Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt

Professur für Ökoklimatologie

Performance of native and invasive plant species under climate change – phenology, competitive ability and stress tolerance

Julia Laube

Vollständiger Abdruck der von der Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt der Technischen Universität München zur Erlangung des akademischen Grades eines

Doktors der Naturwissenschaften

genehmigten Dissertation.

Vorsitzender:

Univ.-Prof. Dr. H. Schäfer

Prüfer der Dissertation:

1. Univ.-Prof. Dr. A. Menzel

2. Prof. Dr. T.H. Sparks (Coventry University, UK)

3. Univ.-Prof. Dr. S.S. Renner (Ludwig-Maximilians-Universität München)

Die Dissertation wurde am   30.04.2015   bei der Technischen Universität München eingereicht und durch die Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt am   16.06.2015   angenommen.

There are "enormously more invasions that never happen (…)

they meet with resistance"

(Elton, 1958)

Word cloud of this thesis, created at www.wordle.net.

Summary

Background and Objectives

Climate change and its expected impacts on ecosystems are among the ecological research topics that demand the most urgent attention. Plant invasions are regarded as a part of global change, which in turn will be affected by a changing climate.

We are aware that climate change will influence individual plant performance, and thus translate into community and ecosystem processes. Changes in average temperatures during the dormant and the growing seasons will have an effect on the timing of a plant's life-cycle and a plant's fitness. An earlier start of the growing season is anticipated to increase the exposure to spring frost events. An increased frequency and intensity of climatic extremes will influence survival, fitness, and reproduction of species. These changes will affect local communities and, in relation to changed competitive abilities of co-occurring species, might lead to changes in local abundance, occurrence, and finally species' range shifts or extinctions.

The focus of this thesis is to assess possible responses of invasive and native species to different facets of climate change. Special emphasis is placed on the influence of competition, seasonal aspects, and climate variability. This cumulative thesis encompasses five publications, which contribute to the following main questions:

- How will invasive plant species respond to changes in winter and spring temperatures and climatic variability?

- Will changes in competitive ability influence invasion processes with climate change?

- Do the seasonal/temporal niches of native and invasive species differ, and is this relevant?

Methods

To address these questions, mainly experimental studies were conducted.

This thesis used climate chamber experiments to assess the possible influence of climate change on the spring phenology of 36 native and invasive woody species. Twigs, harvested at three different dates during winter, were kept in water bottles under three different day lengths, and their spring development until budburst was observed (twig method). Thus, a factorial setting investigated the effects of shortened winter conditions (chilling) and photoperiod on the time needed until budburst (expressed as thermal time / forcing requirement).

A second study was conducted to assess the influence of air humidity on the spring phenology of eleven woody species. The study used the twig method in climate chambers with contrasting air humidities to assess the influence of this factor on the timing of budburst. A further experiment, using bare twigs (without water supply from the vascular tissue) under high air humidity assessed the influence of foliar water uptake.

SUMMARY

A greenhouse experiment (third study) addressed the question of how climate extremes influence the performance of three native and three invasive herb species. The species were exposed to a sequence of frost, drought, and water-logging in five intensities. The climatic stresses were applied to two life-history stages (seedling and adult), and to plants exposed to mild or strong competition.

The triggers of elevational range limits of the native and two invasive balsam species in a mid-mountain range, the Bavarian Forest, were studied by a combination of a field experiment and trait measurements in the field (fourth study). While the trait measurements in natural populations focused on possible plastic responses and/or adaptations to elevation, the experiment studied germination, establishment and reproduction at four elevations. Balsams were sown with or without co-occurring native species to assess possible influences of competition.

The fifth study used a dataset of understorey species from the same mountain area to analyse community assembly rules, functional traits, and current environmental niches of the species to estimate the vulnerability of native species to climate change. The dataset encompassed 330 vegetation relevés and plot-specific environmental data, mainly on soil and climate. In total 24 plant functional traits, together with phylogenetic information of the species were analysed.

Wherever feasible, experiments were combined with field observations, and long-term climate or other environmental data were used to put the results into context.

Results

The first study showed that the spring phenology of woody species is less influenced by day length than previously thought – although effects of day length were detected for one third of the species, these were rather marginal. However, reduced chilling lengths delayed budburst markedly for almost all species, with pronounced species-specific differences. In comparison to climax species, pioneer as well as invasive species showed rather short chilling and small forcing requirements. This suggests that they will be able to react more flexibly to warming spring temperatures with climate change. Invasive species, on average, showed a comparable spring phenology to native species, which is not the case for ornamental, non-invasive woody species. Thus, an optimal timing of spring development might be a prerequisite for establishment success of woody species in a new range. The chronology of budburst among species changed considerably with chilling length. This suggests that warmer winters will have pronounced and species-specific impacts on the acquisition of light in early spring, which is likely to influence the fitness of individual species. The chronology of budburst on the other hand was highly comparable between the longest chilling treatment and field observations, which shows that the twig method is adequate to study the spring phenology of woody species.

