuable insights into the changes in butterfly assemblages along altitude. Our results indicate that environmental filtering favours certain combinations of life-history traits at higher altitudes, but it remains an open question whether these trait combinations reduce the adaptive capacity, competitive strength and fitness of alpine butterfly species under global warming.

Supplement

Table II.S1 Information on species life-history traits, population density and the distribution index.

butterfly species	wing length	migration categories	egg number	egg deposition	egg maturation time	generations	population density	distribution index
Aglais io	28	6	445.5	clutch	7.5	1.5	2.01	65.75
Aglais urticae	23	6	307	clutch	7.5	1.5	2.03	74.73
Anthocharis cardamines	21.5	4	33.5	single egg	3.5	1	8.5	72.15
Aphantopus hyperantus	22	3	101	single egg	3.5	1	138	56.24
Aporia crataegi	31	5	212	clutch	3.5	1	1	52.31
Araschnia levana	17.5	5	146.5	clutch	3.5	2.5	4	33.98
Argynnis adippe	28	4	48.5	single egg	10.5	1	4	50.11
Argynnis aglaja	26.5	3	101	single egg	7.5	1	4	62.69
Argynnis niobe f. eris	26.5	3	146.5	single egg	7.5	1	4	37.90
Argynnis paphia	31	4	48.5	single egg	15.5	1	2.125	57.26
Aricia artaxerxes	11.5	4	179	single egg	3.5	1	162	31.24
Boloria euphrosyne	21	3	70	single egg	5.5	1.5	4	57.26
Boloria pales	18	3*	70*	single egg	3.5*	1	100*	4.73
Boloria thore	21.5	2*	70*	single egg	3.5*	1	5*	4.14

Boloria titania	22	2*	70*	single egg	3.5*	1	30*	6.83
Callophrys rubi	14	4	70	single egg	5.5	1	34	71.74
Carterocephalus palaemon	14	3	33.5	single egg	5.5	1	16	33.39
Coenonympha arcania	18.5	3	48.5	single egg	3.5	1	64	41.56
Coenonympha gardetta	15.5	1*	48.5*	single egg	3.5*	1	100*	2.53
Coenonympha pamphilus	15	3	48.5	single egg	3.5	2	34	74.41
Colias alfacariensis/hyale	23.5	4.5	101	single egg	9.5	2.5	130.5	32.42
Colias crocea	25	8	146.5	single egg	10.5	3.5	130.03	58.55
Cupido minimus	11	2	48.5	single egg	3.5	1.5	34	47.52
Erebia aethiops	24	3	48.5	single egg	5.5	1	16	17.37
Erebia epiphron	18	2	48.5	single egg	3.5	1	34	6.83
Erebia eriphyle	17	2*	80*	single egg	1.5*	1	50*	1.4
Erebia euryale	22	2*	80*	single egg	1.5*	1	250*	9.46
Erebia gorge	18.5	2*	80*	single egg	1.5*	1	30*	4.19
Erebia ligea	25.5	4	33.5	single egg	3.5	1	16	31.56
Erebia manto	20.5	2*	80*	single egg	1.5*	1	20*	4.25
Erebia oeme	21	2*	80*	single egg	1.5*	1	50*	5
Erebia pandrose	22.5	2*	80*	single egg	1.5*	1	20*	11.34
Erebia pharte	18	2*	80*	single egg	1.5*	1	10*	2.69
Erebia pronoe	23	2	80*	single egg	1.5*	1	50*	4.35

Erynnis tages	13.5	3	33.5	single egg	5.5	1.5	16	51.08
Gonepteryx rhamni	28	6	101	single egg	270	1	8.03	65.43
Hamearis lucina	15.5	2	48.5	single egg	3.5	1	16	29.62
Hesperia comma	14.5	3	33.5	single egg	5.5	1	16	45.81
Lasiommata maera	26.5	3	48.5	single egg	3.5	1.5	8.5	53.44
Lasiommata petropolitana	20	3	48.5	single egg	3.5	1	4	19.95
Leptidea sinapis/reali	21.5	4	33.5	single egg	3.5	1.5	16	63.82
Lycaena hippothoe	16.5	3	70	single egg	3.5	1	16	41.13
Lycaena tityrus	15	3	70	single egg	5.5	2	64	36.61
Maniola jurtina	23.5	4	146.5	single egg	10.5	1	508	68.28
Melitaea athalia	19	3	146.5	clutch	7.5	1	132	56.29
Melitaea diamina	20	1	212	clutch	5.5	1	132	27.69
Nymphalis antiopa	32	6	307	clutch	270	1	0.51	52.31
Nymphalis c-album	23	6	48.5	single egg	7.5	1.5	0.53	64.46
Ochlodes sylvanus	15.5	4	48.5	single egg	7.5	1	16	59.14
Papilio machaon	35	5	48.5	single egg	3.5	2	0.25	67.74
Pararge aegeria	20.5	4	33.5	single egg	3.5	1.5	16	64.73
Phengaris arion	18	3	212	single egg	1.5	1	16	30.91
Pieris brassicae	30.5	7	101	clutch	7.5	2.5	32.125	75.97
Pieris bryoniae	20	5*	48.5*	single egg	2.5*	1	100*	5.11

Pieris napi	20	5	48.5	single egg	3.5	2.5	34	80.43
Pieris rapae	25	6	48.5	single egg	3.5	3.5	130.5	74.75
Polyommatus bellargus	15.5	3	146.5	single egg	7.5	2	132	36.34
Polyommatus coridon	16.5	4	70	single egg	10.5	1	508	33.49
Polyommatus icarus	16	4	101	single egg	7.5	2	132	80.48
Polyommatus semiargus	15.5	4	101	single egg	5.5	2	64	54.73
Pyrgus alveus	15	4	48.5	single egg	10.5	1	1	30.59
Pyrgus andromedae	14	3*	33.5*	single egg*	7.5*	1	4*	4.46
Pyrgus malvae	12	3	33.5	single egg	5.5	1	16	54.68
Thymelicus lineola	13	4	48.5	clutch	5.5	1	508	54.19
Thymelicus sylvestris	14	3	70	clutch	5.5	1	508	47.2
Vanessa atalanta	29.5	9	101	single egg	7.5	3.5	0.51	76.72
Vanessa cardui	28	8	101	single egg	7.5	3.5	0.135	80
references	Higgins and Riley 1971	Settele et al. 1999	Settele et al. 1999, Sonderegger 2005	Schweizerischer Bund für Naturschutz 1994, Sonderegger 2005, Weidemann1995	Settele et al. 1999, Sonderegger 2005	Settele et al. 1999, Stettmer et al. 2007	Settele et al. 1999	Kudrna et al. 2011

* data based on external expert opinion or estimated from closely related species

III. Combined effects of climate and management on plant diversity and pollination type in alpine grasslands

Abstract

Aim Climate and habitat management are two key drivers for patterns of biodiversity, but little is known about relative importance, interactions and non-linear effects of climate and management on species richness and trait variation of plants.

Location Alps (Germany).

Methods We studied patterns of species richness and pollination types in 34 alpine grasslands along an altitudinal climatic gradient comparing grazed, mown and non-managed grasslands. Two vegetation assessments were conducted in 2009 on ten 4 m² plots per study site and per survey.

Results In total 484 vascular plant species were recorded. Species richness peaked at intermediate temperatures and was highest in grazed grasslands compared to mown and non-managed grasslands. No significant interaction between management effects and climate was found. Species richness of insect-pollinated plants peaked at lower temperatures (higher altitudes) than species richness of wind-pollinated plant species. The proportion of wind-pollinated plants decreased with decreasing temperature, but the vegetation cover of wind-pollinated plants increased with decreasing temperature.

Main conclusions Our results indicate that managing alpine grasslands by extensive grazing maintains high plant diversity over the full subalpine gradient. Rising temperatures with climate change and an upward shift of the diversity peak of plants might result not only in reduced overall diversity due to reduced grassland area at higher altitudes but also in changed species composition and adaptive potential of pollination types.

Keywords

Climate change, land use change, altitudinal gradient, hump-shaped species richness relationships, life history traits, pollination types, vascular plants, alpine ecosystems

Introduction

Biodiversity changes with climate along altitudinal gradients, but also with changing intensity of land use (Tscharntke *et al.*, 2005; Nogues-Bravo *et al.*, 2008). To understand patterns in biodiversity, not only the impact of natural factors such as climate but also human impact has to be considered (Bock *et al.*, 1995; Körner, 2007; Nogues-Bravo *et al.*, 2008). Further the prevalence of species traits and changing adaptations along altitudinal gradients provide additional insights into the potential response of communities to climate change (Hodkinson, 2005). However, to our knowledge no study so far has considered the relative importance, interactions and non-linear effects of climate and management on plant diversity, community composition and species traits in parallel.

Altitudinal gradients have been used several times to study the effect of seemingly simple environmental factors such as temperature on plant species richness (Körner, 2007). However, empirical altitudinal patterns in plant diversity are strikingly variable and therefore several competing hypotheses are suggested to explain the underlying mechanisms. A linear decline of species richness from warm lowlands to cold highlands is predicted due to i) water-energy limitations (Clarke & Gaston, 2006) or ii) species-area effects (Jones *et al.*, 2003). Hypotheses which predict peaks of species richness at mid-elevation are i) the mid-domain effect (Colwell & Lees, 2000; Zapata *et al.*, 2003; Colwell *et al.*, 2004), ii) source-sink (mass) effects (Grytnes *et al.*, 2008; Kessler, 2009) or iii) the effect of temperature on competition, metabolism and speciation (Moser *et al.*, 2005; Stegen *et al.*, 2009). In the face of climate change, studies contributing data to the discussion on biodiversity patterns along climatic gradients (linear versus hump-shaped relationships) are of increasing importance to interpret existing patterns and predict future scenarios.

Intensity and type of land use and management are key drivers of biodiversity in large-scale managed landscapes of Europe where changes in agriculture in recent decades led to intensification or abandonment of pastures and therefore changing species richness and composition (Tscharntke *et al.*, 2005; Krauss *et al.*, 2010). Defoliation, trampling and deposition of manure are main processes on pastures that affect light competition, plant colonization and extinction dynamics and cause local habitat heterogeneity (Olff & Ritchie, 1998; Bergamini *et al.*, 2001). The effect of different management types interacts with climate, soil fertility, management intensity and the scale at which diversity was measured (Olff & Ritchie, 1998). A stronger effect of management on plant species richness is expected at low altitudes where communities are expected to be competition-dominated, than at higher altitudes, where the occurrence of plant species is determined by a harsh abiotic environment and competition plays a minor role for community composition (Bruun *et al.*, 2006; Clarke & Gaston, 2006). Human land use has superimposed the natural drivers of biodiversity and permanently affects the detectability of natural patterns in diversity (Nogues-Bravo *et al.*, 2008). Even in mountain biosphere reserves the impact of land cover changes is assumed to exceed the effect of recent climate changes on species richness (Becker *et al.*, 2007). This stresses the importance of considering management effects and their interactions with climate when investigating processes that affect natural patterns of species richness and assemblages. But apart from a case study on bryophytes in fens (Bergamini *et al.*, 2001) and some large-scale modelling studies (Thuiller *et al.*, 2004; Pompe *et al.*, 2008) little is known about the combined effects of human land use and climatic gradients on species richness of plants.

The pollination type of plants is an important adaptation to environmental conditions. Pollination plays a crucial role in the life cycle of plants and determines their reproductive success. The distribution of plant pollination types can be explained by several mechanisms. The most important ecological drivers are i) temperature as a limiting factor for pollinator flight ability and activity (Hodkinson, 2005) and for the seed set of plants (Totland, 2001), ii) wind as a pollen vector and as an impeding factor for insect flight at high wind speed (discussed in Kühn *et al.*, 2006), iii) precipitation which washes pollen away (Pellissier *et al.*, 2010), iv) vegetation structure with high inter-individual distances and lower population size reducing the efficiency of wind-pollination (Regal, 1982; Culley *et al.*, 2002; Friedman & Barrett, 2009). A decline in pollinator visitation rates at lower temperatures (higher altitudes) due to reduced flight ability and activity or due to high wind speeds (Totland, 2001; Malo & Baonza, 2002) could result in reduced reproductive success of insect-pollinated plant species and might favor wind-pollinated species (Culley *et al.*, 2002). It has been proposed that wind-pollination would be advantageous in alpine grasslands because of the open structure of grasslands (Culley *et al.*, 2002). But lower proportions of wind-pollinated species at high altitudes could be explained by increasing precipitation with altitude which reduces pollen viability and dispersal distances by wind (Pellissier *et al.*, 2010). Understanding of the ecological importance of pollination type for the adaptation and composition of plant communities in different climatic conditions is incomplete and only a few recent studies have been conducted on this issue (Diaz *et al.*, 1998; Kühn *et al.*, 2006; Pellissier *et al.*, 2010), while studies also including the effect of management on the distribution of pollination types are lacking.

In this study we analysed how the combination of a climatic gradient and different management regimes influences species richness of vascular plants and the distribution of pollination types in alpine grasslands. We hypothesized that:

1. Species richness along the altitudinal gradient steadily declines or peaks at intermediate temperatures.
2. Species richness is higher in grazed sites than in non-managed sites.
3. Management enhances plant diversity more at low than at high altitudes.
4. Proportion of total species richness and cover of insect-pollinated species decline while proportion and cover of wind-pollinated and self-pollinated species increase with increasing altitude

Methods

Study sites

The study region is located in and near the National Park Berchtesgaden in the southeast of Germany (47° 6′ N, 12° 9′ E). The region is characterized by calcareous rocks and mountains up to 2700 m a.s.l.. Depending on the altitude the annual mean temperature varies between +7°C and -2°C, the annual mean precipitation varies between 1500 mm and 2600 mm. Many of the former mountain pastures were abandoned within the last century but managed pastures often located within coniferous forests are still characteristic of the landscape. There are three main valleys in the National Park Berchtesgaden. Slopes and faces around the easternmost valley are very steep and there are no grasslands between 600 and 1300 m a.s.l.. Therefore we excluded grasslands from this valley and selected only sites in the western part of the national park and its vicinity.

34 grasslands (16 without management, 14 grazed, 4 mown) were selected and a study site (60 m x 60 m quadrats) was established on each grassland. The grasslands were divided into four transects that covered altitudinal gradients from about 600 m to 2000 m a.s.l.. Two of the transects were established along the relatively steep slopes of two mountains, while the other two transects were established along gently inclining valleys and their terminal mountains. Criteria for selection of the study sites were: (i) the 34 sites

cover the full altitudinal gradient of grasslands in the study region; (ii) the grasslands were extensively managed (one cut per year on meadows, extensive grazing on pastures) or non-managed (sites were abandoned and in a comparable or similar stage of succession); (iii) the grasslands were not fertilized; (iv) permission was obtained from the farmers and owners.

Data collection

Data on species richness, cover and distribution were recorded in two surveys in 2009. The surveys were conducted in the early summer (June and July) and late summer (August and September). Vegetation assessments were conducted on ten 4 m² plots per study site and per survey. The location of the plots within the study site was randomized with minimum distances of 5 m to neighbouring plots. We sampled different plots in the early and late summer surveys. Sampling effort and sampling size were the same on all sites. Vegetation cover (abundance data) was estimated per plot per species using the DOMIN-scale. For calculations the mean of the cover ranges of the Domin scores per species were used (Currall, 1987). Species cover estimates per site were calculated as the average across the 20 plots per site. Species identification followed Oberdorfer *et al.* (2001).

Data on pollination types of the plant species were drawn from the BIOFLOR database (Klotz *et al.*, 2002). The types were grouped into three major levels: self-pollination (including geitonogamy and cleistogamy), wind-pollination and insect-pollination. For analysis we used only the pollination frequencies “always”, “the rule” or “often”. Only the most frequently occurring pollination type per species was selected so that there was only one main type per species. In total we extracted information on the pollination type of 418 species from the BIOFLOR database. 286 of these species were insect-pollinated, 99 species were wind-pollinated and 33 species were self-pollinated. As there were only very few self-pollinated species in our dataset we concentrated our analyses on cross-pollinated types.

During the field season we measured air temperature in 2 h intervals 1 m above the ground on each site with temperature loggers (Thermochron iButtons DS1921G#F5, Maxim Integrated Products, Inc., Sunnyvale, CA, USA). Loggers were installed at different times depending on the date at which sites became snow-free. For statistical analyses we only use the mean temperatures for the period during which data were available from all sites (16 June 2009 to 07 September 2009). Temperature was used in this study to quantify changing climatic conditions along the altitudinal gradient. Temperature was used instead of altitude as it also takes micro-climatic differences into account resulting e.g. from differences in inclination, exposition, wind speed, atmospheric moisture or cloud cover (Hodkinson, 2005). Nonetheless altitude and temperature were highly correlated (Fig. III.S1).

We gathered information on the management of our plots through farmer interviews and own field observations. In the analysis three management levels were used: grazing (cows and/or sheep); mowing (once a year); no management. Many of the currently non-managed sites were abandoned at least 30-40 years ago.

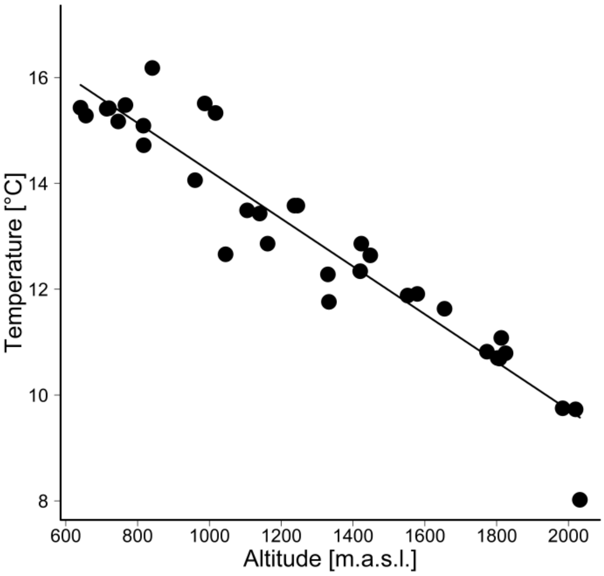


Fig. III.S1 Simple regression of altitude and temperature. $R^2 = 0.921$, $p < 0.001$. Temperature decreased by 0.45 °C per 100 m altitude.

Statistical analysis

Statistical analyses were performed using the software R 2.11.1 for Windows (R Core Team, 2012). Linear models were fitted for the effects of management and temperature on species richness. The quadratic term of temperature was added to the models to check for non-linear relationships. Hierarchical variance partitioning was performed to calculate independent and joint effects of management and temperature (Mac Nally, 1996, 2000; Heikkinen *et al.*, 2004). Linear mixed effects models (*lmer* function) were employed to test for differences between plant pollination types in species richness and vegetation cover in relation to management and temperature. Cover per pollination type was defined as the summed cover of all species per site with the same pollination type. Site identity was used as random factor in order to correct for pseudoreplication. A binomial generalized linear model (*glm* function) with a binomial response (species richness of insect pollinated plants and species richness of wind pollinated plants) was employed to test for the effect of management and temperature on the proportion of species richness per pollination type. Proportions of species richness per pollination type add up to 100 % and hence there are opposing effects on the proportion of the two pollination types. For all models we tested all possible three-way and two-way interactions of the fixed effects. Non-significant interactions were removed from the models and only significant interactions are presented here.

The residuals of “species richness” and “cover per pollination type” were normally distributed and homoscedastic. For “species richness per pollination type” a log-linear model with Poisson errors was fitted using the “glmer” function of R. The estimated scale parameter for this model was 0.903. The generalized linear model fitted for the response variable “proportion of species richness per pollination type” was not overdispersed (Phi = 0.678). Model simplification was performed by removing non-significant terms using likelihood ratio tests (Crawley, 2007). The final models also showed the lowest AIC value.

EstimateS version 8 (Colwell, 2009) was used to compute species accumulation curves and species richness estimators. Accumulation curves and species richness estimators were calculated with ten replicates. Each replicate comprised the species of one plot of the early summer survey and one plot of the late summer survey. We pooled the data from the two vegetation surveys to avoid phenology effects on the estimates. An estimate for the proportion of detected species per site was calculated by dividing the recorded species richness by the estimator ICE (incidence based species richness estimator). Estimated values ranged from 73 to 90 % and were correlated neither with temperature nor with altitude. They also did not differ significantly between management types. Due to the consistently high detection rate we only present results on detected species richness and not on the estimators. Calculation of Moran's I according to Kissling & Carl (2008) using the *correlog* function of the R package *ncf* showed no spatial autocorrelation of species richness.

Results

Species richness

In total 484 species were recorded on 780 plots. A minimum of nine species and a maximum of 53 species per plot (4 m^2) were found. Sites (data from 20 plots) had a minimum species richness of 50 and a maximum of 153.

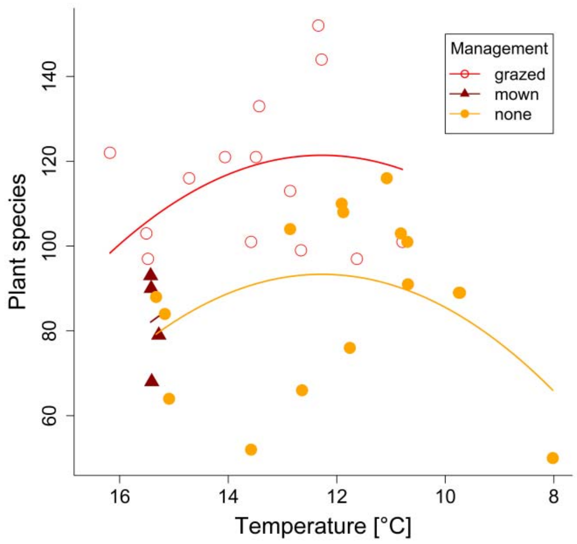


Fig. III.1 Temperature and management on 34 alpine grasslands in relation to species richness of vascular plants. Statistics see Table III.1.

