Effects of climate change, extreme events and management on plants, pollinators and mutualistic interaction networks

15 83

Dissertation zur Erlangung des
naturwissenschaftlichen Doktorgrades
der Julius-Maximilians-Universität Würzburg

vorgelegt von

Bernhard Hoiß

geboren in Bad Reichenhall

Würzburg 2013

Mitglieder der Promotionskommission:

Vorsitzender: ____________________

Gutachter : Prof. Dr. I. Steffan-Dewenter

Gutachter: Prof. Dr. J. Tautz

Eingereicht am: ____________________

Verteidigt am: ____________________

Doktorurkunde ausgehändigt am: ____________________

Table of Contents

Summary (English)

I. Climate change comprises average temperatures rise, changes in the distribution of precipitation and an increased amount and intensity of extreme climatic events in the last decades. Considering these serious changes in the abiotic environment it seems obvious that ecosystems also change. Flora and fauna have to adapt to the fast changing conditions, migrate or go extinct. This might result in shifts in biodiversity, species composition, species interactions and in ecosystem functioning and services. Mountains play an important role in the research of these climate impacts. They are hotspots of biodiversity and can be used as powerful natural experiments as they provide, within short distances, the opportunity to research changes in the ecosystem induced by different climatic contexts. In this dissertation two approaches were pursued: i) surveys of biodiversity, trait dominance and assembly rules in communities depending on the climatic context and different management regimes were conducted (chapters II and III) and ii) the effects of experimental climate treatments on essential ecosystem features along the altitudinal gradient were assessed (chapters IV, V and VI).

II. We studied the relative importance of management, an altitudinal climatic gradient and their interactions for plant species richness and the dominance of pollination types in 34 alpine grasslands. Species richness peaked at intermediate temperatures and was higher in grazed grasslands compared to non-managed grasslands. We found the climatic context and also management to influence the distribution and dominance structures of wind- and insect-pollinated plants. Our results indicate that extensive grazing maintains high plant diversity over the full subalpine gradient. Rising temperatures may cause an upward shift of the diversity peak of plants and may also result in changed species composition and adaptive potential of pollination types.

III. On the same alpine grasslands we studied the impact of the climatic context along an altitudinal gradient on species richness and community assembly in bee communities. Species richness and abundance declined linearly with increasing altitude. Bee species were more closely related at high altitudes than at low altitudes. The proportion of social and ground-nesting species, as well as mean body size and altitudinal range of bees, increased with increasing altitude, whereas the mean geographic distribution decreased. Our results suggest that community assembly at high altitudes is dominated by environmental filtering effects, while the relative importance of competition increases at low altitudes. We conclude that ongoing climate change poses a threat for alpine specialists with adaptations to cool environments but low competitive capacities.

IV. We determined the impacts of short-term climate events on flower phenology and assessed whether those impacts differed between lower and higher altitudes. For that we simulated advanced and delayed snowmelt as well as drought events in a multi site experiment along an altitudinal gradient. Flower phenology was strongly affected by altitude, however, this effect declined through the season. The manipulative treatments caused only few changes in flowering phenology. The effects of advanced snowmelt were significantly greater at higher than at lower sites, but altitude did not influence the effect of the other treatments. The length of flowering duration was not significantly influenced by treatments. Our data indicate a rather low risk of drought events on flowering phenology in the Bavarian Alps.

V. Changes in the structure of plant-pollinator networks were assessed along an altitudinal gradient combined with the experimental simulation of potential consequences of climate change: extreme drought events, advanced and delayed snowmelt. We found a trend of decreasing specialisation and therefore increasing complexity in networks with increasing altitude. After advanced snowmelt or drought networks were more specialised especially at higher altitudes compared to control plots. Our results show that changes in the network structures after climate manipulations depend on the climatic context and reveal an increasing susceptibility of plant-pollinator networks with increasing altitude.

VI. The aim of this study was to determine the combined effects of extreme climatic events and altitude on leaf CN (carbon to nitrogen) ratios and herbivory rates in different plant guilds. We found no overall effect of climate manipulations (extreme drought events, advanced and delayed snowmelt) on leaf CN ratios and herbivory rates. However, plant guilds differed in CN ratios and herbivory rates and responded differently to altitude. CN ratios of forbs (legume and non-legume) decreased with altitude, whereas CN ratios of grasses increased with altitude. Further, CN ratios and herbivory rates increased during the growing season, indicating a decrease of food plant quality during the growing season. Insect herbivory rates were driven by food plant quality. Contrasting altitudinal responses of forbs versus grasses give reason to expect changed dominance structures among plant guilds with ongoing climate change.

VII. This dissertation contributes to the understanding of factors that determine the composition and biotic interactions of communities in different climates. The results

presented indicate that warmer climates will not only change species richness but also the assembly-rules for plant and bee communities depending on the species' functional traits. Our investigations provide insights in the resilience of different ecosystem features and processes towards climate change and how this resilience depends on the environmental context. It seems that mutualistic interactions are more susceptible to short-term climate events than flowering phenology and antagonistic interactions such as herbivory. However, to draw more general conclusions more empirical data is needed.

Zusammenfassung (German)

I. Das Klima ändert sich: die Durchschnittstemperaturen steigen, die Niederschlagsverteilung ändert sich und sowohl die Anzahl als auch die Intensität von klimatischen Extremereignissen hat in den letzten Jahrzehnten zugenommen. In Anbetracht dieser beträchtlichen Veränderungen in der abiotischen Umwelt scheint es offensichtlich, dass sich auch die Ökosysteme verändern. Flora und Fauna müssen sich an die sich schnell verändernden Bedingungen anpassen, wandern oder sie sterben aus. Dies kann zu Veränderungen in der Biodiversität, der Artzusammensetzung, den Ökosystemfunktionen sowie von Ökosystemdienstleistungen führen. Gebirge spielen eine wichtige Rolle in der Erforschung dieser Klimafolgen. Sie sind Biodiversitäts-Hotspots und können als großräumige natürliche Experimente genutzt werden, da sie die Möglichkeit bieten, innerhalb kurzer Distanzen Veränderungen im Ökosystem unter verschiedenen klimatischen Bedingungen zu untersuchen. In dieser Dissertation wurden zwei Ansätze verfolgt: i) Es wurden Untersuchungen zur Abhängigkeit von Biodiversität, der Dominanz von funktionalen Merkmalen sowie den Gesetzmäßigkeiten in der Zusammensetzung von Artengemeinschaften vom klimatischen Kontext sowie verschiedenen Management Regimen durchgeführt. ii) Die Effekte von Klimaexperimenten auf essentielle Ökosystemeigenschaften, biotische Interaktionen und Nahrungsnetze entlang eines Höhengradienten wurden untersucht.

II. Die relative Bedeutung von Höhenlage, Bewirtschaftungsform sowie ihre Interaktionen für den Artenreichtum von Pflanzen und die Dominanz von Bestäubungstypen wurden in 34 alpinen Wiesen untersucht. Der Artenreichtum erreichte bei mittleren Temperaturen ein Maximum und war auf beweideten Flächen höher als auf nicht bewirtschafteten Wiesen. Wir stellten außerdem fest, dass sowohl der klimatische Kontext als auch die Bewirtschaftungsform die Verteilung und Dominanzstrukturen von wind- und insektenbestäubten Pflanzen beeinflusste. Unsere Ergebnisse zeigen, dass extensive Beweidung eine hohe Artenvielfalt über den gesamten subalpinen Gradienten erhält. Steigende Temperaturen könnten eine Verschiebung des Bereiches mit maximaler Artenvielfalt nach oben sowie veränderte Zusammensetzungen von Artengemeinschaften und Veränderungen in der Bedeutung von Bestäubungstypen als Anpassung verursachen.

III. Auf den selben alpinen Wiesen untersuchten wir den Einfluss der klimatischen Gegebenheiten entlang des Höhengradienten auf die Artenzahl und die

Gesetzmäßigkeiten in der Zusammensetzung von Wildbienen Artengemeinschaften. Die Artenzahl und Abundanz nahm mit zunehmender Höhe linear ab. Die Bienenarten in höheren Lagen waren näher miteinander verwandt als in niedrigen Lagen. Der Anteil sozialer, im Boden nistender Arten sowie die mittlere Körpergröße und Höhenverbreitung der Bienen nahm mit zunehmender Höhe zu, wohingegen die mittlere geographische Verbreitung der Arten abnahm. Unsere Ergebnisse legen nahe, dass die Zusammensetzung von Artengemeinschaften in höheren Lagen primär vom Filtereffekt der Umwelt bestimmt wird, wohingegen der Einfluss von Konkurrenz in niedrigen Lagen an Bedeutung gewinnt. Wir folgern, dass der fortschreitende Klimawandel eine Gefährdung für alpine Spezialisten darstellt, die zwar Anpassungen an kühle Bedingungen aber oft eine nur geringe Konkurrenzfähigkeit aufweisen.

IV. Wir untersuchten die Auswirkung von kurzzeitigen klimatischen Ereignissen auf die Blütenphänologie und analysierten, ob sich diese Auswirkungen zwischen hohen und tiefen Lagen unterscheiden. Dazu simulierten wir verfrühte und verspätete Schneeschmelze sowie Dürreereignisse in Experimenten auf multiplen Standorten entlang eines Höhengradienten. Die Blütenphänologie wurde von der Höhenlage stark beeinflusst, dieser Effekt nahm im Laufe der Saison allerdings ab. Die Manipulationen zeitigten nur wenige Effekte auf die Blühphänologie. Die Auswirkungen von verfrühter Schneeschmelze waren auf hohen Flächen signifikant höher als in niedrigen Lagen, es wurden jedoch keine Unterschiede für die anderen Behandlungen zwischen den Höhenstufen gefunden. Die Blühdauer wurde durch die Behandlungen nicht beeinflusst. Unsere Daten zeigen ein relativ geringes Risiko für die Blütenphänologie durch Dürreereignisse in den bayerischen Alpen auf.

V. Veränderungen in der Struktur von Pflanzen-Bestäuber Netzwerken wurden entlang eines Höhengradienten in Kombination mit der experimentellen Simulation von potentiellen Konsequenzen des Klimawandels (extreme Dürre, verfrühte und verspätete Schneeschmelze) untersucht. Wir fanden einen Trend hin zu einem abnehmenden Spezialisierungsgrad und daher einer Zunahme der Komplexität in Netzwerken mit zunehmender Höhe. Die Netzwerke nach verfrühter Schneeschmelze und nach Dürre waren, insbesondere in höheren Lagen, stärker spezialisiert als in den Kontrollflächen. Unsere Ergebnisse zeigen, dass Veränderungen in den Netzwerkstrukturen nach Klimamanipulationen vom klimatischen Zusammenhang abhängen und zeigen auf, dass die Anfälligkeit von Pflanzen-Bestäuber Netzwerken mit der Höhe zunimmt.

VI. Das Ziel dieser Studie war es die kombinierten Auswirkungen von kurzzeitigen klimatischen Ereignissen und Meereshöhe auf das CN (Kohlenstoff zu Stickstoff) Verhältnis in Blättern und den Blattfraß in verschiedenen Pflanzengruppen zu untersuchen. Wir fanden keinen Gesamteffekt der Klimamanipulationen (extremes Dürreereignis, verfrühte und verspätete Schneeschmelze) auf das CN Verhältnis und die Herbivorieraten. Die Pflanzengruppen unterschieden sich jedoch in ihrer Reaktion auf die Meereshöhe hinsichtlich ihres CN Verhältnisses und des Blattfraßes. Das CN Verhältnis in Gräsern nahm mit der Höhe zu, wohingegen das CN Verhältnis in den restlichen krautigen Pflanzen mit zunehmender Höhe abnahm. Außerdem nahmen CN Verhältnis und die Herbivorierate im Laufe der Saison zu, was auf eine Abnahme der Futterqualität im Saisonverlauf hindeutet. Die Herbivorieraten wurden von der Futterqualität der Pflanzen bestimmt. Die gegensätzlichen Muster von Gräsern und anderen krautigen Pflanzen über die Höhe lassen veränderte Dominanzstrukturen zwischen Pflanzengruppen mit fortschreitendem Klimawandel zu erwarten.

VII. Diese Dissertation leistet einen Beitrag zur Identifikation von Gesetzmäßigkeiten in der Zusammensetzung von Artengemeinschaften unter unterschiedlichen klimatischen Bedingungen. Die präsentierten Ergebnisse weisen darauf hin, dass ein wärmeres Klima nicht nur den Artenreichtum, sondern auch diese Gesetzmäßigkeiten für Pflanzen- und Bienenvergesellschaftungen in Abhängigkeit von den funktionellen Merkmalen der Arten verändern wird. Unsere Untersuchungen liefern Erkenntnisse über die Stabilität verschiedener Ökosystemaspekte und -prozesse gegenüber dem Klimawandel und wie diese Stabilität vom Umweltkontext abhängt. Es scheint, dass mutualistische Interaktionen anfälliger sind für kurzfristige Klimaereignisse als die Phänologie von Blüten oder antagonistische Interaktionen wie die Herbivorie. Um allgemeinere Rückschlüsse ziehen zu können bedarf es jedoch dringend weiterer empirischer Daten.

I General Introduction

Climate Change and its consequences

Abiotic changes

Global average temperature raised by 0.74 °C in the last century and the rate of warming even increased in the last decades (Trenberth et al. 2007). The warming in the alpine region was about two to three times as large as for the global average for the 20th century which can mainly be traced back to two very warm decades in the 1980s and 1990s in the alpine region (Auer et al. 2007, Beniston 2012). For the next century rising temperatures are predicted even if the concentrations of greenhouse gases, responsible for climate warming, remain constant (Meehl et al. 2007). Climate changes due to raised amounts of carbon dioxide in the atmosphere will be irreversible for the next centuries (Solomon et al. 2009).

Among the predicted consequences of climate change are shifts in the precipitation patterns (geographical and seasonal shifts) and a shortened snow season especially in the Northern Hemisphere (Solomon et al. 2007). Yet, the snow cover at high altitudes seems to be less sensitive to the temperature changes than at low altitudes and where winter precipitation increases in these regions, the snow season might even elongate (Solomon et al. 2007). Not only mean precipitation and temperatures change, but also the amount and intensity of extreme climatic events increased in the last decades (Trenberth et al. 2007). These extreme events may lead to nature disasters when they hit vulnerable regions. It is very likely that the frequency and intensity of heat waves, drought and heavy precipitation events will further increase with ongoing global warming (Meehl et al. 2007).

Considering these serious changes in the abiotic environment with an increasing amount of extreme events in combination with habitat fragmentation, intensification of land-use and therefore reduced biodiversity (Foley et al. 2005, Tscharntke et al. 2005), it seems obvious that ecosystems will also change. Flora and fauna have to adapt to the fast changing conditions, migrate or they will go extinct. The resulting shifts in biodiversity, species composition, species interactions and in ecosystem functioning and services are largely unknown.

Biotic changes

Climate change already affected biodiversity and composition of communities (Erschbamer et al. 2009, Forister et al. 2010, Devictor et al. 2012), shifted the ranges and distribution of species and led to invasions of species into habitats which they could not colonize before (Rahel and Olden 2008, Thomas 2010, Felde et al. 2011, Chen et al. 2011a). These shifts in communities and ecosystems are expected to carry on with climate change (Urban et al. 2012, Devictor et al. 2012).

Diversity is important for many aspects of ecosystems, such as productivity (Roscher et al. 2005), nutrient-cycling (Hooper and Vitousek 1998), the structure of trophic interactions (Scherber et al. 2010), or stability against species invasions (Fargione and Tilman 2005) and is hence an important driver for many ecosystem functions humans benefit from (Myers 1996). To predict future developments in ecosystem functioning, to evaluate the need for action and to enable adaptation strategies to these changes, data on the influence of land use and climate on biodiversity, species composition and their interactions in communities are therefore of high importance.

The survival of individuals and species under given environmental conditions depend on their characteristics or, in other words, their functional and life-history traits. If climate determines the composition of communities, species in these assemblages may often have similar traits. These traits, important for the persistence of species, can become dominant in communities (Cornwell and Ackerly 2009). However, the traits dominant in communities may shift with changing environmental conditions due to species turnover or intraspecific shifts (Spooner and Vaughn 2008, Cornwell and Ackerly 2009). We therefore need to identify traits with an adaptive value to climatic conditions to be able to evaluate the sensitivity of species and communities to the consequences of climate change (Diamond et al. 2011) and to understand the assembly of communities. This knowledge might also allow predictions about the directions in which our ecosystems will develop in terms of their species composition, ecological functioning and services (Spooner and Vaughn 2008).

A very important feature for ecosystems and their functioning are the numerous interactions between species and the ecosystem services they provide. The sensibility of species, participating in mutualistic interactions, to global change is expected to be particularly high as phenological mismatches may occur when they do not respond in the same extent to the changes as their partners (Bartomeus et al. 2011). Because both partners benefit from a mutualistic interaction they may also be both negatively influenced by its loss. However, there is only sparse empirical data on the sensibility of interactions and interaction-networks to climate change and phenological mismatches.

Mountainous Regions

Mountainous regions play an important role for humans and nature. Humans benefit from many resources and services provided by mountains such as water, energy, minerals, forest and agri-cultural products and areas of recreation (Beniston 2003). In addition to this, mountainous regions harbour many endemic and threatened species and are hotspots of biodiversity. They represent a refuge for species that were supplanted from the lowlands due to the increasing land-use intensity by humans (Lomolino 2001). With their steep environmental gradients and high topological variability, mountains provide a high habitat and climate diversity within only small distances and therefore play an important role in conservation efforts.

Mountains also play an important role in the research of biogeographic questions as well as in climate impact research. Altitudinal gradients are powerful natural experiments as they provide, within short distances, the opportunity to research changes in the ecosystem induced by different geophysical influences, such as the climatic contexts (Körner 2007). To evaluate the effects of global warming, altitudinal gradients can be used in a space-for-time substitution approach. Climatic changes in space along altitudinal gradients can be used as models for the effects of climate change in time (Dunne et al. 2004, Fukami and Wardle 2005, Körner 2007, Lurgi et al. 2012). The interpretation of ecological or evolutionary patterns along altitudinal gradients can become difficult, when the gradients include also changes in variables, such as land use, that are not generally associated with altitude (Körner 2007). Human land use, for example, often superimposes the natural drivers of biodiversity and hampers the detectability of natural patterns (Nogues-Bravo et al. 2008). It is therefore important to consider also the effects and interactions of important co-variables, such as management type and intensity, when investigating the effects of climate on patterns in species richness and assemblages. Comparisons between historical data and new surveys along altitudinal gradients may provide important insights in ecosystem processes under climate change and allow a validation of predicted changes derived from the space-for-time approach. However, for these comparisons, reliable and standardised baseline data are necessary, but these are missing for many taxonomic groups and regions. Surveys to gather these data are therefore needed.

Besides the space-for-time substitution approach, mountains provide the possibility to integrate experimental and gradient methods within one study. The combination of experimental methods and natural gradients provides the possibility to overcome some limitations of the separate approaches (Dunne et al. 2004). Gradient analyses allow insights in long-term adaptations of ecosystems to environmental conditions, but only few conclusions can be drawn on ecosystem reactions to short-term effects. The value of space-for-time substitutions along climatic gradients depends on the assumption that species distributions can keep pace with the rapid climatic changes (Dunne et al. 2004). With experimental methods on the other hand important cofactors can be controlled and phenotypic reactions of different ecosystem aspects to short-term effects of climate change can be studied. Experiments however are often limited in size and time. Furthermore experiments often allow the manipulation of only few factors and ignore context-dependent ecosystem responses (Dunne et al. 2004). In an integrated approach the strengths of both methods can be combined and context-dependent responses to climate change can be assessed. However, to our knowledge, no empirical studies have been published on the context dependent effects of climate change on communities and species interaction networks.

Study systems and study design

Fig. I.1: *Bombus monticola* on *Trifolium pratense*. Photo: B. Hoiß

Important features of ecosystems that can be accessed in a changing climatic context along altitudinal gradients are biodiversity, community structure and assembly rules, and species interactions. Both, biodiversity and species interactions play an important role for the stability of ecosystems (Bascompte et al. 2006, Ives and Carpenter 2007, Tylianakis et al. 2008). Important traits for the survival under given climatic conditions can be identified. Species' traits can be used to predict the reactions of species to climate change, possible future community structures and to explain observed diversity and composition patterns (Forrest and Miller-Rushing 2010, Diamond et al. 2011, Lurgi et al. 2012). As study systems we used plants, insect pollinators, insect herbivores and their mutualistic respectively antagonistic interactions (Fig. I.1). Plants, in their function as primary producers, are the basal component of most ecosystems and their fitness therefore plays an important role for the functioning of these ecosystems (Loreau et al. 2001). Plant pollinator interactions represent crucial processes to maintain biodiversity, reproduction and fitness in both groups and spread plant genes with adaptive values to changing environments. Recent, worldwide declines in wild and domesticated pollinators have been shown, and, at the same time, plants that rely upon them declined as well (Potts et al. 2010). The resilience of these plant-pollinator interactions under changing climatic conditions is not only of ecological, but also of high economic interest (Kearns et al. 1998, Ayres and Lombardero 2000, Klein et al. 2007). The focal pollinators in our studies were wild bees, hoverflies and other diptera. Herbivores also play an essential role in ecosystems. On the one hand they directly affect plants, induce their defence mechanisms, consume plant biomass and thereby alter dominance structures in plant communities. On the other hand herbivores represent an important link in ecosystems in converting nutrients stored in plant tissues into digestible forms for carnivores.

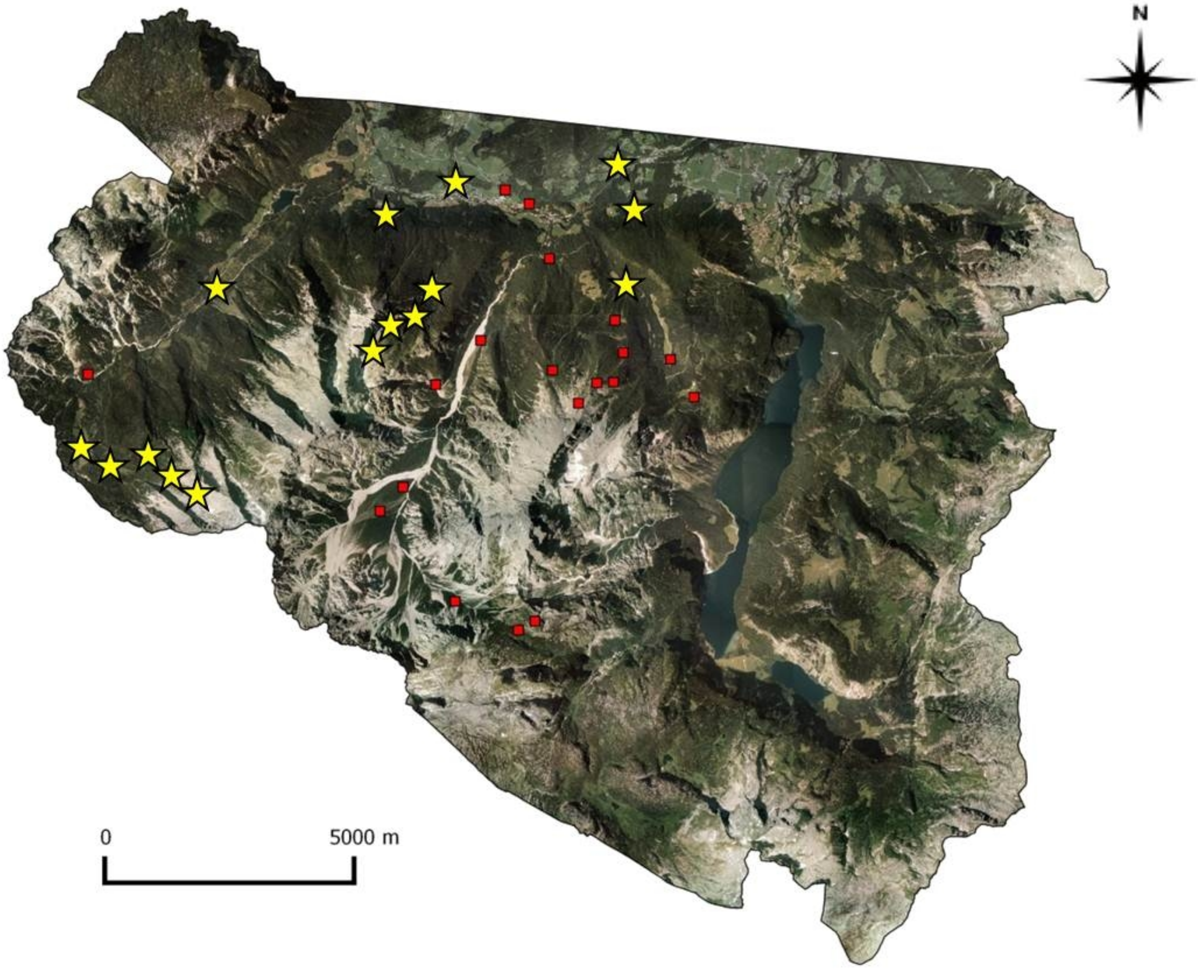

Fig. I.2: 34 Grassland sites in the National Park Berchtesgaden, Germany. Sites that were only used in 2009 are marked with red squares. 15 sites that were used in 2009 and also for the experiments in 2010 are marked with yellow stars.