Bud development patterns during this experiment indicated that air humidity is an additional, so far overlooked, factor influencing the spring phenology of woody species. These initial observations were confirmed by the results of the second study. Budburst occurred earlier under conditions with higher air humidity. Furthermore, bare twigs (without water supply from the vascular tissue) were able to develop to budburst under high air humidity, and a pronounced gain in fresh weight during the course of the experiment suggested that foliar water uptake

occurred. A re-calculation of the data obtained by the first study showed that a discrepancy between experiment and field budburst dates existed when calculated based on temperature. This discrepancy was considerably reduced for calculations based on absolute air humidity. Analysis of long-term climate data showed that the increase in air humidity is a reliable signal of spring. A literature search with respect to water supply and water related changes during winter dormancy and spring development revealed that moisture might be a limiting factor for developing buds. The results led to the question of whether, rather than temperature itself, the closely correlated absolute air humidity might be the primary influence for the spring development of woody species.

In the third study, invasive herb species showed no overall better resistance to climatic stress events than comparable native species. Differences between the congeneric or confamilial native and invasive species were absent or negligible with respect to mortality rates, biomass reduction, and flowering rate. However, the timing of the stress events was highly influential, and seedlings were more vulnerable than adults. Individuals also responded more strongly to the treatments when grown in competition. This shows that experiments on climatic stress events using adult individuals grown alone might not capture important responses. However, the response of invasive species to climatic stress did not differ from that of native species for differing life-history stages or in competition. Thus, the study did not support the idea that an increase in climatic extremes with climate change will favour invasive species due to a higher homeostasis or tolerance to stress.

The trait measurements in the fourth study among natural populations of the three balsam species along the elevational gradient in the Bavarian Forest led to contradictory results. While clear differences between the species were detected (especially with respect to size and frost sensitivity), overall little response to elevation was found. However, the response of plant size to elevation differed among species, and invasive species decreased more in size than the native congener. Equally, the phenological development of the native balsam was also least flexible with elevation. However, these higher trait plasticities of invasive species do not translate into higher fitness. The field experiment showed that all species germinated well above their actual elevational limits, and competition was not important. Establishment and reproduction seemed to be limiting factors. Low frost tolerances, simultaneous germination, and lack of a seed bank likely restrict both invasive species, and invasive himalayan balsam furthermore might not be able to reproduce every year due to the late start of flowering. Thus, both invasive species will be challenged by an increased exposure to spring frost events with climate change, while himalayan balsam might profit from higher growing season temperatures.

Analysis of the vegetation relevés along the elevational gradient (fifth study) in the same area showed that the native understorey communities are mainly influenced by growing season mean temperatures and tree cover. While high elevation species show adaptations that assist reproduction under unstable or short summer conditions, they show several traits that likely will be unfavourable with an increase of competitive pressure. However, there is no indication that the abundance or number of other understorey species restricts the high-elevation species, thus light-limitation triggered by the tree layer seems to be most important. Thus, an upward shift of the tree layer with climate change will pose a particularly serious threat. About one third of the

native understorey species seems to be vulnerable to climate change, no matter whether the current temperature or tree cover niche are considered.

Conclusions

To conclude, this thesis compiles somewhat contradicting results to the question of whether invasive species might profit from climate change. On the one hand, a more flexible spring development is expected to favour invasive woody species, and might give them competitive advantage over native woody species. For the invasive herb species, we found no support for the idea that they show a higher resistance to climatic extreme events. With respect to possible elevational range shifts, a highly nuanced interplay of frost resistance and germination, or frost resistance and reproduction seems to be important for invasive balsam species. Thus, they might profit from climate change, but to a lesser extent than anticipated by mean temperature increases.

Nevertheless, several results indicate that the interplay of phenology or development stage and climate variability will be especially important. The seasonal and temporal niches of invasive and native species differ, and these differences probably will translate into differing responses with respect to climate change. However, so far temporal aspects have been underestimated and should be included more rigorously in future research.

Contents

CONTENTS

1 Introduction

1.1 Climate change, competition and plant invasions

Evidence for ongoing climate change is abundant and unequivocal (IPCC, 2007; IPCC, 2013). Numerous reviews compiled information on ongoing changes in biotic systems attributable to global warming (Walther *et al.*, 2002; Root *et al.*, 2003; Parmesan & Yohe, 2003; Rosenzweig *et al.*, 2008; Bellard *et al.*, 2012). Yet, assessment, quantification and prediction of the impacts of climate change, as well as the search for adaptation strategies, remain among the most challenging research topics to date.