Management and temperature were good predictors for plant species richness. Management explained a major part of the variance ($p < 0.001$; independent effect: $R^2 = 0.354$, joint effect: $R^2 = 0.051$). Species richness was significantly higher in grazed sites than in mown or non-managed sites. (Fig. III.1, Table III.1). The four mown sites were all located in a small range at high temperatures (low altitudes). The graph for the mown management is therefore short and conclusions are only possible for this small range of temperatures. Due to an intercorrelation of management and temperature ($R^2 = 0.312$) management superimposed the temperature effect. But after correcting for management the quadratic term of temperature still showed a significant but smaller influence than management on species richness ($p = 0.042$; independent effect of temperature: $R^2 = 0.136$, joint effect: $R^2 = 0.051$). This reflects a hump-shaped relationship between plant species richness and temperature along the altitudinal gradient (Fig. III.1).

Table III.1 Results of a general linear model with species richness of vascular plants as response variable, temperature, temperature² and management with the three levels grazing, mowing, no management (none) as explanatory variables. The grazed management was used as reference/intercept. The estimates of the management levels mowing and grazing indicate differences from the intercept. $R^2 = 0.490$.

	Estimate	Std. error	t value	P value	
Intercept	-106.138	113.001	-0.939	0.355	
Management mown	-24.287	11.174	-2.173	0.038	*
Management none	-28.070	7.183	-3.908	<0.001	***
Temperature	37.079	17.948	2.066	0.048	*
Temperature²	-1.510	0.709	-2.130	0.042	*

The model did not reveal interactions between management and temperature, indicating that the influence of management on species richness did not change with temperature. The model explained 49.0 % (F = 6.96, $p < 0.001$) of the total variance. Species-richness showed a maximum at a temperature of 12.3 °C (mean temperature from 16 June 2009 till 07 September 2009; see methods – data collection). A model using management and altitude instead of management and temperature as predictor variables was less significant than the original model ($R^2 = 0.452$, F = 5.99, p = 0.001). An additional model including only sites which were non-managed (N = 16 sites) supported a humped relationship irrespective of the management effect (Table III.S1).

Table III.S1 Results of a general linear model with species richness of vascular plants on non-managed sites as response variable and temperature and temperature^2 as explanatory variables. $R^2 = 0.290$.

	Estimate	Std. error	t value	P value	
Intercept	-217.354	142.111	-1.529	0.150	
Temperature	52.732	23.810	2.215	0.045	*
Temperature^2	-2.218	0.979	-2.266	0.041	*

Pollination type

Species-richness of wind- and insect-pollinated plants was non-linear in relation to temperature. Interactions of pollination type and management as well as pollination type and the linear term of temperature improved the model fit significantly. The interaction of pollination type and temperature suggested different slopes (Table III.2): the curve for wind-pollinated plants was more flat and had its maximum at higher temperatures than for insect-pollinated plants (Fig. III.2). This suggests that temperature has a stronger influence on the species richness of insect-pollinated plants than on wind-pollinated plants. Species richness of insect-pollinated species showed a maximum at a mean temperature of 12.3 °C whereas the maximum for wind-pollinated species richness was at 13.9 °C. Species richness was highest in grazed sites and significantly lower in non-managed sites for both wind- and insect-pollination types. Mown sites showed intermediate species-richness for both pollination types (Table III.2). A significant interaction between management and pollination type indicates that different pollination types respond differently to management regimes resulting in opposing effects of management on the proportion of species richness (Table III.2).

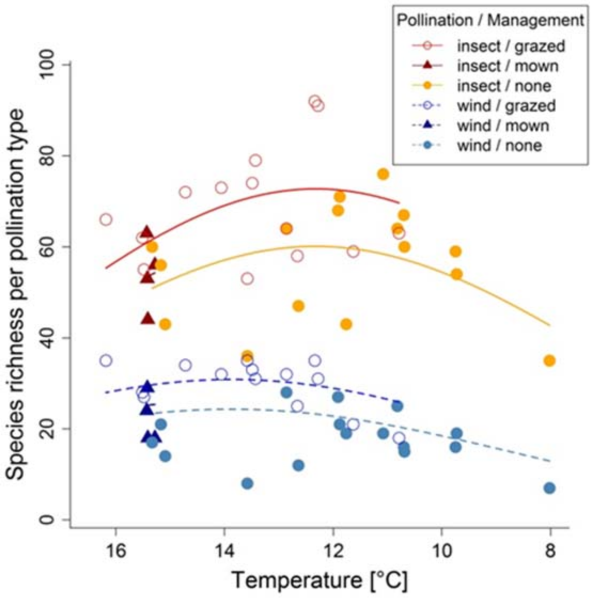


Fig. III.2 Effects of temperature and management on species richness of plants with different pollination types: insect- versus wind-pollinated species. Statistics see Table III.2.

The proportion of species richness of insect-pollinated plants increased with decreasing temperature (Table III.3), while the opposing effect was true for the proportion of wind-pollinated plants which decreased with decreasing temperature (Fig. III.3). The proportion of insect-pollinated plants was significantly higher in non-managed sites than in grazed sites. The proportion of insect-pollinated plants was not significantly different in mown compared to grazed sites (Table III.3). The opposing patterns were found for the proportion of wind-pollinated plant species. Thus wind-pollinated plant species benefited more from management than insect-pollinated plants.

The analysis of the cover of pollination types indicated a different pattern than the analysis of the proportion of species richness. Management showed no influence on the cover but the interaction of pollination type and temperature was highly significant (Table III.4). The slope estimate for temperature was significantly different in wind-pollinated and insect-pollinated plants. Cover of wind-pollinated species increased significantly with decreasing temperatures and became even higher than the cover of insect-pollinated species at mean temperatures below 11.4 °C (Fig. III.4).

Table III.2 Results of a generalized linear mixed effects model (log-link function) with species richness of vascular plants as response variable, temperature, temperature², pollination type (two levels: insect, wind) and management (three levels: grazing, mowing, none) as explanatory variables. The factor levels insect-pollination type and grazed management were associated with the estimate of the intercept. The factor level insect-pollination was associated with the estimate of the Temperature slope. The values for the other factor levels indicate differences from the given intercept and slope. Site identity was used as a random factor to correct for pseudoreplication. 68 observations on 34 sites.

Fixed effects	Estimate	Std. error	z value	P value
Intercept	1.496	1.167	1.282	0.200
Pollination type wind	-1.603	0.363	-4.416	<0.001 ***
Management mown	-0.132	0.117	-1.122	0.262
Management none	-0.191	0.074	-2.563	0.010 *
Temperature	0.453	0.184	2.465	0.014 *
Temperature²	-0.018	0.007	-2.548	0.011 *
Pollination type wind: Management mown	-0.159	0.148	-1.078	0.281
Pollination type wind: Management none	-0.238	0.098	-2.433	0.015 *
Pollination type wind: Temperature	0.057	0.026	2.148	0.032 *

Table III.3 Results of a binomial generalized linear model with the proportion of insect pollinated species richness of vascular plants as response variable, temperature and management (three levels: grazing, mowing, none) as explanatory variables. The grazed management was used as reference/intercept. The estimates of the other management levels indicate differences from the intercept. Estimates are shown in the logit scale.

	Estimate	Std. Error	z value	P value
Intercept	1.593	0.366	4.356	<0.001 ***
Management mown	0.156	0.147	1.059	0.290
Management none	0.236	0.098	2.396	0.016 *
Temperature	-0.056	0.027	-2.104	0.035 *

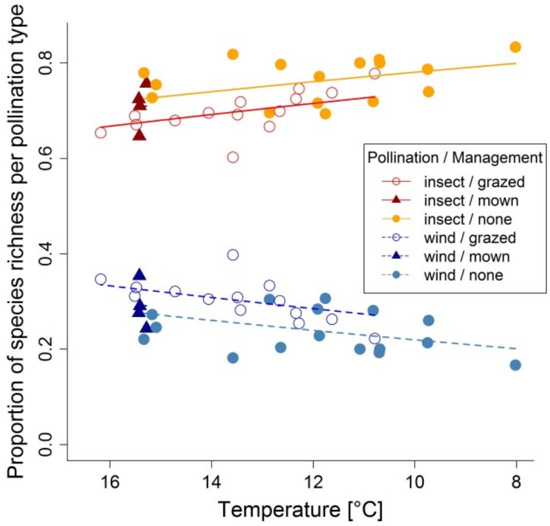


Fig. III.3 Effects of temperature and management on the proportion of species richness per pollination type (insect-pollination, wind pollination). Statistics see Table III.3.

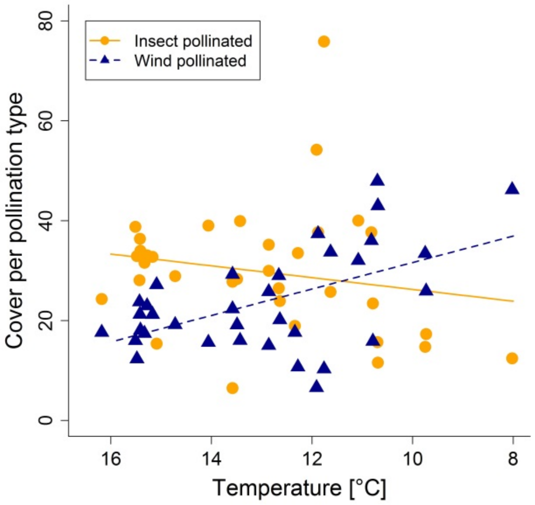


Fig. III.4 Temperature in relation to the cover of different pollination types: insect-pollination, wind-pollination. Statistics see Table III.4.

Table III.4 Results of a linear mixed effects model with cover of vascular plants as response variable, temperature and pollination type (two levels: insect, wind) as explanatory variables. The insect-pollination type was used as reference/intercept. The factor level insect-pollination type was associated with the estimate of the intercept and with the estimate of the temperature slope. The values for the other factor level indicate differences from the given intercept and slope. Site was used as a random factor to correct for pseudoreplication. 68 observations on 34 sites.

Fixed effects	Estimate	Std. Error	t value	P value
Intercept	14.433	12.200	1.183	0.241
Pollination type wind	43.687	17.253	2.532	0.014 *
Temperature	1.180	0.928	1.272	0.208
Pollination type wind: Temperature	-3.831	1.312	-2.919	0.005 **

Discussion

Our results show that species richness peaks at intermediate temperatures. Grazed sites supported higher species richness than mown or non-managed sites. The influence of management on species richness was higher than the influence of temperature. The management effect was constant over the full temperature gradient and the hump-shaped relationship of species richness and temperature was supported at least for the management types grazing and no management. Mown sites were all located at low altitudes and thus do not allow conclusions about diversity patterns along the full temperature gradient.

Species richness – Climate Relationships

A hump-shaped relationship of species richness of plants along altitudinal gradients has been found in several mountainous ecosystems (Sánchez-González & López-Mata, 2005; Bruun *et al.*, 2006; Grytnes & Beaman, 2006; Grytnes *et al.*, 2008), but other studies also showed linear relationships (Austrheim, 2002; Grytnes, 2003).

Hypotheses supporting the humped relationship in our study are the mid-domain-effect (Colwell & Lees, 2000) or mass-effect (Grytnes *et al.*, 2008), which predict a humped relationship due to geometric constraints/borders at both ends of the altitudinal gradient. If geometric constraints were the only responsible factors driving species richness along the altitudinal gradient, species richness of different functional plant groups would peak at the same altitude, which was not the case for plants with different pollination types in our study. Additionally our model using the climatic predictor "temperature" explained the data better than the model using the geometric predictor "altitude". This stresses the importance of climatic drivers for species richness. Precipitation, an important driver for diversity (Clarke & Gaston, 2006), is high in the whole study region (annual precipitation of 1500 mm to 2600 mm) and therefore probably not limiting for physiological processes and thus for species richness or productivity at any part of the gradient. Solar radiation is an important driver for biodiversity in latitudinal gradients (Clarke & Gaston, 2006) but it is an implausible driver for the patterns we found as there are no significant altitudinal changes of mean solar radiation in the Alps (Körner, 2003). Reduced species richness at sites with high temperatures in the lowlands was recorded on managed as well as on non-managed sites. This excludes higher management intensity in the lowlands as a possible driver for lower species richness at higher temperatures. Declining species richness with declining temperature can be explained through reduced metabolic rates (Clarke & Fraser, 2004; Brown *et al.*, 2004) and productivity (Pärtel *et al.*, 2007) at lower temperatures which allow only a reduced range of lifestyles with reduced activity (Clarke & Gaston, 2006), leading to reduced diversity. An explanation for declining species richness with higher temperatures could be that favourable climatic conditions enhance the importance of competition and promote highly competitive species (Bruun *et al.*, 2006) which out-compete alpine specialists and less competitive species. Therefore the observed species richness pattern could be the result of two opposing factors: declining species richness with declining temperatures and increasing species richness with declining competition. But mid-domain- or mass-effects still might contribute to the hump-shaped relationship of plant species richness and temperature. Further, as discussed below, climate-driven trade-offs between different pollination types might contribute to the altitudinal patterns in plant species richness.

Species richness – Management interactions

Several studies in moist, temperate environments are consistent with our results, having found higher species richness in continuously extensively managed sites than in non-managed or abandoned sites (de Bello *et al.*, 2007; Aavik *et al.*, 2008; Marion *et al.*, 2010). However negative effects of grazing on species richness have also been found (e.g. Howe *et al.*, 2002).

Disturbance is an important factor determining species richness in managed versus non-managed sites. Disturbance results in empty patches that can be colonized by rapid colonizers, reduces the biomass of superior competitors and therefore prevents competitive exclusion (Kondoh, 2001). This enables higher species richness in mid- to high-nutrient ecosystems where sufficient water and nutrients enable regrowth after grazing (Proulx & Mazumder, 1998). Precipitation is not limiting for plants in the study region due to a very humid climate (see above). In contrast to our original hypotheses we did not find a stronger positive effect of management on plant species richness at low compared to high altitudes. Possible explanations for this unchanged impact of grazing at all temperatures could be: i) Habitats with freely available water and warmer mean temperatures support a greater biomass (Clarke & Gaston, 2006) and thus increased light-competition, which increases the value of grazing for species richness at high temperatures. ii) At low temperatures in high altitudes grazing opens gaps for new colonizers in the alpine grasslands which are often dominated by vegetatively growing, persistent graminoids (Pellissier *et al.*, 2010). iii) These open patches can also be important at mid temperatures for sink-populations from low- and highland species (mass-effect) which need open patches to recolonize sites where they cannot sustain a permanent viable population (Grytnes *et al.*, 2008). Thus different mechanisms might explain grazing impacts on plant species richness along climatic gradients with a more important role of release from superior competitors at low altitudes (high temperatures) and creation of microhabitats for colonizers at high altitudes (low temperatures), summing up to a similar effect of management on vegetation at different altitudes.

Pollination type

Considering that species richness of wind-pollinated plants peaked at higher temperatures than species richness of insect-pollinated plants and that the proportion of wind-pollinated species declines with decreasing temperature our results seem to contradict theoretical predictions that low temperatures and harsh conditions favor wind-pollination (Regal, 1982; Culley *et al.*, 2002; Hodkinson, 2005; but see Kühn *et al.*, 2006; Pellissier *et al.*, 2010). Kühn *et al.* (2006) argue that extensive management at higher altitudes causes higher species richness and therefore increased proportion of insect-pollinated plants and corresponding decrease in wind-pollinated plants. However, this explanation does not fit with our results as we recorded a decreasing proportion of wind-pollinated plants with altitude independent from management. Reasons why the proportion of wind-pollinated plants decreases at higher altitudes might be i) inter-individual distances of plants and ii) precipitation (Pellissier *et al.*, 2010): i) Heterogeneity of habitats on a small scale in the mountains might constrict the pollination efficiency for most wind-pollinated species. Due to this high habitat heterogeneity distances from one individual or subpopulation to the next are often large. This might reduce the efficiency of wind-pollination as pollen rain from an anemophilous individual dilutes rapidly with distance (Whitehead, 1969; Regal, 1982). Therefore small scale heterogeneity and widely spaced individuals promote insect-pollinated plants which are pollinated specifically and efficiently in comparison to plants that are unspecifically pollinated by wind. ii) Pollen is washed out of the atmosphere by precipitation (Whitehead, 1969). As amounts and probabilities of precipitation increase with higher altitudes in the National Park Berchtesgaden (Konnert, 2004), this could also result in reduced reproductive success of wind-pollinated plants at high altitudes.

Species richness was higher in grazed compared to non-managed sites in wind- and in insect-pollinated plants. But the differences between grazed and non-managed sites were bigger for wind-pollinated species richness, thus causing the observed pattern in the proportion of pollination types. The proportion of insect-pollinated plants was lower in grazed than in non-managed sites, but the opposite was true for wind-pollinated plants. We assume that disturbance of pollinators and destruction of inflorescences by grazers might reduce the reproduction success of insect-pollinated species (Brys *et al.*, 2011) more than that of wind-pollinated species of which a higher proportion can also propagate vegetatively (see above). This indicates that wind pollinated plants are more competitive under increased herbivore mediated disturbance. However this remains speculative and needs further investigation.

The cover (abundance) of wind-pollinated species increased with decreasing temperature while the cover of insect-pollinated species decreased with decreasing temperature. Thus few wind-pollinated species that are well adapted to harsh environmental conditions performed best at low temperatures. This is in contrast to the findings of Pellissier *et al.* (2010) and to our results concerning the proportion of pollination types. A rising proportion of species with vegetative reproduction and clonal growth forms with altitude Pellissier *et al.* (2010) might be the reason for the increasing cover of wind-pollinated species with decreasing temperature. 80% of the wind-pollinated species but only 63% of the insect-pollinated species in our dataset can also propagate vegetatively. Vegetative reproduction can be of advantage in unfavorable years and under harsh climatic conditions. It allows some species to become dominant while others retreat. As wind-pollinated species depend on small inter-individual distances and show pollen-limitation in sparse populations (Rognli *et al.*, 2000; Friedman & Barrett, 2009; Hesse & Pannell, 2011) dominant wind-pollinated species have an advantage, while rare wind-pollinated species have a disadvantage. The higher pollination and seed-set success in dense stands of vegetatively growing and wind-pollinated species might even enforce their dominance.

Conclusions

In conclusion, our results suggest that conservation of high plant diversity in mountain grasslands would benefit from extensive management of grasslands by grazing over the full subalpine gradient. A maximum diversity can be preserved at intermediate temperatures at altitudes between 1400 to 1500 m. The region with this optimum temperature will shift upwards as climate changes. It is therefore important to also manage sites at higher altitudes to preserve areas as refugia for less-competitive grassland species. A concern regarding the upward shift will be a reduced grassland area at higher altitudes and therefore a climate-driven extinction debt in mountain ecosystems due to the species-area relationship (Kuussaari *et al.*, 2009; Krauss *et al.*, 2010). Grazing increased diversity but promoted wind-pollinated species more than insect-pollinated species, and thus influenced not only diversity but also species composition. Wind-pollination may be an adaptation to low temperatures and medium to high wind speeds but not to the specific conditions of the mountains with high amounts of precipitation and often large inter-individual distances. Future climates might change the composition of pollination traits in alpine plant communities with so far unknown consequences for the adaptive potential of mountainous ecosystems to rapid global warming.

IV. Combined effects of extreme climatic events and elevation on nutritional quality and herbivory rates of alpine plants

Abstract

Climatic extreme events can cause disruptions of species interactions. However, the response of plant-herbivore interactions to such events and climatic gradients has been rarely studied, although climatic extremes will increase in frequency and intensity in the future and insect herbivores represent a highly diverse and functionally important group. We set up a replicated climate change experiment along elevational gradients in the German Alps to study the responses of three plant guilds and their insect herbivores to extreme events (extreme drought, advanced and delayed snowmelt) versus control plots under different climatic conditions on 15 grassland sites. Our results indicate that elevational shifts in CN ratios and herbivory rates depend on plant guild and season. CN ratios increased with altitude for grasses, but decreased for legumes and other forbs. In contrast to our hypotheses, extreme climatic events did not significantly affect CN ratios and herbivory rates. Thus, our study provides the first experimental evidence that nutritional quality of plants and antagonistic interactions with insect herbivores are robust against seasonal climatic extremes. Across the three functional plant guilds, herbivory rates increased with nitrogen concentrations. Further, increased CN ratios indicate a reduction in nutritional plant quality with advancing season. Although our results revealed no direct effects of extreme climatic events, the opposing responses of plant guilds along elevation imply that competitive interactions within plant communities might change under future climates, with unknown consequences for plant-herbivore interactions and plant community composition.

Keywords

climate change, CN ratios, drought, field experiment, snow depth

Introduction

Plants and herbivorous insects represent estimated 50 % of all species and herbivory plays a major role in shaping plant community diversity and composition (Strong *et al.*, 1984). Climate change will globally increase temperatures and the frequency of extreme events (IPCC, 2012), but the consequences for plant-herbivore interactions are little understood (Tylianakis *et al.*, 2008). Climate change and extreme events can change the phenology and performance of plants and herbivorous insects (Walther *et al.*, 2002; Bale & Hayward, 2010). This might lead to phenological desyncronisation, increased or decreased herbivory rates, shifts in competitive strength within plant communities and altered population dynamics of plants and herbivores (Tylianakis *et al.*, 2008; Lloret *et al.*, 2012). To analyse the impact of climate change and extreme events on plant-herbivore interactions two different approaches have been realised: First, studies of plant-herbivore interactions along elevational gradients have been used to forecast responses to changing temperature and precipitation patterns (Körner, 2007; Garibaldi *et al.*, 2011). Second, the simulation of extreme climatic events at single locations is a promising experimental approach to evaluate possible responses of plants and their interactions with insects (Jentsch *et al.*, 2007; Beier *et al.*, 2012). However, gradient and experimental approaches have been rarely combined, thereby limiting the conclusions about impacts of climate change either to gradual shifts or to the, in most cases ambient temperate, local climatic context (Dunne *et al.*, 2004; Bütof *et al.*, 2012). However, the strongest effects of climate change are expected in mountainous, arctic and tropical ecosystems (Beniston, 2003; Deutsch *et al.*, 2008). Therefore, a promising approach is the combination of manipulative climate experiments with elevational gradients.