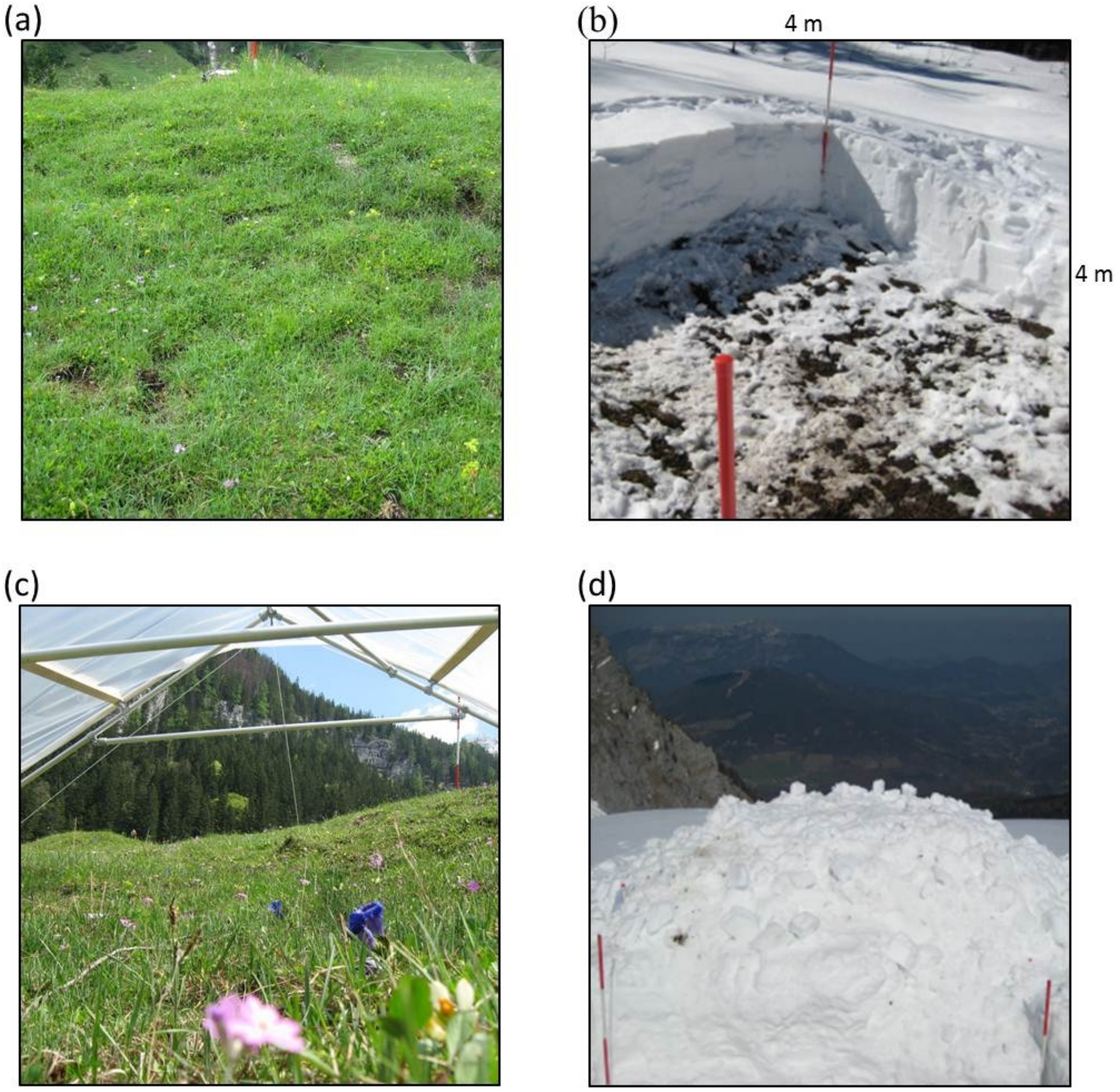

Fig. I.3: Experimental design with four treatments per study site: (a) unmanipulated control, (b) advanced snowmelt, (c) drought treatment with rain-out shelter and (d) delayed snowmelt. The size of each treatment plot was 4 x 4 m. The distance between the plots was 1 m. Photos were taken from different study sites at different dates. Photos: B. Hoiß and A. Leingärtner

In this dissertation two approaches were pursued: i) surveys of biodiversity, trait dominance in communities and assembly rules of communities at 34 grassland sites along an altitudinal gradient in the National Park Berchtesgaden (Fig. I.2) with different management regimes were conducted (see chapters II and III) and ii) consequences of climate change (extreme drought events, advanced and delayed snowmelt) were experimentally simulated (Fig. I.3) at 15 sites along an altitudinal gradient (Fig. I.2) (chapters IV, V and VI).

i) In the first approach surveys on plants and important pollinators (wild bees) were conducted at the same sites under standardised conditions. Important traits of the taxa were assessed to derive, in combination with a phylogenetic approach, assembly rules of communities under different climatic conditions. The aim in a space-for-time substitution approach was to draw conclusions from patterns along the altitudinal gradient for possible developments in communities with ongoing climate change. The information on biodiversity, abundance and community structures on the marked sites can be used as baseline data to assess changes in time in future studies.

ii) The focus in the second approach lay on the effects of experimentally simulated climate change on plant phenology and interactions between plants and insects. An important aspect was the susceptibility of communities and interactions to the simulated consequences of global warming and how this susceptibility depended on the climatic context. The susceptibility of mutualistic interaction networks to extreme events and changed precipitation patterns has received little attention so far. Moreover, even though the resilience of networks and communities to climate change is supposed to depend on the environmental context (Ives and Carpenter 2007, Tylianakis et al. 2008) as far as we know, no research has been published on this combination. Experiments, that simulate extreme events, altered season length or other consequences of climate change, have mainly been conducted at single locations so far (Bütof et al. 2012). We therefore assessed the importance of the local climate context in determining plant flowering phenology, plant-pollinator network structures and susceptibilities to climate change and investigated the effects on herbivory rates and food quality of plant tissues. To simulate the extreme drought we set up 4 x 4 m rain-out shelters at 15 sites along an altitudinal gradient in the National Park Berchtesgaden (Fig. I.4). To simulate advanced snowmelt we removed snow from one plot in early spring until only a thin layer was left and shovelled the snow on an adjacent plot to simulate a delayed snowmelt at all 15 sites (Fig. I.5). In total we moved about 70 tons of snow for these snow-manipulation experiments.

The emphasis in this dissertation lay mainly on plant-pollinator systems. However, some colleagues in the project collaborated at the same sites to gain a comprehensive and complementary dataset on different parameters and taxa. Annette Leingärtner mainly worked with butterflies, plant-herbivore systems and the phenology of insects, hibernating in soil. Christine Cornelius focused on plant phenology and Sergey Rosbak on the assessment of plant traits.

Fig. I.4: Fenced experimental site with a 4 x 4 m rain-out shelter to simulate an extreme drought event. Photo: B. Hoiß

Fig. I.5: Shoveling snow to simulate advanced and delayed snowmelt. Photo: A. Leingärtner

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

This chapter has been published as: 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*, 1–10. (doi:10.1111/j.1472-4642.2012.00941.x)

Running title: Climate, land use and alpine plants

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 and 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 and 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 and 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 and 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 and 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 climatic 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 and 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 and 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 analyzed 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 m^2 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 neighboring 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 (Curall 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. II.S1).

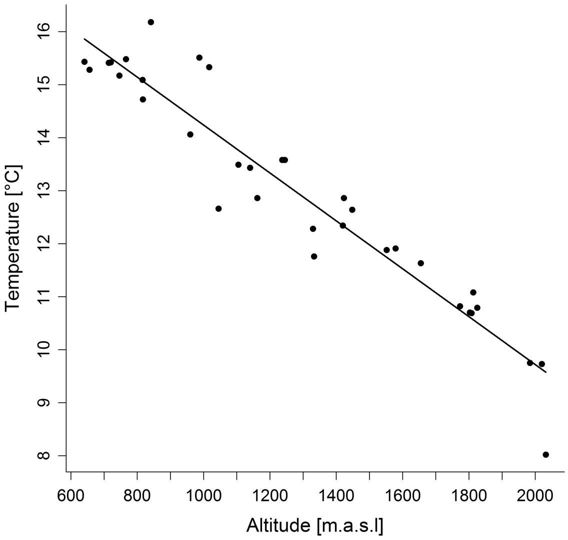

Fig. II.S1: Simple regression of altitude and temperature. $R^2 = 0.912$, $p < 0.001$. Temperature decreased by 0.45 °C per 100 m altitude.

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.

Statistical analysis

Statistical analyses were performed using the software R 2.11.1 for Windows (R Development 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 pseudo replication. 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.

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. (Table II.1, Fig. II.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. II.1). The model did not reveal interactions between management and

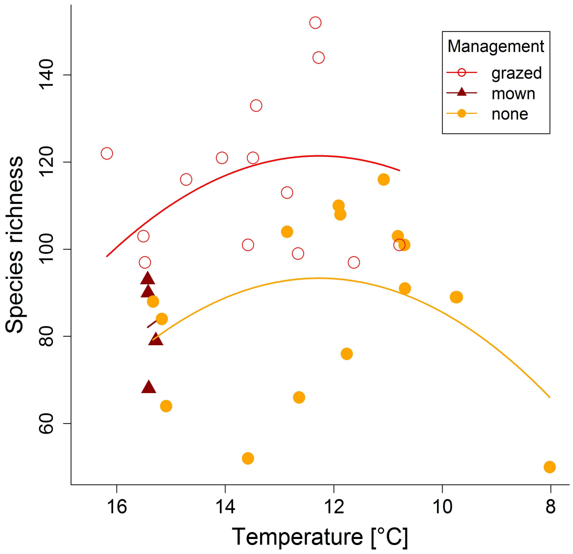

Fig. II.1: Temperature and management on 34 alpine grasslands in relation to species richness of vascular plants. Statistics see Table

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 II.S1).

Table II.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 none 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	*

Table II.S1: Results of a general linear model with species richness of vascular plants on non-managed sites as response variable and temperature and temperature² 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	2.22	0.045	*
Temperature²	-2.218	0.979	-2.266	0.041	*

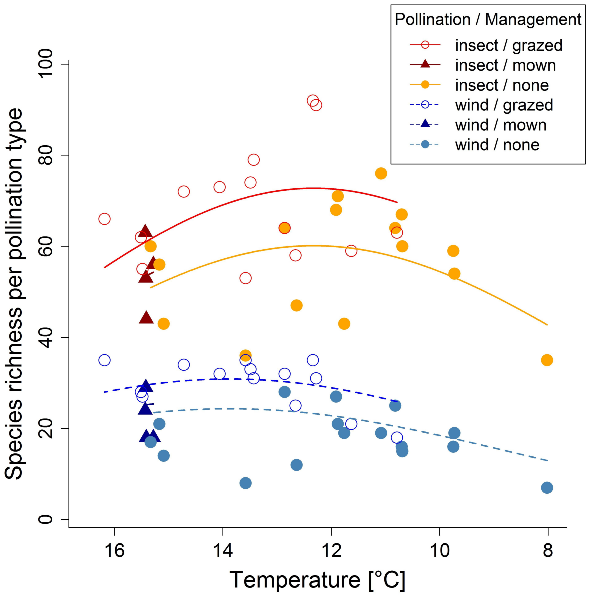

Fig. II.2: Effects of temperature and management on species richness of plants with different pollination types: insect- versus wind-pollinated species. Statistics see Table II.2.

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 II.2): the curve for wind-pollinated plants was more flat and had its maximum at higher temperatures than for insect-pollinated plants (Fig. II.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 II.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 II.2).

Table II.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	*

The proportion of species richness of insect-pollinated plants increased with decreasing temperature (Table II.3), while the opposing effect was true for the proportion of wind-pollinated plants which decreased with decreasing temperature (Fig. II.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 II.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 II.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. II.4).

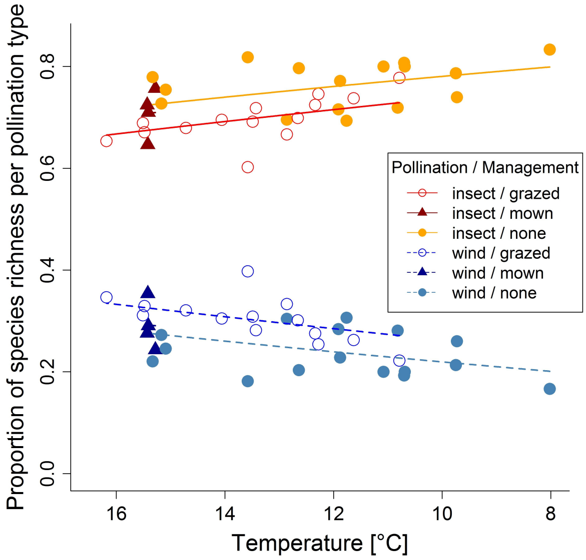

Fig. II.3: Effects of temperature and management on the proportion of species richness per pollination type (insect-pollination, wind-pollination). Statistics see Table II.3.

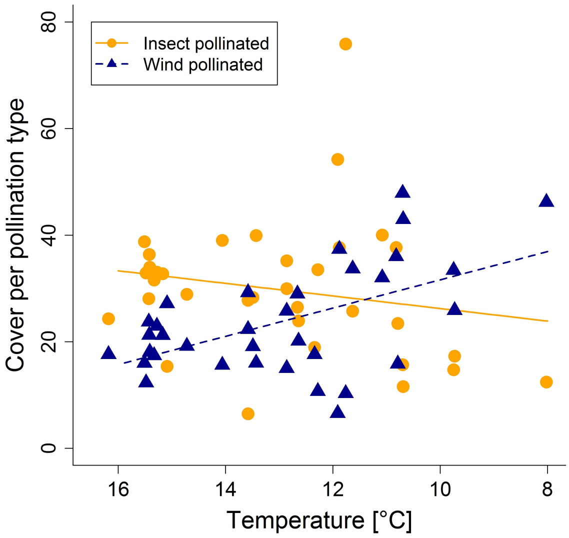

Fig. II.4: Temperature in relation to the cover of different pollination types: insect-pollination, wind-pollination. Statistics see Table II.4.

Table II.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	*

Table II.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	14.43	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 (Sanchez-Gonzalez and Lopez-Mata 2005, Bruun et al. 2006, Grytnes and 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 and 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 and 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 and 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 and 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 and 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 and 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 and 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 can not 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 and Barrett 2009, Hesse and 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.

III Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities.

This chapter has been published as: Hoiss, B., Krauss, J., Potts, S. G., Roberts, S. & Steffan-Dewenter, I. 2012 Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proceedings of the Royal Society B: Biological Sciences*. **279**, 4447–4456. (doi:10.1098/rspb.2012.1581)

Running title: Altitude determines community assembly

Abstract

Knowledge about the phylogeny and ecology of communities along environmental gradients helps to disentangle the role of competition-driven processes and environmental filtering for community assembly. In this study we evaluated patterns in species richness, phylogenetic structure and life history traits of bee communities along altitudinal gradients in the Alps, Germany. We found a linear decline in species richness and abundance but increasing phylogenetic clustering in communities with increasing altitude. The proportion of social and ground-nesting species, as well as mean body size and altitudinal range of bee communities, increased with increasing altitude whereas the mean geographic distribution decreased. Our results suggest that community assembly at high altitudes is dominated by environmental filtering effects, while the relative importance of competition increases at low altitudes. We conclude that inherent phylogenetic and ecological species attributes at high altitudes pose a threat for less competitive alpine specialists with ongoing climate change.

Keywords: altitudinal gradient, phylogeny, environmental filtering, life history traits, communities, assembly-rules, insects

Introduction

Understanding patterns of species richness and community structure, and their underlying drivers, along environmental gradients remains a key challenge in ecology. Knowledge of the phylogenetic clustering of species, the adaptive value of life history traits for species and communities, and the sensitivity of communities to environmental changes can allow predictions to be made of their responses to climate change. Altitudinal gradients can be used as model systems for climatic changes to analyse the role of environmental filtering effects on animal communities (Hodkinson 2005, Beck et al. 2010). To date, studies using altitudinal gradients have primarily focused on diversity patterns in tropical regions, while few studies have been conducted in temperate regions (Beck et al. 2010). The importance of traits along altitudinal gradients has been investigated within single taxa (Dingle and Mousseau 1994, Cronin 2001, Berner et al. 2004), but thorough documentation of changes in community structure, and associated adaptive traits and phylogenetic patterns, along climatic gradients are missing. To fill this gap studies are required which combine phylogenetic methods with the ecological analysis of species distribution patterns and functional traits to explain climate-driven differences in community structure.

Two commonly reported patterns in species richness along altitudinal gradients are: (i) a decline of species richness with altitude, and (ii) a unimodal distribution with a mid-elevation peak (Rahbek 2005). The reported patterns in species richness depend on the geographic region, climate zone and the taxa studied. Various hypotheses have been proposed to explain these diversity patterns (Rahbek 2005, Nogues-Bravo et al. 2008, Field et al. 2009, Hoiss et al. 2013). However, the causes for the diversity patterns, and the driving factors of community assembly, are poorly understood (Hodkinson 2005). The analysis of phylogenetic structure within and between communities, as well as the analysis of trait combinations, are useful approaches to explore the processes which affect the assembly and diversity of insect communities. Several recent studies have examined phylogenetic community structures using the statistical tools provided by Webb et al. (Webb et al. 2002). The assembly of communities is driven by niche-related processes, which are deterministic, or by neutral processes, which are stochastic (Götzenberger et al. 2012). Important factors for niche-related assembly rules are species characteristics and their adaptive values under environmental filtering and competition, while neutral community models predict that only dispersal limitations and not other species characteristics influence the community assembly (Jabot et al. 2008, Cavender-Bares et al. 2009). Phylogenetic clustering of closely related species can be interpreted in terms of niche-related processes (Webb et al. 2002, Machac et al. 2011): only a few lineages of closely related species with similar, conserved characteristics occur under given environmental filtering conditions (phylogenetic niche conservatism) (Webb et al. 2002, Vamosi et al. 2009). Conserved characteristics are passed from common ancestors to their descendants and are common in the descendants. Phylogenetic over-dispersion (i.e. phylogenetic relatedness is lower than expected from the null-model) is the opposing pattern, and can indicate that competition between species with similar conserved traits is the dominant process in community assembly (Webb et al. 2002, Machac et al. 2011). However, there are also many other processes proposed to influence phylogenetic community structure (Cavender-Bares et al. 2009). A subsequent analysis showing that particular life-history traits dominate in communities along altitudinal gradients would reveal the adaptive value of those traits under changing climatic conditions, and the importance of niche-related (abiotic and biotic) processes on community assembly. No patterns in the dominance of traits should be detectable if neutral processes are driving the assembly of communities or if the traits are of no adaptive value.

We use wild bees (Hymenoptera: Apoidea) as our study system, as they are important pollinators and so the composition of bee communities under changing climatic conditions is of high economic and ecological interest; to our knowledge there are no studies on the phylogenetic structure of bee communities along climatic gradients. In our study we employ the net relatedness index (NRI) (Webb et al. 2002) to investigate the phylogenetic structure, and driving ecological processes within wild bee communities along an altitudinal gradient, and the mean phylogenetic distances between communities at similar altitudes to investigate the phylogenetic turnover at a larger spatial scale.

The ability of insects to cope with different climatic conditions has been proposed to depend on several life-history traits (Petanidou et al. 1995, Hodkinson 2005, Dillon et al. 2006, Diamond et al. 2011, Purcell 2011). We analysed the importance of seven traits (sociality, parasitism, nesting behaviour, number of generations per year / voltinism, diet breadth / lecty, body size, and range size). Previous studies suggest that warmer lowlands, with low or no seasonality, promote a higher degree of sociality in arthropods (Purcell 2011). The number of generations per year (voltinism) depends on the generation time and on the length of the season, and is therefore expected to decline with altitude (Chown and Gaston 2010). Wild bees also include some cleptoparasites species (either brood or social parasites) which either lay their eggs in brood cells which the host has already provisioned, or let their brood be raised by workers of their social hosts. The strong seasonality at high altitudes is expected to increase the relative abundance of parasitic bees due to more closely synchronised phenology of hosts and parasites (Petanidou et al. 1995). The proportion of below-ground nesting species is predicted to increase with altitude as below-ground nests may be better protected from extreme climatic conditions than above-ground nests (e.g. stems, wood, walls, rocks, snail shells). An increasing niche breadth with altitude has been shown for some species (e.g. brown hares) in situations where less food was available (Rödel et al. 2004), and in more generalised plant-pollinator networks (Ramos-Jiliberto et al. 2010). Scarce food supply at higher altitudes may therefore lead to a higher proportion of polylectic species with a wider niche breadth. Patterns in body size along altitudinal gradients remain a controversial topic (Chown and Gaston 2010). However, in the majority of studies, lower temperatures and shorter seasons were associated with larger size of animals (Dillon et al. 2006, Chown and Gaston 2010). According to Janzen's hypothesis (Janzen 1967), the temperature variability as well as overlap of seasonal and daily temperature ranges is higher in temperate elevation gradients than in tropical gradients, and thus may lead to an adaptation of species in temperate regions to larger temperature fluctuations and occurrence across larger altitudinal ranges (McCain 2009). This prediction can be extended to daily fluctuations, which are higher at high elevations than at low elevations, so that species at high elevation communities are expected to have, on average, larger altitudinal ranges, but smaller geographic distributions, than species occurring at low altitudes (McCain 2009). We performed a species-based analysis to provide insights into the importance of the above traits for the occurrence of species, and an abundance-based analysis to provide information on the importance of traits for the dominance structure in communities.

Overall in this study, we provide a comprehensive analysis of the changes in bee communities along an environmental gradient. We analysed the community composition along an altitudinal gradient and underlying adaptive life-history traits determining community assembly in alpine grasslands. We developed and tested the following predictions:

1. Species richness shows a linear decrease, or a hump-shaped distribution, with increasing altitude.
2. The phylogenetic community structure is influenced by altitude.
3. The frequency of the occurrence of functional traits in a community is influenced by altitude.
4. Bee species in communities at higher altitudes show, on average, a larger altitudinal range

and a smaller geographical distribution than those at lower altitudes.

Materials and methods

Study sites

The study was carried out on grasslands in the National Park Berchtesgaden and its vicinity (47,10° N, 12,15° E). The National Park is located in the northern limestone Alps in the south-east of Germany. The region is characterised by calcareous rocks, coniferous forests and mountain pastures. Many mountain pastures were extensively managed for centuries but were abandoned within the last 150 years. The region lies in the transition zone of Atlantic and continental climate with up to 2,500 mm of precipitation per year.

We selected 34 study sites (60 x 60 m) on grasslands from 600 m.a.s.l. to 2,000 m.a.s.l. in the western part of the National Park Berchtesgaden. Eighteen of the selected grasslands were extensively managed and 16 grasslands were not managed. The study sites were established along the slopes of two mountains and along two gently inclining valleys and their terminal mountains. Criteria for the selection of the study sites were: (i) the grasslands represent a more or less continuous altitudinal gradient; (ii) the grasslands were extensively managed (one cut per year on meadows, extensive grazing on pastures) or unmanaged; (iii) the grasslands were not fertilized; (iv) permission from the farmers and owners.

Data collection

Wild bees and honey bees were recorded in transect walks from 8 May to 10 September 2009. Sites at lower altitudes were sampled six times and sites at altitudes greater than 1,200 m a.s.l. were sampled five times due to the shorter snow free season. This different number of transect walks did not affect species detectability and calculated saturation (see statistical analysis). The surveys were conducted from 09:30 to 18:00 h on days when the weather was sunny or when temperature at 650 m a.s.l. was above 17° C on cloudy days. The time for a transect within every study site was 50 mins. We focused on a 2 m corridor and caught bees in 10 subtransects of about 25 m length where time was set at 5 mins each. Insects were identified to species level in the laboratory. We avoided collecting *Bombus* queens and instead noted the exact colour code on thorax and abdomen for later determination. Bee species identification followed Scheuchl (2000) for *Anthophoridae*; Scheuchl (2006) for *Megachilidae* and *Melittidae*; Schmid-Egger & Scheuchl (1997) for Andrenidae; Mauss (1996) for *Bombus*; Amiet et al. (2001) for *Lasioglossum* and *Halictus*; Amiet et al. (2001) for *Dufourea*, *Hylaeus* and *Sphecodes*. The taxonomy followed Michener (2007).

The species were assigned to one of two categories of five life-history traits or were considered as undefined when no information was available or when the species took up an intermediate or bimodal trait value. We considered the following trait values: social vs. solitary (including communal), parasitic vs. non-parasitic, below-ground (endogaic) vs. above-ground (epigaic) nesting, polylectic vs. oligolectic (use of more than one plant family vs. only one family or genus as pollen source), univoltine vs. multivoltine (including bivoltine). A sixth trait was the inter-tegular distance (ITD) which is used as an estimator for body size and body mass (Cane 1987). For social bees, we used the ITD of queens as the fitness of a colony is highly dependent on the performance of the nest founding queens (Bommarco et al. 2010). Sources for trait information were the European pollinator database resulting from the ALARM and STEP projects, Westrich (1989), Gogala (1999), Amiet et al. (2001) and ITD measurements made by the authors according to Cane (1987).

For the analysis of the geographical distribution of bee communities we extracted occurrence data of each species in our dataset in Bavaria from the website www.aculeata.eu (Prosi-CAD 2011). We noted the number of quadrants (ordnance maps) in which the species were recorded at least once during the last two centuries. We only used the data for Bavaria, as data quality varies among German federal states and therefore is difficult to compare.

To be able to correct for the effect of flower cover we estimated the cover of all flowering plant species as a percentage of the total area (60 x 60 m) of the study site after each of the transect walks. For statistical analysis we used the mean value of the flower cover over all transect walks per site.

Statistical analysis

The statistical analyses were performed using the software R 2.11 for Windows (R Development Core Team 2012).

To test for correlations between the predictors altitude, flower cover and the categorical predictor management Spearman's *rho* statistic was used. *Rho* was smaller than 0.5 in all combinations implying that there was no strong covariance of the predictors.

Species accumulation curves and species richness estimators were calculated using the *spp.est* function of the R package *fossil*. The ten sub-transects per survey were used as replicates to calculate species richness estimators. To avoid phenology effects the data from the five or six surveys in 2009 were pooled. The proportion of detected species was estimated by dividing the recorded species richness per site by the estimator Jacknife1. The values for the estimated rate of detected species ranged between 58 and 83 % for the Jack1 estimator. The detection rates were not correlated with the number of surveys, altitude, management or flower cover. Due to the relatively high detection rates we used the species richness and not the calculated estimators for our analysis. As the different number of surveys on higher (five surveys) and lower altitudes (six surveys) did not affect the detection rate (t-test: five surveys mean: 70.2 %; six surveys mean: 70.7 %; $p = 0.801$) we used data from all the surveys.

General linear models were fitted with total species richness and total abundance of bees per site as response variables. The full model (type 3 sum of squares) was fitted with altitude, the quadratic term of altitude (to test for a hump-shaped distribution), management and flower cover as predictors. For model simplification likelihood ratio tests were performed and non significant terms were removed from the model (Crawley 2007). Flower-cover was not significant in the species-richness analysis and the quadratic term of altitude could be removed from both models. Flower cover at the site T1 was detected as a highly influential outlier. This site was removed from the species richness and abundance analysis. The model residuals were sufficiently normally distributed and showed variance homogeneity. Moran's I was calculated for the model residuals of species richness. The minimum distance between a pair of sites was 0.33 km, the maximum distance was 12.26 km. We calculated Moran's I for 1 km distance-classes up to 5 km and a global Moran's I using the multiplicative inverted distances as weights. No significant spatial autocorrelation of species richness could be detected at distance classes up to 5 km or in the global Moran's I.

For the phylogenetic analysis a polytomous, ultrametric tree was compiled based on the taxonomy of bees. Branch lengths were calculated and adjusted with the ϱ parameter set to 1 (Grafen 1989) using the R package *ape*. As an estimator for the phylogenetic relatedness of species within sites we calculated the standardized (by the standard deviation of phylogenetic distances in the null communities) net relatedness index (NRI) (Webb et al. 2002, 2008). As the null model for the NRI we calculated for each site the mean and standard deviation of the phylogenetic distances expected for the number of taxa found on the site, based on a random selection of species from the regional species pool found in our study (500 iterations per site). We also calculated the null model by weighting the sampling probability of the taxa by their abundance in the regional species pool. Patterns were almost identical to the patterns in the unweighted estimates presented in the result section. A regression with altitude as predictor and the NRIs of the sites as response variable was performed to assess the influence of environmental conditions on the phylogenetic clustering of bees. Positive NRI values indicate phylogenetic clustering, while negative values indicate phylogenetic over-dispersion. To study the effect of environmental conditions on the phylogenetic structures at a larger spatial scale we calculated the mean phylogenetic distances between sites. For all possible site combinations we estimated the mean of the matrix of pairwise phylogenetic distances between all possible pairwise species combinations with species from the first site as rows and species from the second site as columns in the matrices. We performed an ANOVA using the average of the mean phylogenetic distances (MPD) between site pairs at low ($n = 11$), medium ($n = 11$) and high ($n = 12$) altitudes as response ($n = 34$) with altitudinal categories as the grouping factor. We only used the MPDs between sites in the same altitudinal category (low (l): < 1000 m.a.s.l. , intermediate (m): 1000 – 1500 m.a.s.l., high (h): > 1500 m.a.s.l.).

We used regression analyses to test for shifts in the dominance of traits in bee communities with altitude. Relative frequencies of trait categories per site were used as response variables. For each trait two response variables were estimated: the proportion of species per trait category and the proportion of individuals per trait category (abundance weighted frequencies of traits). Regressions were performed with the proportions of social, parasitic, ground-nesting, multivoltine, oligolectic species and individuals per site as response variables. For the continuous estimator of body size, ITD, we used the mean value of all species or individuals per site. Altitude was the only predictor variable.

Interpolated altitudinal ranges per species were calculated from the altitudinal difference between the highest and lowest occurrence for all species in our dataset (McCain 2009). This approach assumes that species were potentially present between their highest and lowest occurrence. Mean altitudinal ranges per site were calculated based on the altitudinal ranges of the species and were also additionally calculated as individual based mean (abundance weighted mean). Mean geographic distributions of the species and individuals per site were calculated from the occurrence data of Bavaria (see data collection subsection). From this data we performed regressions with mean altitudinal ranges and mean geographic distribution per site as response variables and altitude as predictor.