Invasions of non-native plant species pose serious threats to agriculture, forestry, human health, and the economy (Pimentel *et al.*, 2001; Colautti *et al.*, 2006a; Vilà *et al.*, 2010; EEA, 2012). In total, the amount of economic losses due to invasive species (plants, fungi, and animals) in the European Union is estimated to equal at least € 12 billion annually (EEA, 2012). Nevertheless, problems in Europe so far are smaller compared to other parts of the world, e.g. US$ 120 billion (Pimentel *et al.*, 2005). Invasions impact ecosystem functioning and services (Traveset & Richardson, 2006; Pejchar & Mooney, 2009; Vilà *et al.*, 2010; Strayer, 2012), and pose threats to native biodiversity (Vilà *et al.*, 2011; Pyšek *et al.*, 2012; Gilbert & Levine, 2013). Nevertheless, earlier studies (Wilcove *et al.*, 1998) likely overestimated the importance of invasions on species extinctions (Gurevitch & Padilla, 2004).

Indeed, plant invasions are seen as a part of human-induced global change (Vitousek *et al.*, 1997; Mack *et al.*, 2000), and the link between both topics is close. For example, recent definitions of "invasive species" account for predicted future range expansions of native species, and thus include climate change aspects (Webber & Scott, 2012). Nevertheless, cross-references between invasion and global change biology were minimal at least until 2005 (Davis *et al.*, 2005), and thus more research is needed to assess possible influences of climate change on invasions (Richardson & Pyšek, 2008; Hellmann *et al.*, 2008; Bradley *et al.*, 2010).

1.1.1 Facets of climate change

With global warming, increases in minimum, maximum, and mean temperatures are predicted (IPCC, 2013). While increased maximum temperatures might reach values above the optimum for biosynthesis, and lead to increased transpiration losses and heat stress, so far assessments for Central Europe expect an increase in heat waves to be especially important in natural ecosystems (IPCC, 2014; Kovats *et al.*, 2014). Increasing minimum temperatures and warmer winters are anticipated to influence plants considerably, e.g. via species individual absolute frost tolerances, increased winter transpiration, changed snow cover, and increased survival of herbivores or pests (Kovats *et al.*, 2014). Furthermore, increasing temperatures are expected to prolong the growing season (Chapter 1.2).

This already relates to another important facet of climate change: changes in temperature seasonality and variability. A higher frequency and intensity of temperature extremes are predicted with climate change (IPCC, 2013), which are known to influence plants heavily

(Easterling *et al.*, 2000; Jentsch *et al.*, 2007; Zimmermann *et al.*, 2009; Smith, 2011; Reyer *et al.*, 2013).

Moreover, changed precipitation patterns are predicted (IPCC, 2013), and an increased frequency and severity of summer droughts might also limit plant growth, favour drought-resistant species, or favour species with early life-cycle completion. An increase in the number and intensity of heavy precipitation and flood events (Huntington, 2006; Min *et al.*, 2011; Kovats *et al.*, 2014) will particularly challenge ecosystems in flood basins, or on steep slopes, but will also facilitate the spread of water-dispersed species. An increased frequency and intensity of winter storms in Central Europe (Kovats *et al.*, 2014) is likely to cause damage in forest ecosystems (Schelhaas *et al.*, 2003; Lindner *et al.*, 2010), but will equally contribute to an increase in dispersal distances for wind-transported seed. Given that many plant species are rather poor long-distance dispersers (Cain *et al.*, 2000; Malcolm *et al.*, 2002; IPCC, 2014), such extreme events are of high importance for range shifts, and thus will influence native and invasive species dispersal distances in the future (Higgins & Richardson, 1999; Cain *et al.*, 2000; Nathan, 2006; Reyer *et al.*, 2013).

Amongst other impacts, fertilisation effects and changes in water use efficiency are anticipated with increasing CO_2 levels. Moreover, changes in light quality due to changes in cloud cover, or changes in air humidity are also likely to influence plant species under climate change. Due to multiple changes of several environmental factors, anticipated species-specific responses, and known and unknown feedback-loops, reliable predictions are hard to attain.

Overall, we expect whole ecosystems, and related to this also large-scale ecosystem processes, to respond to some facets of climate change, e.g. changes in growing season lengths, or upward and poleward shifts of the tree line. At the finer species scale, the most common notion is that with climate change, we expect species to adapt, migrate or go extinct (Holt, 1990; Aitken *et al.*, 2008; IPCC, 2014). Generally, species' ability to adapt relates to the breadth of their environmental niche, as well as to their plasticity, which includes aspects of fast adaptation or genetic acclimatisation to new conditions. It also relates to species' ability to grow and reproduce under changed climate conditions, and to cope with changes in biotic interactions.