In the European Alps, particularly at higher altitudes, climate change is already observable by a three times stronger temperature increase than the global-average 20th century warming (Beniston, 2012), shifts in the elevational distribution of plants and insects (Hill *et al.*, 2011; Pauli *et al.*, 2012) and heavier precipitation events in alpine regions, particularly during winter time (Stewart, 2009; Laghari *et al.*, 2012). Nevertheless, the length of the winter season will decrease, the fraction of liquid precipitation will increase and particularly at lower altitudes higher temperatures are predicted to accelerate snowmelt (Räisänen & Eklund, 2012). Therefore, future climate change scenarios predict either higher or lower snow cover depending on altitude and location (Wipf & Rixen, 2010). In contrast, rainfall in summer is predicted to decrease and the frequency of drought events to increase across Europe (Rowell, 2009).

Climatic conditions might affect chemical and physical plant defences against herbivores, CN (carbon to nitrogen) ratios of plants and thereby host plant quality and diet breadth of herbivores (Welker *et al.*, 2005; Jentsch *et al.*, 2011; Pellissier *et al.*, 2012). Low temperatures and a short growing season at higher altitudes have been proposed to increase plant N concentrations and to decrease concentrations of secondary defence compounds due to harsh environmental conditions and low herbivore pressure (Körner, 1989; Garibaldi *et al.*, 2011). Simulated drought can change leaf N concentrations and CN ratios (Sardans *et al.*, 2008, 2012), but standardised drought experiments along climatic gradients also addressing the consequences for plant-animal interactions, are lacking (Tylianakis *et al.*, 2008; Smith, 2011; de Sassi *et al.*, 2012).

Invertebrate herbivores might profit from climatically stressed plants due to increased leaf nitrogen concentrations (White, 1984) and decreased concentrations of secondary defence compounds (Mattson & Haack, 1987; Behmer, 2009; Gutbrodt *et al.*, 2011). In addition, climatic events such as advanced and delayed snowmelt can differently shift the phenology of plants and herbivores, thereby desynchronising interactions and altering herbivory rates (Roy *et al.*, 2004; Torp *et al.*, 2010). Generally, herbivore densities and herbivory rates are expected to be highest at the beginning of the growing season, when leaf N concentrations are highest, and to decrease until leaf senescence. However, compensatory feeding on plants with low leaf N concentration can result in increased herbivory rates (Mattson, 1980). At a plant community level, different plant guilds vary in CN ratios and leaf N concentrations. Legume forbs (thereafter legumes) have in contrast to non-legume forbs (thereafter forbs) and grasses lower CN ratios and higher leaf N concentrations, which can influence the preference of insect herbivores towards legumes and might result in guild specific differences directed by climate change. In this study we performed a replicated climate change experiment to investigate the effects of simulated extreme climatic events (advanced snowmelt, delayed snowmelt, extreme drought versus control plots) on plant-herbivore interactions along an elevational gradient in the Alps from 600 – 2000 m elevation. In each treatment we measured CN ratios and herbivory rates for representative plant species of the plant guilds grasses, legumes and forbs to test the following main predictions:

1. In control plots CN ratios and herbivory rates decrease with increasing elevation and differ between plant guilds.
2. Extreme drought hampers plant defense and increases herbivory rates particularly at low elevations with high herbivore pressure.
3. Advanced snowmelt accelerates plant growth and reduces herbivory pressure by desyncronisation of plant and herbivore phenology.
4. Delayed snowmelt increases herbivory rates due to the availability of young plants with high N concentrations later in the season.
5. Effects of extreme events are more pronounced early in the season and in plant guilds with low plant N concentrations.

Material and methods

Study region

The study was conducted in the National Park Berchtesgaden in the southeast of Germany and its surroundings (47°6’ N, 12°9’ E). The National Park Berchtesgaden is located in the Eastern Alps and is characterised by alpine meadows and mountains. The mountains are up to 2700 m a.s.l.. Average annual rainfall varies between 1500 and 2600 mm and average annual temperature ranges from - 2°C to + 7°C depending on the altitude.

Climate experiment

Between 20th February and 8th April 2010 we selected 15 study sites along an elevational gradient (600 to 2000 m a.s.l.) to test whether winter/spring climate change can affect food quality and herbivore damage of alpine plants. We conducted four climate treatments in 4 x 4 m plots at each study site: (a) advanced snowmelt, (b) delayed snowmelt, (c) extreme drought and (d) control (Fig. IV.1). To simulate advanced snowmelt we removed snow from a randomly chosen plot after the last snowfall in early spring until only a thin layer was left and shoveled the snow on an adjacent plot to increase snow cover and simulate a delayed snowmelt. The four plots were separated by 1 m wide corridors at each site. We removed a snow layer of 73 ± 57 cm (range: 15 - 214 cm) from advanced snowmelt plots. Snow layer depth varied between the study sites depending on altitude, exposition and inclination. The snow layer at the delayed snowmelt plots, after snow shoveling, varied between 16 and 304 cm along the alpine gradient and was on average 111 ± 84 cm. We defined the plots as snow-free when near-surface air temperatures reached more than + 5 °C on at least three consecutive days (Wipf *et al.*, 2006).

To simulate an extreme drought event we constructed 4 x 4 m rain-out shelters with aluminium tubes and cast-iron key clamps (B-One key clamps, Montfoort, the Netherlands) and covered them with a transparent plastic sheet (0.2 mm polyethylene, SPR 5, Hermann Meyer KG, Germany), which allowed nearly 90 % penetration of photosynthetically active radiation (Fig. 1). We set up the rain-out shelters between 26th April and 24th June on average four weeks after snowmelt. The drought period lasted 43 ± 1 days to simulate a 1000-year extreme event for the study region based on data from the German Weather Service (Jentsch *et al.*, 2007). The rain-out shelters had a roof height of 125 cm at the highest point and had two open sides to avoid greenhouse effects and allow air exchange. Mean near-surface air temperature under the rain-out shelters was 14.5 ± 2.1 °C during the drought period and 14.4 ± 2.2 °C on the control plots, thus no significant differences between rain-out shelters and control plots existed (paired t-test: $t_{12} = -0.5$, $P = 0.6$).

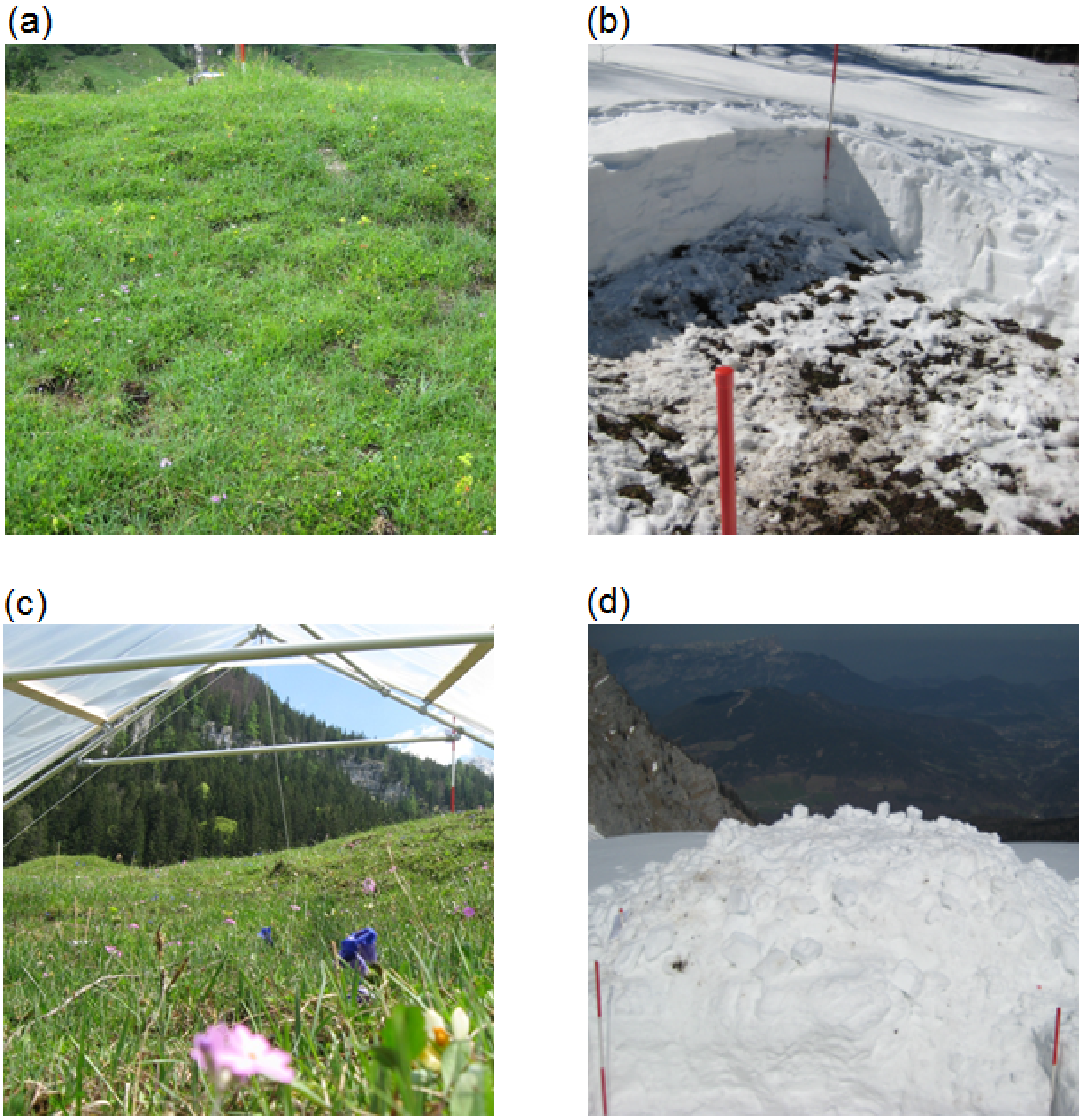


Fig. IV.1 Experimental design with four treatments per study site: (a) unmanipulated control, (b) advanced snowmelt, (c) drought treatment with rain-out shelter and (d) delayed snowmelt. Each treatment plot measured 4 x 4 m and the distance between the plots was 1 m.

Abiotic factors

We measured near-surface air temperatures with temperature loggers (Thermochron iButtons DS1921G#F5, Maxim Integrated Products, Inc., Sunnyvale, CA, USA) in the centre of each of the four treatment plots in 2 h intervals at all 15 study sites. Temperature loggers in the snowmelt treatments measured the subnivean temperatures near soil surface until snow had melted. We installed rain collectors to measure the amount of rain that was excluded from the drought treatment. Mean rainfall over all study sites during the drought period was 379 ± 71 l/m^2 and the amount of rain did not show a directional change along the elevational gradient (simple regression, $F_{1,13} = 1.1$, $P = 0.3$). We monitored soil moisture during the drought period for each treatment separately with a portable soil moisture meter (Delta-T Devices type HH2 + ThetaProbe ML2x sensors, Cambridge, UK).

CN ratios and leaf herbivory

We collected leaf samples at each of the four treatments at three times during the growing season at an interval of three weeks, to measure leaf carbon-to-nitrogen (CN) ratios. Each time we collected three leaves from each of five individual plants per species and treatment. We took samples from 7 ± 2 plant species per study site representing all three plant guilds (grasses, legumes, forbs) with the widest occurrence on the four plots per site. In total we took 751 leaf samples from 42 plant species to determine leaf CN ratios. Leaf samples were oven-dried for 48 h at 75 °C and afterwards analysed with an elemental analyser (vario MICRO cube, Elementar Analysensysteme GmbH, Hanau, Germany).

In parallel, we recorded herbivore damage of the same plant species as used for the CN analyses at three week intervals. We randomly chose five individuals per plant species and treatment and estimated percentage leaf area loss from 0 to 100 % for each leaf by visual inspection. In total we estimated herbivory rates of 25,013 leaves of the three plant guilds (grasses, legumes, forbs). The accuracy of our estimates was checked and improved in advance by first estimating and afterwards analysing samples of randomly collected leaves. The leaf area was transferred to millimetre paper and the exact amount of missing leaf area was calculated to adjust accuracy.

Statistical analysis

We calculated linear mixed effects models (type I sum of squares) for the response variables herbivory and CN ratio with the explanatory variables altitude (continuous), treatment (4 categories), plant guild (3 categories), sampling time (3 categories) and their interactions. The response variable herbivory was arcsine square root transformed to meet the assumptions of normality and homoscedasticity in the statistical models. CN ratio was not transformed. We used mean values for each plant guild (grasses, legumes, forbs) and treatment (advanced snowmelt, delayed snowmelt, extreme drought, control) per study site and sampling time to average the effect of single plant species. We used study site, treatment and plant guild as random effects to account for nesting and in order to correct for pseudoreplication. The models were fitted with likelihood ratio tests. Tukey HSD tests were used to calculate differences between categories of significant main effects.

We tested for relations between CN ratios and herbivory by calculating a linear mixed effects model (type I sum of squares) with herbivory as response variable and CN ratio and plant guild (grasses, legumes, forbs) as explanatory variables. Plant guild was included as explanatory variable in the model to test for plant guild effects and an interaction between CN ratio and plant guild. Study site was used as random effect in the model, because plant guild was nested in study site. Analyses were performed with mean values of CN ratio and herbivory per study site for every plant guild. Model simplification was performed using likelihood-ratio tests.

Differences between the treatments and along the elevational gradient for snowmelt and soil moisture were analysed with linear mixed effects models (type I sum of squares) with treatment and altitude as fixed effects including their interaction and study site as random effect. For soil moisture analyses we calculated mean values per treatment and study site. After simplifying the models with likelihood ratio tests we performed Tukey HSD tests for posthoc comparisons when main effects were significant.

All statistical analyses were performed using the software R 2.15.1 for Windows (R Core Team, 2012).

Results

Snow and drought experiments

The time of complete snowmelt was successfully manipulated along the elevational gradient (Fig. IV.2) without significantly increasing soil water availability (Fig. IV.3). In control treatments snowmelt was finished on average over all study sites on 14th April (104th day of the year). On advanced plots snowmelt was finished on 18th March (77th day of the year) and on delayed plots on 15th April (105th day of the year) showing a mean advanced snowmelt of 27 days and a delayed snowmelt of one day. At higher altitudes treatment plots were naturally covered with more snow than at lower altitudes thus the time lag between advanced and control snowmelt was larger on higher plots compared with lower plots (Fig. IV.2).

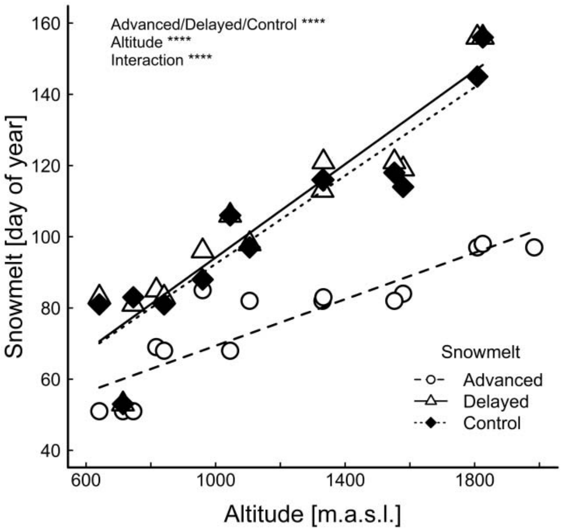


Fig. IV.2 Final day of snowmelt for three different treatments (advanced snowmelt, delayed snowmelt, control) on 15 study sites in relation to altitude. *** P ≤ 0.0001

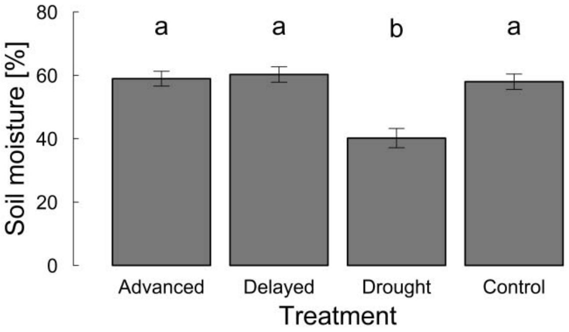


Fig. IV.3 Soil moisture [% volume] during the extreme drought event on four treatments (advanced snowment, delayed snowmelt, extreme drought, control) (mean ± se). Letters indicate non-significant (a – a, P > 0.05) and significant (a – b), P ≤ 0.0001) differences between the treatments according to Tukey HSD post-hoc comparisons.

Soil moisture was significantly lower on drought plots during simulated extreme drought events compared to the other treatment plots ($F_{3,42} = 26.5$, $P < 0.0001$, Fig. 3). Drought plots had on average 40.2 ± 3.0 % soil moisture during the drought manipulation, whereas the other treatment plots had significantly higher soil moisture (control: 58.0 ± 2.4 %, advanced: 58.9 ± 2.3 %, delayed: 60.3 ± 2.4 %). The interaction of altitude and treatment was not significant, indicating a similar treatment effect along the elevational gradient.

CN ratio

The CN ratio of plants was affected by the interaction of altitude, plant guild and sampling time (Table IV.1). Treatment (advanced snowmelt, delayed snowmelt, extreme drought, control) or any interaction with other variables had no significant effect on the CN ratio and was therefore removed as explanatory variable from the model (Table IV.1).

Table IV.1 Mixed effects model statistics of the response variable CN ratio with the explanatory variables altitude, treatment, plant guild, sampling time and their interactions. The explanatory variable treatment was removed from the model as it was neither significant as single variable nor in the interactions. The final model is presented.

	numDF	**denDF**	***F*-value**	***P*-value**
(Intercept)	1	257	1114.37	< 0.0001
altitude	1	13	2.11	0.17
plant guild	2	103	107.83	< 0.0001
sampling time	2	257	31.46	< 0.0001
altitude:plant guild	2	103	20.23	< 0.0001
altitude:sampling time	2	257	0.57	0.57
plant guild:sampling time	4	257	38.03	< 0.0001
altitude:plant guild:sampling time	4	257	4.53	0.002

The highly significant three-way interaction of altitude, plant guild and sampling time indicates that these three explanatory variables played an important role for the CN ratio of plants and depend in their effects on each other. Plant guilds (grasses, legumes, forbs) significantly differed in CN ratio (Fig. IV.4). Legumes had the lowest CN ratio compared with forbs and grasses ($P < 0.0001$), but forbs and grasses were not significantly different in their CN ratio ($P = 0.1$). CN ratios were lowest at the first sampling time, and increased three weeks ($P < 0.001$) and six weeks later ($P = 0.06$). The significant interaction between the explanatory variables altitude and plant guild indicates contrasting shifts in CN ratios of the plant guilds along the elevational gradient (Table IV.1). CN ratios of grasses showed a slight increase with altitude whereas the CN ratios of forbs and legumes decreased with altitude (Fig. IV.4). The significant interaction of plant guild and time indicates that the CN ratios of the three plant guilds changed differently during the growing season.