Results

Species richness

In total we collected 2,328 bees from 87 species (22 genera) with a minimum of six species and a maximum of 24 species per site. Nineteen species belonged to the genus *Bombus*. Seven species were only found above 1,500 m.a.s.l. (*Andrena lapponica*, *Bombus gerstaeckeri*, *Bombus mendax*, *Bombus pyrenaeus*, *Bombus sichelii*, *Dufourea alpina*, *Lasioglossum* *bavaricum*) whereas 34 species were found only below 1000 m.a.s.l. Species richness of bees along an altitudinal gradient was predicted by altitude in the minimal adequate model (Fig III.1a). Management and flower cover showed no significant influence on the number of bee species (Table III.1). The abundance of bees was predicted by flower cover and altitude (Table III.1, Fig III.1b). Both, species richness and abundance showed a linear decline with increasing altitude. Abundance also linearly declined with decreasing flower cover.

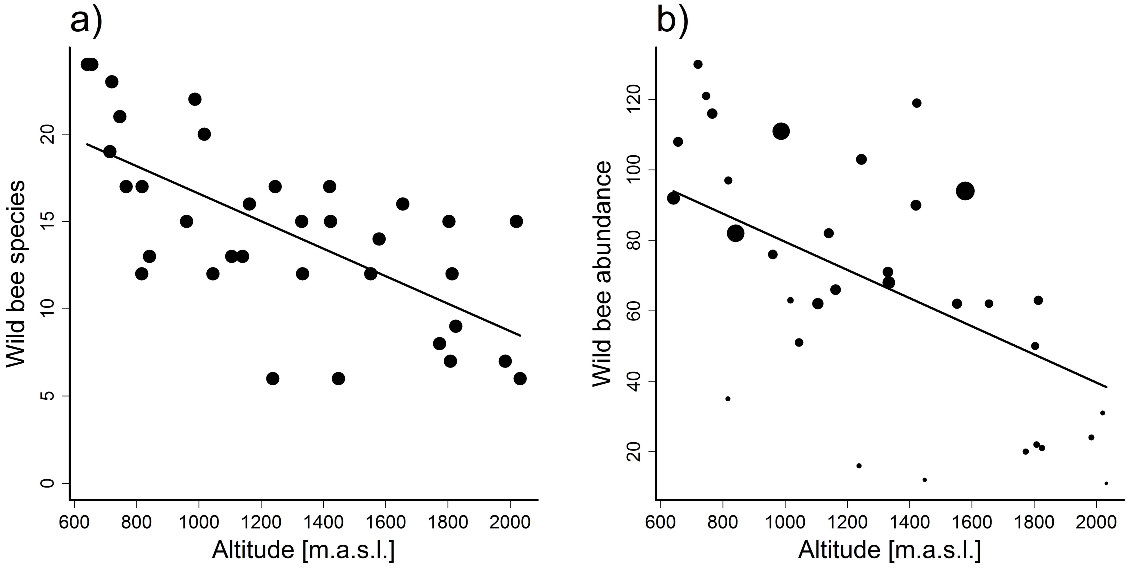

Fig. III.1: Altitude predicts a) species richness of wild bees and b) abundance of wild bees. Point size in the abundance plot is weighted by flower cover (min: 0.41%, max: 10.44%) which is also a good predictor for the abundance of wild bees. Regression lines are drawn from the minimal adequate model estimates. Statistics see Table III.1.

Table III.1: ANOVA table with Type III sum of squares of general linear models with species richness and abundance of bees as response variables. Explanatory variables are flower cover, management (two levels: extensively managed, no management) and altitude.

Response	Predictor	D.f.	F	P
Species richness	Management	1, 29	0.77	0.388
	Flower cover	1, 29	2.26	0.143
	Altitude	1, 29	11.25	0.002
Abundance	Management	1, 29	2.51	0.124
	Flower cover	1, 29	10.79	0.003
	Altitude	1, 29	9.76	0.004

Phylogeny

The net relatedness index (NRI) as an indicator for the phylogenetic community structure increased significantly with altitude (Fig. III.2a) (F1, 32 = 10.63 P = 0.003). This implies that species in communities at higher altitudes are on average more closely related than species in communities at low altitudes. The same pattern was found in an ANOVA at a larger spatial scale where altitude predicted the site-based average of the mean phylogenetic differences (MPD) between sites (F2, 31 = 93.04, P < 0.001)(Fig. III.2b). MPDs between sites at high altitudes were smaller than at intermediate altitudes (*P* < 0.001) and the MPDs between sites at intermediate altitudes were significantly smaller than at low altitudes (*P* < 0.001). Thus species were more closely related at high altitudes, not only within sites, but also between sites than at low altitudes. This suggests, that the phylogenetic turnover at high altitudes is lower than in lowlands.

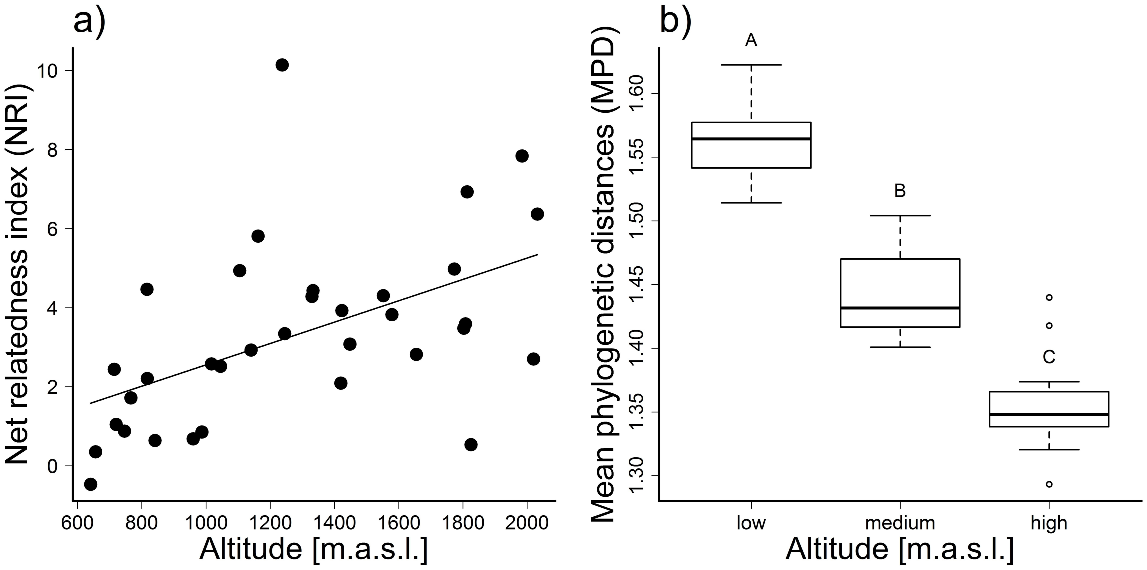

Fig. III.2: Effect of altitude on a) the phylogenetic relatedness of wild bee species within sites (NRI): D.f.= 1, 32, F = 10.63, P = 0.003, y = -0.030+2.62e-3*altitude; and b) the mean phylogenetic distances of wild bees between sites (MPD): D.f. = 2, 31, F = 93.04, P < 0.001. The altitudinal categories are: low (<1,000 m.a.s.l.), medium (1,000 – 1499 m.a.s.l.), high (> 1,500 m.a.s.l.).

Life history Traits

Our analysis revealed significant changes in the relative frequency of life history traits in wild bee communities along an altitudinal gradient (Table III.2). The proportion of social species and individuals as well as the proportion of ground-nesting species and individuals increased significantly with altitude (Fig. III.3a, c). The individual- and species-based means of the inter-tegular distance (ITD) as a proxy for body-size also increased significantly with altitude (Fig. III.3f). In our study altitude did not affect the relative frequency of parasitism, voltinism and lecty in the communities (Fig. III.3b, d, e, Table III.2). To explore how much of the pattern is due to the dominant social bee genus Bombus we also provide the results of the analysis after removing the 19 Bombus species (see Table III.S1 and Fig. III.S1; no significant correlations with altitude except for the rates of sociality and parasitism).

Communities at high elevations consisted mainly of species with a large mean altitudinal range, whereas species in communities at low altitudes showed significantly smaller altitudinal ranges (Fig. III.4a, Table III.2). No significant effect was found on the abundance weighted analysis. The consistently large mean altitudinal ranges in this analysis imply that the communities along the complete altitudinal gradient were dominated by individuals of species with a large altitudinal range. Species with smaller ranges contributed only a few individuals to the communities (Fig. III.4a). Both the species- and the individual-based means of the geographic distribution decreased with the altitude at which the wild bee communities were investigated (Fig. III.4b).

Table III.2: F-statistics and estimates of simple regressions on the effects of altitude [m.a.s.l.] on the proportions of social species, nonparasitic species, ground-nesting species, multivoltine species, oligolectic species and on the mean inter-tegula distance (ITD), altitudinal range and geographical distribution of wild bee communities in 34 sites. The calculations were performed for species based proportions / means of traits and abundance weighted proportions / means of traits. Degrees of freedom = 1, 32 in all cases.

Response species weighted	*F*	*P*	Estimates
Proportion of social species	40.71	< 0.001	y = 37.55+0.03*altitude
Proportion of nonparasitic species	0.80	0.377	n.s.
Proportion of ground-nesting species	6.06	0.019	y = 62.56+9.84e-3*altitude
Proportion of multivoltine species	2.08	0.159	n.s.
Proportion of oligolectic species	2.05	0.162	n.s.
Mean inter-tegula distance (mm)	46.07	< 0.001	y = 2.36+9.26e-4*altitude
Mean altitudinal range (m)	17.07	< 0.001	y = 696.65+0.26*altitude
Mean geographical distribution	8.27	0.01	y = 233.33-0.03*altitude
Response abundance weighted	*F*	*P*	Estimates
Proportion of social species	21.52	< 0.001	y = 67.64+0.02*altitude
Proportion of nonparasitic species	0.27	0.609	n.s.
Proportion of ground-nesting species	10.93	0.002	y = 59.62+0.01*altitude
Proportion of multivoltine species	2.47	0.126	n.s.
Proportion of oligolectic species	0.46	0.501	n.s.
Mean inter-tegula distance (mm)	16.74	< 0.001	y = 2.90+9.03e-4*altitude
Mean altitudinal range (m)	1.85	0.184	n.s.
Mean geographical distribution	9.13	0.005	y = 319.44-0.05*altitude

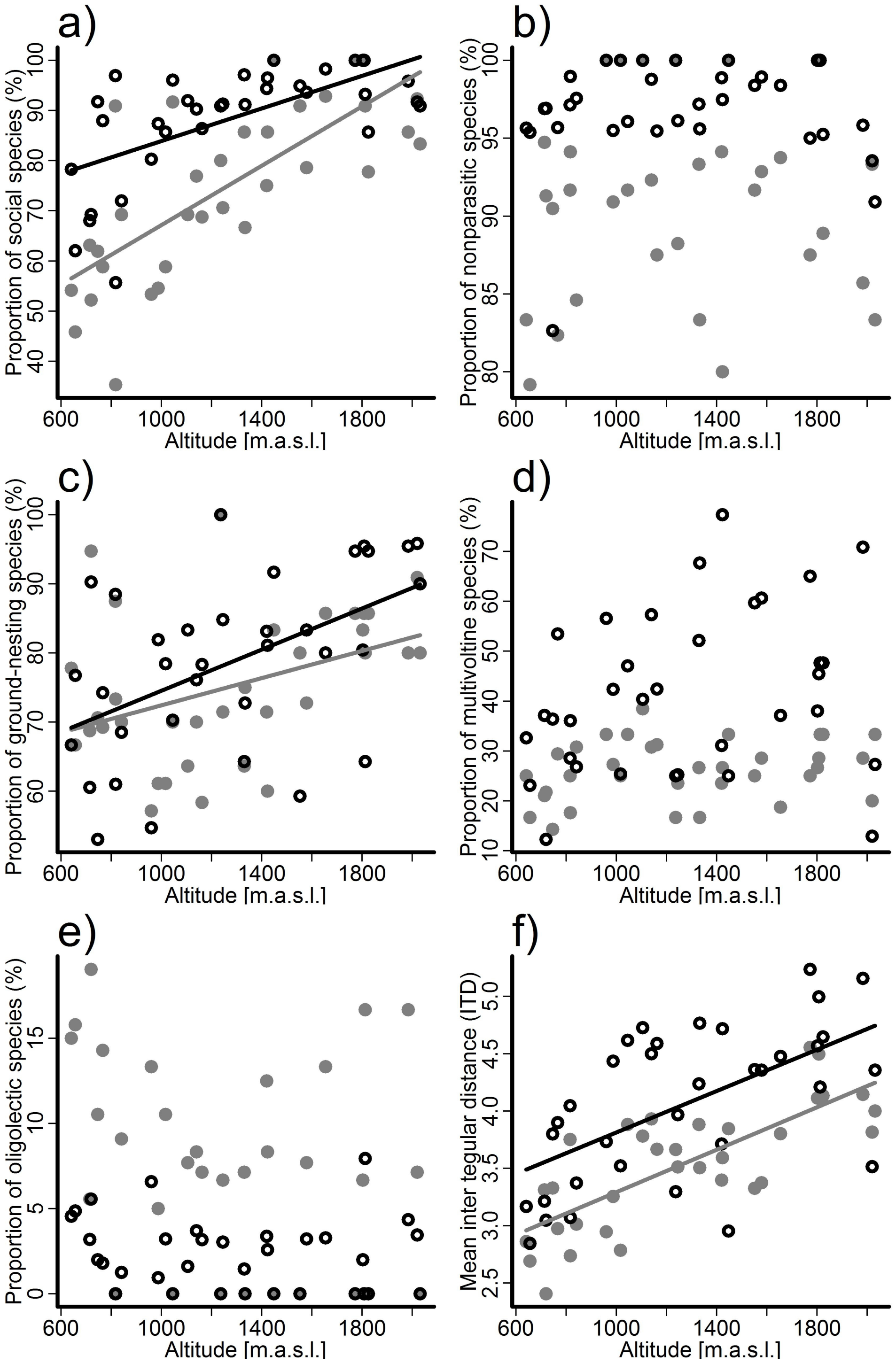

Fig. III.3: Effects of altitude [m.a.s.l.] on the proportion (%) of five categorical life-history traits and on the mean inter-tegular distance (ITD) in wild bee communities on 34 sites. Black circles and lines represent abundance weighted proportions / means of traits, while grey solid points and lines represent species based proportions / means of traits. Lines are presented if simple regressions were significant ($P < 0.05$). The trait categories were: sociality (social vs. solitary), parasitism (non-parasitic vs. parasitic), nesting behaviour (below-ground vs. above-ground nesting), voltinism (multivoltine vs. univoltine) and lecty (oligolectic vs. polylectic).

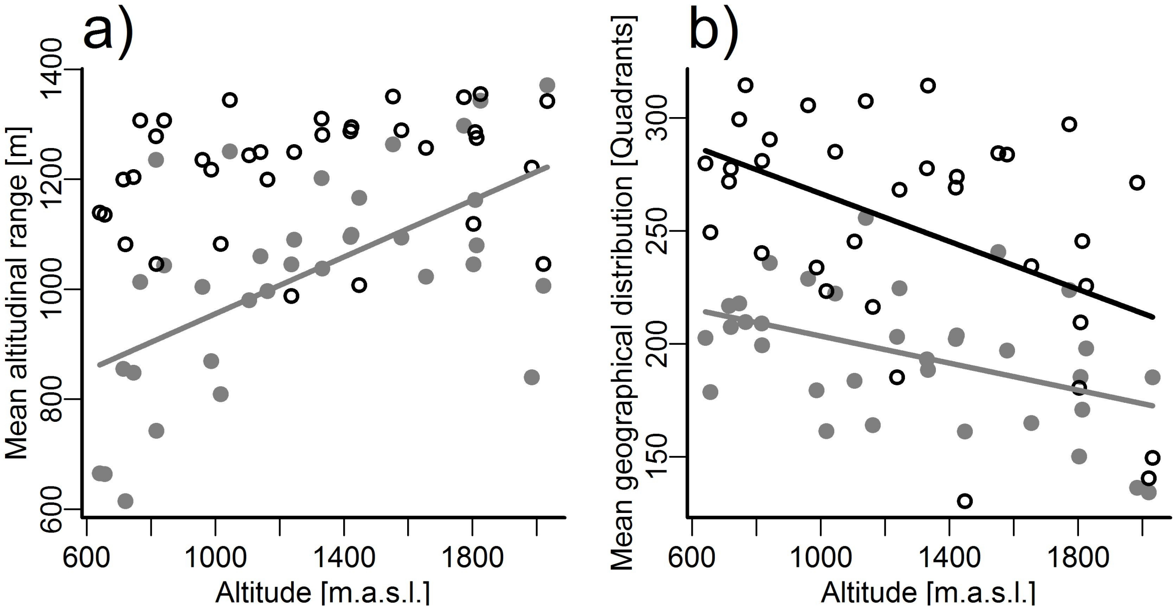

Fig. III.4: Effect of altitude on a) the mean altitudinal range [m] and b) the mean geographical distribution [number of quadrants (10x10 km) at which species were found in Bavaria] of wild bee communities. Black circles and lines represent abundance weighted means, while grey solid points and lines represent species based means. Lines are presented if simple regressions were significant ($P < 0.05$).

Discussion

Species richness

Our results show that altitude strongly influences the diversity, phylogeny and ecology of wild bee communities. Species richness and abundance linearly decreased with increasing altitude and did not show a hump-shaped distribution. Higher flower-cover was correlated with an increase in bee abundance and was probably the result of flowers attracting more foraging individuals, but this did not affect the species richness of wild bees. Nevertheless, the decreasing abundance with increasing altitude, after correcting for flower-cover, suggests decreasing competition for floral resources with altitude. Therefore abiotic mechanisms are most likely to be the cause of the observed decrease in diversity of bees at high altitudes. A linearly decreasing diversity with increasing altitude is consistent with temperature limitation predictions (Clarke and Gaston 2006, McCain 2007) and/or the metabolic theory of ecology (Sanders et al. 2007) which both predict a linear decline of diversity with decreasing temperatures. The same pattern is also expected from species-area effects (Jones et al. 2003), but their general validity on altitudinal gradients remains unclear (Beck and Chey 2008). Other hypotheses, like the mid-domain effect (Colwell and Lees 2000), or the source-sink (mass) effects (Grytnes et al. 2008), predict a unimodal distribution of species richness, but do not seem to influence the diversity pattern of bees significantly in this study. However, not only species richness of communities, but also their composition, changes along the altitudinal gradient and is driven by evolutionary history and ecological processes.

Phylogeny

The influence of evolutionary history and ecological processes on community assembly can be assessed by analysing the phylogenetic structures of communities. In our study, the phylogenetic relatedness within and between communities at high altitudes was on average higher than at low altitudes. The observed increase in the phylogenetic relatedness with altitude indicates that the assembly of communities at high altitudes is determined by environmental filtering processes where related species with adaptive characteristics, supposedly to low temperatures and strong seasonality, are filtered. We interpret the lower phylogenetic relatedness in lowland communities as evidence that the environmental filtering effect of abiotic factors is replaced here by an increased competition between species with similar traits. Under favourable climatic conditions communities can even exhibit an over-dispersed phylogenetic structure and interspecific competition becomes the driving factor for the structure of communities (Machac et al. 2011). Our finding that the phylogenetic turnover was higher between communities from low altitudes than between communities from high altitudes confirms these patterns also on larger spatial scales. Our results are in line with patterns found in tropical hummingbird communities in the Andes (Graham et al. 2009) and ant communities in temperate altitudinal gradients in the USA and in Austria (Machac et al. 2011) which were phylogenetically clustered at higher altitudes. However, for plants, an increasing phylogenetic over-dispersion with increasing altitude has been shown, while bacterial communities were phylogenetically clustered at all altitudes in the Colorado Rocky Mountains (Bryant et al. 2008). The contrasting results reported in these studies suggest that different taxa have different thresholds at which abiotic factors have a filtering effect (Machac et al. 2011). However, the clustering of closely related species in communities at high altitudes, as found in our study, indicates that niche-related assembly rules and abiotic habitat constraints play a key role in community assembly (Graham et al. 2009, Machac et al. 2011). To determine the probable causes of the observed phylogenetic structure in the communities, we examined patterns in community ecology and assessed changes in ecologically relevant species characteristics (traits) along the altitudinal gradient.

Life history Traits

The species characteristics of sociality, nesting behaviour, body size, altitudinal range and geographic distribution changed in bee communities as a response to changing environmental filtering and other niche-based processes at different altitudes, and are therefore possible drivers for the observed changes in species richness, community composition and phylogenetic structures. Altitude did not significantly affect traits associated with parasitism, lecty and voltinism which implies, that these characteristics are of little or no adaptive value under changing altitudinal (climatic) conditions. In the literature, a higher degree of sociality is generally expected in warmer regions with low seasonality due to more overlapping generations, which is a prerequisite for sociality (Purcell 2011). However, a higher proportion of social species in cold regions, as shown in our results, can be potentially explained by a risk spreading strategy: (i) if a generation, of animals dies due to bad weather-conditions this can be compensated for in social species through the next overlapping generation whereas the whole brood of solitary animals might be lost; (ii) if the nest-founding queen dies there is a good chance that at least some workers may survive and raise the brood started by the queen, or even produce new (male) brood (Gadagkar 1990); (iii) if a gyne (mated female) in sub-social species dies the brood can still be raised and protected by other females sharing the same nest (Jones and Riechert 2008). The fact that we showed an increasing proportion of sociality with altitude in the analysis without the social genus, *Bombus*, (see Appendix S1, S2), confirms the adaptive value of sociality in cold environments. However, there is a need for phylogenetically independent data from other geographical regions with additional taxa to reveal more general patterns of sociality along climatic gradients (Purcell 2011).

Our results showed an increase of the mean body size with increasing altitude. Other studies on body size along altitudinal gradients at the community level have found declines, inclines or no trends (Chown and Gaston 2010). A larger body size at higher altitudes can be explained by the hypothesis that a greater size provides an enhanced tolerance against starvation or desiccation (Chown and Gaston 1999). Another explanation for the detected pattern can be that larger animals have a higher energy efficiency (Ellington 1999) which is an advantage in environments where low temperatures, bad weather periods and starvation can be a problem. Probably the main advantage for bees is that larger species can more effectively thermoregulate and fly at lower temperatures, therefore enhancing their foraging ability. We assume that body size, thermoregulation or dispersal ability are traits with adaptive value. However, we cannot disentangle in our study the adaptive value of body size from the possible phylogenetic signal of the genus *Bombus*, as this genus combines the traits of sociality, active thermoregulation and large body size and dominates bee communities at high altitudes in our study. Studying dominant traits along altitudinal gradients in regions where *Bombus* does not occur might help to further disentangle the adaptive values of sociality and body size.

We found an increasing proportion of ground-nesting species with increasing altitude. To our knowledge there are no other studies about the effects of altitude on the nesting behaviour of insects. However, better protection against extreme climatic conditions of below-ground nests on the one hand, and a decline of available above-ground nesting sites (such as shrubs) at higher altitudes on the other hand, are plausible explanations for our findings.

We found a larger mean altitudinal range in species in upland communities, but no significant patterns in the abundance-based analysis. Additionally, we show that the mean geographical distribution was smaller in upland communities than in lowland communities in both the species- and the abundance-based analysis. This is consistent with results from studies on the altitudinal ranges of vertebrates (McCain 2009), which can be explained by an adaptation of Janzen's hypothesis (Janzen 1967), also called Rapoport's rule: species living at high altitudes have broader environmental tolerances and therefore larger altitudinal ranges due to larger seasonal fluctuations (McCain 2009). The fact that abundance weighted altitudinal ranges of communities were constantly high across the altitudinal gradient raises the issue of whether highly abundant, generalist species with large altitudinal and geographical ranges dominate at all altitudes. However, our results show that bee species in communities at high altitudes, even though they have on average a wider environmental range, were restricted in their distribution to mountainous areas in Bavaria, and were less abundant. This suggests that high altitudinal communities consisted of a few widespread generalists, which are dominant at low, but not at high altitudes (such as *B. jonellus*, *Bombus terrestris, Lasioglossum calceatum*), and of less competitive, alpine specialists with large altitudinal ranges but small geographical distributions (such as *B. mendax, B. monticola, B. mucidus, B. wurfleinii, L. fratellum, L. alpigenum*). In contrast, communities at low altitudes consisted of many less abundant species with small altitudinal ranges but were dominated by abundant generalists with large altitudinal ranges and geographical distribution.

Conclusions

Our combined phylogenetic and ecological analyses show that competition driven processes in community assembly are more important at low altitudes than at high altitudes where environmental filtering processes are more important in determining the assembly and phylogenetic structure of communities. The critical characteristics needed for survival under adverse and fluctuating environmental conditions seem to have evolved in a few phylogenetic lineages (e.g. *Bombus* and *Lasioglossum*), and at the expense of competitive strength in most of the bee species in alpine communities. Therefore less competitive alpine species are restricted in their geographic distribution. With warmer climates, the importance of environmental filtering processes is reduced and competition driven processes can be assumed to increase in their importance. This could lead to a threat for alpine specialists with high environmental tolerance but low competitive capacities.

Supplement

Table III.S1: F-statistics and estimates of simple regressions on the effects of altitude [m.a.s.l.] on the proportions (%) of social species, nonparasitic species, ground-nesting species, multivoltine species, oligolectic species and on the mean inter-tegula distance (ITD) of wild bee communities in 34 sites. The genus Bombus was excluded from the analysis. The calculations were performed for species based proportions / means of traits and abundance weighted proportions / means of traits.

Response species weighted	*Df*	*F*	*P*	Estimates
Proportion of social species	1, 31	7.07	0.012	y= 18.07 + 0.024 *altitude
Proportion of nonparasitic species	1, 32	4.70	0.038	y= 90.76 + 0.005 *altitude
Proportion of ground-nesting species	1, 32	0.00	0.406	n.s.
Proportion of multivoltine species	1, 32	0.58	0.454	n.s.
Proportion of oligolectic species	1, 32	0.00	0.607	n.s.
Mean inter-tegula distance (mm)	1, 32	0.00	0.000	n.s.
Response abundance weighted	***Df***	***F***	***P***	**Estimates**
Proportion of social species	1, 31	0.54	0.466	n.s.
Proportion of nonparasitic species	1, 32	5.68	0.023	y= 97.03 + 0.002 *altitude
Proportion of ground-nesting species	1, 32	0.00	0.000	n.s.
Proportion of multivoltine species	1, 32	1.20	0.000	n.s.
Proportion of oligolectic species	1, 32	0.00	0.107	n.s.
Mean inter-tegula distance (mm)	1, 32	1.18	0.000	n.s.