1.1.2   Competitive ability of plant species and climate change

The competitive ability of species is a major factor governing establishment success, growth, reproductive output, and thus abundance, persistence and distribution of plant species (Grime, 1979; Levine *et al.*, 2004; Maestre *et al.*, 2005; Brooker, 2006). However, the absolute importance of species interactions for large-scale processes is still under debate (Ricklefs, 2008; Brooker *et al.*, 2009). The importance of biotic interactions itself is anticipated to change with environmental conditions, known as stress-gradient hypothesis of competition (Bertness & Callaway, 1994; Choler *et al.*, 2001; Maestre *et al.*, 2009; He *et al.*, 2013). Together with niche differences, the individual competitive ability of species, in relation to the competitive ability of co-occurring plant species within a given community, foster coexistence or competitive exclusion (Mayfield & Levine, 2010). The competitive background each individual is facing usually is thought to be a matrix of the competitive abilities of all co-occurring species, named

the "biotic interaction milieu" (McGill *et al.*, 2006), although it has also been supposed that the dominant species, directly neighbouring species (Trinder *et al.*, 2013), or most similar species (Kraft *et al.*, 2007; Thuiller *et al.*, 2010) are most important.

The competitive ability of a species is context-sensitive, and shaped by different, flexible or inflexible traits and processes within a given environment. Thus, the competitive ability of a species has to be considered as highly flexible in several dimensions (Choler *et al.*, 2001; Daehler, 2003; Walther *et al.*, 2009; He *et al.*, 2013):

Niche response: The performance and competitive ability of each species is highest close to its optimum growing conditions (Ellenberg, 1953; McGill *et al.*, 2006) with respect to e.g. water, nutrients, temperature, and is supposed to decrease with distance from this optimum.

Stress response: The decrease in competitive ability with increasingly unfavourable conditions is not uniform. Often, a higher homeostasis can be found within species of intermediate or low optimum competitive ability, while species with very high competitive abilities at optimum growing conditions might tolerate stress least (He *et al.*, 2010).

Temporal response: Different development stages of plants differ in competitive ability (Foster & Gross, 1997; Mangla *et al.*, 2011). Often, plants in early developmental stages are less competitive than adults, which can at least partly be explained by size-dependent aspects of competition (Gaudet & Keddy, 1988; Schwinning & Weiner, 1998; Bennett *et al.*, 2013). Thus, both priority effects during establishment, and the individual development stage of competing species can be (Wilsey *et al.*, 2015), but are not necessarily (Cleland *et al.*, 2015) decisive. Not only development stages or individual age, but also the individual seasonal shape of species, e.g. differing length and timing of the growing seasons, is relevant for competitiveness (Willis *et al.*, 2008; Augspurger, 2008; Chuine, 2010; Cleland *et al.*, 2012).

A high competitive ability is often related to plant functional traits allowing fast growth, e.g. high seed mass, low specific leaf area, and large plant size (Gaudet & Keddy, 1988). However, the influence of traits themselves are only valid given a certain environmental setting. Herbs or grasses profit from all these effects in habitats with regular high disturbance regimes, whereas tree species, with much lower initial growth rates and high investment in permanent tissue, ultimately are more competitive in non-disturbed habitats. Climate change will influence the growing conditions of plants, and will show species-specific impacts on the competitive abilities due to niche, stress, and temporal dependence. Moreover, singular climatic events will influence the competitive ability due to its stress dependence, while the timing of singular events will influence the competitive ability via its temporal dependence.

1.1.3   Influence of competition on plant invasions

Not surprisingly, competitive ability was supposed to play a major role in the success of invasive species early on (Elton, 1958; Richardson & Pyšek, 2008; Gioria & Osborne, 2014). Indeed, many of the main hypotheses on plant invasions still relate to competition (Table 1), and either take the competitive ability of invasive species into account (competitiveness), or relate to the competitive ability of native communities repelling or hindering invasions (biotic resistance, invasibility). Overall, it is believed that biotic resistance can act as both invasion barrier, thus

hindering invasion, and regulator of invasive species' success, e.g. limiting growth, reproduction, dispersal, and impact (Levine *et al.*, 2004).

Table 1: Main hypotheses on plant invasions with direct or indirect relation to competition

Many of the mentioned hypotheses are also known with slightly differing sub-hypotheses, or under different names (Jeschke, 2014). The table is not a complete list of hypotheses on plant invasions, but rather gives an overview of the most widely known or discussed hypotheses. Comp: indicates whether competition is of direct or indirect importance to the hypothesis; Topic: indicates whether the hypothesis relates to invasiveness (as a trait of invasive species), invasibility (as a trait of recipient communities), or both. Expectation with climate change: ~ no general trend expected or known; - possibly disadvantageous for invasive species; + possibly advantageous for invasive species.