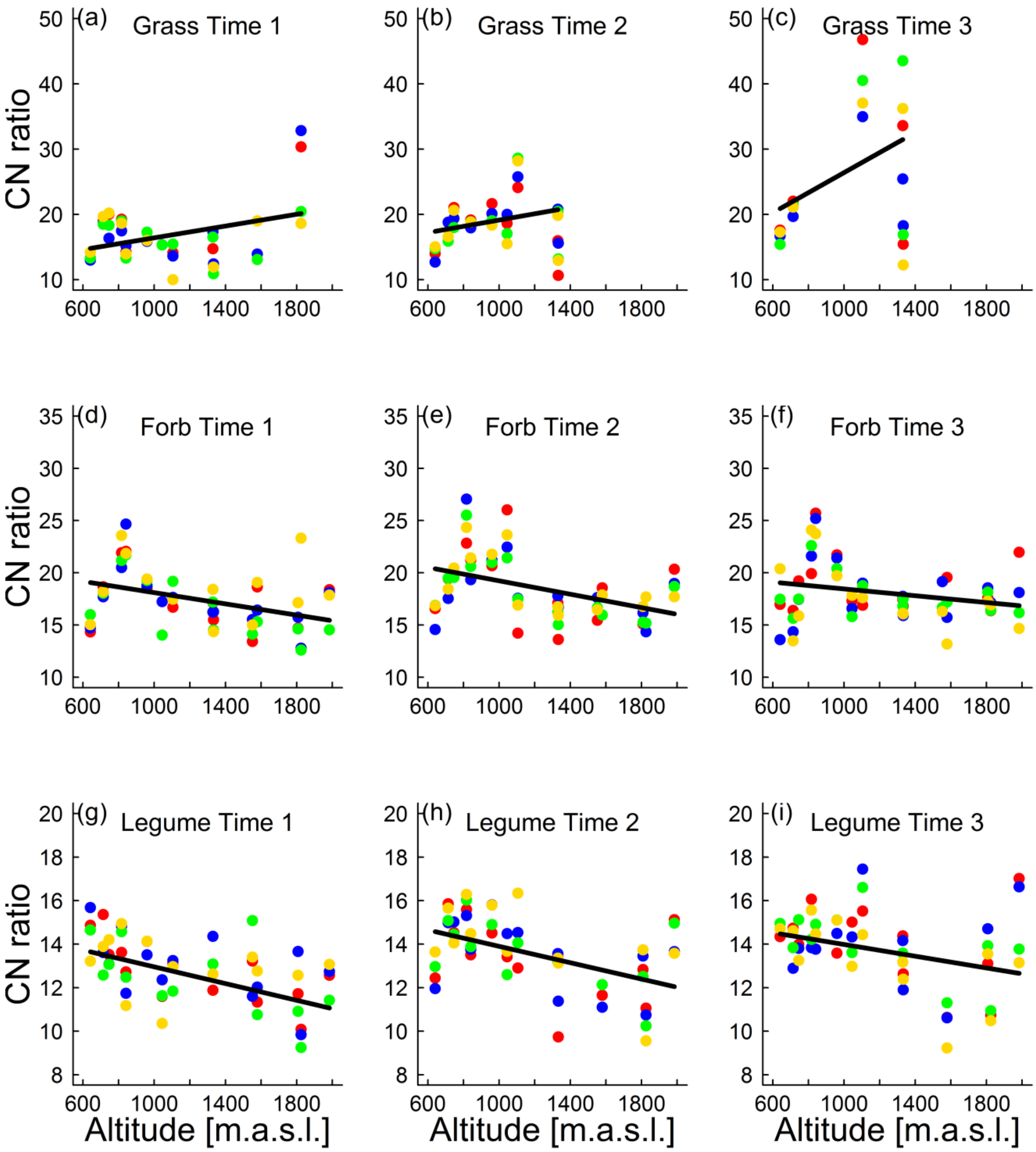


Fig. IV.4 Effects of altitude, treatment and their interaction on CN ratio of three plant guilds (grasses, legumes, forbs) at three sampling times (a - i). CN data are presented as mean values per study site and treatment. Points symbolise the study sites and different colours represent the four treatments (blue: advanced snowmelt, green: delayed snowmelt, yellow: extreme drought, red: control). Black lines are based on the simplified model and show different slopes for CN ratio with altitude. Statistics see Table IV.1.

Herbivory

Herbivory rates were affected by the interaction of altitude, plant guild and sampling time (Table IV.2). Treatment and any interaction with treatment had no effect on herbivory (Fig. IV.5a), therefore we removed the explanatory variable treatment and the interactions with treatment from the final model. Grasses, legumes and forbs had different herbivory rates which also changed with sampling time (Fig. IV.5b). Legumes had a significantly higher herbivory rate compared to grasses and forbs ($P < 0.001$), while grasses and forbs were not different in their herbivory rates ($P = 0.9$). At the first sampling time the herbivory rate was lowest but not significantly different to the herbivory rate three weeks later ($P = 0.14$). Six weeks later the herbivory rate further increased, leading to significant differences between sampling times (Time 1 – Time 3: $p < 0.0001$, Time 2 – Time 3: $P = 0.02$). The three-way interaction of altitude with plant guild and sampling time did not reveal clear overall elevational patterns in herbivory rates.

Table IV.2 Mixed effects model statistics of the response variable herbivory with the explanatory variables altitude, treatment, plant guild, sampling time and their interactions. The explanatory variable treatment was removed from the model as it was neither significant as single variable nor in the interactions. Herbivory was arcsine square root transformed. The final model is presented.

	numDF	**denDF**	***F*-value**	***P*-value**
(Intercept)	1	266	273.70	< 0.0001
altitude	1	13	0.33	0.58
plant guild	2	103	41.90	< 0.0001
sampling time	2	266	12.91	< 0.0001
altitude:plant guild	2	103	1.14	0.32
altitude:sampling time	2	266	2.77	0.06
plant guild:sampling time	4	266	1.25	0.29
altitude:plant guild:sampling time	4	266	2.89	0.02

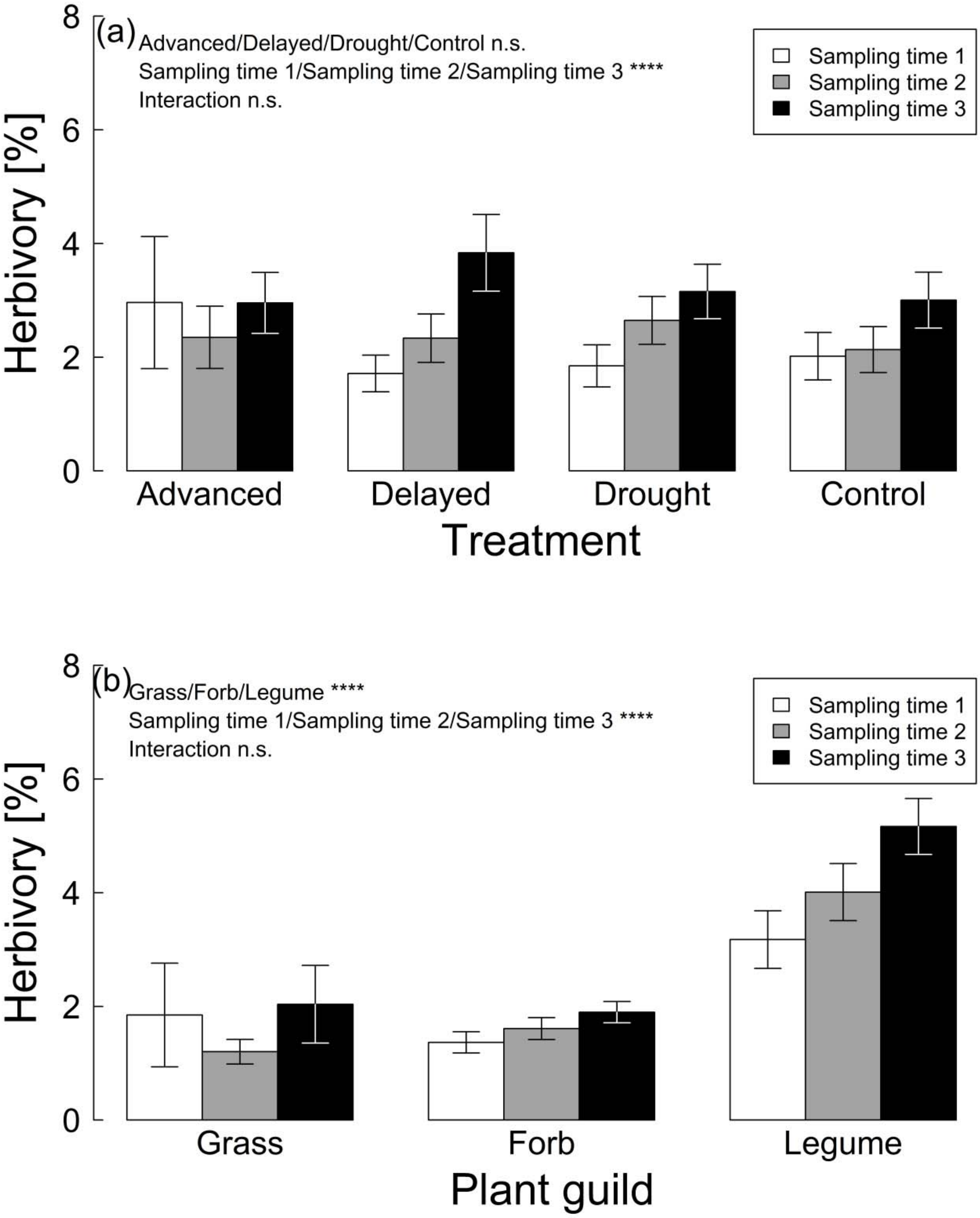


Fig. IV.5 Herbivory rates [%] as a function of (a) treatment (advanced snowmelt, delayed snowmelt, extreme drought, control) and (b) plant guild (grasses, legumes, forbs) at three sampling times (mean ± se). **** $P \leq 0.0001$, n.s. $P > 0.1$. Statistics see Table IV.2.

CN ratio - herbivory relationship

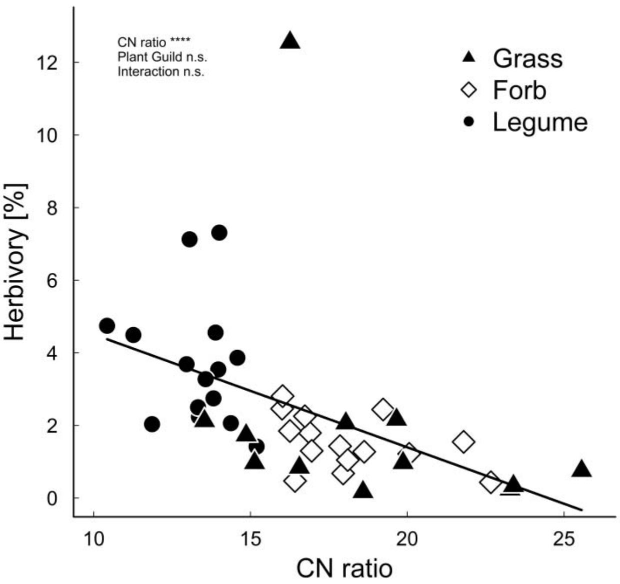


Fig. IV.6 Relation between herbivory rate [%] and CN ratio of three plant guilds (grasses, legumes, forbs). The black line shows the significant relation between herbivory and CN ratio. **** $P \leq 0.0001$, n.s. $P > 0.1$.

The CN ratio significantly affected herbivory rates (Fig. IV.6), in that the more leaf nitrogen the plants had (low CN ratio) the higher was the herbivory rate of the plants. We found no interaction between CN ratio and plant guild suggesting identical slopes for the plant guilds. The explanatory variable plant guild did not explain further variation in herbivory rates in addition to the CN ratio.

Discussion

Our results indicate that elevational shifts in CN ratios and herbivory rates depend on plant guild and season. Thus, the three plant guilds differed in CN ratios and herbivory rates and responded differently to altitude. In contrast to our predictions, extreme climatic events did neither affect CN ratios nor herbivory rates, suggesting that nutritional quality of plants and antagonistic interactions with insect herbivores are robust against seasonal climatic extremes. Across the three plant guilds, herbivory rates were highest when CN ratios were lowest, demonstrating that high N content is related to increased plant damage by herbivores.

CN ratio

We expected that advanced snowmelt and drought would result in lower CN ratios compared to delayed snowmelt and control plots, particularly early in the season. However, we found no treatment effects on CN ratios. We are not aware of other experimental studies that manipulated snow depth at multiple sites along a climatic gradient while two climate experiments in arctic environments gave ambiguous results for snow cover manipulations (Welker *et al.*, 2005; Aerts *et al.*, 2009). By replicating the climate experiment at multiple sites we can exclude that contrasting temperature conditions at low or high altitudes affected the response of plant CN ratios to snowmelt manipulations. Hence, plant CN ratios seem to be more robust against snowmelt changes than previously assumed.

The extreme drought treatment in our study did not change plant CN ratios despite the simulation of a 1000 years drought event. We predicted lower CN ratios, because decreased soil moisture can result in slowed growth and higher concentration of plant leaf minerals (Huberty & Denno, 2004). Importantly, in our experiment the drought simulation did not increase temperatures on the plots and therefore we could independently analyse the response of plants to drought events. Thus, significant changes in CN ratios in other studies that simulated higher temperatures and drought in combination (Sardans *et al.*, 2012), might be more related to temperature increases than reduced soil moisture. We could not control for air humidity, thus plant species might have experienced higher air humidity during the simulated drought event than under natural extreme drought conditions, but this is also the case for other climate experiments.

Although we found no effects of extreme events, climatic conditions along the elevational gradient affected CN ratios and herbivory in concert with plant guild specific responses and seasonal shifts. Nitrogen fixing legumes had the lowest leaf CN ratios compared with grasses and forbs. Within all plant guilds, leaf CN ratios increased over time, indicating a decrease of leaf nitrogen concentration during the growing season, which adds to related results in woody plants (Hansen *et al.*, 2006a; Torp *et al.*, 2010). At our first sampling occasion, leaf N contents were highest compared to the following sampling occasions. Mechanisms explaining seasonal decreases in leaf nutrient concentrations are the accumulation of carbon during the growing season, which operates as a dilution effect, and the recovery of nutrients from leaves before leaf senescence (Körner, 2003). The significant interaction with plant guild and sampling time indicates that altitude influenced the CN ratios of grasses, legumes and forbs in different directions. Legumes and forbs had at all three sampling times lower CN ratios at higher altitudes, but within grass species CN ratios increased with altitude. Thus, the opposing response of plant guilds to altitude suggest that under future warmer climates, food plant quality of legumes and forbs could be lower and of grasses higher compared to current climatic conditions. This might change competitive interactions between plant guilds and biotic interactions, with important implications for ecosystems under future climates.

Herbivory

In contrast to our predictions insect herbivory was not affected by simulated climate change, presumably because nutritional quality of plants remained unchanged. However, our data imply that herbivores are strongly driven by plant leaf nutrients. The CN ratios were a very good predictor to explain herbivory rates and herbivores preferred food plants with a lower CN ratio and therefore higher N content in the leaves. Related to this, the leaf nutrient contents of the different plant guilds (grasses, legumes, forbs) influenced the herbivory rates. Legumes had on average the highest herbivory rates compared with grasses and forbs, which can be explained by low leaf CN ratios and therefore high N contents in legumes. Additionally, we found changes in the herbivory rates during the growing season. Herbivory rates of all plant guilds increased with time, although CN ratios of the plant guilds were highest later in the season. This might be explained by an increased consumption rate of herbivores, to compensate for low host plant quality (Berner *et al.*, 2005; Behmer, 2009), but also indicates that herbivore phenologies are not only triggered by seasonal dynamics in nutritional value of plants, but also by other factors such as more ambient temperatures. While herbivory rates changed with season, we found no overall effect of altitude on herbivory rates, in contrast to our predictions. However, herbivory rates varied between plant guilds and sampling time along the elevational gradient. Other studies suggest that the abundance of herbivorous insects and leaf herbivory rates decrease with increasing elevation (Hodkinson, 2005; Garibaldi *et al.*, 2011), although increasing food plant quality might increase herbivory at higher elevations (Körner, 1989). Thus, the lower CN ratios of legumes and forbs at higher altitudes with potentially increased herbivory rates might be counteract by lower herbivory rates on grasses and elevational declines of herbivore populations, and therefore no overall pattern in insect herbivory rates along the elevational gradient occurred.

In conclusion, our results indicate that shifts in the snowmelt date and extreme drought events in the German Alps had no strong effect on food plant quality and insect herbivory rates. Although mean effects of climate manipulations on plant species and herbivores were not significant in our experiment, the opposing responses of plant guilds to altitude imply that competitive interactions within plant communities might change under future climates, with unknown consequences for plant-herbivore interactions. Therefore, we recommend long term experiments simulating multiple extreme climatic events along climatic elevational or latitudinal gradients to reveal the complex dynamics and potential risks of future climate change for biotic interactions and ecosystem stability.

V. Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient

Abstract

Plant communities in the European Alps are assumed to be highly affected by climate change since temperature rise in this region is above the global average. It is predicted that higher temperatures will lead to advanced snowmelt dates and that the number of extreme weather events will increase. The aims of this study were to determine the impacts of extreme climatic events on flower phenology and to assess whether those impacts differed between lower and higher altitudes. In 2010 an experiment simulating advanced and delayed snowmelt as well as drought event was conducted along an altitudinal transect ca. every 250m (600-2000 m a.s.l.) in the Berchtesgaden National Park, Germany. The study showed that flower phenology is strongly affected by altitude; however there were few effects of the manipulative treatments on flowering. The effects of advanced snowmelt were significantly greater at higher than at lower sites, but no significant difference was found between both altitudinal bands for the other treatments. The response of flower phenology to temperature declined through the season and the length of flowering duration was not significantly influenced by treatments.

The stronger effect of advanced snowmelt at higher altitudes might be a response to differences in treatment intensity across the gradient. Consequently, shifts in the date of snowmelt due to global warming may affect species more at higher than at lower altitudes since changes may be more pronounced at higher altitudes. Our data indicate a rather low risk of drought events on flowering phenology in the Bavarian Alps.

Key words

Advanced snowmelt; Alps; BBCH; Climate change; Delayed snowmelt; Flowering

Introduction

In the past 100 years global annual mean temperatures increased by about 0.7 °C (IPCC, 2007), however, some regions were more affected by climate change than others. For the European Alps a much stronger temperature increase of about 2 °C was detected (Auer *et al.*, 2007). In the future, it is predicted that temperature will further rise, that rainfall distribution will change and that extreme weather events, such as torrential rain and drought will significantly increase in frequency (IPCC, 2007). Furthermore, a general reduction in the duration of snow cover will be caused by warmer temperatures, because the zero-degree isotherm will be displaced to higher altitudes (Beniston, 2003; Laghari *et al.*, 2012). However, climate change scenarios for future snow conditions are rather vague. An increase in heavy snowfall events in winter may therefore also lead to a prolongation of snow cover duration.

Due to a changing environment, alpine plant communities have already experienced and will further suffer negative impacts (e.g. Körner, 1992; Grabherr *et al.*, 1994; Sala *et al.*, 2000; Erschbamer *et al.*, 2009). The effects of climate change on alpine vegetation will be especially pronounced at high altitudes since abiotic factors such as climate prevail over biotic factors in those regions (Körner & Miglietta, 1994; Theurillat J-P. & Guisan A., 2001).

Phenology, the study of the timing of recurring natural events, can be a tool for assessing climate change impacts on plant growth and development. Several studies showed that the most important factors for plant development in alpine areas were temperature, date of snowmelt and photoperiod (e.g. Price & Waser, 1998; Blionis *et al.*, 2001; Keller & Körner, 2003). However, in the future, drought might also play an important role in the development of plants in the Alps due to an increasing probability of the occurrence of extreme weather events.

Shifts in plant phenology due to warmer temperatures have already been widely documented by analysing long-term datasets (e.g. Schwartz & Reiter, 2000; Sparks *et al.*, 2000; Abu-Asab M.S. *et al.*, 2001; Fitter & Fitter, 2002; Menzel *et al.*, 2005, 2006) or have been confirmed by experimental studies (Marion *et al.*, 1997; Hollister & Webber, 2000; Kudernatsch *et al.*, 2008; De Frenne *et al.*, 2010). Higher temperatures mainly advance plant phenology (e.g. Sparks *et al.*, 2000; Menzel *et al.*, 2006; Kudernatsch *et al.*, 2008), which increases the risk of late frost damage in spring (Inouye, 2000, 2008; Wipf *et al.*, 2009) and may cause shifts in plant community composition due to die off (Molau, 1997). Furthermore, changes in plant flowering patterns can cause an overlap of the flowering times of different species which, in early summer, can lead to greater competitive pressure, because pollinator activity is very low at this time of year (Molau, 1997). Shifts in plant flowering times may also decrease population levels of pollinators (Inouye & McGuire, 1991) which may in turn also increase competitive pressure.

Timing, depth and duration of snow cover determine the beginning of the growing season in alpine areas (Inouye & Wielgolaski, 2003). Thus, the development of many species in alpine or Arctic regions is highly dependent on the timing of snowmelt (Inouye *et al.*, 2002; Stinson, 2004; Inouye, 2008). A prolongation in snow cover duration often delays plant phenology (Weaver & Collins, 1977; Inouye, 2008; Torp *et al.*, 2010; Cooper *et al.*, 2011) whereas a shortening of snow cover duration mostly advances the timing of plant development (e.g. Price & Waser, 1998; Inouye *et al.*, 2003; Dunne *et al.*, 2003; Wipf *et al.*, 2009; Wipf, 2010; Lambert *et al.*, 2010; Chen *et al.*, 2011). However, phenological responses are highly species-specific and differ between functional groups (Wipf & Rixen, 2010). An advanced snowmelt could potentially increase plant fitness by prolonging the growth period and hence resource allocation (Galen & Stanton, 1993; Stinson, 2004). However, an earlier start of flowering also increases the risk of late frost damage in spring, thus an earlier snowmelt may not necessarily lead to advanced flowering (see Inouye, 2008). In the Australian Alps, for example, the timing of snowmelt only slightly affected the timing of flowering for tested species (Venn & Morgan, 2007).

As for other plants, the responses of alpine plants to drought include wilting, reduced plant growth (Sangtarash *et al.*, 2009) and seed set or even extinction (Galen, 2000). Phenological responses to drought, however, are not consistent for both alpine and other plants. Jentsch *et al.* (2009) reported an advance of mid-flowering date by 4 days after a drought event, whereas Bloor *et al.* (2010) and Bernal *et al.* (2011) did not detect a significant effect of drought on grasses or shrub species. In contrast, a delay in flowering phenology under dry conditions was reported for Mediterranean plants (Penuelas *et al.*, 2004; Llorens & Penuelas, 2005; Prieto *et al.*, 2008; Miranda *et al.*, 2009).

In general, there have been several studies dealing with the impacts of a changing abiotic environment (shifts in the date of snowmelt or the occurrence of drought) on plant phenology. However, as far as we know, there have only been a few studies combining manipulative experiments with an altitudinal gradient (but see Dunne *et al.*, 2003; Stinson, 2004) to assess whether impacts due to climate change differ between lower and higher altitudes. Altitudinal gradients naturally provide different temperature scenarios, because air temperature decreases by 0.54 °C to 0.58 °C per 100 m increase in altitude (Rolland, 2003). Thus, this study not only focuses on treatment effects but also combines temperature changes which are indirectly derived from altitudinal change. Consequently, the aim of this study was to test whether shifts in the date of snowmelt or drought events affect (i) the timing and (ii) the length of flowering phenology of different grassland species. Furthermore we test if those impacts change with (iii) elevation or (iv) season.