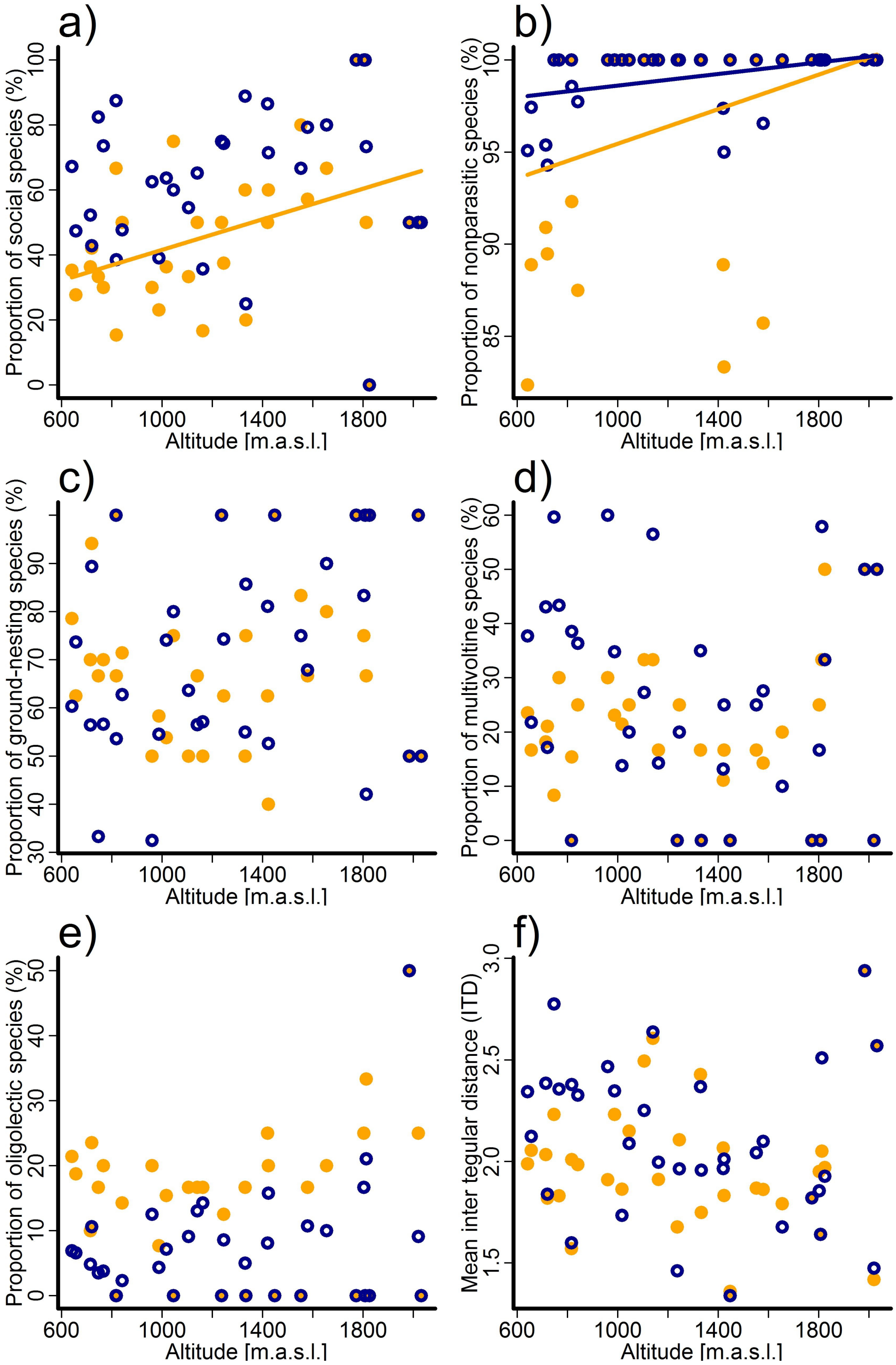

Fig. III.S1: Effects of altitude [m.a.s.l.] on the proportion (%) of five categorical life-history traits and on the mean inter-tegular distance (ITD) in wild bee communities on 34 sites excluding the genus Bombus. Blue circles and lines represent abundance weighted proportions / means of traits, while yellow solid points and lines represent species based proportions / means of traits. Lines are presented if simple regressions were significant ($P < 0.05$). The trait categories were: sociality (social vs. solitary), parasitism (non parasitic vs. parasitic), nesting behaviour (below-ground vs. above-ground nesting), voltinism (multivoltine vs. univoltine) and lecty (oligolectic vs. polylectic).

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

This chapter has been published as: Cornelius, C., Leingärtner, A., Hoiss, B., Krauss, J., Steffan-Dewenter, I. & Menzel, A. 2012 Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient. *Journal of Experimental Botany* **64**, 241–251. (doi:10.1093/jxb/ers321)

Running title: Grassland phenology after manipulative experiments

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.

Keywords: 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 (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 and Miglietta 1994, Theurillat and Guisan 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 (Price and Waser 1998, Blionis and Vokou 2001, Keller and 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 (Schwartz 2000, Sparks et al. 2000, Abu-Asab et al. 2001, Fitter and Fitter 2002, Menzel et al. 2005, 2006) or have been confirmed by experimental studies (Marion et al. 1997, Hollister and Webber 2001, Kudernatsch et al. 2008, De Frenne et al. 2009). 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 and 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 and 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 and 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 (Price and Waser 1998, Inouye et al. 2003, Dunne et al. 2003, Wipf et al. 2009, Wipf 2009, Lambert et al. 2010, Chen et al. 2011b). However, phenological responses are highly species-specific and differ between functional groups (Wipf and Rixen 2010). An advanced snowmelt could potentially increase plant fitness by prolonging the growth period and hence resource allocation (Galen and Stanton 1995, 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 (Inouye 2008). In the Australian Alps, for example, the timing of snowmelt only slightly affected the timing of flowering for tested species (Venn and 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 (Peñuelas et al. 2004, Llorens and Penuelas 2005, Prieto et al. 2008, de Dios 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 and Beierkuhnlein 2008). 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 (Biologische Bundesanstalt, Bundessortenamt and Chemical 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 (Ordinal Logistic Regression) 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 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. (Tab. 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/m2 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.

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. IV.1, IV.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. IV.1, IV.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. IV.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. IV.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. IV.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. IV.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).

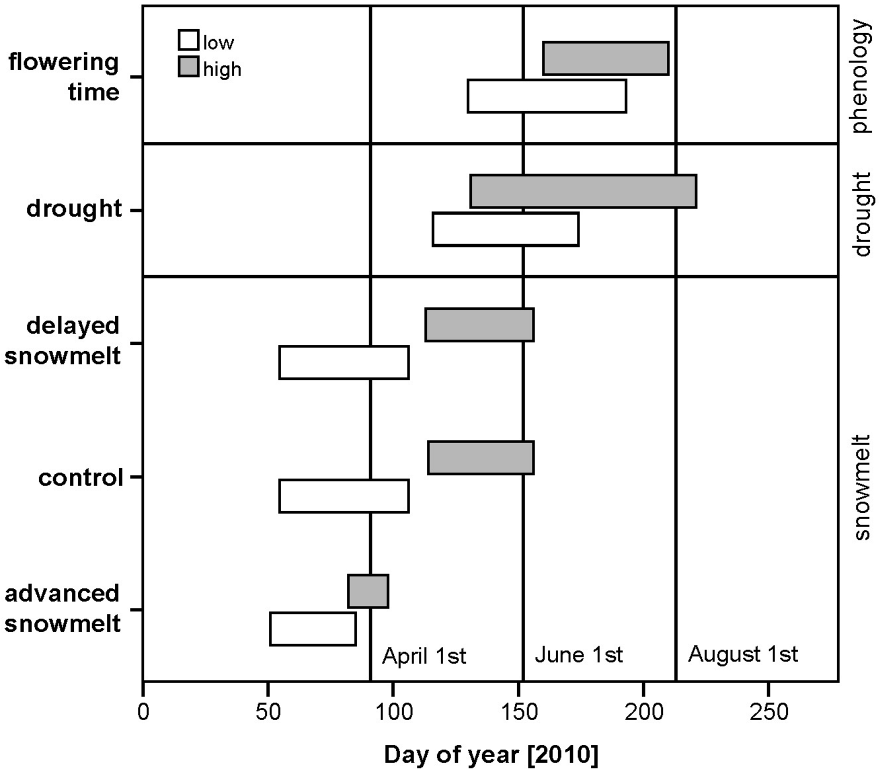

Fig. IV.1: Range in the date of snowmelt (advanced snowmelt, control, delayed snowmelt), duration of drought treatment and flowering time of all species over the lower (600 m to 1300 m) and the higher (1300 m to 2000 m) altitudinal gradient in 2010.

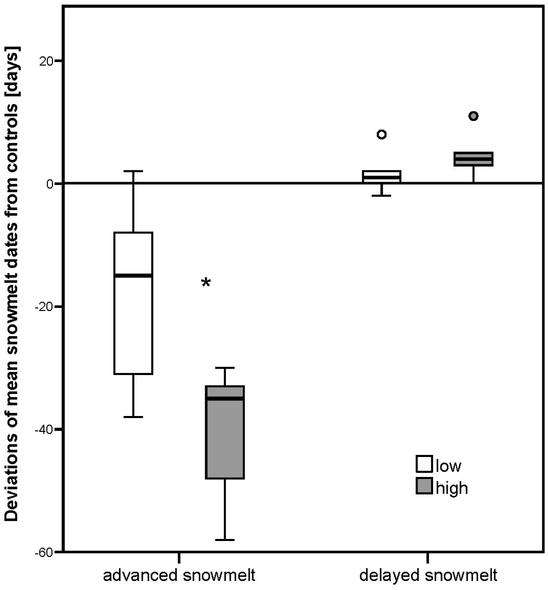

Fig. IV.2: Deviations from controls of mean snowmelt dates on advanced and delayed snowmelt plots, derived from each altitudinal site singly and then separated by low (600 m to 1300 m) and high altitudes (1300 m to 2000 m). Asterisk indicates significant differences in snow melting date between lower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

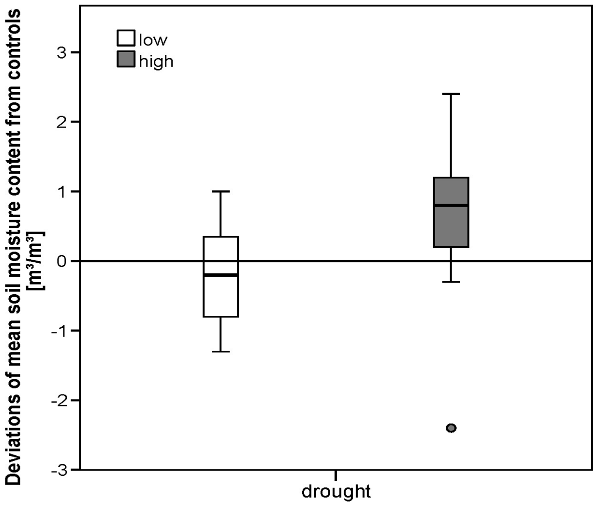

Fig. IV.3: Deviations of soil moisture content on drought plots from controls, derived from each altitudinal site singly and then separated by low (600 m to 1300 m) and high sites (1300 m to 2000 m).

Phenological shifts due to altitude

Linear regression models mostly showed significant responses of flowering phenology to altitude (Tab. IV.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, R2= 0.593).

Table IV.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.

	f	N	R2	P	regression coefficients [days/100m](±SE)	altitudinal ranges [low-high] (m)
Alchemilla vulgaris L.	BF	4	0.12	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 Vill.	BF	3	0.776	0.314	5.2 (± 2.8)	273 [1552-1825]
(Campanulaceae)	FF	5	0.535	0.160	1.4 (± 0.8)	865 [960-1825]
	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 (L.) Raeusch	BF	4	0.917	**0.043**	3.6 (± 0.8)	762 [817-1579]
(Rosaceae)	FF	5	0.916	**0.011**	3.1 (± 0.5)	762 [817-1579]
	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 Willd.	BF					#
	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]

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 (Tab. IV.2, IV.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 (Tab. IV.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 (Tab. IV.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 (Tab. IV.2, IV.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, Tab. IV.3).

The timing of phenophases, averaged over all species, was about 1 to 7 days earlier on advanced snowmelt 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 (Tab. IV.4). For P. erecta flower duration was much longer at lower altitudes (33 days) than at higher altitudes (18 days) averaged over all treatments (Tab. IV.4).

Table: IV.2: Mixed-effect 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). 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.	0.622	**140**	**137**	NA	**139**	0.153	**140**	**137**	**139**	**139**	0.369	**174**	**177**		**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.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
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**	NA	0.223	**170**	**162**	**178**	NA	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.	NA	NA	NA	NA	NA	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 IV.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.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
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.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lotus corniculatus L.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.242	202	200	200	202
Potentilla erecta (L.) Raeusch	0.318	**179**	**173**	**183**	**178**	0.192	**180**	**175**	**184**	**181**	**0.036**	NA	**199** a	**200** b	**195** a b
Prunella vulgaris L.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Ranunculus acris L.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
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.	NA	NA	NA	NA	NA	0.610	**199**	**196**	**201**	**198**	0.410	**210**	**207**	**211**	**210**

Table IV.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). NA data not available.

		Duration [days]				
		P	co	ad	de	dr
Alchemilla vulgaris L.	mean (l)		NA	NA	NA	NA
	treatment (l)	NA				
	mean (h)		30	37	25	27
	treatment (h)	**0.01**	a	a b c	b	c
Briza media L.	mean (l)		9	9	8	7
	treatment (l)	0.552				
	mean (h)		NA	NA	NA	NA
	treatment (h)	NA				
Campanula scheuchzeri Vill.	mean (l)		NA	NA	NA	NA
	treatment (l)	NA				
	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)		NA	NA	NA	NA
	treatment (h)	NA				
Lotus corniculatus L.	mean (l)		22	30	31	
	treatment (l)	0.696				
	mean (h)		NA	NA	NA	NA
	treatment (h)	NA				
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)		NA	NA	NA	NA
	treatment (h)	NA				
Ranunculus acris L.	mean (l)		NA	NA	NA	NA
	treatment (l)	NA				
	mean (h)		NA	NA	NA	NA
	treatment (h)	NA				
Ranunculus montanus Willd.	mean (l)		NA	NA	NA	NA
	treatment (l)	NA				
	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)		NA	NA	NA	NA
	treatment (h)	NA				

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 and Chmielewski 2001, Dittmar and Elling 2005, Migliavacca et al. 2008, Vitasse et al. 2009, Moser et al. 2009), 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 and 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 and Waser 1998, Dunne et al. 2003, Wipf 2009, 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 and Collins 1977, Torp et al. 2010, Chen et al. 2011b, 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 and 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 and Waser 1998, Dunne et al. 2003, Wipf 2009).

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 and 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. IV.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 and 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 (2009) 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 and 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.

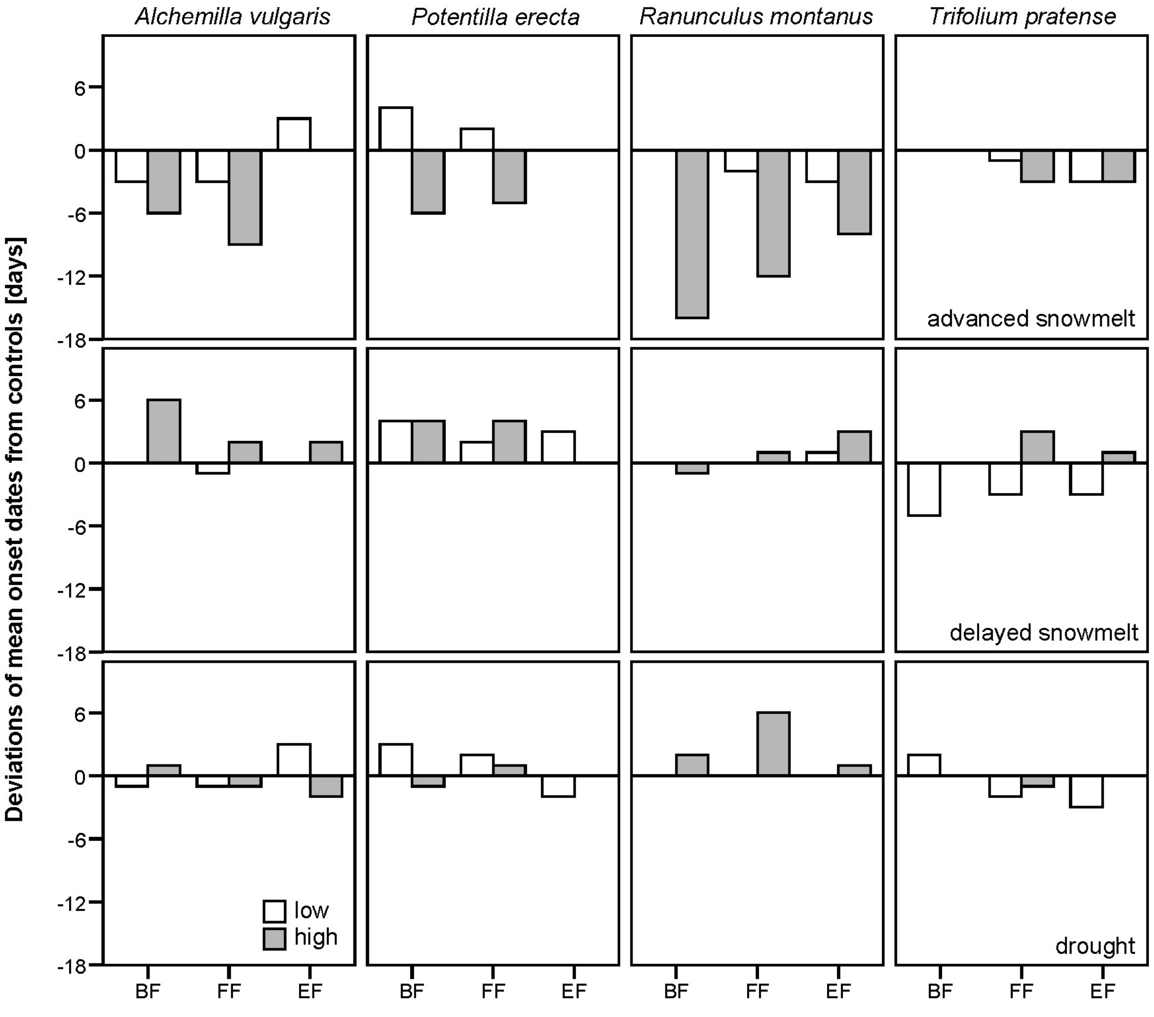

Fig. IV.4: Deviations from controls of mean onset dates from the ANCOVA model for each studied phenophase (BF: beginning of flowering, FF: full flowering, EF: end of flowering) separately by low (600 m to 1300 m) and high sites (1300 m to 2000 m) for the four species (*Alchemilla vulgaris* L., *Potentilla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

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. IV.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 and 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. (2012) 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.

Conclusions

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.

V Climatic context predicts resilience of mutualistic networks

This chapter is in preparation for publication as: Hoiss, B., Krauss, J. & Steffan-Dewenter, I., Climatic context predicts resilience of mutualistic networks.

Running title: Climatic context predicts network stability

Abstract

Shifts in ecological networks due to climate change cause population and species extinctions. The susceptibility of networks to global warming is expected, but not shown yet, to depend on the environmental context. In this study we assess changes in the structure of plant-pollinator networks along altitudinal gradients combined with the experimental simulation of potential consequences of climate change: extreme drought events, advanced and delayed snowmelt. We found a trend of decreasing specialisation and therefore increasing complexity in networks with increasing altitude. Networks after advanced snowmelt or drought were more specialised especially at higher altitudes compared to control plots. Our results show that changes in the network structures after climate manipulations depend on the climatic context and reveal an increasing susceptibility of networks with increasing altitude.

Keywords: altitudinal gradient, plant-pollinator interactions, quantitative network descriptors, H2', extreme events, snowmelt, drought

Introduction

Global warming and climatic extreme events can disrupt species interactions and alter the structure of trophic networks (Memmott et al. 2007, Tylianakis et al. 2008, Johnson et al. 2010). Changes in interactions have been shown to be the most important causes of population and species extinctions due to climate change (Cahill et al. 2013). Knowledge about the reactions of ecological networks to climate change is therefore crucial for our understanding of the susceptibility and resilience of ecosystems and communities. As it is unlikely that networks react the same way under different conditions it is important to integrate the climatic context in predictions or experiments on the effects of climate change on ecosystem processes (Dunne et al. 2004, Tylianakis et al. 2008).

Network Descriptors

Different characteristics and changes of bipartite interaction networks can be described with a variety of indices. In the last decade quantitative descriptors, which include also informations on visitation frequencies (interaction strengths), were developed and are proposed to allow i) a better understanding of the organisation of mutualistic networks and their susceptibilities than qualitative descriptors and ii) comparisons between different studies and systems (Bersier et al. 2002, Bascompte et al. 2006, Blüthgen et al. 2006). Some parameters to describe networks are the H2' index, generality / vulnerability and web asymmetry. H2' is a quantitative parameter that measures the degree of specialisation in networks. It describes the degree of niche partitioning in the entire network (Blüthgen et al. 2006). The H2' index has been shown to be robust against differences in network size and degree distribution (Blüthgen et al. 2007). Quantitative generality and vulnerability are computed as the weighted mean of the effective number of links per species which is derived from the interaction diversity of this species (Bersier et al. 2002). It describes the degree of generalisation within one trophic level. Generality is used for the higher trophic level, vulnerability for the lower trophic level. Web asymmetry is a simple, qualitative measure for the relation of species richness of the two trophic levels.

Gradients and climatic context

Altitudinal gradients provide, within short distances, the opportunity to research patterns in the ecosystem induced by different local climatic contexts. One important feature of ecosystems that can be accessed in a changing climatic context along altitudinal gradients is biodiversity. Main patterns that have been found are a decreasing diversity with increasing altitude and a unimodal pattern with a mid-elevational peak (McCain and Grytnes 2010). Another important feature of ecosystems are the networks of interactions between species. They play an important role for the evolution and maintenance of biodiversity as well as for the stability of ecosystems (Bascompte et al. 2006, Ives and Carpenter 2007, Tylianakis et al. 2008). However, only little is known about the effects of climate change on mutualistic interaction networks (Rafferty and Ives 2011) and only few studies assess the influence of altitude on interactions and network structures at the community level (Olesen and Jordano 2002, Ramos-Jiliberto et al. 2010). At the latitudinal gradient one recent meta study found specialisation in mutualistic interaction networks to decrease from higher to lower latitudes (Schleuning et al. 2012). Several possible mechanisms might influence the network-structure and stability along an altitudinal and therefore climatic gradient. Plants are often more widely separated and tend to be smaller at high altitudes (Hodkinson 2005). The abundance of insect-pollinated plant species has been shown to decrease compared to wind-pollinated species with increasing altitude (Hoiss et al. 2013). This can result in lower densities of resource species for pollinators at higher altitudes. According to the optimal foraging strategy these low densities lead to longer search times and therefore promote more generalised pollinators and more generalised food-web structures (Schleuning et al. 2012). Additionally pollinators experience a release from competition at higher altitudes due to lower diversity and abundance in pollinators (Hoiss et al. 2012), which could result in wider realised food niches and therefore also in more generalised network structures with increasing altitude.

Effects of climate change

Rising temperatures in the course of global warming change the phenologies of many plants and insects (reviewed by Hegland et al. 2009). Species often differ in the magnitude and rates of adaptation to climate change which leads to disruptions in their interactions (Kudo et al. 2004, Parmesan 2007, Both et al. 2009, Johnson et al. 2010). These mismatches might also occur as a consequence of extreme events, or changes in the date of snowmelt influencing the start of the vegetation period. Changes in the structure and stability of trophic networks, and thus their tolerance to species extinctions can be the results of these mismatches (Kudo et al. 2004, Memmott et al. 2007). However, the susceptibility of mutualistic interaction networks to extreme events and changed precipitation patterns has received little attention so far. Moreover, even though the resilience of networks and communities to climate change is supposed to depend on the environmental context (Ives and Carpenter 2007, Tylianakis et al. 2008) as far as we know, no research has been published on this combination. Experiments, that simulate extreme events, altered season length or other consequences of climate change, have mainly been conducted at single locations so far (Bütof et al. 2012). An increasing generalisation in networks with altitude as proposed above can be expected to result in a decreasing susceptibility to the effects of climate change. Generalised species are able to interact with a broad range of partners and are therefore supposed to be more resilient to disruptions of interactions with some of their initial partners.

Climate predictions

Communities and mutualistic networks will face different consequences of climate changes in Europe. The global mean temperature is predicted to increase (IPCC 2007), the probability and extent of drought extreme events in summer is likely to increase (Meehl and Tebaldi 2004, Field et al. 2012), and an increase of mean and extreme winter precipitation is expected in high latitudes and mountainous regions (Saha et al. 2006, Solomon et al. 2007, Laghari et al. 2012). The effects of climate change are more pronounced with increasing altitude and the temperature increase is stronger at high altitudes (Beniston 2012). The predicted higher amount of precipitation in winter may influence the length of vegetation periods and the phenology of species. Different scenarios are possible for the date of snowmelt and therefore for the length of vegetation periods: advanced snowmelt (liquid precipitation in winter and faster snowmelt due to high temperatures) or delayed snowmelt (larger snow packs mainly at higher altitudes due to the increased amount of precipitation in winter). Due to the more pronounced effects of climate change at high altitudes it can be expected that the shifts in the date of snowmelt are larger here which has the potential to change network structures at high altitudes more than at low altitudes.

In order to assess the importance of the local climate context in determining network structure and susceptibility to climate change, we experimentally simulated advanced and delayed snowmelt and drought events along an altitudinal gradient in the German Alps.

We tested the hypotheses that i) the structure of mutualistic plant-pollinator networks depends on the local climatic context; ii) a changed phenology of plants (due to climatic manipulations) affects the structure of plant-pollinator networks due to (phenological) mismatches; iii) the effect of climatic manipulations on the network structure depends on the local climatic context.

Materials and methods

Study sites

The study was carried out on grasslands in the National Park Berchtesgaden and its vicinity (47,10° N, 12,15° E). The National Park is located in the northern limestone Alps in the south-east of Germany. We selected 15 study sites (10 x 10 m) on extensively or not managed grasslands across an altitudinal gradient ranging from 600 to 2,000 m.a.s.l..

Climate experiment

At each study site we set up four climate treatments in 4 x 4 m plots: (a) advanced snowmelt, (b) delayed snowmelt, (c) extreme drought (d) control. In early spring we moved snow, except for a thin layer to prevent damage at the plants, from one treatment plot to an adjacent treatment plot to simulate advanced and delayed snowmelt. We achieved a mean advanced snowmelt of 27 days and a delayed snowmelt of one day. The advance in snowmelt increased with altitude (for more details see Cornelius et al. 2012). Four weeks after snowmelt we set up 4 x 4 m rain-out shelters for 43 ± 1 days to simulate a 1000-year extreme drought event for the study region (Jentsch et al. 2007). Plots were regarded as snow-free when near-surface air temperatures reached more than + 5 °C on at least three consecutive days (Wipf et al. 2006). Near-surface air temperatures were measured with temperature loggers (Thermochron iButtons DS1921G#F5, Maxim Integrated Products, Inc., Sunnyvale, CA, USA) in each of the four treatment plots in 2 h intervals. The amount of rain we excluded with the rain-out shelters (379 ± 71 l/m^2) did not change significantly along the altitudinal gradient (simple regression, $F_{1,13} = 1.1$, $P = 0.3$). But we found significant differences between the treatments in soil moisture during the drought period, using a portable soil moisture meter (Delta-T Devices type HH2 + ThetaProbe ML2x sensors, Cambridge, UK) (see chapters IV and VI).

Network data

We recorded quantitative pollination network data from 22 May to 06 September 2010. Depending on the time of snowmelt, we conducted 6 to 8 surveys on the treatments control, delayed and advanced and 3 to 6 surveys on the treatment drought after the rain-out shelters were removed. One survey included two observation periods of 5 minutes per treatment and therefore a total of 40 minutes per site. Network-data was recorded between 9:30 and 18:00 h on days when the weather was sunny or when temperature at 650 m.a.s.l. was above 17°C. The flower-visitors were determined to species level except for a few individuals which could only be morphotyped. From the network-datasets we calculated network-indices for each of the 60 networks (15 sites x 4 treatment plots) using the R package *bipartite*.

For our analysis we used three quantitative network parameters which are more robust to sampling differences and more conservative in detecting differences between habitats than their qualtitative counterparts (Tylianakis et al. 2007): i) H'2 represents a scale-independent index to estimate the degree of complementarity specialisation of a network (Blüthgen et al. 2006, Blüthgen and Klein 2011). It has been shown to be robust against differences in network size and form (Blüthgen et al. 2007). ii) Generality of pollinators is calculated as the weighted ratio of plant species per pollinator species (Dormann et al. 2009) iii) Vulnerability is analogous to generality the weighted ratio of pollinator species per plant species (generality of plants). We also used web asymmetry as a simple qualitative web metrics. It provides information on the relation of plant vs. pollinator species participating in the networks.