| Hypotheses | Explanation | Comp | Topic | expectation with changes in | |
				climatic means	climatic variability
Competitive Traits "Ideal Weed"	Invasive species are more competitive than average native species, which is related to high growth rates, size, and rapid resource-allocation (Elton, 1958; Rejmánek & Richardson, 1996; Daehler, 2003; van Kleunen *et al.*, 2010b).	direct	invasiveness	~	- trade-offs (e.g. size vs. stress resistance) + fast recovery
Novel Weapons	Invasive species show new traits, e.g. new chemical compounds like allelopathic substances, increasing the competitiveness of the invasive species, and decreasing competitiveness of native species (Callaway & Ridenour, 2004; Hierro *et al.*, 2005).	direct	invasiveness	~	~
Trait Plasticity	Invasive species show a higher trait plasticity, which might lead to competitive advantage (Daehler, 2003; Davidson *et al.*, 2011).	indirect	invasiveness	+ fast adaptation (phenotypic or genetic)	+ fast adaptation - trade-offs (e.g. size vs. stress resistance)
Broad Environmental Niche	Invasive species show a broader environmental niche (Rejmánek, 1996; Dukes & Mooney, 1999; Hellmann *et al.*, 2008), which should lead to higher competitive ability under many environmental conditions.	indirect	invasiveness	+	+
Profiteers of disturbance	High dispersal ability allows invasive species to invade rapidly into disturbed sites, and thus leads to relief of competition (Sher & Hyatt, 1999; Hood & Naiman, 2000; Colautti *et al.*, 2006b).	indirect	invasiveness	+ rapid range changes possible	+ rapid reach of damaged or disturbed habitats
Differing Temporal Niche "Window of Opportunity"	Invasive species show differing temporal niches, and thus profit from a temporal relief of competition, e.g. longer growing season in autumn (Shea & Chesson, 2002; Fridley, 2012).	indirect	both	+ if temporal niche is more flexible	+ if temporal niche is more flexible - if higher exposure to spring or autumn frosts

| Hypotheses | Explanation | Comp | Topic | expectation with changes in | |
				climatic means	climatic variability
Fluctuating-Resource	Invasive species react more flexibly to fluctuating resources, and thus the competitive ability increases temporarily. Invasive species take up newly emerging resources, or use fluctuating resources more efficiently (Sher & Hyatt, 1999; Davis *et al.*, 2000; Colautti *et al.*, 2006b).	indirect	both	~	+ increase in resource availability after climatic extremes
Enemy-Release	Release of enemies such as herbivores in the non-native range leads to higher biomass, leading to higher competitive ability (Maron & Vilà, 2001; Keane & Crawley, 2002; Colautti *et al.*, 2004).	indirect	both	- decline in specialised enemies of natives	~
	Release of enemies allows allocation of more resources to competitively advantageous traits, e.g. higher growth rates (Blossey & Nötzold, 1995; Callaway & Ridenour, 2004).			~	- trade-off with large plant size + faster recovery
	Native species have more enemies, and more specialised enemies, and thus suffer more strongly from enemies, and thus show a reduced competitive ability (Colautti *et al.*, 2004; Eppinga *et al.*, 2006).			- decline in specialised enemies of natives	~
Biodiversity-Invasibility	Native diversity increases biotic resistance. More diverse communities are less prone to invasions (Elton, 1958; Levine & D'Antonio, 1999).	direct	invasibility	+ reduced biotic resistance with loss of native species	+ reduced biotic resistance with loss of native species
Invasional Meltdown	Native communities get destabilised by the presence of invasive species, and thus are less resistant to further invasions (Simberloff, 2006).	indirect	invasibility	+ accelerated	+ accelerated
Invasibility-Related-ness Darwin's Naturalis-ation	Competition strength increases with relatedness, thus less closely related invasive species face smaller competition than more closely related natives (MacArthur & Levins, 1967; Richardson *et al.*, 2000; Webb *et al.*, 2002).	direct	invasibility	~	~

To conclude, competition by either invasive species, recipient communities, or both is anticipated to be of high relevance for invasion success. However, as discussed earlier (Chapter 1.1), and as shown in Table 1, both parameters are expected to change with climate change, and are highly flexible with respect to environmental conditions, seasonality, and timing.

1.1.4   Climate change and plant invasions

Plant invasions show a distinct global latitudinal pattern, with generally small numbers of invasive species in the tropics, an increase towards intermediate latitudes (Pyšek & Richardson, 2006), and a sharp drop off towards the highest latitudes (Lockwood *et al.*, 2007). Mirroring the decreasing number of invasive species at high latitudes, the amount and abundance of invasive

species also globally decrease with elevation (Pyšek *et al.*, 2002; Becker *et al.*, 2005; McDougall *et al.*, 2005; McDougall *et al.*, 2011; Marini *et al.*, 2013).