Materials and Methods

Study site and experimental design

The study area was located in the northern part of the Berchtesgaden National Park, which is the only German national park in the Alps and is characterized by a large altitudinal range within a small area (StMUG, 2001).

Eleven observational sites were located along two valleys in the national park and ranged from ca. 800 m to ca. 2000 m a.s.l. To ensure a larger altitudinal gradient three sites below 800 m beyond the borders of the park were added, starting at ca. 600 m. One other site outside the two valleys was also included to ensure a site at ca. every 250 m altitude difference. Thus, observations were conducted at a total of 15 different sites. Aspects of sites were different; eight faced north, three faced west, three south and one was on level ground.

Annual mean temperature in the park ranges between -2 °C and 7 °C and annual mean precipitation is 1500-2600 mm depending on altitude (StMUG, 2001). For sites below 1000 m a.s.l. maximum snow cover is reached in February at a mean depth of about 50 cm. Sites over 1000 m have their maximum snow cover in March, ranging between 3 m and 5 m at highest altitudes (StMUG, 2001).

The lapse rate of air temperature (decrease in temperature with elevation) was about 0.45 °C per 100 m elevation (mean from March to August; Konnert, 2004). Growing season lengths (derived from days above a 10 °C threshold) varied from 5 months at 600 m to ca. 1 month at 2000 m (Konnert, 2004).

Experimental plots were established at each of the 15 study sites along the entire altitudinal gradient, consisting of three different treatments and a control, each plot sized 4 m x 4 m. Plots were contained within a 10 m x 10 m square, arranged in a 2 x 2 array. Treatments were the simulation of advanced and delayed snowmelt as well as a drought event.

Advanced and delayed snowmelt

Advanced and delayed snowmelt was simulated by shovelling snow from advanced snowmelt plots onto delayed snowmelt plots until only a thin snow layer was left on the former, thus the vegetation on the advanced snowmelt plots was not disturbed. Shovelling took place between the end of February and the beginning of April in 2010 depending on altitude. Snow depth along the gradient varied from 15 to 214 cm on advanced snowmelt plots before shovelling. After shovelling, snow depth on delayed snowmelt plots ranged from 16 to 304 cm depending on altitude. Snow melting date was defined as the day when near-surface air temperatures reached more than + 5 °C on at least three consecutive days (for description of temperature measurements see Environmental data).

Drought event

The drought event was simulated by rain-out shelters which were installed, on average, four weeks after snowmelt in control plots depending on altitude (installed: end of April to end of June; removed: beginning of June to beginning of August). The drought period lasted 43 ± 1 days, which is regarded as a 1000-year extreme event in this region (Jentsch *et al.*, 2007). To allow air exchange rain-out shelters were open at the front and rear. Rain-out shelters were 125 cm high and constructed with aluminium tubes and cast-iron key clamps (B-One key clamps, Montfoort, Netherlands). Shelter poles were covered with a transparent plastic sheet (0.2 mm polyethylene, SPR 5, Hermann Meyer KG, Germany), which transfers nearly 90% of photosynthetically active radiation. The drought period ended when the shelters were removed. Over the altitudinal gradient no significant difference in average or maximum near-surface air temperature (for description of temperature measurements see Environmental data) between drought and control plots was detected with a paired *t*-test (P = 0.6 and P = 0.9) in the drought period. Minimum temperature, however, was significantly different between drought and control plots for the same period (paired *t*-test P = 0.012).

Species and phenological observations

Phenological observations of 10 different species, 8 herbs and 2 grasses, were conducted once a week from April to September 2010 on each plot following the BBCH code (**B**iologische Bundesanstalt, **B**undessortenamt and **Ch**emical Industry). The code is a detailed growth stage key which includes intermediate stages as well as stages marking the end of phenophases. It allows the observation of the entire development cycle of all mono- and dicotyledonous plants using a decimal coding system (Meier, 2001). Using a detailed observation key like this, it is not necessary to be present at the exact start of the phenological stage since the key allows recording the frequency distribution of phenophases of a certain number of individual plants on each sampling date. Classical onset dates, as used in climate research studies could be interpolated from these data using the OLR (**O**rdinal **L**ogistic **R**egression) method described by Cornelius *et al.*

(2011). The OLR method provides information about the progression of stages (including the beginning, speed of passage and the end of secondary growth stages) and allows stages are to be of unequal length (ordinal scale approach). Furthermore, OLR is based on the frequency distribution over time which includes the entire progression of plants in the model and not only the progression of a single stage.

In this study the focus was on flower phenology, especially the beginning of flowering (forbs: first flowers open; grasses: first anthers visible), full flowering (forbs: 50% of flowers open; grasses: 50% of anthers mature) and end of flowering (forbs: petals dehydrated or fallen; grasses: all spikelets/panicles have completed flowering but some dehydrated anthers may remain). *Campanula scheuchzeri* Vill. develops only one flower per individual, thus definitions needed to be adjusted for the beginning of flowering (flower slightly open) and full flowering (flower expanded to full size). In each plot 20 individuals per species were observed where possible. This number of individuals was considered large enough for further statistical analysis and small enough to make all observations achievable within a week. As plants of each species were not individually marked, partly different groups of individual plants were likely observed on consecutive sampling dates.

The average altitudinal range of species in this study was about 705 m but varied between 127 m for full flowering of *Ranunculus acris* L. and 1343 m for end of flowering of *Ranunculus montanus* Willd. (Table V.1). All observed dates were converted to day of year (1 January = 1, etc.; DOY).

Environmental data

Temperature data was derived from iButton data loggers (Thermochron iButtons DS1921G#F5, Maxim Integrated Products, Inc., Sunnyvale, CA, U.S.) which were located in the middle of each treatment plot; recording temperature at 2 h intervals. For snowmelt treatments iButton loggers were used to determine snow melting dates from subnivean temperatures, which were measured near the soil surface. Due to technical faults of the iButton data loggers there is no information about snow melting dates for sites at 817 m and 1920 m. The amount of rain excluded from drought plots through rain-out shelters was estimated with the help of rain collectors next to the site. Averaged over all sites mean precipitation was 379 ± 71 l/m^2 during the drought period. Linear regression analysis revealed no significant relationship between the amount of precipitation between sites along the altitudinal gradient ($P = 0.3$). Soil moisture content was measured with a portable soil moisture meter (Delta-T Devices type HH2 + ThetaProbe ML2x sensors, Cambridge, UK) on average four times per plot during the drought period.

Table V.1 Results of linear regression analysis of study site mean dates of three phenophases (BF: beginning of flowering, FF: full flowering, EF: end of flowering) on altitude. Numbers in bold are significant ($P < 0.05$). Altitudinal ranges showing the maximum difference in elevation and the elevation of the lowest and highest site for each species and phenophase. # No variation recorded in this variable for this event.

		N	R^2	P	regression coefficients [days/100m](±SE)	altitudinal ranges [low-high] (m)
Alchemilla vulgaris L.	BF	4	0.119	0.655	0.8 (± 1.6)	534 [1045-1579]
(Rosaceae)	FF	7	0.827	**0.005**	4.8 (± 1.0)	865 [714-1579]
	EF	7	0.550	**0.050**	2.4 (± 1.0)	619 [960-1579]
Briza media L.	BF	7	0.844	**0.003**	3.4 (± 0.7)	689 [641-1330]
(Poaceae)	FF	7	0.731	**0.014**	2.4 (± 0.7)	689 [641-1330]
	EF	7	0.853	**0.003**	3.2 (± 0.6)	689 [641-1330]
Campanula scheuchzeri	BF	3	0.776	0.314	5.2 (± 2.8)	273 [1552-1825]
Vill.	FF	5	0.535	0.160	1.4 (± 0.8)	865 [960-1825]
(Campanulaceae)	EF	8	0.642	**0.017**	1.9 (± 0.6)	865 [960-1825]
Dactylis glomerata L.	BF	5	0.713	0.072	3.9 (± 1.4)	464 [641-1105]
(Poaceae)	FF	5	0.526	0.166	2.5 (± 1.4)	464 [641-1105]
	EF	5	0.331	0.311	1.3 (± 1.1)	464 [641-1105]
Lotus corniculatus L.	BF	6	0.794	**0.017**	3.6 (± 0.8)	1111 [714-1825]
(Fabaceae)	FF	6	0.878	**0.006**	3.1 (± 0.6)	1111 [714-1825]
	EF	11	0.683	**0.002**	1.7 (± 0.4)	1270 [714-1984]
Potentilla erecta.	BF	4	0.917	**0.043**	3.6 (± 0.8)	762 [817-1579]
(L.) Raeusch	FF	5	0.916	**0.011**	3.1 (± 0.5)	762 [817-1579]
(Rosaceae)	EF	9	0.074	0.479	0.8 (± 1.0)	1167 [641-1808]
Prunella vulgaris L.	BF	3	0.900	0.205	7.0 (± 2.3)	288 [817-1105]
(Lamiaceae)	FF	5	0.816	**0.036**	2.7 (± 0.7)	865 [714-1579]
	EF	8	0.769	**0.004**	2.5 (± 0.6)	938 [641-1579]
Ranunculus acris L.	BF					#
(Ranunculaceae)	FF	3	0.894	0.211	7.9 (± 2.7)	127 [714-841]
	EF	3	0.999	**0.019**	5.7 (± 0.2)	246 [714-960]
Ranunculus montanus	BF					#
Willd.	FF	3	0.953	0.139	5.1 (± 1.1)	780 [1045-1825]
(Ranunculaceae)	EF	8	0.954	**<0.001**	4.9 (± 0.4)	1343 [641-1984]
Trifolium pratense L.	BF	5	0.648	0.100	3.4 (± 1.4)	984 [841 -1825]
(Fabaceae)	FF	7	0.647	**0.029**	4.1 (± 1.3)	1111 [714-1825]
	EF	10	0.684	**0.003**	4.1 (± 1.0)	1111 [714-1825]

Statistical analyses

Linear regression models with data from control plots over the entire altitudinal gradient were conducted to test the effect of altitude on the timing of phenophases (beginning of flowering, full flowering and end of flowering) for each species. To test whether response to altitude changed with timing of mean onset dates, weighted linear regression of significant altitudinal regression coefficients on mean dates was carried out. We weighted the dependent variable in dependence on its residuals. A mixed-effect analysis of covariance (ANCOVA) with Type I sums of squares was used for each species and phenophase (beginning of flowering, full flowering and end of flowering) separately to test whether there were differences in phenology due to experimental treatments. In this model, site nested within altitude was considered as a random factor and treatment as a fixed factor. Altitude was included as a covariate to remove the effect of altitude from the treatment comparison. Tukey's HSD for multiple comparisons was used when the model was significant. Mean onset dates were derived from the adjusted means from the mixed-effect model. The ANCOVA was conducted separately for lower (600–1300 m) and higher sites (1300–2000 m) to detect changes in the response to experimental treatments over the altitudinal gradient.

Paired *t*-tests were used to test whether soil moisture content differed between control and treated plots during the drought period. Further *t*-tests were conducted to see whether there were differences in treatment effects between lower and higher sites.

All statistical analyses were performed with SPSS 19.0 (SPSS, Chicago, IL, USA, 2010).

Results

Abiotic treatment effects

Averaged over the lower gradient from 600 m to 1300 m, snow melted ca. 18 days earlier on advanced snowmelt plots than on control plots (between 20 February (DOY 51) and 23 March (DOY 82)) (Figs. V.1, V.2). At higher altitudes (1300 m to 2000 m) snow melting date on advanced snowmelt plots was between 23 March (DOY 82) and 8 April (DOY 98) which was about 40 days earlier in comparison to control plots (Figs. V.1, V.2). A *t*-test showed a significant difference in the advance of snow melting dates in comparison to control plots at lower and higher sites on advanced snowmelt plots (P = 0.014). On delayed snowmelt plots, mean snow melting date was about 2 days later at lower and about 5 days later at higher sites than on control plots (Fig. 2). Date of snowmelt on delayed plots was between 22 February (DOY 53) and 16 April (DOY 106) at lower sites and between 23 April (DOY 113) and 5 June (DOY 156) at higher sites (Fig. V.1). A *t*-test showed no significant differences in the delay of snowmelt in comparison to controls between lower and higher sites on delayed snowmelt plots (P = 0.157, Fig. V.2). During the drought period, soil moisture content was, averaged over all sites, significantly different between control and drought plots (paired *t*-test, P < 0.001), however the difference did not change with altitude, since a *t*-test was not significant different between lower and higher sites (P = 0.301, Fig. V.3). No significant difference in soil moisture content was found between controls and either advanced or delayed snowmelt plots (paired *t*-test, P = 0.786 or P= 0.932).

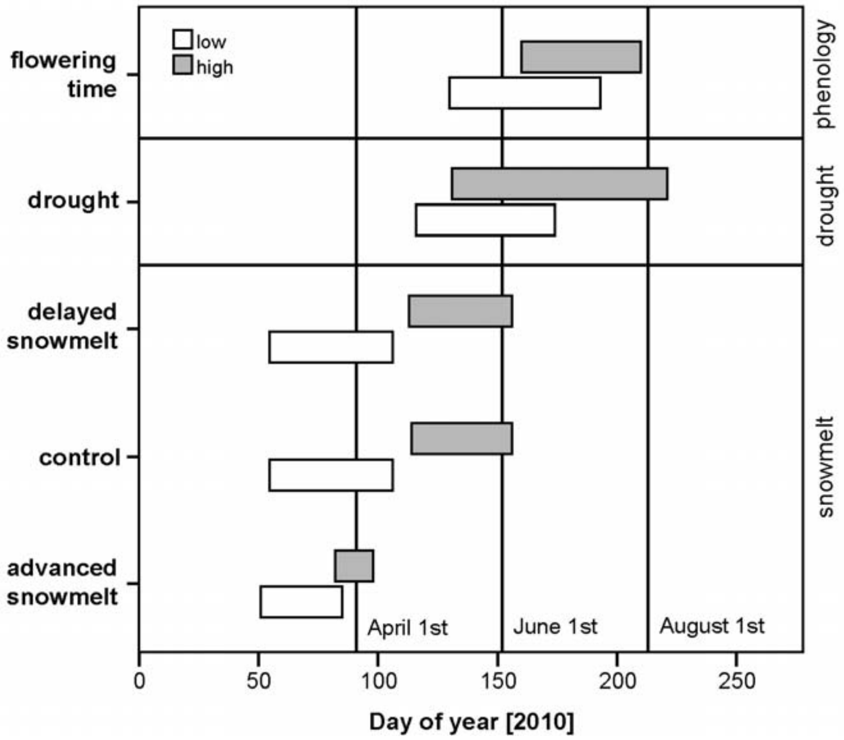


Fig. V.1 Range in the date of snowmelt (advanced snowmelt, control, delayed snowmelt), duration of drought treatment and flowering time of all species over the lower (600 m to 1300 m) and higher (1300 m to 2000 m) altitudinal gradient in 2010.

Phenological shifts due to altitude

Linear regression models mostly showed significant responses of flowering phenology to altitude (Table V.1). Averaged over all phenophases and species there was a delay in onset dates of 3.4 days per 100 m increase in elevation. However, the altitudinal response differed strongly between species, being greatest for the end of flowering of *R. acris* (5.7 days per 100 m), and the smallest for the end of flowering of *Lotus corniculatus* L. (1.7 days per 100 m).

Weighted linear regression analysis showed that phenophases occurring later in the year were significantly less responsive to altitudinal change than phenophases early in the year ($P = 0.043$, $R^2 = 0.593$).

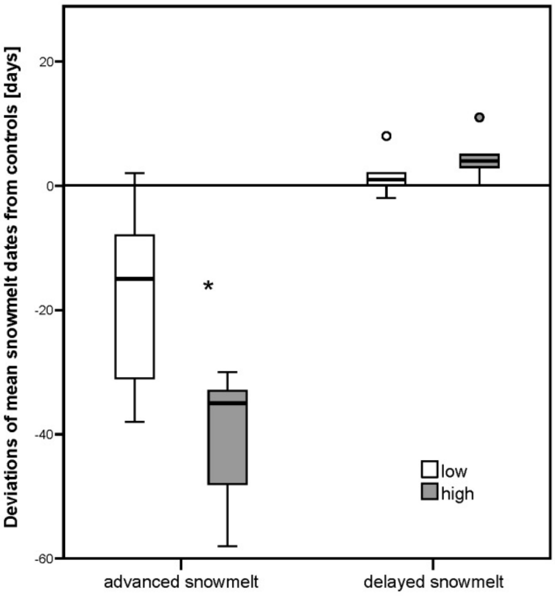


Fig. V.2 Deviations from controls of mean snowmelt dates on advanced and delayed snowmelt plots, derived from each altitudinal site singly and then separated by low (600 m to 1300 m) and high altitudes (1300 m to 2000 m). Asterisk indicates significant differences in snow melting date between lower and higher sites ($P < 0.05$).

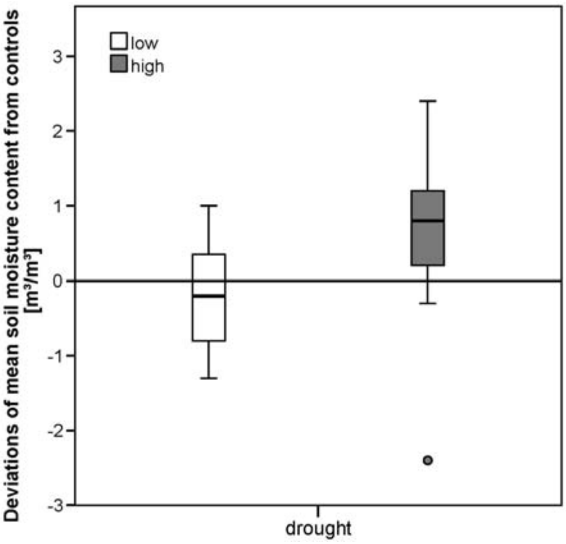


Fig. V.3 Deviations of soil moisture content on drought plots from controls, derived each altitudinal site singly and then separated by low (600 m to 1300 m) and high sites (1300 m to 2000 m).

Phenological differences due to treatments

ANCOVA showed few significant differences in the timing of phenophases between treatments with differences mainly found at higher sites, except for *Prunella vulgaris* L. which showed a significant shift at the lower gradient (Tables V.2, V.3).

Tukey´s HSD post-hoc tests showed a significant advance of 6 to 12 days for the beginning of flowering and full flowering of *Alchemilla vulgaris* L. on advanced snowmelt plots in comparison to control and other treatment plots (Table V.3). Full flowering and end of flowering of *R. montanus* were also 8 to 18 days earlier on advanced snowmelt plots in comparison to the other treatments (Table 3). A significant delay of 5 to 9 days in the end of flowering of *C. scheuchzeri* and *P. vulgaris* was recorded on delayed snowmelt plots (Tables V.2, V.3). For *Potentilla erecta* (L.) Raeusch the end of flowering was significantly advanced on drought plots (by 3–8 days) in comparison to advanced and delayed snowmelt plots (no data available for control plots, Table V.3).

The timing of phenophases, averaged over all species, was about 1 to 7 days earlier on advanced snowmelts plots in comparison to control plots (including non-significant results). The timing was 2 to 3 days later or about the same (0 to -2 days) on delayed snowmelt and drought plots, respectively.

On advanced snowmelt plots, effects were much greater at higher than at lower sites (mean response of -1 day on lower and -5 days on higher sites). On delayed snowmelt plots the response was the same for lower and higher sites (mean delay of 3 days). Average response to drought was -2 days for lower sites but no significant difference in phenology was found at higher sites.

The effect of an advanced snowmelt appeared to be more pronounced earlier in the year showing a response of -7 days on higher sites for the beginning of flowering and only -1 day for the end of flowering. The effect of delayed snowmelt and drought appeared to be consistent throughout the year.

Changes in the duration of flower phenology

ANCOVA showed that, for all species, manipulative treatments had no significant effect on the duration of flower phenology except for *A. vulgaris* showing a prolongation of 7 days on advanced snowmelt plots in comparison to the control plots (Table V.4). For *P. erecta* flower duration was much longer at lower altitudes (33 days) than at higher altitudes (18 days) averaged over all treatments (Table V.4).

Table V.2 Mixed-effect analysis of covariance (ANCOVA) showing differences in phenological onset dates (beginning of flowering, full flowering, end of flowering) between treatments (control (co), advanced snowmelt (ad), delayed snowmelt (de), drought (dr)) for the lower part (600 m–1300 m) of the altitudinal gradient. Numbers in bold are significant (P < 0.05). N/A data not available. Mean onset dates are derived as adjusted means from the model. Tukey´s HSD was conducted for multiple comparisons if the model was significant; Letters indicate a significant difference between respective treatments.