Data analysis

Analyses were conducted in R version 2.15.1 (R Development Core Team 2012). To test our hypothesis that simulated changes in the date of snowmelt and extreme drought events alter the structure of plant pollinator networks we fitted mixed effects models using the lme function from the R package *nlme*. We fitted one model for each of the four network indices as response variables: H'2, web asymmetry, generality and vulnerability. Predictors in these models were altitude, treatment (a factor with 4 levels: control, delayed snowmelt, advanced snowmelt and drought) and the interaction altitude*treatment. The control plot was defined as reference level. We also fitted the same models for a dataset including only the first three surveys on each treatment plot to check whether our results are robust against lower sampling effort. We used the site ID as random-factor to account for nesting. Likelihood ratio tests were performed to identify the minimal adequate models. The model residuals were sufficiently normally distributed and showed variance homogeneity.

Results

Our network dataset comprises 4726 interactions involving 377 pollinator species and 122 plant species. The most abundant pollinators were Diptera (3575 interactions), followed by Hymenoptera (989 interactions). We recorded a minimum of 12 and a maximum of 164 interactions per treatment plot. Species richness of plants and pollinators involved in the networks showed a hump-shaped distribution along the altitudinal gradient (Fig. V.S2 & V.S3). Flower cover and density did not vary significantly with altitude nor with treatments (Fig. V.S4 & V.S5).

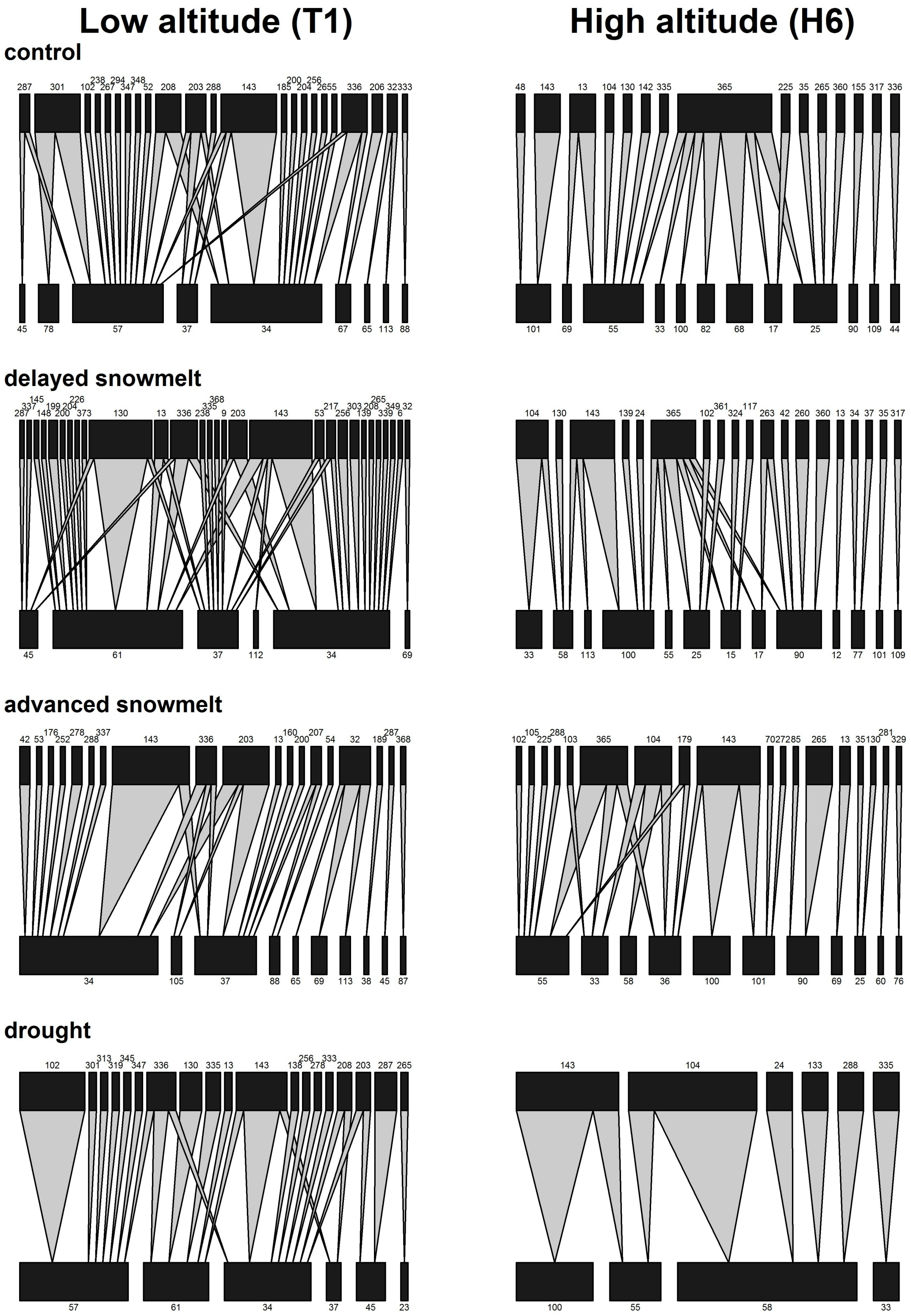

Fig. V.1: Examples of bipartite network-structures in four treatment plots on a low altitude site (T1: 714 m a.s.l.) and a high altitude site (H6: 1808 m. a.s.l.). Upper black bars indicate pollinator species, lower black bars indicate plant species. The width of the black bars shows the abundance of the species in the network. The width of the grey links between the two trophic levels depicts the interaction-strength.

We found significant changes of the network structure along the altitudinal gradient, depending on the climate treatments (Fig. V.1). This suggests that networks in different climatic context differ in their reaction to shifts in the phenology of plants due to changes in the date of snowmelt or extreme drought events. We show that the degree of specialisation (H'2) was similar at low altitudes for all treatments, but diverged with increasing altitude (Fig. V.2, Tab. V.1): The degree of specialisation tended to decrease with altitude on the control plots ($p = 0.068$, $t = -1.99$, $DF = 13$) from $H2' = 0.60$ at 600 m to 0.37 at 2000 m.a.s.l. (Tab. V.1). In the delayed snowmelt treatment the trend did not differ significantly from control, but after advanced snowmelt and drought treatment the specialisation degree increased with altitude and the slopes were therefore significantly different from the control trend (Fig. V.2, Tab. V.1).

For the generality (G) of pollinators we found patterns similar as for the H'2 index. The significant interaction between altitude and treatment indicates that generality of pollinators after advanced snowmelt or an extreme drought event showed a different trend along the altitudinal gradient than in the control and delayed snowmelt treatments. Generality decreased with altitude in the plots with advanced snowmelt and drought treatment, whereas it increased in the control and delayed snowmelt plots (Fig. V.2, Tab. V.2).

No significant relationships were found in the vulnerability (generality of plants) index (Fig. V.2).

The positive web asymmetry index shows that in general more pollinator than plant species were participating in all networks, but this relation decreased with altitude (Fig. V.2, Intercept $= 0.551$, slope $= -1.27E-4$, $t = -2.40$, $P = 0.032$). This fact indicates that species richness of pollinators decreased faster with increasing altitude than the species richness of plants.

We found very similar patterns for H'2, generality and vulnerability in our models using network-data based only on the first three surveys in every treatment (Fig. V.S1, Table V.S1 & Table V.S2). Only for web asymmetry we could not confirm the pattern found in the full dataset. This confirms that the quantitative network indices as well as our results are robust against differences in sample size.

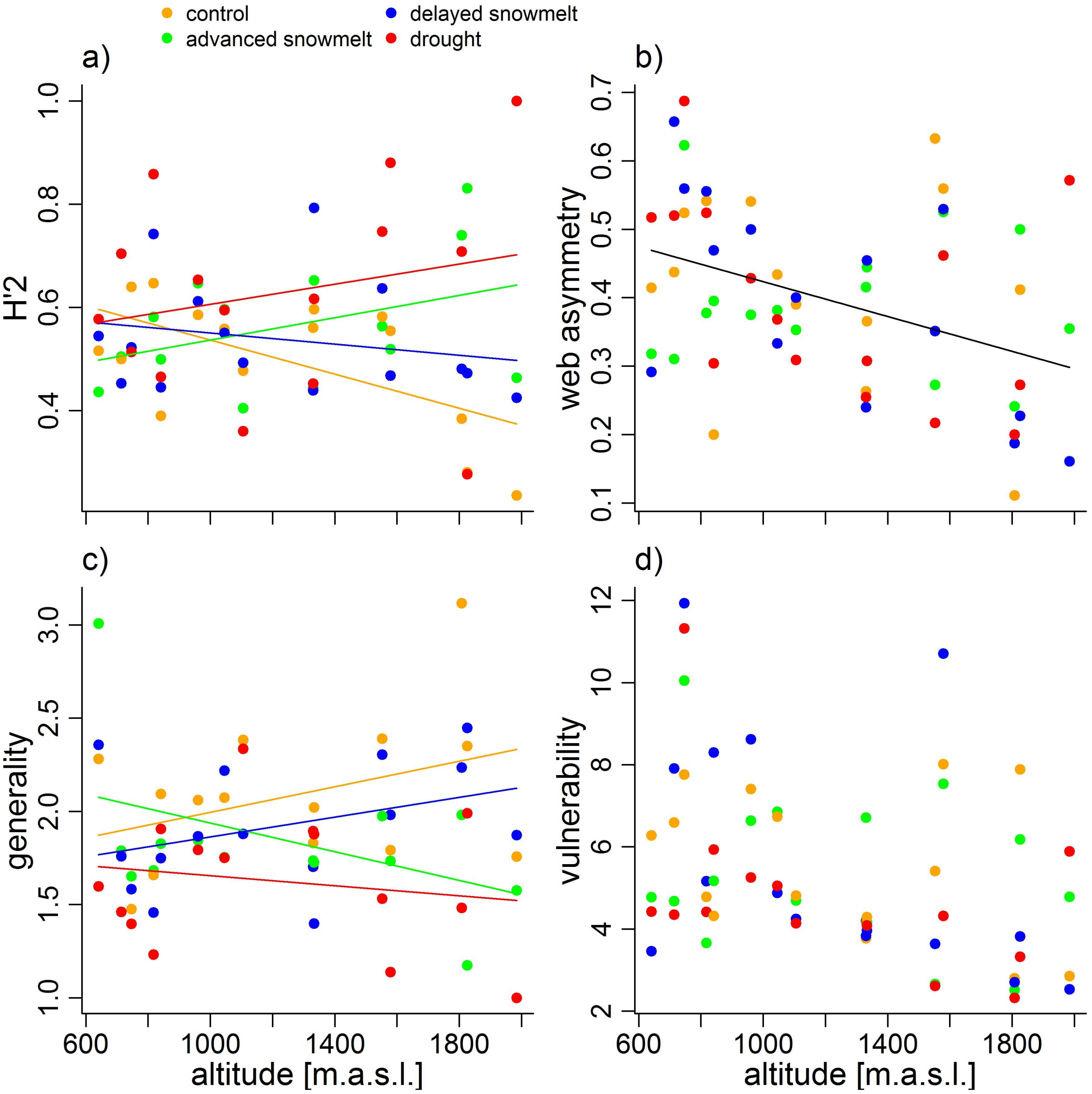

Fig. V.2: Effects of experimentally simulated climate-change scenarios along an altitudinal gradient on four different descriptors of mutualistic plant-pollinator networks. For statistics see Tables V.1, V.2 and results section.

Table V.1: Results of a linear mixed effects model with H2' as response variable. Altitude and experimental treatments were used as explanatory variables. The treatment consisted of four levels: control (co), advanced snowmelt (ad), delayed snowmelt (de) and drought (dr). The control treatment serves as reference slope/ intercept. Site identity was used as random factor to correct for pseudoreplication. Sixty observations on fifteen sites.

Fixed effects	Estimate	SE	DF	t value	P value
Intercept (Treatment co)	7.00E-1	1.07E-1	39	6.547	<0.001
Altitude:treatment co	-1.65E-4	8.29E-5	13	-1.993	0.068
Treatment ad	-2.74E-1	1.39E-1	39	-1.967	0.056
Treatment de	-9.76E-2	1.39E-1	39	-0.702	0.487
Treatment dr	-1.94E-1	1.39E-1	39	-1.392	0.172
Altitude:treatment ad	2.74E-4	1.08E-4	39	2.542	0.015
Altitude:treatment de	1.11E-4	1.08E-4	39	1.034	0.307
Altitude:treatment dr	2.63E-4	1.08E-4	39	2.443	0.019

Table V.2: Results of a linear mixed effects model with generality of pollinators as response variable. Altitude and experimental treatments were used as explanatory variables. The treatment consisted of four levels: control (co), advanced snowmelt (ad), delayed snowmelt (de) and drought (dr). The control treatment serves as reference slope/ intercept. Site identity was used as random factor to correct for pseudoreplication. Sixty observations on fifteen sites.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	1.65E+0	2.81E-1	39	5.888	0.000
altitude	3.42E-4	2.17E-4	13	1.577	0.139
treatmentad	6.69E-1	3.09E-1	39	2.167	0.036
treatmentde	-5.48E-2	3.09E-1	39	-0.178	0.860
treatmentdr	1.37E-1	3.09E-1	39	0.445	0.659
alt:treatmentad	-7.27E-4	2.39E-4	39	-3.043	0.004
alt:treatmentde	-7.71E-5	2.39E-4	39	-0.323	0.749
alt:treatmentdr	-4.77E-4	2.39E-4	39	-1.998	0.053

Discussion

Gradient

Our climate change experiment along an altitudinal gradient shows that the resilience of mutualistic networks depends on the climatic context. We found a trend of increasing generalisation and therefore increasing complexity with increasing altitude in untreated networks. The complexity of networks is regarded as crucial for their stability (Montoya et al. 2006) and the changing resilience of plant-pollinator networks along the climatic gradient may therefore be a consequence of the changes in the structure of these networks. Our results support the hypothesis that the climatic context determines the structure of plant-pollinator networks. Possible reasons for the observed increasing generalisation with altitude are: i) Decreasing densities of insect-pollinated plant species at higher altitudes which lead to longer foraging times and impede the specialisation of pollinators (Schleuning et al. 2012). However, this explanation is implausible for our findings, as flower cover and flower cover per species (density) did not decrease with altitude. The other three explanations have a higher probability to be the mechanism behind the found patterns, but remain also speculative: ii) A reduced competition between pollinators due to decreasing diversity and abundance with altitude (Hoiss et al. 2012), which causes wider realised food niches in pollinators; iii) A decreasing web-asymmetry with altitude, as shown in our results, meaning that pollinator diversity in the networks decreases faster with altitude than plant diversity. This again implies a reduced competition between pollinators and therefore more generalised, wider food niches; iv) The flower duration increases with altitude (Körner 2003). Longer flowering plants do not depend on pollinators co-occurring at a special point of time but are able to use a wider range of pollinators and are therefore supposed to be more generalised. More randomly organized interaction networks at higher altitudes under harsh abiotic conditions have also been found in Andean plant-pollinator networks (Ramos-Jiliberto et al. 2010) and fluctuations in the nestedness of mutualistic plant-ant networks have been found to depend on the abiotic factors temperature and precipitation (Rico-Gray et al. 2011). Reduced relative abundance of resource species has been suggested as mechanism behind a decreasing specialisation in mutualistic networks towards the tropics (Schleuning et al. 2012), whereas unpredictable environments in terms of abiotic climatic factors have been assumed to promote more generalised interactions (Devoto et al. 2005). However, further studies are needed to understand the organisation of networks along climatic gradients and the ecological mechanisms.

Extreme Events

Our climate-change experiment showed realistic changes in expected drought (reduced soil moisture from 58.9% to 40.2%) and advanced snow melt (27 days), but shifted the delayed snowmelt only by one day. These changes in climate resulted in diverse responses of the phenology of plants in the same study plots (Cornelius et al. 2012). The altered plant phenology could have affected also the structure of plant-pollinator networks. Our results show that changes in the network structures after climate manipulations increased with increasing altitude and thus revealed an increasing susceptibility. The results in our study therefore confirm our hypothesis, that the impact of climate change depends on the local climate context. Advanced snowmelt and drought caused an increasing specialisation degree with altitude compared to control plots. No changes in the network structure in plots with delayed snowmelt were found, presumably due to the very small delay in snowmelt that was achieved with the treatment. However, the reactions in the networks contradict our hypothesis that more generalised networks (as found at higher altitudes) should be more resilient to the effects of climate change. This raises the question what caused these observed patterns and how can they be explained?

In general, more specialised network structures after climate manipulations can be explained by the shifted phenology of flowers resulting in a reduced overlap with the active phase of their pollinators. However, the increasing specialisation pattern after drought and advanced snowmelt at higher altitudes originated mainly from the insects level. Insects showed a decreased generality after treatments with altitude, whereas the vulnerability (generality) of plants stayed unchanged compared to control plots. The fact that network asymmetry did not change with the treatments shows that the relation of plant vs. pollinator species in the networks did not change significantly. Differences in the generality of insects can therefore mainly be explained by differences in the interaction-strengths: insects at higher altitudes focused their foraging effort after drought events or advanced snowmelt on few plant species, while the number of plant species, they interacted with, was more or less constant. One requirement for the constant level of generality in plants is, that the average diversity of flower-visitors per plant species remains more or less constant. This implies, that the shift of the pollinators to few generalised plant species as food resources occurred in a similar amount in most of the pollinator species.

Still, the ecological mechanisms behind these shifts in the interaction strengths are speculative. Possible mechanisms could be that i) the flower duration increases with altitude (Körner 2003) which might cause an increasing specialisation of pollinators on plants usually co-occurring in their temporal niche, but a higher generalisation within this group of plants. This hidden temporal complementarity causes a reduced redundancy after the phenological shift of plants compared to systems at lower altitudes, where flower durations are shorter and pollinators are not able to specialise on the species in one temporal niche. ii) Species richness of plants and bees decreases at high altitudes (Hoiss et al. 2012, 2013) which leads to smaller networks in which partners lost through mismatches cannot be replaced. The consequence is a lower redundancy and the ability to maintain ecosystem processes (pollination) is reduced. iii) The stronger effect of advanced snowmelt at high altitudes might also be explained by the increasing treatment intensity with altitude. However, the drought effect was constant along the altitudinal gradient and still showed an increasing effect on the network structure with altitude.

Conclusions

In conclusion we confirm the pattern, that pollination systems are resilient to climate changes in temperate regions at lower altitudes (Devoto et al. 2007), but found an increasing susceptibility with increasing altitude. These findings, based on empirical data, support the patterns observed in a recent modelling study (Encinas-Viso et al. 2012): i) mutualistic communities are more fragile in cool environments with short seasons and ii) changes in the phenology (altered phenology of plants in our experiment (Cornelius et al. 2012)) lead to shifts in the patterns in mutualistic communities. This is also supported by another study, finding that networks are mainly shaped by biological constraints, such as potential interactions that do not occur for example due to phenological mismatches (Olesen et al. 2011). It therefore seems that the interaction of changes in the phenology and the climatic context is highly important for the resilience of ecosystems. However, more empirical data is badly needed and there is also a need for a more profound theoretical framework on the ecological mechanisms behind the different susceptibilities. Another step towards a deeper understanding of the effects of climate change on ecosystems would be the assessment of the consequences of different network-structures for the fitness of individuals, populations and communities. For example further research on changes in network structures should record fitness, fecundity and reproduction success of the involved species.

Supplement

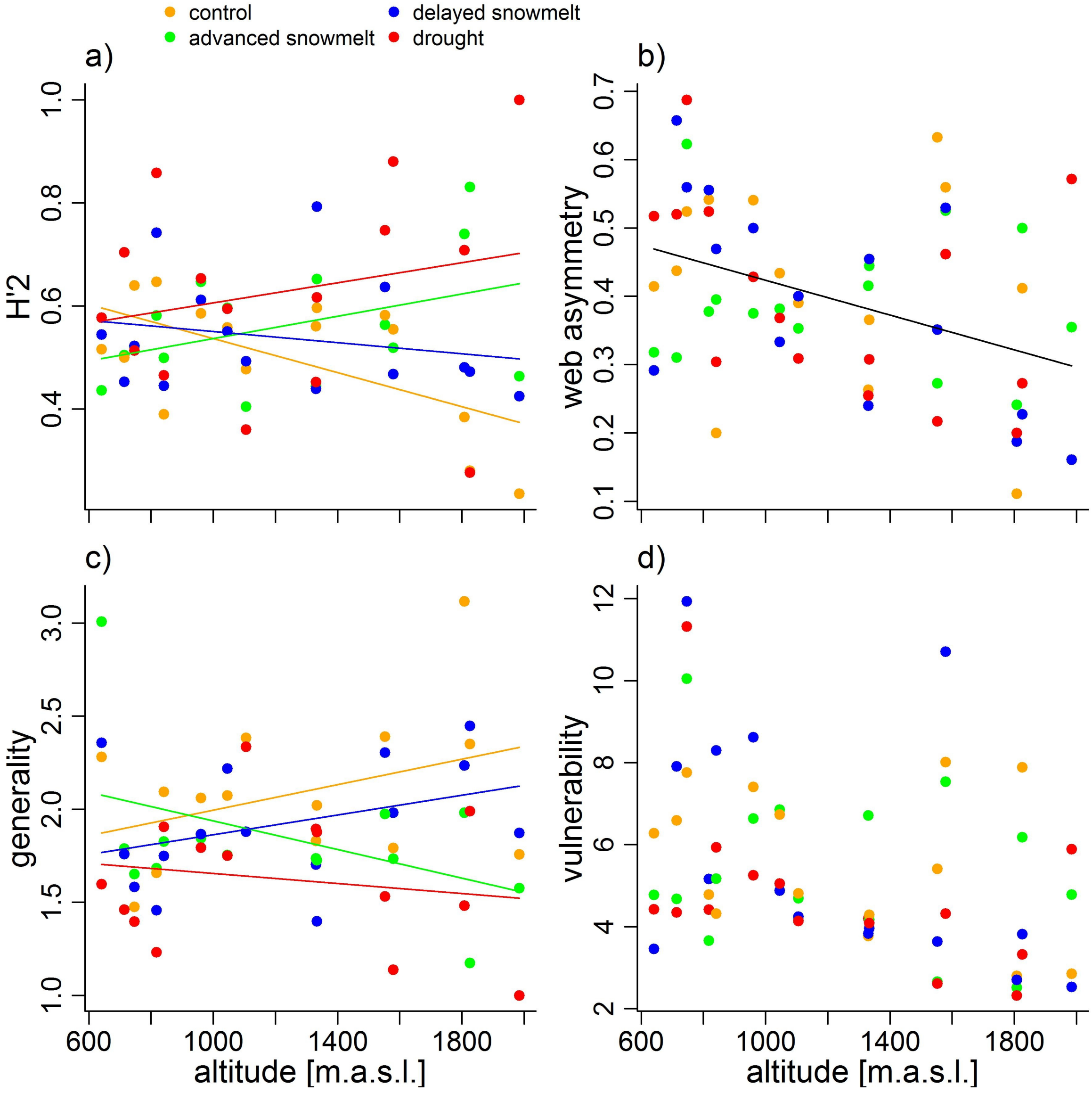

Fig. V.S1: Effects of altitude and experimentally simulated climate-change scenarios on the structure of mutualistic plant-pollinator networks. To check whether our results are robust against differences in sampling effort we based this analysis on the first three surveys per plot and compared it with the analysis including all surveys (Fig. V.1, Table V.1, V.2). We were able to perform three surveys on the plots with the fewest replicates (drought plots at high altitudes). The structure of the networks is depicted by the four different descriptors: H'2, generality, vulnerability, web asymmetry. The treatment consisted of four levels: control (co), advanced snowmelt (ad), delayed snowmelt (de) and drought (dr). Lines are only drawn if the interaction between altitude and treatment or the main effects were statistical significant at the level of 5%. For statistics and estimates see also tables V.S1 and V.S2.

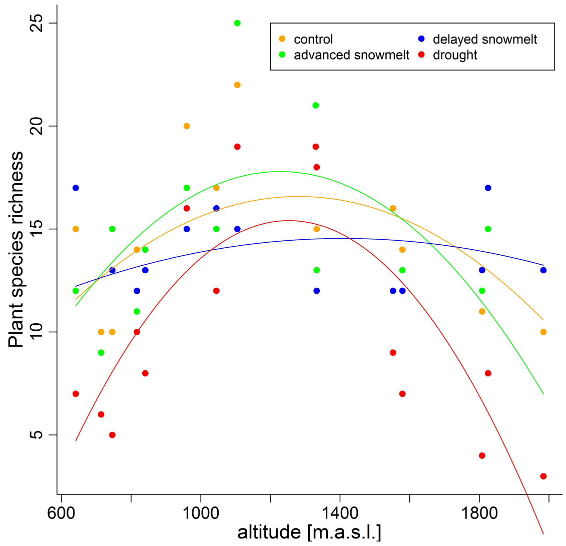

Fig. V.S2: Species richness of plants involved in the observed plant-pollinator networks along an altitudinal gradient. The interaction of altitude and the climatic treatments (control, advanced snowmelt, delayed snowmelt and drought) influences the number of plants involved in plant-pollinator interactions. Sixty observations on fifteen sites.

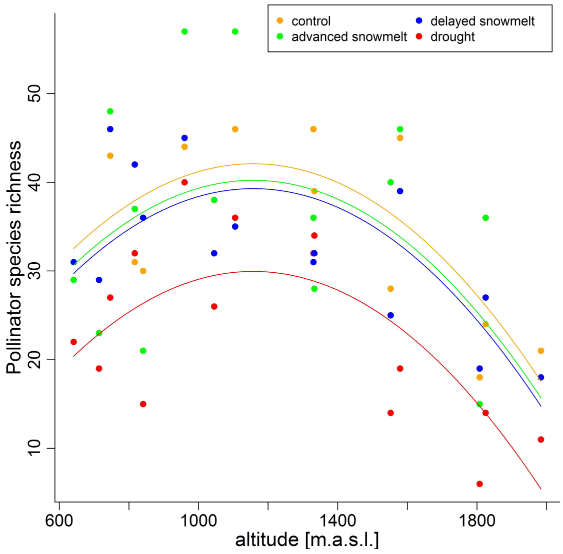

Fig. V.S3: Hump-shaped distribution of the species richness of pollinators involved in mutualistic plant-pollinator networks along an altitudinal gradient in four different treatments (control, advanced snowmelt, delayed snowmelt and drought). Sixty observations on fifteen sites.

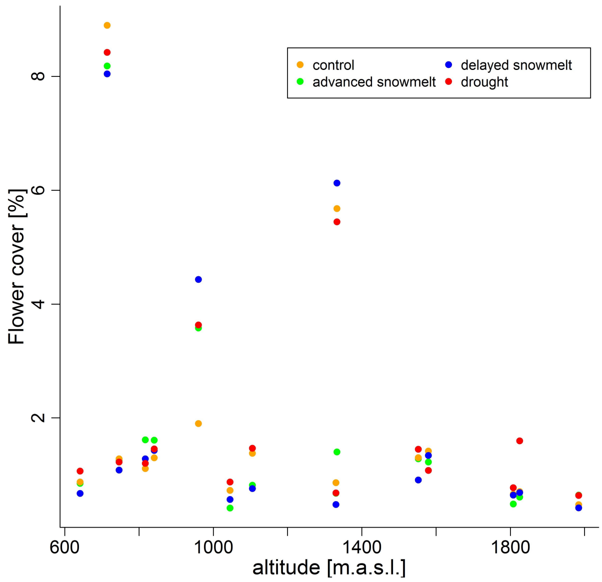

Fig. V.S4: Total flower cover averaged over the number of surveys in four climatic treatments (control, advanced snowmelt, delayed snowmelt, drought) along an altitudinal gradient. No significant influence of altitude, treatment and their interaction on flower cover was detected (at the significance level of 5%).