However, a growing number of invasive species, increasing invaded areas, and invasions at high latitudes and elevations, as well as increasing impacts have been observed since the 1970s (Lockwood *et al.*, 2007). The upward shift of invasive species to higher elevations (Pauchard *et al.*, 2009), and the poleward shift of invasive species (Clements & Ditommaso, 2011), recently even to Antarctic environments (Frenot *et al.*, 2005) suggest that ongoing climate change contributes considerably to this trend (Becker *et al.*, 2005; Pauchard *et al.*, 2009; Walther *et al.*, 2009). Generally, climate change is anticipated to ease several stages of the invasion process (Figure 1).
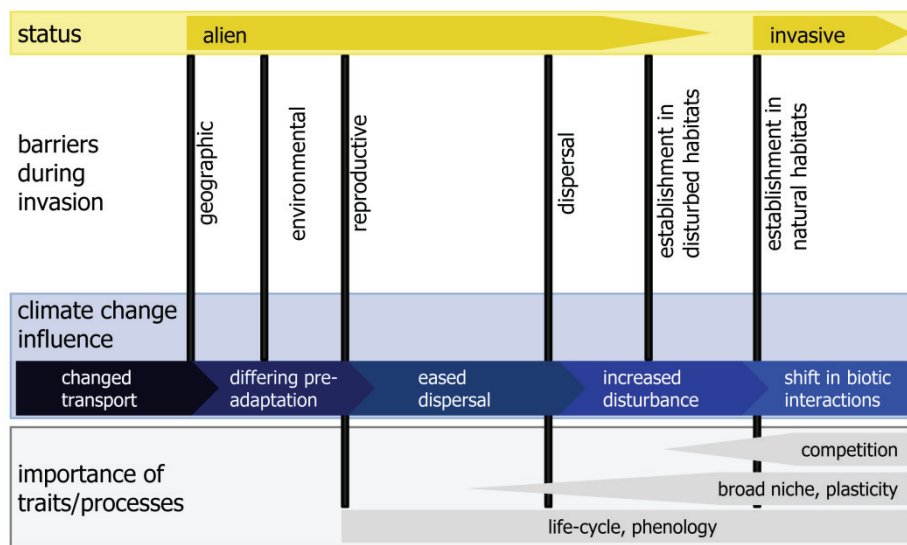
Figure 1: Stages of the invasion process.

Status: Alien status could be further divided into synanthropic, casual, and naturalised. The relevant barriers during the invasion process follow Richardson *et al.* (2000). The expected influence of climate change roughly follows Hellmann *et al.* (2008) and Theoharides & Dukes (2007). Other traits and processes are more important during earlier stages (e.g. attraction or usefulness of species to humans, propagule pressure), which are not shown.

We expect new and possibly invasive species to arrive due to changed transport routes (e.g. the North-East-Passage for species unintentionally transported in ballast water or containers), or due to novel introductions with adaptations of agriculture, forestry, and horticulture to climate change (Hellmann *et al.*, 2008; Walther *et al.*, 2009). However, several theoretical considerations (Table 1) support the idea that invasive species might also profit directly or indirectly from climate change in later stages of the invasion process (Dukes & Mooney, 1999; Thuiller *et al.*, 2007; Vilà *et al.*, 2007; Theoharides & Dukes, 2007; Hellmann *et al.*, 2008; Diez *et al.*, 2012).

Three basic assumptions principally lead to this expectation: niche of species, biotic interactions, and dispersal ability.

INTRODUCTION

- Fundamental niche and trait plasticity

The literature supposes that invasive species have broader ecological niches than native species (Dukes & Mooney, 1999; Richardson *et al.*, 2000; Vilà *et al.*, 2007; Theoharides & Dukes, 2007; Hellmann *et al.*, 2008). Among the pool of invasive species, more generalists, and fewer specialists occur (Dukes & Mooney, 1999; Theoharides & Dukes, 2007).

Whether fuelled by multiple introductions from formerly allopatric source populations, hybridisation, or rapid genetic drifts in the new range (Lambrinos, 2004; Whitney & Gabler, 2008; Clements & Ditommaso, 2011; Moles *et al.*, 2012; Alexander, 2013; Moran & Alexander, 2014), invasive species seem to overcome genetic bottlenecks. Invasive species can occupy broader climatic niches in the new range than in the native range (Broennimann *et al.*, 2007; Webber *et al.*, 2012), although this is under debate (Petitpierre *et al.*, 2012). However, a broad environmental niche in the native range also seems to be a prerequisite for successful invasions abroad (Richardson *et al.*, 2000; Vilà *et al.*, 2007; Pyšek & Richardson, 2007; Pyšek *et al.*, 2009b; Pyšek *et al.*, 2015), and the ability to occur in many different habitats in the native range partly explains the success in the invasive range (Rejmánek, 1996; Rejmánek, 2000). In line with this, invasive species are known to generally show a high phenotypic plasticity (Daehler, 2003; Davidson *et al.*, 2011), although this is not unequivocal (Theoharides & Dukes, 2007; Godoy *et al.*, 2011; Palacio-Lopez & Gianoli, 2011). It is not yet resolved whether high plasticity is a decisive trait per se, or if the aspects of rapid acclimatisation or evolution contribute to this (Lambrinos, 2004; Vilà *et al.*, 2007; Whitney & Gabler, 2008; Hellmann *et al.*, 2008; Bradley *et al.*, 2010; Clements & Ditommaso, 2011; Alexander, 2013). A fast adaptation to new environments seems to be one possible factor for the success of invasive species, which might relate to rather short generation times (Rejmánek, 1996; Hellmann *et al.*, 2008; Bradley *et al.*, 2010).