	Beginning of flowering					Full flowering					End of flowering				
	P	co	ad	de	dr	P	co	ad	de	dr	P	co	ad	de	dr
Alchemilla vulgaris L.	0.622	**140**	**137**	N/A	**139**	0.153	**140**	**137**	**139**	**139**	0.369	**174**	**177**	N/A	**177**
Briza media L.	0.485	**173**	**172**	**174**	**172**	0.236	**175**	**177**	**179**	**173**	0.103	**181**	**181**	**182**	**180**
Campanula scheuchzeri Vill.	N/A														
Dactylis glomerata L.	0.106	**170**	**168**	**170**	**167**	0.354	**172**	**170**	**173**	**170**	0.265	**177**	**175**	**178**	**175**
Lotus corniculatus L.	0.253	**166**	**156**	**170**	N/A	0.223	**170**	**162**	**178**	N/A	0.160	**189**	**188**	**200**	**198**
Potentilla erecta (L.) Raeusch	0.218	**149**	**153**	**153**	**152**	0.744	**156**	**158**	**158**	**158**	0.714	**189**	**189**	**192**	**187**
Prunella vulgaris L.	0.800	**183**	**183**	**181**	**185**	0.290	**185**	**183**	**187**	**185**	**0.047**	**193**	**191** a	**196** a b	**191** b
Ranunculus acris L.	0.695	**143**	**140**	**144**	**141**	0.402	**144**	**143**	**144**	**142**	0.763	**159**	**157**	**158**	**158**
Ranunculus montanus Willd.	N/A					0.590	**130**	**128**	**130**	**130**	0.801	**136**	**133**	**137**	**136**
Trifolium pratense L.	0.391	**167**	**167**	**162**	**169**	0.147	**173**	**172**	**170**	**171**	0.634	**184**	**181**	**181**	**181**

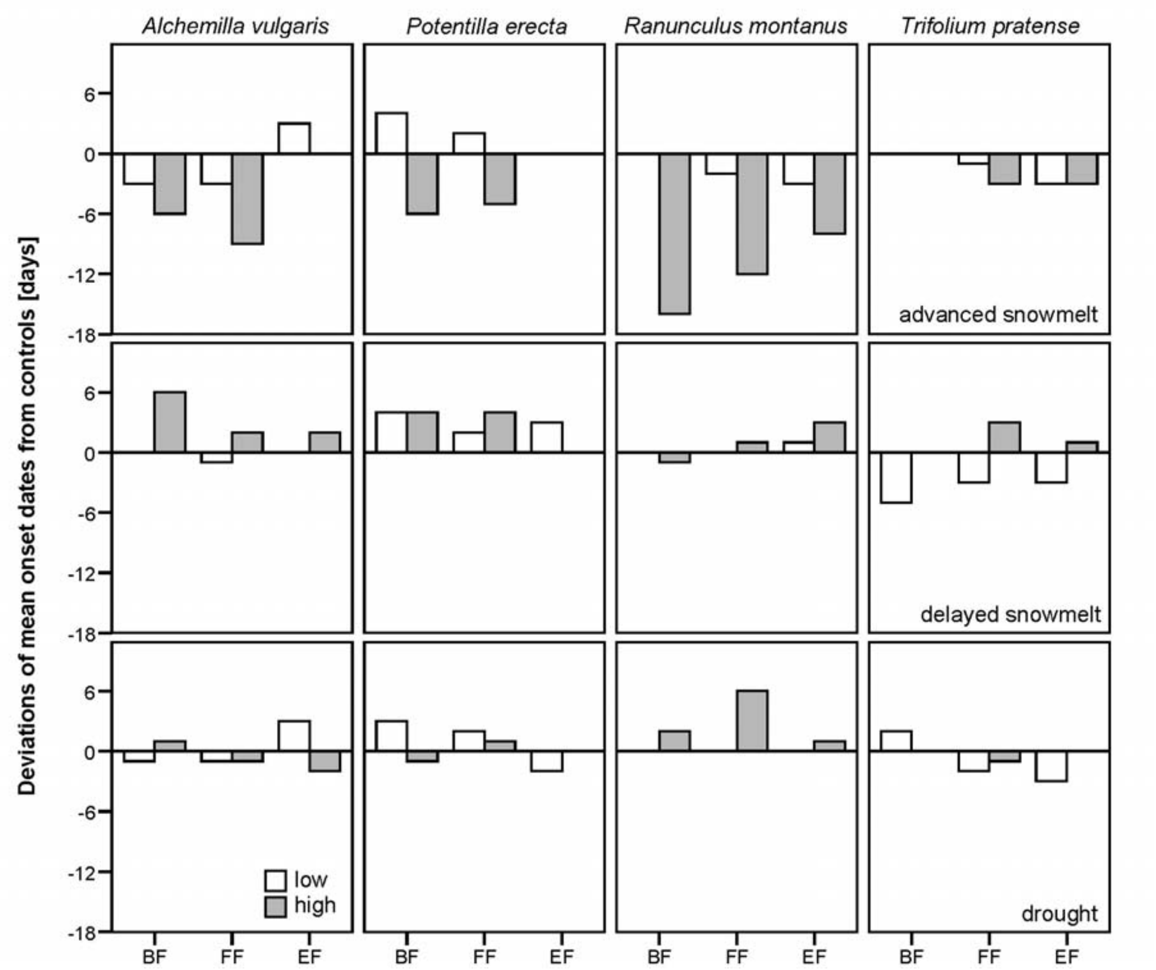
Table V.3 Mixed-effect analysis of covariance (ANCOVA) showing differences in phenological onset dates (beginning of flowering, full flowering, end of flowering) between treatments (control (co), advanced snowmelt (ad), delayed snowmelt (de), drought (dr)) for the higher part (1300 m–2000 m) of the altitudinal gradient. Numbers in bold are significant (P < 0.05). NA data not available. Mean onset dates are derived as adjusted means from the model. Tukey´s HSD was conducted for multiple comparisons if the model was significant; Letters indicate a significant difference between respective treatments.

	Beginning of flowering					Full flowering					End of flowering				
	P	co	ad	de	dr	P	co	ad	de	dr	P	co	ad	de	dr
Alchemilla vulgaris L.	**0.005**	**160** a	**154** a b c	**166** b	**161** c	**0.028**	**170** a	**161** a b c	**172** b	**169** c	0.255	**187**	**187**	**189**	**185**
Briza media L.	N/A														
Campanula scheuchzeri Vill.	0.122	**209**	**211**	**213**	**207**	0.123	**210**	**211**	**214**	**207**	**<0.001**	**216** a	**219** b	**225** a b c	**217** c
Dactylis glomerata L.	N/A														
Lotus corniculatus L.	N/A										0.242	202	200	200	202
Potentilla erecta (L.) Raeusch	0.318	**179**	**173**	**183**	**178**	0.192	**180**	**175**	**184**	**181**	**0.036**		**195** a	**200** b	**192** a b
Prunella vulgaris L.	N/A														
Ranunculus acris L.	N/A														
Ranunculus montanus Willd.	0.092	**169**	**153**	**168**	**171**	**0.005**	**170** a	**158** a b c	**171** b	**176** c	**0.006**	**178** a	**170** a b c	**181** b	**179** c
Trifolium pratense L.	N/A					0.610	**199**	**196**	**201**	**198**	0.410	**210**	**207**	**211**	**210**

Table V.4 Mixed-effect analysis of covariance (ANCOVA) showing differences in the length of flowering period (days from beginning of flowering to end of flowering) between treatments (control (co), advanced snowmelt (ad), delayed snowmelt (de), drought (dr) over a lower (l) (600 m–1300 m) and a higher (h) (1300 m–2000 m) altitudinal gradient. Numbers in bold are significant (P < 0.05). Tukey´s HSD was conducted for multiple comparisons if the model was significant; letters symbols indicate a significant difference between respective treatments (treatment). N/A data not available.

		Duration [days]				
		P	co	ad	de	dr
Alchemilla vulgaris L.	mean (l)			N/A		
	treatment (l)					
	mean (h)	**0.010**	30	37	25	27
	treatment (h)		a	a b c	b	c
Briza media L.	mean (l)		9	9	8	7
	treatment (l)	0.552				
	mean (h)			N/A		
	treatment (h)					
Campanula scheuchzeri Vill.	mean (l)			N/A		
	treatment (l)					
	mean (h)		11	11	12	14
	treatment (h)	0.253				
Dactylis glomerata L.	mean (l)		11	9	11	11
	treatment (l)	0.396				
	mean (h)			N/A		
	treatment (h)					
Lotus corniculatus L.	mean (l)		22	30	31	
	treatment (l)	0.696				
	mean (h)			N/A		
	treatment (h)					
Potentilla erecta (L.) Raeusch	mean (l)		33	31	35	31
	treatment (l)	0.591				
	mean (h)		18	22	17	15
	treatment (h)	0.082				
Prunella vulgaris L.	mean (l)		12	10	15	9
	treatment (l)	0.935				
	mean (h)			N/A		
	treatment (h)					
Ranunculus acris L.	mean (l)			N/A		
	treatment (l)					
	mean (h)			N/A		
	treatment (h)					
Ranunculus montanus Willd.	mean (l)			N/A		
	treatment (l)					
	mean (h)		10	20	16	9
	treatment (h)	0.241				
Trifolium pratense L.	mean (l)		12	12	15	10
	treatment (l)	0.283				
	mean (h)			N/A		
	treatment (h)					

Fig. V.4 Deviations from controls of mean onset dates from the ANCOVA model for each studied phenophase (BF: beginning of flowering, FF: full flowering, EF: end of flowering) separately by low (600 m to 1300 m) and high sites (1300 m to 2000 m) for the four species (*Alchemilla vulgaris* L., *Potentilla erecta* (L.) Raeusch, *Ranunculus montanus* Willd, *Trifolium pratense* L.) observed on both low and high altitudes.



Discussion

The present study showed strong responses of the flower phenology of different grassland species to altitude. Furthermore, we demonstrated that advanced snowmelt had a greater influence on flower phenology at higher than at lower sites due to a stronger treatment effect at higher altitudes. However, altitude had no significant effect on responses to delayed snowmelt or drought, whereas treatment effects were rather small over the entire gradient. Flowering duration was mostly not influenced by manipulative treatments at both higher and lower sites.

Phenological response to altitudinal change

Averaged over all species and phenophases, there was a delay in flower phenology of 3.4 days per 100 m increase. This is in accordance with Cornelius *et al.* (2013) who showed a delay of flower and leaf phenology of 3.8 days per 100 m increase for tree and herbaceous species in the same region. However, the response to altitude change is species-specific, ranging between 1.7 and 5.7 days per 100 m which is similar to the 1.7 to 6.9 days per 100 m shown by Cornelius *et al.* (2013). Most altitudinal studies refer to tree species (e.g. Rötzer & Chmielewski, 2001; Dittmar & Elling, 2006; Migliavacca *et al.*, 2008; Vitasse *et al.*, 2009; Moser *et al.*, 2010), however, Ziello *et al.* (2009) showed, based on COST725 data for the Alpine region, a delay in the beginning of flowering of *Dactylis glomerata* L. of 2.8 days per 100 m. This is slightly less sensitive to altitude than the non-significant response of *D. glomerata* in our study (3.9 days per 100 m). We assume that if we had a greater number of observations in the present study these values would have been more similar.

Phenophases later in the year were significantly less sensitive to altitude than phenophases early in the year, which was also confirmed by Cornelius *et al.* (2013). A weaker response to temperature of species flowering in May and June in comparison to earlier spring flowering species was also shown by Fitter & Fitter (2002) and Menzel *et al.* (2006), who found that, because of high temperature variability in spring, the earlier the species, the stronger the sensitivity to temperature. However, in the present study as well as that of Cornelius *et al.* (2013), early (March to May) and late (September to October) species and phases are missing. Thus, it appears that response to temperature is declining not only in spring but consistently throughout the year.

Phenological response to treatments

The experiment showed only a few significant differences in the timing of flowering due to the manipulative treatments. Earlier snowmelt advanced flower phenology in most cases although the effect was only significant for four species and phenophases. An earlier snowmelt is in accordance with other studies (Price & Waser, 1998; Dunne *et al.*, 2003; Wipf, 2010; Lambert *et al.*, 2010). For example, Wipf *et al.* (2009) showed an advance of flower phenology of up to 10 days (present study 1 to 7 days). The response of species to later snowmelt is rather small; only the end of flowering phenophase was sometimes significantly delayed. Delayed timing due to later snowmelt was also shown in other studies (Weaver & Collins, 1977; Torp *et al.*, 2010; Chen *et al.*, 2011; Cooper *et al.*,

2011) that demonstrated a delay in beginning of flowering and peak flowering of about 6 to 8 days for alpine species. In our study the response was smaller with a non-significant delay of 2 to 3 days between delayed snowmelt and control plots. Hoye *et al.* (2007), however, showed that the result of delayed snowmelt was not necessarily later flowering but could also be unchanged. Thus, response to delayed snowmelt also appears to be species-specific. Wipf & Rixen (2010) suggested that, in general, the least responsive and least consistent responses to shifts in the date of snowmelt were in the grasses, while forbs were a little more responsive. Furthermore, the advanced snowmelt treatment was very early in the year, thus early flowering species such as *A. vulgaris* or *R. montanus* were affected, whereas an effect on late flowering species such as *C. scheuchzeri* or *P. vulgaris* was rather unlikely. Late-flowering species as well as phenophases later in the season were less responsive to snowmelt than early-flowering species or phenophases early in the season because those are controlled by temperature (Price & Waser, 1998; Dunne *et al.*, 2003; Wipf, 2010).

Across species and phenophases the drought treatment did not influence flowering significantly except for *P. vulgaris.* No effect of drought on plant phenology was also found for different grass species in an alpine meadow in France (Bloor *et al.*, 2010) or for the onset of growth of *Globularia alypum* L. in a Mediterranean shrubland (Bernal *et al.*, 2011). However, flowering of *G. alypum* was delayed by drought (Prieto *et al.*, 2008). A delay in flowering time after a drought period was also demonstrated for other Mediterranean plants (Llorens & Penuelas, 2005). In contrast, Jentsch *et al.* (2009) showed an advance of the mid-flowering date by 4 days after a drought period of 32 days. Thus, plant response to drought appears to be highly species-specific (Bernal *et al.*, 2011) and ecosystem dependent. In the present study, soil moisture content on drought plots was 42% on average, which was probably not low enough to simulate a drought event that affects plant phenology (Fig. 3).

The flowering durations of species were mostly not significantly affected by the manipulative treatments. As far as we know, studies dealing with the impacts of snowmelt date on flower duration are rare and contradictory. Price & Waser (1998) showed that early snowmelt was associated with longer flowering duration which agrees with our prolongation of the flowering duration of *A. vulgaris* on advanced snowmelt plots. However, Wipf (2010) demonstrated that flowering duration was not affected by snowmelt timing which agrees with the results of all other species in our study. Studies dealing with the impacts of drought on flowering duration are also rare and contradictory. Jentsch *et al.* (2009) reported a lengthening of the flowering period after a drought event, whereas Llorens & Penuelas (2005) reported both a shortening and a lengthening of the flowering duration of two different Mediterranean dwarf shrubs. In our study, the intensity of drought was likely not sufficient to cause shifts in flowering duration. However, general conclusions from ambiguous results as shown in these studies should be drawn with care due to slight differences in flowering duration definitions between studies.

Shifts in the phenological response due to changes in altitude

We had data for both the lower and the higher altitudes for only a few species. Ideally, species would have been distributed over the entire altitudinal gradient and also located in each treatment plot. However due to restrictions in their natural distribution, species are often not spread over the entire gradient. Thus, only four species were monitored on both lower and higher sites. For those species impacts of treatments on flower phenology were additionally illustrated in Fig. 4. For advanced snowmelt plots, treatment effects were more pronounced at higher sites, however other treatments showed no significant difference between altitude bands. Thus, on advanced snowmelt plots the phenological response is most likely stronger at higher altitudes due to a larger treatment effect and not because species react more sensitively at higher than at lower altitudes. For delayed snowmelt and drought plots no significant differences in treatment effects between lower and higher altitudes were detected. Thus, phenological differences were not significant, which indicates that species responded similarly at different altitudes. Defila & Clot (2005) showed from a 50-year time series in Switzerland that the total proportion of significant trends was higher in the alpine (higher than 1000 m a.s.l.) regions (42%) and smaller in the lowland (lower than 600 m a.s.l, 33%). However, considering the intensity of trends, the results showed an advance of full flowering of 32 days in the lowland and 20 days in the alpine region.

The length of flowering of *P. erecta* was greater at lower altitudes for all treatments which led to the conclusion that duration was probably influenced by higher temperatures at lower sites. Tyler (2001) showed that the length of the flowering period was only slightly influenced by temperature because the timing of the onset of both start and end of phenophases advances in response to temperature increase; thus, the total length is not affected. However, Cornelius *et al.* (2013) showed that, although for most species flowering duration was not influenced by temperature, some species prolonged their flowering duration mainly due to a weaker response of end of flowering which is related to the declining sensitivity to temperature change over the season as also shown in the present study.

Conclusion

Our results suggest that changes in the abiotic environment such as shifts in the date of snowmelt only influence the timing of flowering if the effect is rather distinctive. As this will likely be the case at higher altitudes, species there may be more affected by global climate change. Furthermore, this study showed that a 1000-year extreme drought event in the Bavarian Alps did not substantially influence the phenology of grassland species. Thus, the risk of severe impacts of droughts on flowering phenology will be rather low here. Consequently, shifts in temperature and in the date of snowmelt will constitute the main factors which alter plant phenology under future climate change, however; the magnitude of change will strongly depend on the species.

VI. Elevation and experimental snowmelt manipulation affect emergence phenology and abundance of soil-hibernating arthropods

Abstract

1. Effects of climate change are already apparent and especially in alpine regions further changes can be expected. Arthropods, the most diverse taxon within terrestrial ecosystems are highly sensitive towards ecological and climate changes, however community responses to changed climatic conditions are mostly unknown.

2. In this study, we simulated advanced snowmelt on 15 plots along an elevational gradient in the German Alps. At each study site we established soil-emergence traps for sampling soil-hibernating arthropods on an advanced and control snowmelt treatment during the growing season. We analysed the abundance and emergence phenology of the five most common arthropod orders (Araneae, Coleoptera, Diptera, Hemiptera, Hymenoptera) and the species richness of Coleoptera.

3. We found increasing abundance and species richness of Coleoptera along the elevational gradient, indicating that at higher altitudes more individuals and species hibernate in the soil. Abundances of Diptera also increased with elevation. In contrast, abundances of Hemiptera declined with increasing elevation, while abundances of Araneae and Hymenoptera did not show significant elevational patterns. Arthropods at higher elevation emerged on average five weeks later than arthropods at lower elevation, because of a longer lasting snow cover. The advanced snowmelt treatment resulted in higher abundances of Araneae and Hymenoptera compared to the control plots, indicating that the time of snowmelt influenced the abundance of predators like spiders or parasitic wasps more than those of herbivores.

4. An earlier emergence of certain arthropod guilds and a change in abundance of guilds might desynchronise species interactions leading to a possible loss of biodiversity.

Keywords

Advanced snowmelt, Coleoptera, emergence trap, elevational gradient, phenology, snow shovelling experiment

Introduction

Elevational gradients in species richness are a long-standing topic in ecology that receive renewed interest as a model system for ecosystem responses to climate change (Körner, 2007; McCain & Grytnes, 2010). However, in contrast to species-area relationships as another major ecological gradient where parallel abundance-area relationships have been intensively studied (Connor *et al.*, 2000), very few studies systematically address abundance-elevation relationships at the community level (Hodkinson, 2005; Hoiss *et al.*, 2012). Arthropods are the most dominant group in species richness and abundance on earth with approximately 5 – 10 million species (Stork, 1988; Odegaard, 2000). Arthropods comprise many different functional guilds ranging from pollinators to predators and herbivores and are sensitive indicators for changing environmental conditions (Kremen *et al.*, 1993). According to current climate change scenarios not only increasing mean temperatures but also changes in snow cover and snowmelt date are predicted (Räisänen & Eklund, 2012). Between 1972 and 2000 the date of snowmelt has advanced 9 to 15 days (Dye, 2002). Mountainous regions are particularly affected, when warmer temperatures cause shifts from snow to rain dominated precipitation regimes (Stewart, 2009). A large fraction of arthropods hibernates as larvae, pupae or adults in soil, and thus the emergence of soil-hibernating arthropods may depend on the date of snowmelt, soil and air temperature (Hoye & Forchhammer, 2008). However, little is known about the factors that trigger arthropod emergence and synchronise it with environmental conditions (Hodkinson, 2005). In particular, the combined effects of air temperature and snowmelt timing on soil-hibernating arthropods are mainly unknown. The reduction of snow cover might not only change emergence phenology, but in combination with freezing temperatures can also result in a decrease of arthropod individuals due to higher mortality rates (Bale & Hayward, 2010).

Within arthropods Coleoptera are the most species-rich group accounting for about 40 % of all arthropods and estimated 25 % of all described species (Erwin, 1982; Hamilton *et al.*, 2013). The high functional diversity within Coleoptera including herbivorous, predatory, coprophagous and necrophagous species indicates an important role for ecosystem functioning like seed dispersal (Vander Wall *et al.*, 2005), nutrient recycling (Slade *et al.*, 2007) and herbivore control. Changes in ecosystem functioning due to climate change are already apparent, and with rising temperatures further changes can be expected (McCarty, 2001). However, responses of soil-hibernating Coleoptera and other arthropods to changing climate and variations in precipitation regimes are hardly known. Elevational gradients provide a valuable model system to study the interacting effects of mean temperature and snowmelt regimes, because snow cover and snowmelt naturally vary between the different altitudinal ranges.

In this study we analysed the effects of advanced snowmelt on soil-hibernating arthropods along an elevational gradient by addressing the following questions:

1. How does the abundance of five major arthropod taxa and the species richness of Coleoptera change along an elevational gradient?
2. Does experimentally advanced snowmelt affect the total abundance of soil-hibernating arthropods?
3. How does emergence phenology differ along elevation and between advanced versus control snowmelt plots?

Material and methods

The study was located in the National Park Berchtesgaden, the only German National Park in the Alps. We selected 15 study sites along an elevational gradient between 641 and 1984 m.a.s.l..

On each of the 15 study sites we simulated advanced snowmelt by removing snow from a 4 x 4 m plot until only a thin snow layer of approximately 5 cm was left. We shovelled the snow depending on the altitude between the end of February and the beginning of April in 2010. The snow cover along the altitudinal gradient ranged from 15 to 214 cm before the snow was removed. Complete snowmelt at the advanced snowmelt plots was on average over all study sites 29 ± 5 (mean ± se) days earlier than on the control plots.