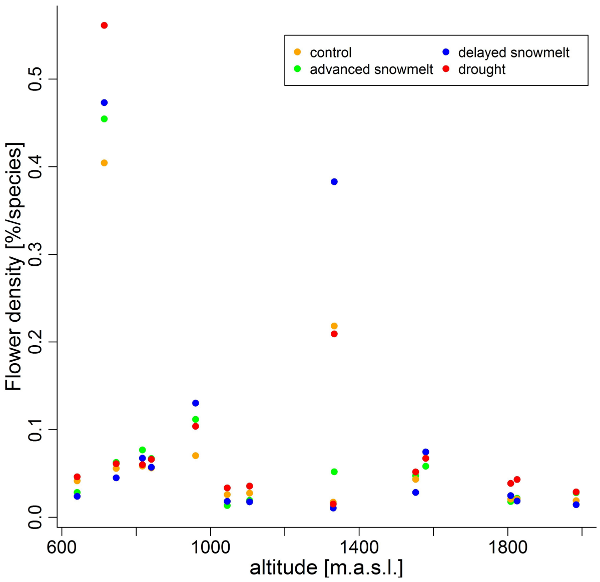

Fig. V.S5: Flower density (flower cover in % per species) averaged over the number of surveys in four climatic treatments (control, advanced snowmelt, delayed snowmelt, drought) along an altitudinal gradient. No significant influence of altitude, treatment and their interaction on flower cover was detected (at the significance level of 5%).

Table V.S1: Results of a linear mixed effects model with H2' as response variable using network-data from the first three surveys per plot. Altitude and climate treatments (control (co), advanced snowmelt (ad), delayed snowmelt (de) and drought (dr)) were used as explanatory variables. The control treatment serves as reference slope/ intercept. Site identity was used as random factor to correct for pseudoreplication. Sixty observations on fifteen sites.

Fixed effects	Estimate	SE	DF	t value	P value
Intercept (Treatment co)	7.23E-1	1.37E-1	38	5.284	<0.001
Altitude:treatment co	-2.20E-4	1.06E-4	13	-2.081	0.058
Treatment ad	-2.06E-1	1.77E-1	38	-1.166	0.251
Treatment de	1.43E-2	1.77E-1	38	0.081	0.936
Treatment dr	-2.13E-1	1.84E-1	38	-1.157	0.254
Altitude:treatment ad	2.96E-4	1.37E-4	38	2.162	0.037
Altitude:treatment de	3.51E-5	1.37E-4	38	0.257	0.799
Altitude:treatment dr	3.28E-4	1.40E-4	38	2.34	0.025

Table V.S2: Results of a linear mixed effects model with generality of pollinators as response variable using network-data from the first three surveys per plot. Altitude and experimental climate treatments were used as explanatory variables. The treatment consisted of four levels: control (co), advanced snowmelt (ad), delayed snowmelt (de) and drought (dr). The control treatment serves as reference slope / intercept. Site identity was used as random factor to correct for pseudoreplication. Sixty observations on fifteen sites.

Fixed effects	Estimate	SE	DF	t value	P value
Intercept (Treatment co)	1.10E+0	2.69E-1	39	4.094	<0.001
Altitude:treatment co	4.74E-4	2.08E-4	13	2.279	0.040
Treatment ad	8.18E-1	3.30E-1	39	2.477	0.018
Treatment de	-1.52E-2	3.30E-1	39	-0.046	0.964
Treatment dr	1.32E-1	3.30E-1	39	0.399	0.692
Altitude:treatment ad	-7.98E-4	2.56E-4	39	-3.124	0.003
Altitude:treatment de	2.77E-5	2.56E-4	39	0.109	0.914
Altitude:treatment dr	-3.28E-4	2.56E-4	39	-1.285	0.206

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

This chapter is in preparation for publication as: Annette Leingärtner, Bernhard Hoiss, Jochen Krauss, Ingolf Steffan-Dewenter, Combined effects of extreme climatic events and elevation on nutritional quality and herbivory rates of alpine plants

Running title: Plant-herbivore interactions & climate change

Abstract

The response of plant-herbivore interactions to extreme climatic 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 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 showed a reduction in nutritional plant quality with advancing season. Although our results indicate 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, food plant quality, phenology, plant functional groups, plant-herbivore interactions, 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 and 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, Wu et al. 2011, 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 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 and Eklund 2012). Therefore, future climate change scenarios predict either higher or lower snow cover depending on altitude and location (Wipf and 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, 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 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 desyncronising 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. I.3). 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. I.3). 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: t12 = -0.5, P = 0.6).

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/m2 and the amount of rain did not show a directional change along the elevational gradient (simple regression, F1,13 = 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 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 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 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 Development Core Team 2012).

Results

Snow and drought experiments

Snowmelt timing was successfully manipulated along the elevational gradient (Fig. VI.1) without significantly increasing soil water availability (Fig. VI.2). 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. VI.1).

Soil moisture was significantly lower on drought plots during simulated extreme drought events compared to the other treatment plots (F3,42 = 26.5, $P < 0.0001$, Fig. VI.2). 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.

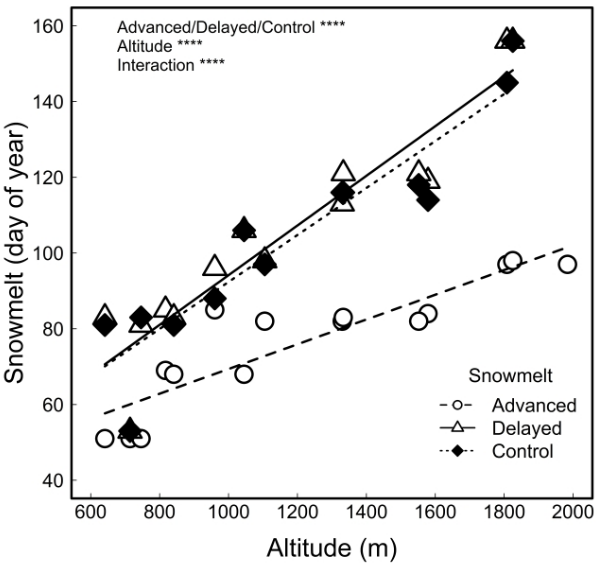

Fig. VI.1: Final day of snowmelt for three different treatments (advanced snowmelt, delayed snowmelt, control) on 15 study sites in relation to altitude. **** $P \leq 0.0001$

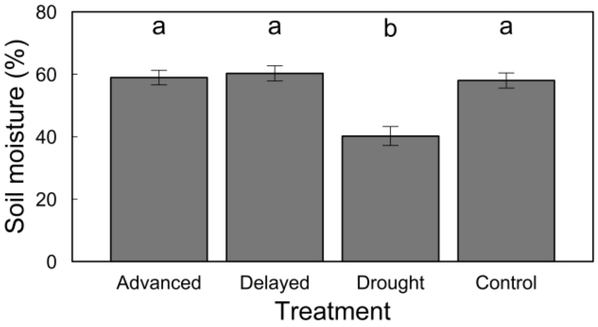

Fig. VI.2: Soil moisture (% volume) during the extreme drought event on four treatments (advanced snowmelt, delayed snowmelt, extreme drought, control) (mean ± se). Letters indicate non-significant (a – a, $P > 0.05$) and significant (a – b, $P \leq 0.0001$) differences between the treatments according to Tukey HSD post-hoc comparisons.

CN ratio

The CN ratio of plants was affected by the interaction of altitude, plant guild and sampling time (Table VI.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 VI.1). 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. VI.3). 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 VI.1). CN ratios of grasses showed a slight increase with altitude whereas the CN ratios of forbs and legumes decreased with altitude (Fig. VI.3). The significant interaction of plant guild and time indicates that the CN ratios of the three plant guilds changed differently during the growing season.

Table VI.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

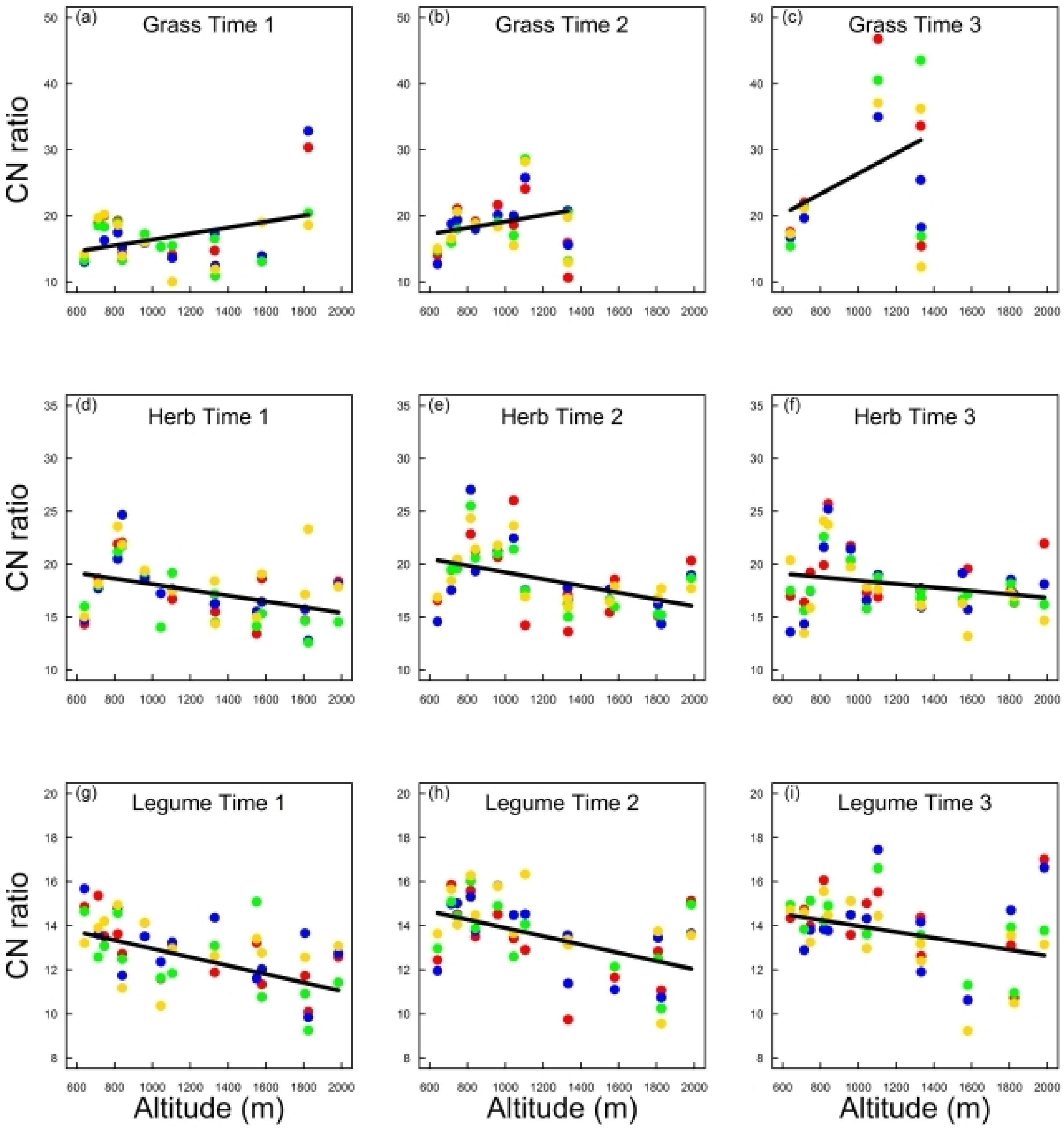

Fig. VI.3: Effects of altitude, treatment and their interaction on CN ratio of three plant guilds (grasses, legumes, forbs) at three sampling times (a - i). CN data are presented as mean values per study site and treatment. Points symbolise the study sites and different colours represent the four treatments (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 VI.1.

Herbivory

Herbivory rates were affected by the interaction of altitude, plant guild and sampling time (Table VI.2). Treatment and any interaction with treatment had no effect on herbivory (Fig.

VI.4a), 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 VI.4b). 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 VI.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

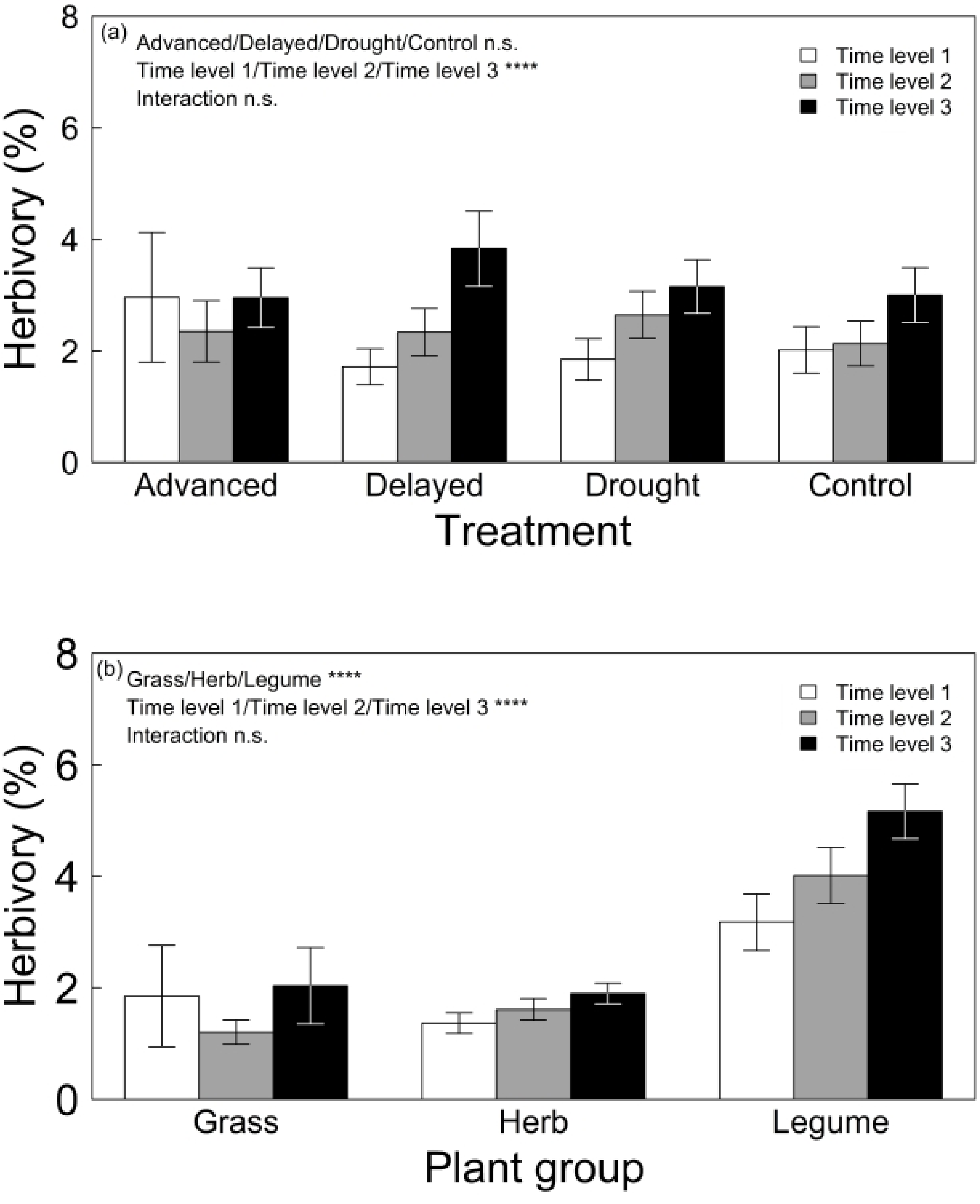

Fig. VI.4: Herbivory rates (%) as a function of (a) treatment (advanced snowmelt, delayed snowmelt, extreme drought, control) and (b) plant guild (grasses, legumes, forbs) at three sampling times (mean ± se). **** $P \leq 0.0001$, n.s. $P > 0.1$. Statistics see Table VI.2.

CN ratio - herbivory relationship

The CN ratio significantly affected herbivory rates (Fig. VI.5), in that the more leaf nitrogen the plants had (low CN ratio) the higher was the herbivory rate of the plants. We found no

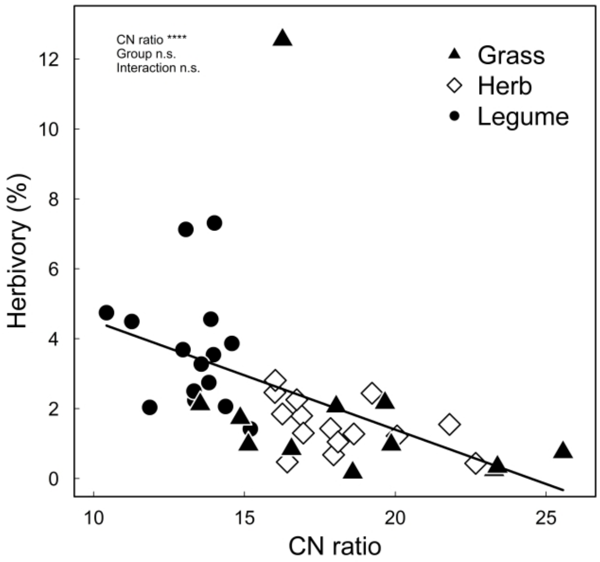

Fig. VI.5: Relation between herbivory rate (%) and CN ratio of three plant guilds (grasses, legumes, forbs). The black line shows the significant relation between herbivory and CN ratio. **** P ≤ 0.0001, n.s. P > 0.1.

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 and 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 fixating 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. 2005, 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.

Conclusions

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 none 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.

VII General Discussion

Altitudinal gradients

The first part of this dissertation provides a comprehensive analysis of the changes in bee communities along an environmental gradient (chapter III) and of the relative importance and interactions of a climatic gradient and different management regimes on species richness of vascular plants and their pollination types in alpine grasslands (chapter II). Knowledge about the phylogeny and ecology of communities along environmental gradients helps to disentangle the role of competition-driven processes and environmental filtering for community assembly. Given that climate is an important abiotic factor, patterns that are now found at low altitudes can be expected to shift to higher altitudes with ongoing global warming. A space-for-time substitution approach along the altitudinal gradient in combination with management effects enables the detection of species' adaptations to different climatic contexts, but also facilitates the development of management adaptation strategies to maintain species and biodiversity in mountainous regions.

In our study species richness of plants peaked at intermediate altitudes and was higher in grazed grasslands compared to non-managed grasslands. No significant interaction between management effects and climate was found. This indicates that the effect of management on species richness did not depend on temperature or 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.

In wild bee communities we found a linear decline in species richness and abundance with increasing altitude. Phylogenetic clustering increased with altitude, which implies that species in communities at higher altitudes are on average more closely related than species in communities at low altitudes. The proportion of social and ground-nesting species, as well as mean body size and altitudinal range of bee communities, increased with increasing altitude. The changes in the dominance of these traits in the communities reveal their adaptive value to given climatic conditions. The number of parasitic species, the number of generations per year and diet breadth did not respond to the climatic gradient and therefore seem not to play an important role for the performance of bees under changing climatic conditions. The mean geographic distribution of wild bee species decreased with increasing altitude. This finding underlines the function of mountains as hotspots of endemicity (Lomolino 2001).

Our results indicate that managing alpine grasslands by extensive grazing maintains high plant diversity over the full subalpine gradient, but management does not directly influence composition or species richness of bee communities. Rising temperatures with climate change might result in an upward shift of the diversity peak of plants and therefore result not only in reduced overall diversity due to reduced grassland area at higher altitudes (Rahbek 1995), but also in a changed composition of pollination traits in alpine plant communities with so far unknown consequences for the adaptive potential of mountainous ecosystems to rapid global warming. The linear decrease in wild bee species richness may originate from the fact, that the lower limit in our study was 600 m.a.s.l. and maximum bee diversity can be found in warmer climates than covered in our study (Nogues-Bravo et al. 2008). Global warming might therefore lead to an increasing bee species richness in mountainous region. We show that bee community assembly at high altitudes was dominated by environmental filtering effects, while the relative importance of competition increased at low altitudes. The critical characteristics needed for survival under adverse and fluctuating environmental conditions seem to have evolved in few phylogenetic lineages, and at the expense of competitive strength in most of the bee species in alpine communities (chapter III). Ongoing climate change might therefore increase bee species richness in temperate mountainous regions, but inherent phylogenetic and ecological species attributes at high altitudes pose a threat for less competitive alpine specialists.

Integrating gradients and manipulative experiments

In the second part of the dissertation we pursued, in cooperation with colleagues in the FORKAST project, an integrated approach. We studied the effects of experimental climate treatments on essential ecosystem features along the altitudinal gradient. Experiments along altitudinal gradients can provide novel information about the response of plants, insects and their interactions to impacts of global climate change under different climatic contexts. The aims of the presented studies were to determine the impacts of climatic short-term or extreme events on flower phenology (chapter IV), the structure of plant-pollinator networks (chapter V), leaf CN ratios and herbivory rates (chapter VI) and to assess whether those impacts depend on altitude and therefore on the climatic context. To investigate these coherences, an experiment simulating advanced and delayed snowmelt as well as drought extreme events was conducted along an altitudinal transect (600-2000 m a.s.l.) in the Berchtesgaden National Park, Germany in 2010.

We found flower phenology to be strongly affected by altitude (chapter IV). Plant species showed diverse responses to the treatments but only few significant differences were found in the timing of phenophases between treatments. Averaged over all species, the timing of phenophases was advanced through earlier snowmelt. The response to later snowmelt was rather small: a delayed end of the flowering phase was detected in some species. Drought had no effect on plant phenology except for one species. Our results are in line with a recent review, showing that plant phenology responds to manipulated timing of snowmelt and that reactions differ between species groups (Wipf and Rixen 2010). The effects of advanced snowmelt were significantly greater at high than at low altitudes, but no significant influence of altitude on the effects of the other treatments was found. The response of flower phenology to the altitudinal gradient and to the advanced snowmelt treatment declined through the season and the length of flowering duration was not significantly influenced by treatments.

How mutualistic plant-pollinator networks change along the altitudinal gradient and whether their susceptibility to global warming depends on the environmental context was analysed in chapter V. We found an influence of altitude on the network-structure. But other than the strong relationship found between plant phenology and altitude, we just detected a statistical relatively weak trend for a decreasing specialisation and therefore increasing complexity in networks with increasing altitude. However this relationship has also been found in Andean plant-pollinator networks which are more randomly organized at higher altitudes under harsh abiotic conditions than networks at lower altitudes (Ramos-Jiliberto et al. 2010). The structures of mutualistic plant-ant networks have also been found to depend on the abiotic factors temperature and precipitation (Rico-Gray et al. 2011). In our study networks after advanced snowmelt or drought were more specialised especially at higher altitudes compared to control plots, whereas delayed snowmelt showed no effect on the network structure. Our results (i) reveal that mutualistic communities are more fragile in cool environments (Encinas-Viso et al. 2012) and (ii) suggest that even small changes in plant phenology (chapter IV) can lead to shifts in the patterns in mutualistic interactions. Mutualistic networks therefore seem to be more sensible to climate change than can be expected by regarding the phenology of a single taxon alone. This finding is supported by a review in which indirect effects of climate change through changes in interactions on population and species fluctuations and extinctions have been shown to be higher than direct effects of climate change (Cahill et al. 2013).

In contrast to the effects we found in plant-pollinator networks no effect of the climate change treatments on leaf nutrient contents and herbivory rates in plants could be detected (chapter VI). Likewise, a study in sub-arctic Sweden reveals only small effects of climate change manipulations on leaf nutrients and suggests only small impacts of phenotypic responses in plant-mediated nutrient cycling pathways and rates induced by climate change (Aerts et al. 2009). However, in our study the three functional plant groups forbs, legumes and grasses differed in CN ratios and herbivory rates and responded differently to altitude, with lower CN ratios for forbs and legumes (but not grasses) at higher altitudes. Additionally, we found the point in time when leafs were sampled during the growing season to affect herbivory rates. Plant species with the lowest CN ratios showed highest herbivory rates. Food plant quality decreased during the growing season and herbivores presumably compensated low food quality with increased consumption rates.

In our three studies on the combined effects of a climatic gradient and manipulative short-term climate experiments we detected an overall influence of the altitudinal and therefore climatic gradient on all the ecosystem compartments researched, but the strength of this relationship differed between study objects. We found the effects of the short-term treatments to depend strongly on the ecosystem feature studied. The climatic context played an important role for the effect of the treatment for plant phenology and plant-pollinator interactions, whereas herbivory rates and the CN ratios in plants seemed to be unaffected by treatments. This diversity in responses underlines the importance to study different taxa and processes to understand the consequences of climate change on ecosystems.

In the presented studies, responses, especially in plant phenology, were stronger to advanced snowmelt than to delayed snowmelt or drought. One reason for this pattern might be that the treatment intensities for drought and delayed snowmelt were to low. Snowmelt was delayed on average by only 1 day which is quite low compared to an advanced snowmelt of 27 days. Even though soil moisture after drought treatment was about 30 % lower, compared to control plots, the remaining soil-moisture of about 40 % was possibly still high enough to provide enough water for most plant species. However, as our drought treatment affected the structure of plant-pollinator networks in a similar extent as did advanced snowmelt the drought possibly affected other important traits of plants, important for pollination, such as the amount of produced nectar and pollen or flowery scents, more than flower phenology. A possibility to increase the intensity of the drought treatment would be to use sheet piling to seal the treatment plots against water in the soil outside the plots and to drain surface water. However this is a difficult task in alpine environments where rocks outcrop on almost every site. A possibility to increase the effect of delayed snowmelt would be to use glacier foil to delay snow melting. This is a rather expensive and time consuming method.

In our experiments we manipulated 4 x 4 m plots. These experiments affected plants, their phenology and probably also other traits (such as nectar or pollen production or plant defence induction). The mobile insects visiting these plants remain largely unaffected by the small-scale treatments. Effects on insects and interactions are therefore always indirect effects, mediated by changes in the plants, microorganisms or soil in the plots. These indirect effects are large in plant-pollinator systems, whereas they are small in plant-herbivore systems. A subsequent research could be to assess changes in the ecosystem in which the mobile insects are trapped and also manipulated.

The stronger effect of advanced snowmelt at high than at low altitudes on plant phenology and plant-pollinator networks might be a response to differences in treatment intensity across the gradient. Consequently, since shifts due to global warming in the date of snowmelt may be more pronounced at higher altitudes, they may also affect species more at higher than at lower altitudes. However the intensity of the drought was the same over the full gradient and the reaction in network properties was still larger at higher altitudes. It therefore seems that it is not just treatment intensity but also the interaction of short-term climatic events and the climatic context which are responsible for the extent of ecosystem responses.

Conclusions

In conclusion we found a maximum species richness in plants at intermediate altitudes between 1400 to 1500 m in the National Park Berchtesgaden whereas species richness in bees decreased linearly from low to high altitudes. For both, plants and bees we found that competition driven processes in community assembly are more important at low altitudes than at high altitudes where environmental filtering processes are more important in determining the assembly and phylogenetic structure of communities. With warmer climates, the importance of environmental filtering processes is reduced and competition driven processes can be assumed to increase in their importance. This could lead to i) a shift of the species richness maximum in plants towards higher altitudes. Consequently, the reduced grassland area at higher altitudes may lead to a climate-driven extinction debt in mountain ecosystems due to the species-area relationship (Kuussaari et al. 2009, Krauss et al. 2010); ii) a threat for alpine specialists in plants as well as in bees with high environmental tolerance but low competitive capacities. 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. However, the management types studied in this dissertation did not affect bee diversity. The results presented in this dissertation indicate that warmer climates will not only change species richness but also the assembly-rules for plant and bee communities depending on the species' functional traits. Contrasting altitudinal responses in the herbivory rates in plant guilds might also contribute to changes in the competitive interactions among these guilds with ongoing global warming (chapter VI).

Our investigations provide new insights in the resilience of different ecosystem features and processes towards climate change and how this resilience depends on the environmental context. All the studied ecosystem features reacted to long-term changes in climate along the altitudinal gradient. The food quality of plants for herbivores, measured as C:N ratio, as well as the herbivory rate, which was highly correlated with the C:N ratio, did not react to climatic short-term changes (extreme drought and shifts in the date of snowmelt). We found a rather low influence of drought events on the flowering phenology and only rather distinctive shifts in the date of snowmelt changed flowering phenology. Network-structures however were changed significantly by both drought and snowmelt timing via changes in the plants growing on the manipulated sites. It therefore seems that mutualistic interactions are more susceptible to short-term climate events than flowering phenology and antagonistic interactions such as herbivory. This partly supports the finding of Cahill et al. (2013) that climate change often affects the survival of populations and species by changes in their interactions. The responses to the short-term events especially in plant-pollinator networks but also in plant phenology depended on the climatic context. This shows that the climatic context is highly important for the responses and resilience of ecosystems to the consequences of climate change. However, to draw more general conclusions more empirical data is urgently needed and there is also a need for a more profound theoretical framework on the ecological mechanisms behind the different climate-driven changes in biodiversity and ecosystem functioning.