Many alien species of the British Isles seem to originate from warmer climates (Hulme, 2009), and thus a pre-adaptation to warmer temperatures has to be assumed. Moreover, the spread of many invasive species is known to be temperature limited (Richardson & Bond, 1991; Beerling, 1993; Willis & Hulme, 2002; Vilà *et al.*, 2007), and experiments reveal that at least some invasive species perform better under increased temperatures (Verlinden & Nijs, 2010). Thus, invasive species might profit from increases in temperature directly, or might profit with respect to broad niches and higher trait plasticity.

- Biotic interactions

Native species are thought to be adapted ideally to present state conditions (Thuiller *et al.*, 2007; Hellmann *et al.*, 2008), hence a decrease in competitive ability of native species with climate change is generally assumed. A reduced competitiveness of native species will reduce biotic resistance and thus will indirectly promote invasions (Thuiller *et al.*, 2007; Hellmann *et al.*, 2008; Diez *et al.*, 2012). Taken to the extreme, climate change might drive native species out of optimal growing conditions, but invasive species into optimal conditions. Experiments show that native species became less productive and competitive, and invasive species showed homeostasis at higher temperatures (Verlinden & Nijs, 2010), during heat waves (White *et al.*, 2001), or droughts (Collinge *et al.*, 2011; Jimenez *et al.*, 2011; Mason *et al.*, 2012). Native

species are more often involved in highly specialised biotic interactions (e.g. with pollinators), which are supposed to be highly vulnerable under changing conditions (Hellmann *et al.*, 2008). Invasive species are less involved, or lack highly specialised interactions, and hence are less vulnerable to diverging life-cycles, or decrease in abundance of the relevant interaction partner with climate change (Vilà *et al.*, 2007; Hellmann *et al.*, 2008).

Generally, a destabilisation of present ecosystems due to loss of climax species, and an increment of early successional species (Dukes & Mooney, 1999) might also favour invasive species, which often are pioneer species. Most invasive species are generalists, which will be favoured in comparison to more specialised native species (Dukes & Mooney, 1999; Theoharides & Dukes, 2007). Changes in present communities are anticipated to create empty niches prone to invasion, or more drastically, the creation of novel ecosystems (Hobbs *et al.*, 2009) is expected. Invasive species are able to invade novel environments (Bradley *et al.*, 2010).

Thus, the impacts of climate change on invasive species might be mediated via reduced performance and competitive ability of native communities (Brooker, 2006).

- Dispersal

Although results for many other traits are ambiguous, it seems clear that invasive species generally are highly successful dispersers (Theoharides & Dukes, 2007; Hellmann *et al.*, 2008; Bradley *et al.*, 2010). While for many native species the average dispersal distances, and dispersal speed supposedly will be too low to keep pace with warming (Malcolm *et al.*, 2002; IPCC, 2014), there is little doubt that invasive species will be able to keep up, whether naturally or by human assistance (Rejmánek, 1996; Richardson *et al.*, 2000; Vilà *et al.*, 2007). Apart from range shifts, many invasive species might also profit from high dispersal abilities whenever empty niches or destabilised ecosystems need to be reached first. This might favour invasive species with respect to climatic extremes (Diez *et al.*, 2012).

To sum up current concerns, many traits that contributed to invasive success of the species, such as a broad ecological niche and especially broad climatic tolerances, fast adaptation or acclimatisation to new environments, short generation times, and high dispersal ability, are thought to be highly advantageous in a changing climate.

1.2 Importance of phenology, seasonality, and timing

Phenology, which describes the timing of recurring stages in plant and animal life, has been recognised to be a key factor in ecosystem processes. Start and end of the vegetation period, which are mostly driven by climate, result in feedbacks to the climate system, via oxygen production, evapotranspiration, biogenic volatile organic compounds (BVOC) emission, and surface layer changes (Schwartz, 1992; Menzel, 2002; Peñuelas *et al.*, 2009; Richardson *et al.*, 2013). The seasonality of vegetation activity triggers carbon-uptake (Picard *et al.*, 2005; Piao *et al.*, 2008; Richardson *et al.*, 2010; Richardson *et al.*, 2012; Melaas *et al.*, 2013), ecosystem

respiration (Piao *et al.*, 2008; Migliavacca *et al.*, 2011), and gross primary and biomass production (Cramer *et al.*, 2001; Keenan *et al.*, 2012).

It is well known that phenological onset dates are highly responsive to temperature changes (Menzel & Fabian, 1999; Sparks *et al.*, 2000; Sparks & Menzel, 2002; Menzel *et al.*, 2006b; Cleland *et al.*, 2007; Thackeray *et al.*, 2010). Climate change will prolong the growing season, with both an earlier start in spring (Menzel & Fabian, 1999; Schwartz & Reiter, 2000; Peñuelas *et al.*, 2002; Menzel *et al.*, 2006b; Cleland *et al.*, 2007) and a later end of the vegetation period in autumn (Richardson *et al.*, 2010; Garonna *et al.*, 2014; Gallinat *et al.*, 2015; Keenan & Richardson, 2015, in press).