We established two soil emergence traps (advanced snowmelt, control) at each study site after the snow was completely melted on the control plots, which differed depending on elevation. On the top of the traps we placed closed plastic boxes with an inner passage that were filled with water and one drop of detergent to catch emerging arthropods. We emptied the boxes once a week from May to September. In total, the emergence trap boxes were emptied between 9 to 17 times (weeks) depending on their elevation. Caught arthropods were determined to order level and Coleoptera, the most species-rich order of arthropods, were determined to species level (Freude *et al.*, 1999). For statistical analyses we only considered the five most abundant arthropod orders in our samples with more than 1000 individuals in total over all study sites and sampling weeks.

Statistical analyses

All statistical analyses were performed using the software R 2.15.1 for Windows (R Core Team, 2012). Linear mixed effects models were calculated with the sequence of explanatory variables: (1) altitude, (2) treatment (advanced snowmelt, control) and (3) their interaction term with type I sum of squares. The response variables were the abundances of the arthropod orders and the species richness of the order Coleoptera. Study site was used as random effect. Model simplification was performed with likelihood ratio tests using maximum likelihood. The sampling period varied between 9 weeks (29th to 37th week of the year) for study sites at high elevation and 17 weeks (20th to 37th week of the year) for study sites at low elevation. To avoid sampling bias, we only used the first 9 sampling weeks after snowmelt for all study sites to ensure the same sample size and comparable sampling periods for study sites at different elevations.

To assess the phenology of the arthropod orders we plotted the mean abundance of each order per altitudinal range (low, intermediate, high) and sampling week (20th to 37th week of the year). There were five study sites within each altitudinal range. The low located sites ranged from 641 to 841 m.a.s.l., the intermediate located sites from 960 to 1333 m.a.s.l. and the high located sites from 1552 to 1984 m.a.s.l.. We calculated paired t-tests between the abundances in advanced and control snowmelt plots for each arthropod order and altitudinal range. To detect possible differences in the emergence of soil-hibernating arthropods immediately after snowmelt, we chose the first week after snowmelt when soil emergence traps were installed on all five study sites per altitudinal range for the paired t-tests. Depending on the altitudinal range the first week after snowmelt was different: 20th week of the year for the low located sites, 21st week of the year for the intermediate located sites and 27th week of the year for the high located sites.

Results

In total, 41,840 individuals of five arthropod orders were collected in the soil emergence traps: Araneae (1,477 individuals), Coleoptera (1,454 individuals), Diptera (28,238 individuals), Hemiptera (4,431 individuals) and Hymenoptera (6,240 individuals). A random sample of 1000 Hymenoptera individuals consisted to over 90 % of parasitoids. Both, elevation and the advanced snowmelt treatment affected the abundance of soil-hibernating arthropods (Table VI.1). The abundance of Coleoptera and Diptera increased with altitude whereas the abundance of Hemiptera decreased with altitude (Table VI.1, Fig. VI.1 a, b, c). Abundances of Araneae and Hymenoptera showed no significant changes with altitude (Table VI.1, Fig. VI.1 d, e).

The interaction terms between altitude and advanced snowmelt were not significant for any arthropod order or for species richness of Coleoptera (Table VI.1). However and interestingly, advanced snowmelt increased the total abundance of Araneae and Hymenoptera (Table VI.1, Fig. VI.1 d, e). Thus, during the nine weeks after snowmelt significantly more individuals emerged from advanced compared to control snowmelt plots.

Within the order Coleoptera 192 species were determined, and further 15 morphospecies could be only determined to genus level (Table VI.S1). Similarly to their abundance the species richness of Coleoptera increased with increasing elevation (Table VI.1, Fig. VI.2). Species richness of Coleoptera was not significantly affected by advanced snowmelt (Table VI.1, Fig. VI.2). The most dominant species was *Anthophagus alpinus* with 145 individuals in total on 10 study sites. 47% of all sampled Coleoptera species were present with one individual and 118 Coleoptera species only occurred at one study site (Table VI.1).

We further analysed the seasonal distribution of soil-hibernating arthropods along the elevational gradient and potential temporal shifts in emergence rates caused by advanced snowmelt. Soil-hibernating arthropods emerged three to seven weeks later at high-elevation sites than at low-elevation sites (Fig. VI.3). However, we found no significant differences between the emergence rates in advanced and control snowmelt plots in the first week after snowmelt (paired t-tests: $p \geq 0.08$). For exact p-values for each arthropod order within each altitudinal range see the supplementary material (Table VI.S2).

Table VI.1 Results of linear mixed effects models with the abundances of the different arthropod orders and the species richness of the order Coleoptera as response variables, altitude, treatment and their interaction as explanatory variables. Full models with restricted maximum likelihood are shown. Significant effects are highlighted in bold.

explanatory variables		**abundance**										**species richness**	
	df	Araneae		Coleoptera		Diptera		Hemiptera		Hymenoptera		Coleoptera	
		F	p	F	p	F	p	F	p	F	p	F	p
altitude	1, 13	2.22	0.160	8.12	**0.014**	7.10	**0.020**	5.01	**0.043**	2.32	0.152	10.37	**0.007**
treatment	1, 13	4.78	**0.048**	0.39	0.541	1.00	0.335	1.22	0.289	4.93	**0.045**	3.20	0.097
altitude : treatment	1, 13	3.42	0.087	0.12	0.739	0.26	0.619	0.68	0.423	0.07	0.794	0.001	0.972

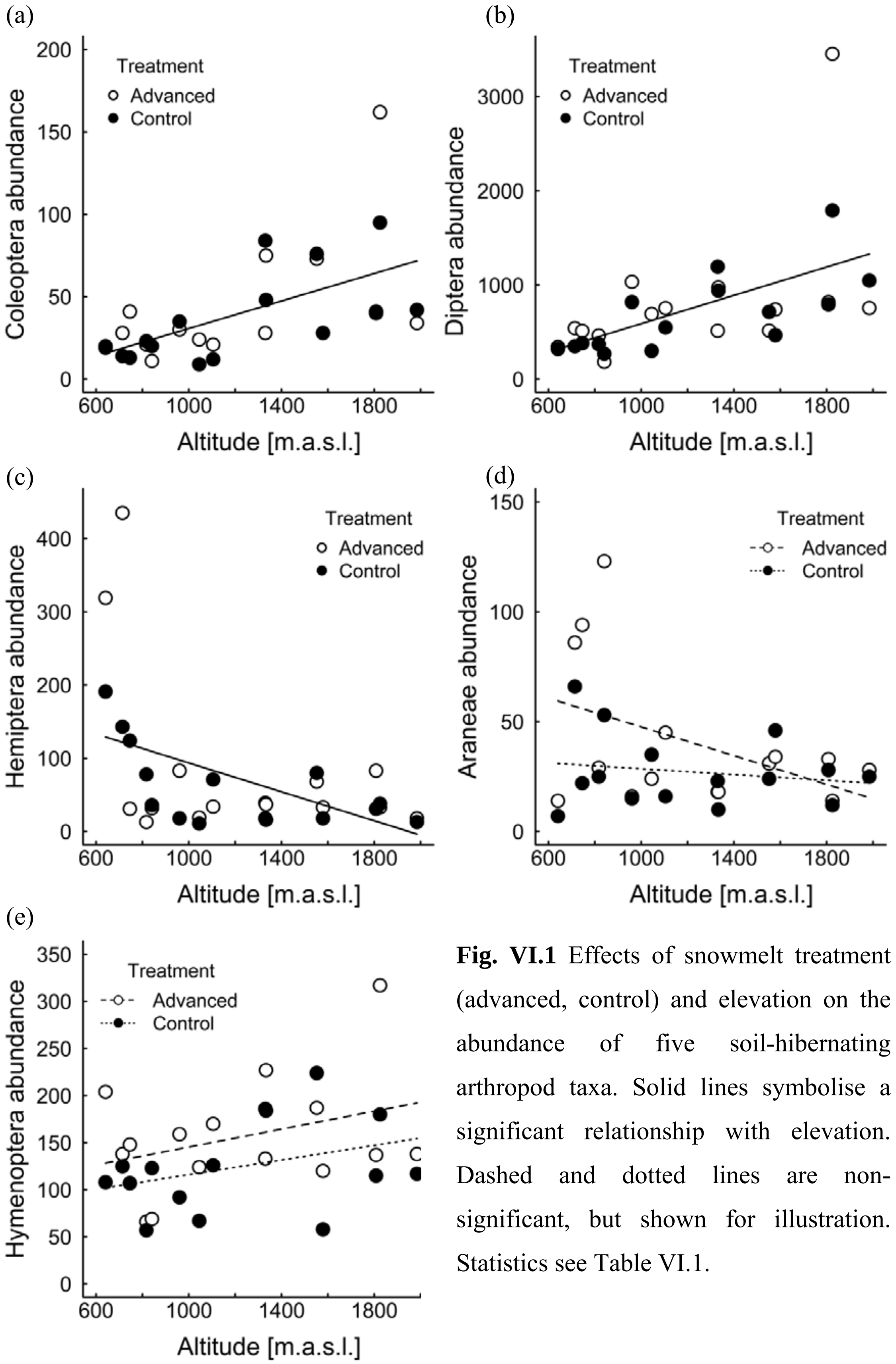


Fig. VI.1 Effects of snowmelt treatment (advanced, control) and elevation on the abundance of five soil-hibernating arthropod taxa. Solid lines symbolise a significant relationship with elevation. Dashed and dotted lines are non-significant, but shown for illustration. Statistics see Table VI.1.

Discussion

Our results indicate that soil-hibernating arthropods have distinct differences in their elevational abundance distribution. Coleoptera and Diptera increased in abundance with elevation, whereas Hemiptera decreased and Araneae and Hymenoptera showed no elevational patterns. Furthermore, we found an increasing species richness of Coleoptera along the elevational gradient. The first emergence of all soil-hibernating arthropod orders shifted along the elevational gradient. Interestingly, the advanced snowmelt treatment triggered emergence rates and thereby increased the total abundances of Araneae and Hymenoptera.

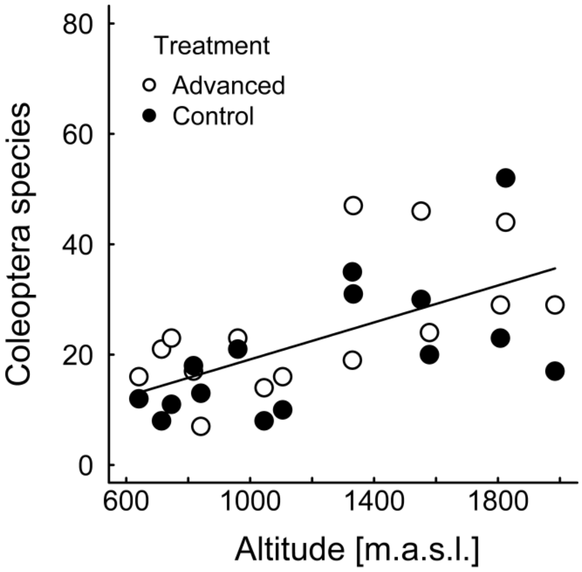


Fig. VI.2 Effects of snowmelt treatment (advanced, control) and elevation on the species richness of Coleoptera. Solid line symbolises a significant relationship with elevation.

Arthropods along the elevational gradient

Arthropods are broadly distributed along elevational gradients and both biotic and abiotic factors shape arthropod abundance patterns along elevation (Hodkinson, 2005). Declining densities can be expected due to decreasing temperatures to suboptimal levels for arthropods, harsher conditions and declining resource availability at higher elevation (Lee *et al.*, 2012; Hoiss *et al.*, 2012). However, abundance patterns can also show increasing trends with elevation, because competition pressure may decrease towards higher elevation. Furthermore, there are also studies showing no abundance patterns with elevation (Lawton *et al.*, 1987; Kelly, 1998). Our results show that soil-hibernating Coleoptera are more abundant and also more species rich at higher than at lower elevation. One explanation for the increasing abundance of Coleoptera with elevation is the lack of other overwintering possibilities than in the soil like trees, shrubs and dead wood. Similarly to Coleoptera abundances, we found that Diptera abundances were also higher at higher altitudes. With increasing elevation Diptera take over the position as dominant pollinators from the thermophilic bees, because Diptera prefer humid regions whereas bees are more abundant in dry regions (Devoto *et al.*, 2005). Humidity increases with elevation, therefore more favourable larval habitats for Diptera are available at higher located sites in contrast to lower located sites (Kearns, 1992). The colours of the alpine flowers also indicate that Diptera are more abundant at higher elevation than in the lowlands, because the proportion of white and yellow flowers increases with increasing elevation, which mainly attracts Diptera (Arnold *et al.*, 2009). In contrast to the abundances of Coleoptera and Diptera we found a linear decrease of Hemiptera abundance with increasing elevation. Possible explanations for the decrease of abundance are the harsh environmental conditions, short seasons at higher elevation and a lower ability to hibernate at high elevations. An adaptation to short season length could be the switch from a one year life cycle at lower elevation to a two year life cycle at higher elevation. However, not all species can change their life cycle, which presumably results in lower abundances at higher elevation. In a study conducted with two Hemiptera species, the population density decreased with elevation for the obligate univoltine species, whereas population density for the semivoltine species was not influenced by altitude (Hodkinson *et al.*, 1999). For Araneae and Hymenoptera we found no elevational patterns. Araneae are predators and the Hymenoptera in our traps were mainly parasitoids. The density of Araneae is mainly driven by prey availability (Lee *et al.*, 2012), therefore we suppose that the soil-hibernating Araneae in our study region found enough prey along the full elevational gradient. Hymenoptera represent the greatest number of parasitoids within all orders accounting for 75 % of all described parasitoid species (Eggleton & Belshaw, 1992). In total, approximately 10 % of all described insect species are parasitoids (Heraty, 2009). Parasitoids play a major role in regulating arthropod populations and they are involved in various trophic interactions, however large-scale patterns of parasitoids are poorly known (Santos & Quicke, 2011). Furthermore, host-parasitoid interactions are a sensitive system, which can be desynchronised by climate change (Jeffs & Lewis, 2013). Our analyses concerning soil-hibernating Hymenopteran parasitoids along an elevational gradient reveal that the parasitoids were equally distributed along the gradient. Similarly to Araneae, the distribution of Hymenopteran parasitoids is dependent on host availability. Additionally, Hymenopteran parasitoids are dependent on an optimal synchronisation between host and parasitoid phenology, whereas parasitoids as higher trophic level are assumed to be more sensitive to climate (Voigt *et al.*, 2003).

Phenology of arthropods

The season length decreases with increasing elevation, which is mainly caused by a delayed onset of spring. A recent study in the National Park Berchtesgaden revealed a delay in the timing of plant phenology of 3.8 days for every 100 m increase in elevation (Cornelius *et al.*, 2013). Our phenology data of soil-hibernating arthropods along an elevational gradient might follow this shift in plant phenology. Studies on the phenology of arthropods are rare (Hoye & Forchhammer, 2008) and as far as we know there is no other study about the phenology of soil-hibernating arthropods along elevational gradients. The five studied arthropod orders showed different phenologies during the growing season. Diptera for example were mainly present at the beginning and decreased during the growing season, whereas the Hymenoptera peaked in the middle and had a second peak at the end of the season. The different phenologies are presumably driven by different life cycles, because Diptera as pollinators need to be active during the main flowering periods in spring and summer, whereas parasitoid Hymenoptera are dependent on hosts and therefore should occur later in the year.

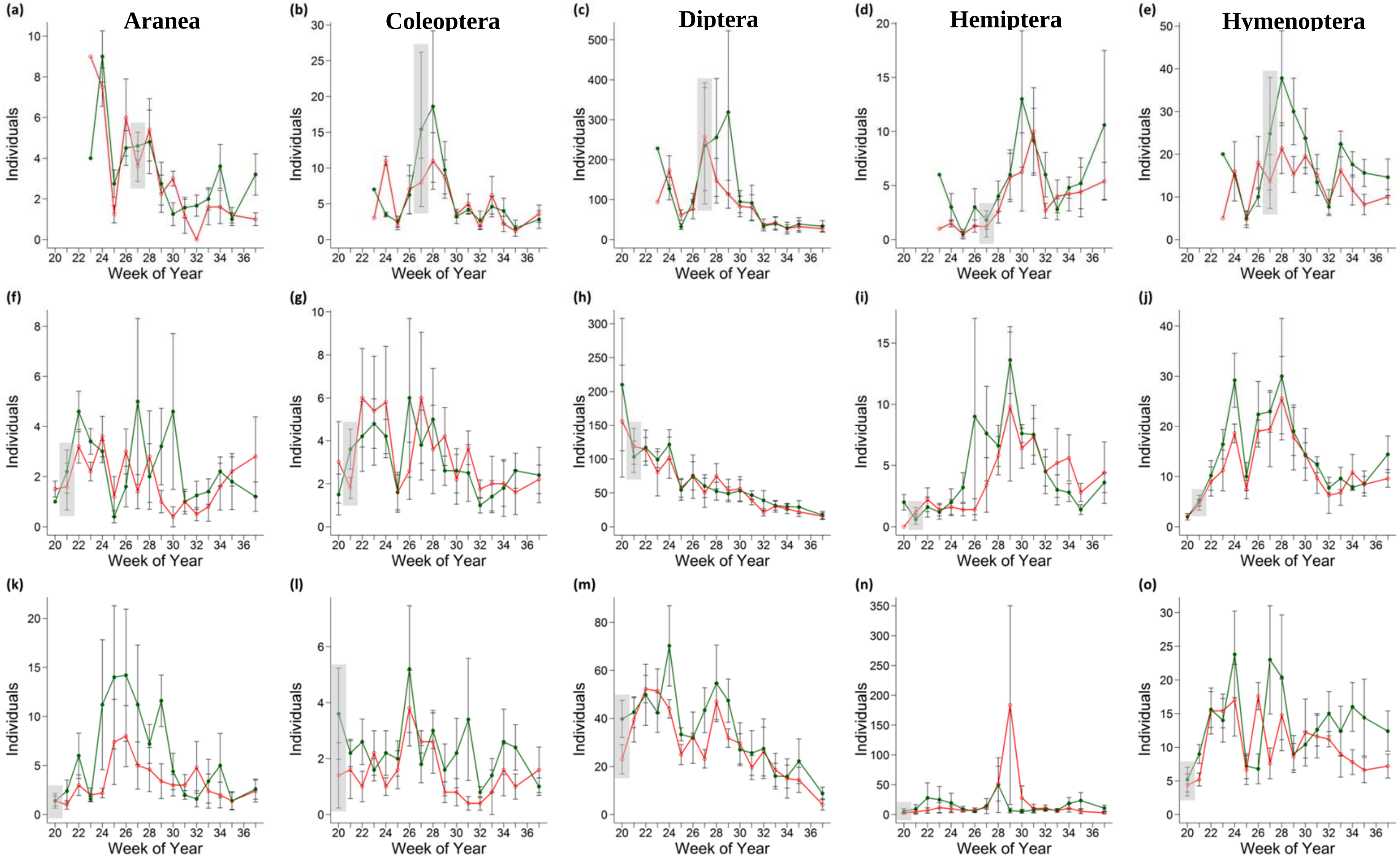

(a)
Aranea
(b)
Coleoptera
(c)
Diptera
(d)
Hemiptera
(e)
Hymenoptera
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)
(n)
(o)
Individuals
Week of Year
0 2 4 6 8 10
0 5 10 15 20 25 30
0 100 200 300 400 500
0 5 10 15 20
0 10 20 30 40 50
0 2 4 6 8
0 2 4 6 8 10
0 50 100 150 200 250 300
0 5 10 15
0 10 20 30 40
0 5 10 15 20
0 2 4 6
0 20 40 60 80
0 50 100 150 200 250 300 350
0 5 10 15 20 25 30
20 22 24 26 28 30 32 34 36

Fig. VI.3 Phenological data of five arthropod orders in control (red) and advanced (green) snowmelt treatments at three altitudinal ranges (high range a - e: 1552 – 1984 m.a.s.l, intermediate range f - j: 960 – 1333 m.a.s.l., low range k - o: 641 – 841 m.a.s.l.,.) from May to September (20th – 37th week of the year). Grey bars symbolise the first week after complete snowmelt in control plots for all five sites per elevational range.

Changes caused by advanced snowmelt

Predictions concerning the timing of snowmelt are difficult and vague, because future snow cover under climate change is expected to become more variable in space and time due to altered precipitation regimes (Stendel *et al.*, 2008; Wipf & Rixen, 2010). Highly variable snowmelt timing will strongly affect arthropods in areas with long lasting snow cover like the Arctic and the alpine region, because there the growing seasons are short and species are especially dependent on a co-occurrence with their resources (Hoye & Forchhammer, 2008). Nevertheless, when environmental conditions are too unfavourable for arthropods to emerge, some evolved a strategy to cope with these circumstances by hibernating a further winter. In contrast, when environmental conditions are especially favourable, because of advanced snowmelt and longer growing seasons, than higher emergence rates can be expected.

Our results indicate that advanced snowmelt influenced the termination of diapause within the orders Araneae and Hymenoptera resulting in higher abundances during the growing season. Regulation of diapause is species-specific and in the most common facultative form also dependent on environmental conditions (Denlinger, 2002). Under favourable environmental conditions diapause is terminated earlier, but thresholds vary among groups. Particularly herbivores, mainly present in the orders Coleoptera and Hemiptera, need to time their emergence exactly to synchronise with the occurrence of a specific stage of their feeding plants (Ragland *et al.*, 2009). Thus, herbivorous arthropods should stay in diapause and hibernate a further winter, when environmental conditions are not favourable.