References

Aavik, T., U. Jogar, J. Liira, I. Tulva, and M. Zobel. 2008. Plant diversity in a calcareous wooded meadow - The significance of management continuity. Journal of Vegetation Science 19:475–484.

Abu-Asab, M. S., P. M. Peterson, S. G. Shetler, and S. S. Orli. 2001. Earlier plant flowering in spring as a response to global warming in the Washington, DC, area. Biodiversity and Conservation 10:597–612.

Aerts, R., T. V. Callaghan, E. Dorrepaal, R. S. P. Van Logtestijn, and J. H. C. Cornelissen. 2009. Seasonal climate manipulations result in species-specific changes in leaf nutrient levels and isotopic composition in a sub-arctic bog. Functional Ecology 23:680–688.

Amiet, F., A. Müller, and R. Neumeyer. 2001. Apidae 2. *Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha*. Schweizerische Entomologische Gesellschaft, Neuchâtel.

Auer, I., R. Böhm, A. Jurkovic, W. Lipa, A. Orlik, R. Potzmann, W. Schöner, M. Ungersböck, C. Matulla, and K. Briffa. 2007. HISTALP—historical instrumental climatological surface time series of the Greater Alpine Region. International Journal of Climatology 27:17–46.

Austrheim, G. 2002. Plant diversity patterns in semi-natural grasslands along an elevational gradient in southern Norway. Plant Ecology 161:193–205.

Ayres, M. P., and M. J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Science of The Total Environment 262:263–286.

Bale, J. S., and S. A. L. Hayward. 2010. Insect overwintering in a changing climate. Journal of Experimental Biology 213:980–994.

Bartomeus, I., J. S. Ascher, D. Wagner, B. N. Danforth, S. Colla, S. Kornbluth, and R. Winfree. 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. Proceedings of the National Academy of Sciences 108:20645–20649.

Bascompte, J., P. Jordano, and J. M. Olesen. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science 312:431–433.

Beck, J., F. Altermatt, R. Hagmann, and S. Lang. 2010. Seasonality in the altitude-diversity pattern of Alpine moths. Basic and Applied Ecology 11:714–722.

Beck, J., and V. Chey. 2008. Explaining the elevational diversity pattern of geometrid moths from Borneo: a test of five hypotheses. Journal of Biogeography 35:1452–1464.

Becker, A., C. Körner, J. Brun, A. Guisan, and U. Tappeiner. 2007. Ecological and land use studies along elevational gradients. Mountain Research and Development 27:58–65.

Behmer, S. T. 2009. Insect Herbivore Nutrient Regulation. Annual Review of Entomology 54:165–187.

Beier, C., C. Beierkuhnlein, T. Wohlgemuth, J. Penuelas, B. Emmett, C. Körner, H. de Boeck, J. H. Christensen, S. Leuzinger, I. A. Janssens, and K. Hansen. 2012. Precipitation manipulation experiments - challenges and recommendations for the future. Ecology Letters 15:899–911.

De Bello, F., J. Leps, and M. Sebastia. 2007. Grazing effects on the species-area relationship: Variation along a climatic gradient in NE Spain. Journal of Vegetation Science 18:25–34.

Beniston, M. 2003. Climatic change in mountain regions: a review of possible impacts. Climatic Change 59:5–31.

Beniston, M. 2012. Impacts of climatic change on water and associated economic activities in the Swiss Alps. Journal of Hydrology 412–413:291–296.

Bergamini, A., M. Peintinger, B. Schmid, and E. Urmi. 2001. Effects of management and altitude on bryophyte species diversity and composition in montane calcareous fens. Flora 196:180–193.

Bernal, M., M. Estiarte, and J. Peñuelas. 2011. Drought advances spring growth phenology of the Mediterranean shrub *Erica multiflora*. Plant Biology 13:252–257.

Berner, D., W. U. Blanckenhorn, and C. Körner. 2005. Grasshoppers cope with low host plant quality by compensatory feeding and food selection: N limitation challenged. Oikos 111:525–533.

Berner, D., C. Körner, and W. U. Blanckenhorn. 2004. Grasshopper populations across 2000 m of altitude: is there life history adaptation? Ecography 27:733–740.

Bersier, L. F., C. Banasek-Richter, and M. F. Cattin. 2002. Quantitative descriptors of food-web matrices. Ecology 83:2394–2407.

Blionis, G., and D. Vokou. 2001. Pollination ecology of *Campanula* species on Mt Olympos, Greece. Ecography 24:287–297.

Bloor, J. M. G., P. Pichon, R. Falcimagne, P. Leadley, and J.-F. Soussana. 2010. Effects of Warming, Summer Drought, and CO2 Enrichment on Aboveground Biomass Production, Flowering Phenology, and Community Structure in an Upland Grassland Ecosystem. Ecosystems 13:888–900.

Blüthgen, N., and A.-M. Klein. 2011. Functional complementarity and specialisation: The role of biodiversity in plant–pollinator interactions. Basic and Applied Ecology 12:282–291.

Blüthgen, N., F. Menzel, and N. Blüthgen. 2006. Measuring specialization in species interaction networks. BMC ecology 6:9.

Blüthgen, N., F. Menzel, T. Hovestadt, B. Fiala, and N. Blüthgen. 2007. Specialization, constraints, and conflicting interests in mutualistic networks. Current Biology 17:341–346.

Bock, J., C. Jolls, and A. Lewis. 1995. The Effects of Grazing on Alpine Vegetation - a Comparison of the Central Caucasus, Republic-of-Georgia, with the Colorado Rocky-Mountains, USA. Arctic and Alpine Research 27:130–136.

Bommarco, R., J. Biesmeijer, B. Meyer, S. Potts, J. Poyry, S. Roberts, I. Steffan-Dewenter, and E. Ockinger. 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. Proceedings of the Royal Society B-Biological Sciences 277:2075–2082.

Both, C., M. van Asch, R. Bijlsma, A. van den Burg, and M. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? Journal of Animal Ecology 78:73–83.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Bruun, H., J. Moen, R. Virtanen, J. Grytnes, L. Oksanen, and A. Angerbjorn. 2006. Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. Journal of Vegetation Science 17:37–46.

Bryant, J. A., C. Lamanna, H. Morlon, A. J. Kerkhoff, B. J. Enquist, and J. L. Green. 2008. Microbes on mountainsides: Contrasting elevational patterns of bacterial and plant diversity. Proceedings of the National Academy of Sciences 105:11505–11511.

Brys, R., R. P. Shefferson, and H. Jacquemyn. 2011. Impact of herbivory on flowering behaviour and life history trade-offs in a polycarpic herb: a 10-year experiment. Oecologia 166:293–303.

Bütof, A., L. R. von Riedmatten, C. F. Dormann, M. Scherer-Lorenzen, E. Welk, and H. Bruelheide. 2012. The responses of grassland plants to experimentally simulated climate change depend on land use and region. Global Change Biology 18:127–137.

Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Y. Ryu, G. C. Sbeglia, F. Spagnolo, J. B. Waldron, O. Warsi, and J. J. Wiens. 2013. How does climate change cause extinction? Proceedings of the Royal Society B: Biological Sciences 280.

Cane, J. H. 1987. Estimation of bee size using intertegular span (Apoidea). Journal of the Kansas Entomological Society 60:145–147.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12:693–715.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011a. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. Science 333:1024–1026.

Chen, W., Y. Wu, N. Wu, and P. Luo. 2011b. Variation in phenology and population distribution pattern of three alpine species along the snowmelt gradient.pdf. Bulletin of Botanical Research 31:206–212.

Chown, S. L., and K. J. Gaston. 1999. Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. Biological Reviews 74:87–120.

Chown, S. L., and K. J. Gaston. 2010. Body size variation in insects: a macroecological perspective. Biological Reviews 85:139–169.

Clarke, A., and K. P. P. Fraser. 2004. Why does metabolism scale with temperature? Functional Ecology 18:243–251.

Clarke, A., and K. Gaston. 2006. Climate, energy and diversity. Proceedings of the Royal Society B: Biological Sciences 273:2257–2266.

Colwell, R. K. 2009. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2. User's Guide and application.

Colwell, R. K., and D. C. Lees. 2000. The mid-domain effect: geometric constraints on the geography of species richness. Trends in Ecology & Evolution 15:70–76.

Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2004. The mid-domain effect and species richness patterns: What have we learned so far? American Naturalist 163:E1–E23.

Cooper, E. J., S. Dullinger, and P. Semenchuk. 2011. Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. Plant Science 180:157–167.

Cornelius, C., N. Estrella, H. Franz, and A. Menzel. 2013. Linking altitudinal gradients and temperature responses of plant phenology in the Bavarian Alps. Plant Biology 15:57–69.

Cornelius, C., A. Leingärtner, B. Hoiss, J. Krauss, I. Steffan-Dewenter, and A. Menzel. 2012. Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient. Journal of Experimental Botany 64:241–251.

Cornelius, C., H. Petermeier, N. Estrella, and A. Menzel. 2011. A comparison of methods to estimate seasonal phenological development from BBCH scale recording. International Journal of Biometeorology 55:867–877.

Cornwell, W. K., and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecological Monographs 79:109–126.

Crawley, M. J. 2007. The R Book1. Auflage. John Wiley & Sons, West Sussex.

Cronin, A. L. 2001. Social flexibility in a primitively social allodapine bee (Hymenoptera: Apidae): results of a translocation experiment. Oikos 94:337–343.

Culley, T., S. Weller, and A. Sakai. 2002. Evolution of wind pollination in angiosperms. Trends in Ecology & Evolution 17:361–369.

Curall, J. 1987. A transformation of the Domin scale. Vegetatio 72:81–87.

Defila, C., and B. Clot. 2005. Phytophenological trends in the Swiss Alps, 1951–2002. Meteorologische Zeitschrift 14:191–196.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences 105:6668–6672.

Devictor, V., C. van Swaay, T. Brereton, L. Brotons, D. Chamberlain, J. Heliola, S. Herrando, R. Julliard, M. Kuussaari, A. Lindstrom, J. Reif, D. B. Roy, O. Schweiger, J. Settele, C. Stefanescu, A. Van Strien, C. Van Turnhout, Z. Vermouzek, M. WallisDeVries, I. Wynhoff, and F. Jiguet. 2012. Differences in the climatic debts of birds and butterflies at a continental scale. Nature Climate Change 2:121–124.

Devoto, M., D. Medan, and N. H. Montaldo. 2005. Patterns of interaction between plants and pollinators along an environmental gradient. Oikos 109:461–472.

Devoto, M., M. Zimmermann, and D. Medan. 2007. Robustness of plant-flower visitor webs to simulated climate change. Ecol Austral 17:37–50.

Diamond, S. E., A. M. Frame, R. A. Martin, and L. B. Buckley. 2011. Species' traits predict phenological responses to climate change in butterflies. Ecology 92:1005–1012.

Diaz, S., M. Cabido, and F. Casanoves. 1998. Plant functional traits and environmental filters at a regional scale. Journal of Vegetation Science 9:113–122.

Dillon, M., M. Frazier, and R. Dudley. 2006. Into thin air: physiology and evolution of alpine insects. Integrative and Comparative Biology 46:49–61.

Dingle, H., and T. A. Mousseau. 1994. Geographic variation in embryonic development time and stage of diapause in a grasshopper. Oecologia 97:179–185.

De Dios Miranda, J., F. M. Padilla, and F. I. Pugnaire. 2009. Response of a Mediterranean semiarid community to changing patterns of water supply. Perspectives in Plant Ecology, Evolution and Systematics 11:255–266.

Dittmar, C., and W. Elling. 2005. Phenological phases of common beech (*Fagus sylvatica* L.) and their dependence on region and altitude in Southern Germany. European Journal of Forest Research 125:181–188.

Dormann, C., J. Fründ, N. Blüthgen, and B. Gruber. 2009. Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks. Open Ecology Journal 2:7–24.

Dunne, J., J. Harte, and K. Taylor. 2003. Subalpine meadow flowering phenology responses to climate change: Integrating experimental and gradient methods. Ecological Monographs 73:69–86.

Dunne, J., S. Saleska, M. Fischer, and J. Harte. 2004. Integrating experimental and gradient methods in ecological climate change research. Ecology 85:904–916.

Ellington, C. P. 1999. The novel aerodynamics of insect flight: applications to micro-air vehicles. Journal of Experimental Biology 202:3439 –3448.

Encinas-Viso, F., T. A. Revilla, and R. S. Etienne. 2012. Phenology drives mutualistic network structure and diversity. Ecology Letters.

Erschbamer, B., T. Kiebacher, M. Mallaun, and P. Unterluggauer. 2009. Short-term signals of climate change along an altitudinal gradient in the South Alps. Plant Ecology 202:79–89.

Fargione, J. E., and D. Tilman. 2005. Diversity decreases invasion via both sampling and complementarity effects. Ecology Letters 8:604–611.

Felde, V. A., J. Kapfer, and J. A. Grytnes. 2011. Upward shift in elevational plant species ranges in Sikkilsdalen, central Norway. Ecography.

Field, C. B., V. Barros, T. F. Stocker, D. Qin, D. J. Dokken, K. L. Ebi, M. D. Mastrandrea, K. J. Mach, G. K. Plattner, S. K. Allen, and others. 2012. Managing the risks of extreme events and disasters to advance climate change adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change Cambridge University Press, Cambridge, UK, and New York, NY, USA.

Field, R., B. A. Hawkins, H. V. Cornell, D. J. Currie, J. A. F. Diniz-Filho, J. F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, and others. 2009. Spatial species-richness gradients across scales: a meta-analysis. Journal of Biogeography 36:132–147.

Fitter, A., and R. Fitter. 2002. Rapid Changes in Flowering Time in British Plants. Science 296:1689–1691.

Foley, J., R. DeFries, G. Asner, C. Barford, G. Bonan, S. Carpenter, F. Chapin, M. Coe, G. Daily, H. Gibbs, J. Helkowski, T. Holloway, E. Howard, C. Kucharik, C. Monfreda, J. Patz, I. Prentice, N. Ramankutty, and P. Snyder. 2005. Global consequences of land use. Science 309:570–574.

Forister, M., A. McCall, N. Sanders, J. Fordyce, J. Thorne, J. O'Brien, D. Waetjen, and A. Shapiro. 2010. Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. Proceedings of the National Academy of Sciences of the

United States of America 107:2088–2092.

Forrest, J., and A. J. Miller-Rushing. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 365:3101–3112.

De Frenne, P., A. Schrijver, B. J. Graae, R. Gruwez, W. Tack, F. Vandelook, M. Hermy, and K. Verheyen. 2009. The use of open-top chambers in forests for evaluating warming effects on herbaceous understorey plants. Ecological Research 25:163–171.

Friedman, J., and S. Barrett. 2009. Wind of change: new insights on the ecology and evolution of pollination and mating in wind-pollinated plants. Annals of Botany 103:1515–1527.

Fukami, T., and D. A. Wardle. 2005. Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. Proceedings of the Royal Society B-Biological Sciences 272:2105–2115.

Gadagkar, R. 1990. Evolution of Eusociality: The Advantage of Assured Fitness Returns. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 329:17–25.

Galen, C. 2000. High and Dry: Drought Stress, Sex-Allocation Trade-offs, and Selection on Flower Size in the Alpine Wildflower *Polemonium viscosum* (Polemoniaceae). The American Naturalist 156:72–83.

Galen, C., and M. L. Stanton. 1995. Responses of Snowbed Plant Species to Changes in Growing-Season Length. Ecology 76:1546–1557.

Garibaldi, L. A., T. Kitzberger, and E. J. Chaneton. 2011. Environmental and genetic control of insect abundance and herbivory along a forest elevational gradient. Oecologia 167:117–129.

Gogala, A. 1999. Bee Fauna of Slovenia: Checklist of Species (Hymenoptera: Apoidea). Scopolia 42:1–79.

Götzenberger, L., F. de Bello, K. A. Brathen, J. Davison, A. Dubuis, A. Guisan, J. Leps, R. Lindborg, M. Moora, M. Partel, L. Pellissier, J. Pottier, P. Vittoz, K. Zobel, and M. Zobel. 2012. Ecological assembly rules in plant communities - approaches, patterns and prospects. Biological Reviews 87:111–127.

Grabherr, G., M. Gottfried, and H. Pauli. 1994. Climate effects on mountain plants. Nature 369:448–448.

Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 326:119–157.

Graham, C. H., J. L. Parra, C. Rahbek, and J. A. McGuire. 2009. Phylogenetic structure in tropical hummingbird communities. Proceedings of the National Academy of Sciences 106:19673–19678.

Grytnes, J. 2003. Species-richness patterns of vascular plants along seven altitudinal transects in Norway. Ecography 26:291–300.

Grytnes, J., and J. Beaman. 2006. Elevational species richness patterns for vascular plants on Mount Kinabalu, Borneo. Journal of Biogeography 33:1838–1849.

Grytnes, J., E. Heegaard, and T. Romdal. 2008. Can the mass effect explain the mid-altitudinal peak in vascular plant species richness? Basic and Applied Ecology 9:373–382.

Gutbrodt, B., K. Mody, and S. Dorn. 2011. Drought changes plant chemistry and causes contrasting responses in lepidopteran herbivores. Oikos 120:1732–1740.

Hansen, A. H., S. Jonasson, A. Michelsen, and R. Julkunen-Tiitto. 2005. Long-term experimental warming, shading and nutrient addition affect the concentration of phenolic compounds in arctic-alpine deciduous and evergreen dwarf shrubs. Oecologia 147:1–11.

Hegland, S., A. Nielsen, A. Lazaro, A. Bjerknes, and O. Totland. 2009. How does climate warming affect plant-pollinator interactions? Ecology Letters 12:184–195.

Heikkinen, R., M. Luoto, R. Virkkala, and K. Rainio. 2004. Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural–forest mosaic. Journal of Applied Ecology 41:824–835.

Hesse, E., and J. R. Pannell. 2011. Density-dependent pollen limitation and reproductive assurance in a wind-pollinated herb with contrasting sexual systems. Journal of Ecology 99:1531–1539.

Hill, J. K., H. M. Griffiths, and C. D. Thomas. 2011. Climate Change and Evolutionary Adaptations at Species' Range Margins. Annual Review of Entomology 56:143–159.

Hodkinson, I. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. Biological Reviews 80:489–513.

Hoiss, B., J. Gaviria, A. Leingärtner, J. Krauss, and I. Steffan-Dewenter. 2013. Combined effects of climate and management on plant diversity and pollination type in alpine grasslands. Diversity and Distributions:1–10.

Hoiss, B., J. Krauss, S. G. Potts, S. Roberts, and I. Steffan-Dewenter. 2012. Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. Proceedings of the Royal Society B: Biological Sciences 279:4447–4456.

Hollister, R. D., and P. J. Webber. 2001. Biotic validation of small open-top chambers in a tundra ecosystem. Global Change Biology 6:835–842.

Hooper, D. U., and P. M. Vitousek. 1998. Effects of Plant Composition and Diversity on Nutrient Cycling. Ecological Monographs 68:121–149.

Howe, H. F., J. S. Brown, and B. Zorn-Arnold. 2002. A rodent plague on prairie diversity. Ecology Letters 5:30–36.

Hoye, T. T., S. M. Ellebjerg, and M. Philipp. 2007. The impact of climate on flowering in the High Arctic - The case of Dryas in a hybrid zone. Arctic Antarctic and Alpine Research 39:412–421.

Huberty, A. F., and R. F. Denno. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. Ecology 85:1383–1398.

Inouye, D. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362.

Inouye, D., M. Morales, and G. Dodge. 2002. Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Nina, in the context of climate change. Oecologia 130:543–550.

Inouye, D. W. 2000. The ecological and evolutionary significance of frost in the context of climate change. Ecology Letters 3:457–463.

Inouye, D. W., and A. D. McGuire. 1991. Effects of Snowpack on Timing and Abundance of Flowering in *Delphinium nelsonii* (Ranunculaceae): Implications for Climate Change. American Journal of Botany 78:997.

Inouye, D. W., F. Saavedra, and W. Lee-Yang. 2003. Environmental influences on the phenology and abundance of flowering by *Androsace septentrionalis* (Primulaceae). American Journal of Botany 90:905–910.

Inouye, D., and F. Wielgolaski. 2003. High altitude climates. Pages 195–214 *in* M. Schwartz, editor. Phenology: An Integrative Environmental Science. Kluwer Academic Publisher, Dordrecht.

IPCC. 2007. Climate Change 2007: Synthesis Report: Working Groups I, II and III to the Fourth Assessment. Cambridge University Press, Cambridge.

IPCC. 2012. *Managing the risks of extreme events and disasters to advance climate change adaptation.* A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change. (C. Field, V. Barros, T. Stocker, D. Qin, D. Dokken, K. Ebi, M. Mastrandrea, K. Mach, G. Plattner, S. Allen, M. Tignor, and Midgley, Eds.). Cambridge University Press, Cambridge, UK, and New York, NY, USA.

Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. Science 317:58–62.

Jabot, F., R. S. Etienne, and J. Chave. 2008. Reconciling neutral community models and environmental filtering: theory and an empirical test. Oikos 117:1308–1320.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. The American Naturalist 101:233–249.

Jentsch, A., and C. Beierkuhnlein. 2008. Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. Comptes Rendus Geoscience 340:621–628.

Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. Frontiers in Ecology and the Environment 5:365–374.

Jentsch, A., J. Kreyling, J. Boettcher-Treschkow, and C. Beierkuhnlein. 2009. Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. Global Change Biology 15:837–849.

Jentsch, A., J. Kreyling, M. Elmer, E. Gellesch, B. Glaser, K. Grant, R. Hein, M. Lara, H. Mirzae, S. E. Nadler, L. Nagy, D. Otieno, K. Pritsch, U. Rascher, M. Schädler, M. Schloter, B. K. Singh, J. Stadler, J. Walter, C. Wellstein, J. Wöllecke, and C. Beierkuhnlein. 2011. Climate extremes initiate ecosystem-regulating functions while maintaining productivity. Journal of Ecology 99:689–702.

Johnson, D. M., U. Buntgen, D. C. Frank, K. Kausrud, K. J. Haynes, A. M. Liebhold, J. Esper, and N. C. Stenseth. 2010. Climatic warming disrupts recurrent Alpine insect outbreaks. Proceedings of the National Academy of Sciences 107:20576–20581.

Jones, J., W. Li, and S. Maberly. 2003. Area, altitude and aquatic plant diversity. Ecography 26:411–420.

Jones, T. C., and S. E. Riechert. 2008. Patterns of reproductive success associated with social structure and microclimate in a spider system. Animal Behaviour 76:2011–2019.

Kearns, C. A., D. W. Inouye, and N. M. Waser. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. Annual review of ecology and systematics:83–112.

Keller, F., and C. Körner. 2003. The Role of Photoperiodism in Alpine Plant Development. Arctic, Antarctic, and Alpine Research 35:361–368.

Kessler, M. 2009. The impact of population processes on patterns of species richness: lessons from elevational gradients. Basic and Applied Ecology 10:295–299.

Kissling, W., and G. Carl. 2008. Spatial autocorrelation and the selection of simultaneous autoregressive models. Global Ecology and Biogeography 17:59–71.

Klein, A. M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B: Biological Sciences 274:303–313.

Klotz, S., I. Kühn, and W. Durka. 2002. BIOFLOR - Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schriftenreihe für Vegetationskunde 38. Bundesamt für Naturschutz, Bonn.

Kondoh, M. 2001. Unifying the relationships of species richness to productivity and disturbance. Proceedings of the Royal Society B: Biological Sciences 268:269–271.

Konnert, V. 2004. Standortkarte Nationalpark Berchtesgaden. Nationalparks Berchtesgaden, Berchtesgaden.

Körner, C. 1989. The nutritional status of plants from high altitudes. Oecologia 81:379–391.

Körner, C. 1992. Response of alpine vegetation to global climate change. Catena Supplement 22:85–96.

Körner, C. 2003. Alpine plant life, 2nd edition. Springer, Berlin.

Körner, C. 2007. The use of "altitude" in ecological research. Trends in Ecology & Evolution 22:569–574.

Körner, C., and F. Miglietta. 1994. Long term effects of naturally elevated CO 2 on mediterranean grassland and forest trees. Oecologia 99:343–351.

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

Kudernatsch, T., A. Fischer, M. Bernhardt-Römermann, and C. Abs. 2008. Short-term effects of temperature enhancement on growth and reproduction of alpine grassland species. Basic and Applied Ecology 9:263–274.

Kudo, G., Y. Nishikawa, T. Kasagi, and S. Kosuge. 2004. Does seed production of spring ephemerals decrease when spring comes early? Ecological research 19:255–259.

Kühn, I., S. Bierman, W. Durka, and S. Klotz. 2006. Relating geographical variation in pollination types to environmental and spatial factors using novel statistical methods. New Phytologist 172:127–139.

Kuussaari, M., R. Bommarco, R. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, F. Roda, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2009. Extinction debt: a challenge for biodiversity conservation. Trends in Ecology & Evolution 24:564–571.

Laghari, A. N., D. Vanham, and W. Rauch. 2012. To what extent does climate change result in a shift in Alpine hydrology? A case study in the Austrian Alps. Hydrological Sciences Journal 57:103–117.

Lambert, A. M., A. J. Miller-Rushing, and D. W. Inouye. 2010. Changes in snowmelt date and summer precipitation affect the flowering phenology of *Erythronium grandiflorum* (glacier lily; Liliaceae). American Journal of Botany 97:1431–1437.

Llorens, L., and J. Penuelas. 2005. Experimental Evidence of Future Drier and Warmer Conditions Affecting Flowering of Two Co-occurring Mediterranean Shrubs. International Journal of Plant Sciences 166:235–245.

Lloret, F., A. Escudero, J. M. Iriondo, J. Martínez-Vilalta, and F. Valladares. 2012. Extreme climatic events and vegetation: the role of stabilizing processes. Global Change Biology 18:797–805.

Lomolino, M. 2001. Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography 10:3–13.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. Grime, A. Hector, D. Hooper, M. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. Wardle. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294:804–808.

Lurgi, M., B. C. López, and J. M. Montoya. 2012. Climate change impacts on body size and food web structure on mountain ecosystems. Philosophical Transactions of the Royal Society B: Biological Sciences 367:3050–3057.

Mac Nally, R. 1996. Hierarchical partitioning as an interpretative tool in multivariate inference. Australian Journal of Ecology 21:224–228.

Mac Nally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: The distinction between – and reconciliation of – “predictive” and “explanatory” models. Biodiversity and Conservation 9:655–671.

Machac, A., M. Janda, R. R. Dunn, and N. J. Sanders. 2011. Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. Ecography 34:364–371.

Malo, J. E., and J. Baonza. 2002. Are there predictable clines in plant-pollinator interactions along altitudinal gradients? The example of *Cytisus scoparius* (L.) Link in the Sierra de Guadarrama (Central Spain). Diversity and Distributions 8:365–371.

Marion, B., A. Bonis, and J. Bouzille. 2010. How much does grazing-induced heterogeneity impact plant diversity in wet grasslands? Ecoscience 17:229–239.

Marion, G. M., G. H. R. Henry, D. W. Freckman, J. Johnstone, G. Jones, M. H. Jones, E. Levesque, U. Molau, P. Mølgaard, and A. N. Parsons. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. Global Change Biology 3:20–32.

Mattson, W. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and systematics:119–161.

Mattson, W. 1987. Role of Drought in Outbreaks of Plant-Eating Insects. Bioscience 37:110–118.

Mauss, V. 1996. Bestimmungsschlüssel für Hummeln, 6th edition. Deutscher Jugendbund für Naturbeobachtung, Hamburg.