In conclusion, strong variations in snowmelt timing in combination with advanced snowmelt are expected to become more frequent with ongoing climate change. Soil-hibernating arthropods in the alpine region will especially be affected by these changes and future phenology shifts presumably result in desynchronisation between herbivore-plant and predator-prey interactions.

Supplement

Table VI.S1 Coleoptera species list

	Species name	Altitude [m.a.s.l.] of colonised sites
1)	*Abax parallelus*	1552
2)	*Acidota cruentata*	1984
3)	*Acrotrichis spec.*	1333
4)	*Adelocera murina*	960
5)	*Adrastus axillaris*	714
6)	*Adrastus pallens*	817
7)	*Agonum* spec.	1330
8)	*Agriotes obscurus*	714, 817, 1330
9)	*Agrypnus murina*	817
10)	*Aleochara marmotae*	1330, 1808, 1825
11)	*Aleuonota rufotestacea*	614
12)	*Altica* spec.	1552
13)	*Amara aulica*	817
14)	*Amara lunicollis*	641, 714
15)	*Amara montivaga*	714
16)	*Amara similata*	1105
17)	*Amphichroum canaliculatum*	960, 1330, 1333
18)	*Anaspis frontalis*	1579
19)	*Anotylus sculpturatus*	641, 1984
20)	*Anthonomus rubi*	1330, 1552, 1808
21)	*Anthophagus alpinus*	817, 960, 1045, 1330, 1333, 1552, 1579, 1808, 1825, 1984
22)	*Anthophagus angusticollis*	960, 1333, 1552, 1579, 1808, 1825, 1984
23)	*Anthophagus bicornis*	1333, 1808, 1825
24)	*Aphodius gibbus*	1579, 1808, 1825, 1984
25)	*Apion flavipes*	1552
26)	*Apion* spec.	1579
27)	*Apion tenue*	746, 841
28)	*Apion trifolii*	746, 960

29)	*Asiorestia melanostoma*	714, 746, 960, 1333, 1552, 1825
30)	*Asiorestia transversa*	960
31)	*Atheta fungi*	714, 960
32)	*Atheta hygrotopora*	641
33)	*Atheta puncticollis*	960, 1330, 1579, 1825
34)	*Atheta pygmaea*	1984
35)	*Atheta* spec.	714, 746, 817, 841, 960, 1045, 1105, 1330, 1333, 1552, 1579, 1825
36)	*Athous haemorrhoidalis*	1045, 1330, 1552, 1825
37)	*Athous subfuscus*	1333
38)	*Bembidion biguttatum*	641
39)	*Bembidion* spec.	714
40)	*Bibloporus bicolor*	714, 1333
41)	*Brachygluta tristis*	817
42)	*Bryaxis glabricollis*	746
43)	*Bryaxis nodicornis*	746, 1105, 1330
44)	*Bryocharis cingulata*	1984
45)	*Bryoporus rufus*	1330, 1808
46)	*Byrrhus gigas*	1552, 1808
47)	*Byturus ochraceus*	817
48)	*Calathus micropterus*	1333
49)	*Cantharis livida*	960
50)	*Cantharis obscura*	1105, 1579
51)	*Cantharis pellucida*	714, 1045, 1105
52)	*Carabus fabricii*	1808, 1825
53)	*Carabus granulatus*	960
54)	*Carabus sylvestris*	1579, 1808, 1984
55)	*Carpelimus corticinus*	641, 746
56)	*Cateretes pedicularius*	746, 841, 817, 960, 1105, 1330
57)	*Catops fuscus*	1333, 1552, 1808, 1825, 1984
58)	*Cercyon convexiusculus*	714, 746, 960
59)	*Ceutorhynchidius troglodytes*	746
60)	*Ceutorhynchus hutchinsiae*	1825

61)	*Chaetocnema hortensis*	841
62)	*Chrysolina marginata*	1330
63)	*Chrysolina staphylaea*	1330
64)	*Chrysolina varians*	1330, 1333, 1552
65)	*Colon brunneum*	641,746
66)	*Cratosilis denticollis*	746, 960, 1105, 1330, 1552, 1808, 1984
67)	*Cryptocephalus labiatus*	1552
68)	*Cryptopleuron minutum*	746
69)	*Ctenicera cuprea*	1333, 1579, 1808, 1984
70)	*Ctenicera pectinicornis*	746, 1045, 1579
71)	*Cychrus attenuatus*	1808
72)	*Cychrus caraboides*	641
73)	*Dalopius marginatus*	714, 817, 1105, 1330, 1333, 1579
74)	*Dascillus cervinus*	641, 746, 960
75)	*Dasytes alpigradus*	1984
76)	*Derocrepis rufipes*	746
77)	*Domene scabricollis*	1045
78)	*Donus comatus*	641, 746, 1045, 1333, 1579
79)	*Donus velutinus*	1045
80)	*Dromius agilis*	1579
81)	*Dryops ernesti*	841, 1045
82)	*Endomychus coccineus*	960
83)	*Enicmus minutus*	641
84)	*Epuraea oblonga*	1825
85)	*Epuraea pusilla*	1825
86)	*Epuraea unicolor*	1330, 1808, 1825
87)	*Euconnus pubicollis*	641
88)	*Eusphalerum abdominale*	746, 1045, 1330, 1333, 1552, 1808, 1825, 1984
89)	*Eusphalerum alpinum*	641, 714, 746, 817, 960, 1045, 1333, 1552, 1808, 1825, 1984
90)	*Eusphalerum anale*	1333
91)	*Eusphalerum sorbi*	641, 817, 960, 1045, 1105, 1330, 1333, 1552, 1579, 1808, 1825

92)	*Falagria thoracica*	1330
93)	*Gabrius* spec.	841, 960
94)	*Galleruca tanaceti*	641
95)	*Geotrupes alpinus*	1984
96)	*Glocianus punctiger*	960
97)	*Gonioctena* spec.	1333
98)	*Gymnaetron* spec.	1808
99)	*Harpalus latus*	714, 1333, 1579
100)	*Hermaeophaga mercurialis*	746
101)	*Hoplia argentea*	641, 714
102)	*Hydnobius punctatus*	1579
103)	*Hypera adspersa*	1045
104)	*Hypera viciae*	1552, 1808
105)	*Lamprohiza splendidula*	641, 1330
106)	*Lebia cruxminor*	1579
107)	*Leiodes* spec.	641, 960, 1579, 1825
108)	*Leiosoma kirschi*	960
109)	*Lesteva longelytrata*	1045
110)	*Limonius aeneoniger*	1579
111)	*Liogluta microptera*	817, 1333, 1825
112)	*Longitarsus apicalis*	641, 960
113)	*Longitarsus luridus*	714, 1330, 1579, 1808, 1984
114)	*Longitarsus suturellus*	641, 960, 1579, 1984
115)	*Longitarsus tabidus*	641, 714, 746, 1579
116)	*Malthodes* spec.	841, 1333, 1552, 1984
117)	*Melanophthalma* spec.	641
118)	*Melanotus castanipes*	841
119)	*Meligethes aeneus*	1825
120)	*Metopsia* spec.	641
121)	*Microplontus millefolii*	714
122)	*Microscydmus nanus*	817, 1825
123)	*Monochamus sutor*	1105
124)	*Mycetoporus longulus*	841

125)	*Mycetoporus niger*	1984
126)	*Mycetoporus ruficornis*	714
127)	*Nebria hellwigii*	1825
128)	*Nebria jockischi*	1330
129)	*Necrophilus subterraneus*	1333, 1552
130)	*Necrophorus vespilloides*	841, 1330, 1552
131)	*Neuraphes coronatus*	1105, 1984
132)	*Omalisus fontisbellaquaei*	1579
133)	*Omalium excavatum*	1825
134)	*Oreina alpestris*	960, 1045, 1330, 1333, 1579, 1808, 1825
135)	*Oreina viridis*	1808, 1825
136)	*Othius myrmecophilus*	1330
137)	*Otiorhynchus coecus*	1984
138)	*Otiorhynchus foraminosus*	641, 841
139)	*Otiorhynchus gemmatus*	1333, 1552
140)	*Otiorhynchus morio*	1105, 1330, 1333, 1579, 1825
141)	*Otiorhynchus nodosus*	1579
142)	*Otiorhynchus porcatus*	960, 1825
143)	*Otiorhynchus scaber*	746
144)	*Otiorhynchus subdentatus*	1333
145)	*Otiorhynchus varius*	1579
146)	*Oxypoda annularis*	1330
147)	*Oxypoda spectabilis*	641
148)	*Paederus litoralis*	841
149)	*Panagaeus bipustulatus*	746
150)	*Pella lugens*	841
151)	*Phaedon pyritosus*	960
152)	*Philonthus carbonarius*	817
153)	*Philonthus cognatus*	960
154)	*Philonthus decorus*	960, 1333, 1825, 1984
155)	*Philonthus fulivipes*	960
156)	*Philonthus fuscipennis*	960, 1825
157)	*Philonthus marginatus*	1984

158)	*Philonthus montivagus*	1333, 1552, 1579, 1808, 1825, 1984
159)	*Philonthus puella*	1333
160)	*Philonthus varians*	714, 841, 960
161)	*Phosphuga atrata*	746, 960
162)	*Phyllopertha horticola*	641, 714, 841
163)	*Pissodes piceae*	1105
164)	*Pityokteines spinidens*	1552, 1825
165)	*Platydracus stercorarius*	641
166)	*Poecilus cupreus*	817
167)	*Polygraphus subopacus*	817
168)	*Potosia cuprea*	746
169)	*Proteinus* spec.	1333
170)	*Pseudathous hirtus*	841
171)	*Pterostichus burmeisteri*	1330, 1333
172)	*Pterostichus vernalis*	1579
173)	*Ptiliolum* spec.	960
174)	*Ptomaphagus variicornis*	641
175)	*Quedius dubius*	1333, 1579, 1825
176)	*Quedius mesomelinus*	1333
177)	*Quedius paradisianus*	714, 746, 1333, 1552, 1579, 1808, 1825, 1984
178)	*Quedius punctatellus*	1105, 1825
179)	*Quedius* spec.	817,1333
180)	*Quedius unicolor*	1825
181)	*Rhagonycha atra*	1552
182)	*Rhagonycha fulva*	714, 746, 817, 960, 1105
183)	*Rhagonycha limbata*	746, 1045
184)	*Rhizophagus bipustulatus*	1825
185)	*Rhyncolus chloropus*	841, 960
186)	*Sciaphilus asperatus*	1105
187)	*Scymnus haemorrhoidalis*	714
188)	*Scymnus impexus*	1825
189)	*Selatosomus aeneus*	1330, 1579
190)	*Semiadalia alpina*	1579

191)	*Serica brunnea*	960, 1105, 1330, 1808
192)	*Smaragdina flavicollis*	714
193)	*Sphaeroderma rubidum*	817, 1105
194)	*Stenus circularis*	817
195)	*Stenus similis*	960, 1045, 1579
196)	*Synuchus vivalis*	714
197)	*Tachinus signatus*	641, 714, 746, 960, 1045, 1333, 1825
198)	*Tachyporus austriacus*	817, 960
199)	*Tachyporus chrysomelinus*	714, 817, 960, 1045, 1552
200)	*Tachyporus nitidulus*	817
201)	*Tachyta nana*	960
202)	*Thinotus morion*	641
203)	*Timarcha metallica*	1333
204)	*Trichotichnus laevicollis*	817, 841, 960, 1045, 1105, 1333, 1552, 1579, 1808
205)	*Trimium brevicorne*	641, 714, 746, 1105, 1552
206)	*Xantholinus* spec.	817
207)	*Zyras humeralis*	841

Table VI.S2 Comparisons of emergence rates of five arthropod groups in the first week after snowmelt (week 20 low sites, week 21 intermediate sites, week 27 high sites) between control and advanced snowmelt plots (p-values are shown).

	Araneae	**Coleoptera**	**Diptera**	**Hemiptera**	**Hymenoptera**
High sites	0.14	0.39	0.54	0.21	0.38
Intermediate sites	0.65	0.19	0.71	0.30	0.69
Low sites	1	0.36	0.08	0.60	0.76

VII. General Discussion

Altitudinal gradients

A major goal in ecology is to understand how species and communities are distributed along spatial gradients and what influences and determines their distribution. Particularly under climate change species and community patterns along altitudinal gradients are of great interest. Under the assumption that species communities along altitudinal gradients change in the same way as climate change will change species communities over time, predictions about species community responses to climate change might be possible. However, species- and abundance-based life-history trait analyses at the community level revealing trait combinations that promote adaption to certain climatic conditions are rare. Thus, this dissertation focused in the chapters II and III on butterfly, diurnal moth and plant species richness patterns along an altitudinal gradient in the Bavarian Alps. Furthermore, life-history traits prevailing in butterfly assemblages and plant pollination types at different altitudes were analysed.

Species richness of butterflies and diurnal moths linearly declined with increasing altitude and the dominance of life-history traits prevailing in alpine butterfly assemblages changed along altitude. The proportion of larger-winged butterflies, as well as the number of eggs per female butterfly and the abundance-based dispersal ability increased with increasing altitude, whereas the egg maturation time within butterfly assemblages decreased with increasing altitude. These changes in the dominance of certain life-history traits in butterfly assemblages along the altitudinal gradient reveal their adaptive value to given climatic conditions. The way of egg deposition and the number of generations per year did not change along the altitudinal gradient, indicating that these life-history traits play a minor role for the performance of butterflies under changing climatic conditions. The mean population density and distribution range in butterfly assemblages decreased with increasing altitude, suggesting that high altitude regions are hotspots for endemic species (Myers *et al.*, 2000).

Plant species richness peaked at intermediate altitudes and more plant species were found at grazed grassland sites than at mown or abandoned grassland sites. The management was the main factor affecting plant species richness independently of temperature and altitude. Species richness of insect-pollinated plants peaked at lower temperatures (higher altitudes) than species richness of wind-pollinated plant species. The proportion of wind-pollinated plants decreased with decreasing temperature, but the vegetation cover of wind-pollinated plants increased with decreasing temperature.

Our results indicate that managing alpine grasslands by extensive grazing along the entire altitudinal gradient maintains high plant diversity. The highest plant diversity was found at intermediate altitudes between 1400 and 1500 m.a.s.l., however this hotspot of plant diversity will shift upwards with climate change when temperatures rise. An upwards shift of plant species may result in a decrease of biodiversity, because with increasing altitude the available area is progressively reduced due to the conical shape of mountains (Jones *et al.*, 2003). Rising temperatures with climate change may also cause changes in trait combinations of butterfly and plant communities, because our results indicate that environmental filtering favours certain combinations of life-history and pollination traits at higher altitudes. With increasing altitude insect-pollination becomes more dominant presumably due to the unfavourable conditions for wind-pollination prevailing at high altitudes with large inter-individual distances of plants and high amounts of precipitation (Pellissier *et al.*, 2010). However, it remains an open question whether special trait combinations favoured by environmental filtering will reduce the competitive strength and fitness of high altitude butterfly and plant species under climate change.

Manipulation experiments

In addition to species richness analyses along elevational gradients and studies revealing trait combinations prevailing under different climatic conditions we also performed manipulation experiments to study ecosystem responses to climate change. Experiments along elevational gradients can provide novel information about the consequences of e.g. variations in snowmelt timing and long lasting drought periods on plant-herbivore interactions and the phenology of plants and arthropods under different climatic contexts. Thus, the focus in the chapters IV, V and VI lay on the impacts of simulated extreme events and elevation on the nutritional quality and herbivory rates of alpine plants, the flower phenology of grassland species and the emergence phenology and abundance of soil-hibernating arthropods.

We found that grasses, legumes and forbs varied in CN ratios and herbivory rates and responded differently to altitude, indicating that elevational shifts in CN ratios and herbivory rates depend on plant guild (chapter IV). Furthermore, CN ratios and herbivory rates changed during the season, with increasing CN ratios and herbivory rates towards the end of the season, suggesting that herbivores compensated low host plant quality with increased consumption rates (Behmer, 2009). However, we did not find any effects of the manipulation experiments on leaf CN ratios and herbivory rates, indicating that nutritional quality of plants and antagonistic interactions with insect herbivores are robust against seasonal climatic extremes. Our results are in line with an experimental study conducted in northern Sweden, showing that seasonal climate manipulations had only minor effects on CN ratios (Aerts *et al.*, 2012).

In contrast, flower phenology was influenced by the manipulative treatments, however not all manipulations showed significant differences in the timing of flowering (chapter V). Earlier snowmelt advanced flower phenology up to 7 days, whereas plants at higher altitudes were more affected than plants at lower altitudes. However, delayed snowmelt and extreme drought delayed the timing of phenophases maximally about 3 days, with no differences within the treatments along the altitudinal gradient. Similar results were found in a High Arctic study showing an advanced onset of flowering in areas of early snowmelt, but not necessarily a delayed onset of flowering in areas of late snowmelt (Hoye *et al.*, 2007). In general, over all phenophases and species we found a strong effect of altitude on flower phenology with a delay in onset dates of 3.4 days per 100 m increase in elevation. During the season the response of flower phenology to altitude and advanced snowmelt declined. However, the climate manipulations had no influence on the flowering duration. The differences in flower phenology between low and high altitudes after earlier snowmelt presumably occurred due to stronger treatment effects at higher altitudes, whereas delayed snowmelt and drought effects were rather similar over the entire gradient.

How elevation and advanced snowmelt affected the emergence phenology and the abundance of soil-hibernating arthropods was analysed in chapter VI. We found different elevational distribution patterns for the studied arthropod orders with increasing abundances for Coleoptera and Diptera, decreasing abundance for Hemiptera and no elevational patterns for Araneae and Hymenoptera. The species richness of Coleoptera showed the same increasing pattern as the abundance of Coleoptera with elevation. Changes in environmental conditions along elevational gradients like temperature and precipitation changes influence distribution patterns, however other organisms such as host plants, parasitoids or predators are also involved in shaping species and abundance patterns along elevation (Hodkinson, 2005). In accordance with the plant phenology the phenology of soil-hibernating arthropods also shifted along the elevational gradient with an up to seven weeks later emergence at higher elevations. The advanced snowmelt treatment had no influence on the emergence phenology of soil-hibernating arthropods, however advanced snowmelt increased the total abundance of Araneae and Hymenoptera.

The three studies about combined effects of elevation and manipulation experiments revealed that the elevational gradient had a strong influence on the studied ecosystem compartments, whereas the strength of this relationship varied between species and communities. The effects of the manipulation experiments were rather small, however the advanced snowmelt treatment showed effects on the phenology of plant species and the abundance of Araneae and Hymenoptera. Our results indicate that variations in snowmelt timing and extreme drought events only marginally affect food plant quality and insect herbivory rates of alpine plants in the Bavarian Alps. Furthermore, changes in the timing of flowering presumably only happens when the date of snowmelt is distinctively shifted, which will likely be the case at higher altitudes, indicating that species there may be more affected by climate change. Although the manipulation experiments had no severe impacts on the nutritional quality of plants, the opposing responses of grasses, legumes and forbs along the altitudinal gradient with increasing nitrogen for legumes and forbs but decreasing nitrogen for grasses imply that competitive interactions within plant communities might change under future climates, with unknown consequences for plant-herbivore interactions. These varying responses underline the importance of long term manipulation experiments along climatic gradients to detect potential risks of future climate change for the biotic components of ecosystems. However, our results indicate that the risk of strong effects of extreme drought periods on flowering phenology is rather low in the study region, whereas presumably the intensity of the drought treatment was too low. The soil moisture was reduced by 30 % on drought plots, which was probably not enough to simulate a drought event that affects flowering phenology (Beier *et al.*, 2004). Importantly, we could analyse the pure drought effect without the influence of temperature, as the drought simulations did not increase temperatures under the rain-out shelters. Therefore, the drought effect detected in other studies presumably is merely a temperature effect (Jentsch *et al.*, 2009).

Earlier snowmelt caused higher abundances of Araneae and parasitoid Hymenoptera, whereas the abundances of Coleoptera, Diptera and Hemiptera were not affected by earlier snowmelt. This indicates that different functional groups including predators and herbivores may respond differently to changing environmental conditions under future climate change, which presumably will result in biodiversity losses due to desynchronisations of species interactions. Therefore, we recommend studying different taxa and processes to understand the consequences of climate change on ecosystems.

Conclusions

The climate is changing and extreme climatic events such as long lasting drought periods or variations in snowmelt timing will occur more frequently. Ecosystems respond to these changes, however the responses depend on the strength of the changes and vary among groups. Butterfly and moth species richness declined towards higher altitudes, whereas the maximum species richness of plants was at intermediate altitudes. Furthermore, the dominance of traits in community assembly changed for butterflies and plants along the altitudinal gradient. Our results indicate that environmental filtering is the main process determining the assembly of communities at higher altitudes, whereas competition-driven processes are more important at lower altitudes. With ongoing global warming, species shifts towards higher altitudes are expected, but a reduced grassland area at higher altitudes may result in diversity losses. Additionally, specific trait combinations prevailing in high altitude assemblages presumably hamper the adaptation to changing conditions under global warming and therefore species adapted to high altitude conditions will likely be outcompeted by more competitive lowland species. Contrasting altitudinal responses in the nutritional quality of grasses, legumes and forbs might also contribute to changes in competitive interactions among these guilds under future climate change. In conclusion, alpine ecosystems are a sensitive hotspot of endemic species, however severe impacts of climate change are expected for alpine flora and fauna due to community composition changes and possible extinctions. In order to mitigate possible ecosystem responses to climate change more studies analysing the complex dynamics and potential risks of future climate change for biotic interactions and ecosystem stability are needed.

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Author Contributions

Chapter II

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AL, JK and ISD designed the study. AL set up the soil emergence traps, collected and analysed the data; AL, JK and ISD interpreted the results; AL wrote the first draft of the manuscript and all authors contributed to revisions.

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