McCain, C. M. 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. Global Ecology and Biogeography 16:1–13.

McCain, C. M. 2009. Vertebrate range sizes indicate that mountains may be “higher” in the tropics. Ecology Letters 12:550–560.

McCain, C. M., and J. A. Grytnes. 2010. Elevational gradients in species richness. Encyclopedia of Life Sciences.

Meehl, G. A., T. F. Stocker, W. D. Collins, P. Friedlingstein, A. T. Gaye, J. M. Gregory, A. Kitoh, R. Knutti, J. M. Murphy, A. Noda, S. C. B. Raper, I. G. Watterson, A. J. Waver, and Z.-C. Zhao. 2007. Global climate projections. Pages 237–336 Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Meehl, G. A., and C. Tebaldi. 2004. More Intense, More Frequent, and Longer Lasting Heat Waves in the 21st Century. Science 305:994–997.

Meier, U. 2001. BBCH-Monograph. Growth stages of mono- and dicotyledonous plants. Blackwell Wissenschafts-Verlag Berlin, Berlin.

Memmott, J., P. Craze, N. Waser, and M. Price. 2007. Global warming and the disruption of plant-pollinator interactions. Ecology Letters 10:710–717.

Menzel, A., N. Estrella, and A. Testka. 2005. Temperature response rates from long-term phenological records. Climate Research 30:21–28.

Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Ahas, K. Alm-KüBler, P. Bissolli, O. Braslavská, A. Briede, F. M. Chmielewski, Z. Crepinsek, Y. Curnel, åSlöG Dahl, C. Defila, A. Donnelly, Y. Filella, K. Jatczak, F. MåGe, A. Mestre, øYvind Nordli, J. PeñUelas, P. Pirinen, V. RemišOvá, H. Scheifinger, M. Striz, A. Susnik, A. J. H. Van Vliet, F.-E. Wielgolaski, S. Zach, and A. Zust. 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12:1969–1976.

Michener, C. D. 2007. The Bees of the World, 2nd edition. Johns Hopkins Univ Pr, Baltimore.

Migliavacca, M., E. Cremonese, R. Colombo, L. Busetto, M. Galvagno, L. Ganis, M. Meroni, E. Pari, M. Rossini, C. Siniscalco, and U. Morra di Cella. 2008. European larch phenology in the Alps: can we grasp the role of ecological factors by combining field observations and inverse modelling? International Journal of Biometeorology 52:587–605.

Molau, U. 1997. Responses to natural climatic variation and experimental warming in two tundra plant species with contrasting life forms: *Cassiope tetragona* and *Ranunculus nivalis*. Global Change Biology 3:97–107.

Montoya, J. M., S. L. Pimm, and R. V. Solé. 2006. Ecological networks and their fragility. Nature 442:259–264.

Moser, D., S. Dullinger, T. Englisch, H. Niklfeld, C. Plutzar, N. Sauberer, H. Zechmeister, and G. Grabherr. 2005. Environmental determinants of vascular plant species richness in the Austrian Alps. Journal of Biogeography 32:1117–1127.

Moser, L., P. Fonti, U. Buntgen, J. Esper, J. Luterbacher, J. Franzen, and D. Frank. 2009. Timing and duration of European larch growing season along altitudinal gradients in the Swiss Alps. Tree Physiology 30:225–233.

Myers, N. 1996. Environmental services of biodiversity. Proceedings of the National Academy of Sciences 93:2764–2769.

Nogues-Bravo, D., M. Araujo, T. Romdal, and C. Rahbek. 2008. Scale effects and human impact on the elevational species richness gradients. Nature 453:216–219.

Oberdorfer, E., A. Schwabe, and T. Müller. 2001. Pflanzensoziologische Exkursionsflora für Deutschland und angrenzende Gebiete, 8th edition. Ulmer, Stuttgart.

Olesen, J. M., J. Bascompte, Y. L. Dupont, H. Elberling, C. Rasmussen, and P. Jordano. 2011. Missing and Forbidden Links in Mutualistic Networks. Proceedings of the Royal Society B: Biological Sciences 278:725–732.

Olesen, J. M., and P. Jordano. 2002. Geographic patterns in plant-pollinator mutualistic networks. Ecology 83:2416–2424.

Olff, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology & Evolution 13:261–265.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology 13:1860–1872.

Pärtel, M., L. Laanisto, and M. Zobel. 2007. Contrasting plant productivity-diversity relationships across latitude: The role of evolutionary history. Ecology 88:1091–1097.

Pauli, H., M. Gottfried, S. Dullinger, O. Abdaladze, M. Akhalkatsi, J. L. B. Alonso, G. Coldea, J. Dick, B. Erschbamer, R. F. Calzado, D. Ghosn, J. I. Holten, R. Kanka, G. Kazakis, J. Kollar, P. Larsson, P. Moiseev, D. Moiseev, U. Molau, J. M. Mesa, L. Nagy, G. Pelino, M. Puscas, G. Rossi, A. Stanisci, A. O. Syverhuset, J.-P. Theurillat, M. Tomaselli, P. Unterluggauer, L. Villar, P. Vittoz, and G. Grabherr. 2012. Recent Plant Diversity Changes on Europe’s Mountain Summits. Science 336:353–355.

Pellissier, L., K. Fiedler, C. Ndribe, A. Dubuis, J.-N. Pradervand, A. Guisan, and S. Rasmann. 2012. Shifts in species richness, herbivore specialization, and plant resistance along elevation gradients. Ecology and Evolution 2:1818–1825.

Pellissier, L., B. Fournier, A. Guisan, and P. Vittoz. 2010. Plant traits co-vary with altitude in grasslands and forests in the European Alps. Plant Ecology 211:351–365.

Peñuelas, J., I. Filella, X. Zhang, L. Llorens, R. Ogaya, F. Lloret, P. Comas, M. Estiarte, and J. Terradas. 2004. Complex spatiotemporal phenological shifts as a response to rainfall changes. New Phytologist 161:837–846.

Petanidou, T., W. N. Ellis, and A. C. Ellis-Adam. 1995. Ecogeographical patterns in the incidence of brood parasitism in bees. Biological Journal of the Linnean Society 55:261–272.

Pompe, S., J. Hanspach, F. Badeck, S. Klotz, W. Thuiller, and I. Kühn. 2008. Climate and land use change impacts on plant distributions in Germany. Biology Letters 4:564–567.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution 25:345–353.

Price, M. V., and N. M. Waser. 1998. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. Ecology 79:1261–1271.

Prieto, P., J. Penuelas, R. Ogaya, and M. Estiarte. 2008. Precipitation-dependent flowering of *Globularia alypum* and *Erica multiflora* in mediterranean shrubland under experimental drought and warming, and its inter-annual variability. Annals of Botany 102:275–285.

Prosi-CAD. 2011, November 17. Website für Freunde der aculeaten Hymenopteren. See http://www.aculeata.eu/

Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. Ecology 79:2581–2592.

Purcell, J. 2011. Geographic patterns in the distribution of social systems in terrestrial arthropods. Biological Reviews 86:475–491.

R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rafferty, N. E., and A. R. Ives. 2011. Effects of experimental shifts in flowering phenology on plant–pollinator interactions. Ecology letters 14:69–74.

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography 18:200–205.

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters 8:224–239.

Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. Conservation Biology 22:521–533.

Räisänen, J., and J. Eklund. 2012. 21st Century changes in snow climate in Northern Europe: a high-resolution view from ENSEMBLES regional climate models. Climate Dynamics 38:2575–2591.

Ramos-Jiliberto, R., D. Dominguez, C. Espinoza, G. Lopez, F. Valdovinos, R. Bustamante, and R. Medel. 2010. Topological change of Andean plant-pollinator networks along an altitudinal gradient. Ecological Complexity 7:86–90.

Regal, P. J. 1982. Pollination by wind and animals: ecology of geographic patterns. Annual Review of Ecology and Systematics 13:497–524.

Rico-Gray, V., C. Díaz-Castelazo, A. Ramírez-Hernández, P. R. Guimarães, and J. Nathaniel Holland. 2011. Abiotic factors shape temporal variation in the structure of an ant–plant network. Arthropod-Plant Interactions:1–7.

Rödel, H. G., W. Völkl, and H. Kilias. 2004. Winter browsing of brown hares: evidence for diet breadth expansion. Mammalian Biology - Zeitschrift für Säugetierkunde 69:410–419.

Rognli, O., N. Nilsson, and M. Nurminiemi. 2000. Effects of distance and pollen competition on gene flow in the wind-pollinated grass Festuca pratensis Huds. Heredity 85:550–560.

Rolland, C. 2003. Spatial and seasonal variations of air temperature lapse rates in Alpine regions. Journal of Climate 16:1032–1046.

Roscher, C., V. M. Temperton, M. Scherer-Lorenzen, M. Schmitz, J. Schumacher, B. Schmid, N. Buchmann, W. W. Weisser, and E. D. Schulze. 2005. Overyielding in experimental grassland communities – irrespective of species pool or spatial scale. Ecology Letters 8:419–429.

Rötzer, T., and F.-M. Chmielewski. 2001. Phenological maps of Europe. Climate Research 18:249–257.

Rowell, D. P. 2009. Projected Midlatitude Continental Summer Drying: North America versus Europe. Journal of Climate 22:2813–2833.

Roy, B. A., S. Güsewell, and J. Harte. 2004. Response of plant pathogens and herbivores to a warming experiment. Ecology 85:2570–2581.

Saha, S. K., A. Rinke, and K. Dethloff. 2006. Future winter extreme temperature and precipitation events in the Arctic. Geophysical Research Letters 33.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global Biodiversity Scenarios for the Year 2100. Science 287:1770 –1774.

Sanchez-Gonzalez, A., and L. Lopez-Mata. 2005. Plant species richness and diversity along an altitudinal gradient in the Sierra Nevada, Mexico. Diversity and Distributions 11:567–575.

Sanders, N. J., J. Lessard, M. C. Fitzpatrick, and R. R. Dunn. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecology and Biogeography 16:640–649.

Sangtarash, M. H., M. M. Qaderi, C. C. Chinnappa, and D. M. Reid. 2009. Differential responses of two < i>Stellaria longipes</i> ecotypes to ultraviolet-B radiation and drought stress. Flora-Morphology, Distribution, Functional Ecology of Plants 204:593–603.

Sardans, J., J. PeñUelas, M. Estiarte, and P. Prieto. 2008. Warming and drought alter C and N concentration, allocation and accumulation in a Mediterranean shrubland. Global Change Biology 14:2771–2771.

Sardans, J., A. Rivas-Ubach, and J. Peñuelas. 2012. The C:N:P stoichiometry of organisms and ecosystems in a changing world: A review and perspectives. Perspectives in Plant Ecology, Evolution and Systematics 14:33–47.

Sassi, C. de, O. T. Lewis, and J. M. Tylianakis. 2012. Plant-mediated and nonadditive effects of two global change drivers on an insect herbivore community. Ecology 93:1892–1901.

Scherber, C., N. Eisenhauer, W. W. Weisser, B. Schmid, W. Voigt, M. Fischer, E.-D. Schulze, C. Roscher, A. Weigelt, E. Allan, H. Beßler, M. Bonkowski, N. Buchmann, F. Buscot, L. W. Clement, A. Ebeling, C. Engels, S. Halle, I. Kertscher, A.-M. Klein, R. Koller, S. König, E. Kowalski, V. Kummer, A. Kuu, M. Lange, D. Lauterbach, C. Middelhoff, V. D. Migunova, A. Milcu, R. Müller, S. Partsch, J. S. Petermann, C. Renker, T. Rottstock, A. Sabais, S. Scheu, J. Schumacher, V. M. Temperton, and T. Tscharntke. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553–556.

Scheuchl, E. 2000. Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs, Band 1: Schlüssel der Gattungen und der Arten der Familie Anthophoridae, 2nd edition. Eigenverlag, Velden.

Scheuchl, E. 2006. Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs, Band 2: Schlüssel der Arten der Familien Megachilidae und Melittidae, 2nd edition. Eigenverlag, Velden.

Schleuning, M., J. Fründ, A.-M. Klein, S. Abrahamczyk, R. Alarcón, M. Albrecht, G. K. S. Andersson, S. Bazarian, K. Böhning-Gaese, R. Bommarco, B. Dalsgaard, D. M.

Dehling, A. Gotlieb, M. Hagen, T. Hickler, A. Holzschuh, C. N. Kaiser-Bunbury, H. Kreft, R. J. Morris, B. Sandel, W. J. Sutherland, J.-C. Svenning, T. Tscharntke, S. Watts, C. N. Weiner, M. Werner, N. M. Williams, C. Winqvist, C. F. Dormann, and N. Blüthgen. 2012. Specialization of mutualistic interaction networks decreases toward tropical latitudes. Current Biology.

Schmid-Egger, C., and E. Scheuchl. 1997. Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs, Band 3: Schlüssel der Arten der Familie Andrenidae, 1st edition. Eigenverlag, Velden.

Schwartz, M. 2000. Changes in North American spring. International Journal of climatology 20:929–932.

Smith, M. D. 2011. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. Journal of Ecology 99:656–663.

Solomon, S., G. K. Plattner, R. Knutti, and P. Friedlingstein. 2009. Irreversible climate change due to carbon dioxide emissions. Proceedings of the national academy of sciences 106:1704–1709.

Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller. 2007. Regional Climate Projections. Climate change 2007. The physical basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Sparks, T. H., E. P. Jeffree, and C. E. Jeffree. 2000. An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. International Journal of Biometeorology 44:82–87.

Spooner, D. E., and C. C. Vaughn. 2008. A trait-based approach to species' roles in stream ecosystems: climate change, community structure, and material cycling. Oecologia 158:307–317.

Stegen, J., B. Enquist, and R. Ferriere. 2009. Advancing the metabolic theory of biodiversity. Ecology Letters 12:1001–1015.

Stewart, I. T. 2009. Changes in snowpack and snowmelt runoff for key mountain regions. Hydrological Processes 23:78–94.

Stinson, K. A. 2004. Natural selection favors rapid reproductive phenology in *Potentilla pulcherrima* (Rosaceae) at opposite ends of a subalpine snowmelt gradient. American Journal of Botany 91:531–539.

StMUG. 2001. Nationalparkplan. (Bayerisches Staatsministerium für Landesentwicklung und Umweltfragen, Ed.). Munich, Germany.

Strong, D. R., J. H. Lawton, and R. S. (Sir.). 1984. Insects on Plants: Community Patterns and Mechanisms. Harvard University Press, Cambridge.

Theurillat, J.-P., and A. Guisan. 2001. Potential impact of climate change on vegetation in the European Alps: a review. Climatic change 50:77–109.

Thomas, C. D. 2010. Climate, climate change and range boundaries. Diversity and Distributions 16:488–495.

Thuiller, W., M. Araujo, and S. Lavorel. 2004. Do we need land-cover data to model species distributions in Europe? Journal of Biogeography 31:353–361.

Torp, M., J. Witzell, R. Baxter, and J. Olofsson. 2010. The effect of snow on plant chemistry and invertebrate herbivory: experimental manipulations along a natural snow gradient. Ecosystems 13:741–751.

Totland, O. 2001. Environment-dependent pollen limitation and selection on floral traits in an alpine species. Ecology 82:2233–2244.

Trenberth, K. E., P. D. Jones, P. Ambenje, D. Bojariu, D. Easterling, A. Klein Tank, D. Parker, F. Rahimzadeh, J. A. Renwick, M. Rusticucci, B. Soden, and P. Zhai. 2007. Observations: Surface and Atmospheric Climate Change. Pages 237–336 Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Tscharntke, T., A. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecology Letters 8:857–874.

Tyler, G. 2001. Relationships Between Climate and Flowering of Eight Herbs in a Swedish Deciduous Forest. Annals of Botany 87:623–630.

Tylianakis, J., R. Didham, J. Bascompte, and D. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363.

Tylianakis, J., T. Tscharntke, and O. Lewis. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. Nature 445:202–205.

Urban, M. C., J. J. Tewksbury, and K. S. Sheldon. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proceedings of the Royal Society B: Biological Sciences.

Vamosi, S. M., S. B. Heard, J. C. Vamosi, and C. O. Webb. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. Molecular Ecology 18:572–592.

Venn, S. E., and J. W. Morgan. 2007. Phytomass and phenology of three alpine snowpatch species across a natural snowmelt gradient. Australian Journal of Botany 55:450–456.

Vitasse, Y., S. Delzon, C. C. Bresson, R. Michalet, and A. Kremer. 2009. Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. Canadian Journal of Forest Research 39:1259–1269.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Weaver, T., and D. Collins. 1977. Possible effects of weather modification (increased snowpack) on *Festuca idahoensis* meadows. Journal of Range Management 30:451.

Webb, C., D. Ackerly, M. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33:475–505.

Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24:2098 –2100.

Welker, J. M., J. T. Fahnestock, P. F. Sullivan, and R. A. Chimner. 2005. Leaf mineral nutrition of Arctic plants in response to warming and deeper snow in northern Alaska. Oikos 109:167–177.

Westrich, P. 1989. Die Wildbienen Baden-Württembergs - Spezieller Teil. Ulmer Verlag, Stuttgart.

White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63:90–105.

Whitehead, D. 1969. Wind pollination in the angiosperms - evolutionary and environmental considerations. Evolution 23:28–35.

Wipf, S. 2009. Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. Plant Ecology 207:53–66.

Wipf, S., and C. Rixen. 2010. A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. Polar Research 29:95–109.

Wipf, S., C. Rixen, and C. Mulder. 2006. Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community. Global Change Biology 12:1496–1506.

Wipf, S., V. Stoeckli, and P. Bebi. 2009. Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. Climatic Change 94:105–121.

Wu, Z., P. Dijkstra, G. W. Koch, J. PeñUelas, and B. A. Hungate. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Global Change Biology 17:927–942.

Zapata, F., K. Gaston, and S. Chown. 2003. Mid-domain models of species richness gradients: assumptions, methods and evidence. Journal of Animal Ecology 72:677–690.

Ziello, C., N. Estrella, M. Kostova, E. Koch, and A. Menzel. 2009. Influence of altitude on phenology of selected plant species in the Alpine region (1971–2000). Climate Research 39:227–234.

Author Contributions

Chapter II

This chapter is published as

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*, DOI: 10.1111/j.1472-4642.2012.00941.x.

The work distribution among authors was as follows

BH, J.K. and ISD and conceived the ideas; BH and JG collected the data; BH analysed the data and interpreted the results; BH wrote the manuscript; JG, AL, JK and ISD proof-read the manuscript.

Acknowledgements

We thank David Inouye, Oliver Schweiger and Emily Martin for valuable comments on the manuscript; The Berchtesgaden National Park and the owners of the study sites for providing infrastructure and their allowance; Roland Kaiser and Thomas Eberl for plant species identification and Andrea Holzschuh and Marcell Peters for statistical discussions;

Funding

This study was performed within the framework of the joint research centre FORKAST and was funded by the "Bavarian Climate Programme 2020”.

Bernhard Hoiß
Julian Gaviria
Annette Leingärtner

Jochen Krauß
Ingolf Steffan-Dewenter

Chapter III

This chapter is published as

Hoiss, B., Krauss, J., Potts, S. G., Roberts, S. & Steffan-Dewenter, I. 2012 Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proceedings of the Royal Society B: Biological Sciences.* **279**, 4447–4456. (doi:10.1098/rspb.2012.1581)

The work distribution among authors was as follows

BH, JK and ISD designed the study; BH collected data, analysed data, performed phylogenetic analysis; BH, JK and ISD interpreted the results; SGP and SR provided trait data; BH wrote the first draft of the manuscript and all authors contributed to revisions.

Acknowledgements

We thank Annette Leingärtner, Alice Claßen and Michaela Bellach for valuable comments on the manuscript; The Berchtesgaden National Park and the owners of the study sites for providing infrastructure and their allowance; Peter Hartmann and Reiner Theunert for the verification of our bee identifications; Marcell Peters for statistical discussions.

Funding

This study was performed within the framework of the joint research center FORKAST and was funded by the "Bavarian Climate Programme 2020”

Bernhard Hoiß Simon G. Potts Stuart Roberts

Jochen Krauß Ingolf Steffan-Dewenter

Chapter IV

This chapter is published as

Cornelius, C., Leingärtner, A., Hoiss, B., Krauss, J., Steffan-Dewenter, I. & Menzel, A. 2012 Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient. *Journal of Experimental Botany* **64**, 241–251. (doi:10.1093/jxb/ers321)

The work distribution among authors was as follows

AL & BH selected the sites; AL, BH, JK & ISD designed the experiments; AL & BH set up the experiments; AL & BH measured and analysed explanatory variables (snow-depth, temperature , soil moisture); CC observed phenology and processed the data; CC performed statistical analysis; AM provided suggestions for experimental performance; BH, JK an AM provided suggestions for statistical analysis; CC wrote the manuscript; JK, ISD & AM proof-read the manuscript.

Acknowledgements

We thank Tim Sparks for his valuable comments on this paper. We also thank the Berchtesgaden National Park for providing infrastructure and Inga Eschenlohr for her field work.

Funding

The study was performed within the framework of the joint research centre FORKAST and was funded by the “Bavarian Climate Programme 2020”.

Christine Cornelius	Annette Leingärtner	Bernhard Hoiß
Jochen Krauß	Ingolf Steffan-Dewenter	Annette Menzel

Chapter V

This chapter is yet to be submitted

Hoiss, B., Krauss, J. & Steffan-Dewenter, I. in prep. Climatic context predicts resilience of mutualistic networks.

The work distribution among authors was as follows

BH, JK & ISD designed the experiments; BH selected the sites and set up the experiments; BH did the field work and determined plants, bees and hoverflies; BH performed statistical analysis and interpreted the results; BH wrote the manuscript; JK & ISD proof-read the manuscript.

Acknowledgements

We thank Emily Martin, Annette Leingärtner and Michaela Bellach for valuable comments on the manuscript; Annette Leingärtner for the great cooperation in planning and implementing our experiment; The Berchtesgaden National Park and the owners of the study sites for providing infrastructure and their allowance; Bernhard Merz, Hans-Peter Tschorsnig, Dr. Andreas Stark, Krzysztof Szpila, Sabine Prescher, Verner Michelsen and Dieter Doczkal for the *Diptera* determinations; Tine Cornelius, Inga Eschenlohr and Sergey Rosbakh for their help with snow shovelling and Julian Gaviria and Katharina Kallnik for carrying the aluminium tubes.

Funding

The study was performed within the framework of the joint research centre FORKAST and was funded by the “Bavarian Climate Programme 2020”.

Bernhard Hoiß Jochen Krauß Ingolf Steffan-Dewenter

Chapter VI

This chapter is yet to be submitted

Leingärtner, A., Hoiss, B., Krauss, J. & Steffan-Dewenter, I. in prep. Combined effects of extreme climatic events and altitude on food quality and herbivory rates of alpine plants.

The work distribution among authors was as follows

AL, BH, JK & ISD designed the experiments; AL & BH selected the sites and set up the experiments; AL did the field work; AL performed statistical analysis; BH supported statistical analysis; AL wrote the manuscript; BH, JK & ISD proof-read the manuscript.

Acknowledgements

We thank Gudrun Schneider for valuable comments on the manuscript; Andrea Hilpert for her help in the field; Andrea Hilpert and Matthias Jäger for analysing leaf CN ratios; The Berchtesgaden National Park and the owners of the study sites for providing infrastructure and their allowance; Tine Cornelius, Inga Eschenlohr and Sergey Rosbakh for their help with snow shovelling and Julian Gaviria and Katharina Kallnik for carrying the aluminium tubes.

Funding

This study was pursued within the framework of the joint research centre FORKAST and was funded by the “Bavarian Climate Programme 2020”. Annette Leingärtner also thanks the FAZIT-STIFTUNG for funding.

Annette Leingärtner Bernhard Hoiß Jochen Krauss

Ingolf Steffan-Dewenter

Acknowledgements

I thank Ingolf Steffan-Dewenter for the opportunity to work on a fascinating topic in the wonderful Alps, for the given supervision and motivation and for the uninterrupted funding. I thank Jochen Krauss for his supervision, his often motivating words and for many statistical and technical discussions. Prof. Dr. Tautz: thank you for your efforts in reviewing my doctoral thesis.

I thank the wonderful working group in Würzburg for the warm and constructive atmosphere. I thank Michaela Bellach, Emily Martin, Alice Claßen and Gudrun Schneider for many valuable comments on my manuscripts. Thanks also to Andrea Holzschuh for statistical discussions and Marcell Peters for statistical support and discussions about all the interesting topics in the research on altitudinal gradients.

Annette Leingärtner was the best colleague I could imagine. Thank you for the great cooperation in the project, for your immense work during the field seasons, for many talks and for your sunny character.

I thank Helmut Franz and the Berchtesgaden National Park for providing support, infrastructure and their allowance. The owners of the study sites outside the National Park for their cooperation and allowance.

I thank the FORKAST colleagues, especially Tine Cornelius, Sergey Rosbak and Gita Benadi. I enjoyed the cooperation with you. Annette Leingärtner, Tine Cornelius, Inga Eschenlohr and Sergey Rosbakh for their help with snow shovelling, Annette Leingärtner, Julian Gaviria and Katharina Kallnik for their help in carrying the heavy parts of our rainout-shelters.

Thanks to Andrea Hilpert for her help during the field season 2010 and for her and Arno Wielgoss' invaluable introduction into the "way of life" in Würzburg.

For their help in the identification of plants, bees, and flies I thank Roland Kaiser, Thomas Eberl, Peter Hartmann, Reiner Theunert, Bernhard Merz, Hans-Peter Tschorsnig, Andreas Stark, Krzysztof Szpila, Sabine Prescher, Verner Michelsen and Dieter Doczkal.

I thank the "Bavarian Climate Programme 2020" for the funding of the joint research centre FORKAST which made this dissertation possible.

Finally a hug to my parents and Eva-Maria for their constant support, patience and love.

Publication list

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*, 1–10. (doi:10.1111/j.1472-4642.2012.00941.x)

Hoiss, B., Krauss, J., Potts, S. G., Roberts, S. & Steffan-Dewenter, I. 2012 Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proceedings of the Royal Society B: Biological Sciences.* **279**, 4447–4456. (doi:10.1098/rspb.2012.1581)

Cornelius, C., Leingärtner, A., Hoiss, B., Krauss, J., Steffan-Dewenter, I. & Menzel, A. 2012 Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient. *Journal of Experimental Botany* **64**, 241–251. (doi:10.1093/jxb/ers321)

Hoiss, B., Krauss, J. & Steffan-Dewenter, I., in prep., Climatic context predicts resilience of mutualistic networks.

Annette Leingärtner, Bernhard Hoiss, Jochen Krauss, Ingolf Steffan-Dewenter, in prep., Combined effects of extreme climatic events and elevation on nutritional quality and herbivory rates of alpine plants.

Erklärung

Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Dissertation mit dem Titel "Effects of climate change, extreme events and management on plants, pollinators and mutualistic interaction networks" 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, 15.03.2013 Bernhard Hoiß

Lebenslauf

Name: Bernhard Hoiß

Geburtstag und Ort: 03.03.1981 in Bad Reichenhall, Deutschland

2009-2013 Promotion am Lehrstuhl für Tierökologie und Tropenbiologie der Universität Würzburg bei Prof. Dr. Ingolf Steffan-Dewenter, gerfördert vom "Klimaprogramm Bayern 2020"

2008 Anstellung in der Ökologieabteilung des Ingenieurbüros Dr. Blasy - Dr. Øverland Beratende Ingenieure GmbH & Co. KG in Eching am Ammersee

2006-2007 Diplomarbeit an der Universität Regensburg zum Thema: "Leben im Gletschervorfeld – populationsbiologische und -genetische Untersuchungen am Moos-Steinbrech (*Saxifraga bryoides*)" am Lehrstuhl für Botanik bei Prof. Dr. Poschlod.

2001-2007 Studium Biologie Diplom an der Universität Regensburg

2000-2001 Zivildienst (11 Monate)

2000 Abschluss der Allgemeinen Hochschulreife in Laufen