Temperature sensitivity and thus response to a changing climate differ for early and late phenophases (Menzel *et al.*, 2001; Menzel *et al.*, 2006a), ontogenetic development phases (Augspurger & Bartlett, 2003; Augspurger, 2008; Richardson & O'Keefe, 2009; Vitasse, 2013; Vitasse *et al.*, 2014b), trophic levels (Thackeray *et al.*, 2010), plant functional types (Rollinson & Kaye, 2012; Panchen *et al.*, 2014; Polgar *et al.*, 2014), but is also highly species-specific (Murray *et al.*, 1989; Heide, 1993; Willis *et al.*, 2008; Vitasse *et al.*, 2009; Richardson & O'Keefe, 2009; Caffarra & Donnelly, 2011; Basler & Körner, 2012; Bolmgren *et al.*, 2013; Bock *et al.*, 2014; Zohner & Renner, 2014; Panchen *et al.*, 2014).

An optimal timing of growth onset relates to competitive advantage, and generally trades off with the risk of spring frost damage (Körner & Basler, 2010; Lenz *et al.*, 2013; Vitasse *et al.*, 2014a; Vitasse *et al.*, 2014b). These factors all relate strongly to competitive ability and thus individual fitness of species (Walther, 2004; Willis *et al.*, 2008; Augspurger, 2008; Polgar & Primack, 2011; Cleland *et al.*, 2012). An optimal timing of flowering secures pollination success, and a simultaneous flowering within and across populations facilitates outcrossing, while a variability in flower timing, for example, enhances the chance of insect pollination, but needs to match temporal patterns of insect activity (Ehrlen, 2015). An early flowering is needed for large-sized fruits to ripen in time (Bolmgren & Cowan, 2008). The timing of fruit ripening is relevant for reproduction success, and for animal-dispersed seed also relates to dispersal distances due to differing availability of animals and offer of fruits (Ehrlen, 2015). Thus, phenology relates to reproduction success, dispersal, and ultimately distribution of species.

Apart from these well-studied phenomena, other seasonal patterns are also of great importance. For example, leaf senescence in autumn trades off with nutrient recapture, carbon uptake, and respiratory losses (Richardson *et al.*, 2010; Migliavacca *et al.*, 2011; Gallinat *et al.*, 2015). Seed dormancy and germination patterns relate to growing season length and seedling frost risk. Moreover, different development stages are more or less sensitive to frost (Lenz *et al.*, 2013), differ in response to competition (Fayolle *et al.*, 2009), and the need for resources and nutrients likely also changes with development stage (Trinder *et al.*, 2013). Therefore, the timing of the complete annual life-cycle needs to match climatic seasonality. To a large extent, the vulnerability of species to climate change is thus related to the ability to adjust the annual life-cycle to changing conditions. For example, annuals might suffer from spring frosts, summer droughts, or autumn frosts depending solely on germination and reproduction timing, while frost tolerance will be of secondary importance.

It has been recognised that seasonal patterns are related to the success of invasive species. Invasive species often show a longer flowering season (Pyšek & Richardson, 2007; Wolkovich & Cleland, 2011; Knapp & Kühn, 2012), and use the extended autumn niche better than many native species (Harrington *et al.*, 1989; Fridley, 2012). In spring, invasive tree species leaf out earlier than natives (Harrington *et al.*, 1989; Xu *et al.*, 2007; Polgar *et al.*, 2014), and invasive herb and grass species germinate earlier (Cleland *et al.*, 2015; Wilsey *et al.*, 2015) or react more flexibly to temperature changes than native species (Willis *et al.*, 2010; Hulme, 2011). This might allow them to take advantage of full light conditions before the closure of the canopy (Augspurger, 2008; Polgar *et al.*, 2014), or be advantageous as a temporal window of competition relief (Gioria & Osborne, 2014). Invasive species tracking climate change have been shown to increase in abundance (Willis *et al.*, 2010) and distribution (Hulme, 2011). Taken together, an optimal temporal niche is a pre-requisite for species survival, performance, and distribution under present conditions. However, the temporal niche of species itself is not a fixed trait, but a highly flexible, species-specific reaction to mainly climatic triggers.

1.3   Background and objectives

1.3.1   General knowledge gaps

The competitive ability of single species, together with the competitive ability of recipient communities, as well as the importance of competitive interactions in a given community will all be influenced by climate change. Thereof, changes in mean growing conditions, changes in climatic variability, and changes in the seasonal timing of climate patterns are thought to be influential.

Many facets of climate change are anticipated to promote current plant invasions. The establishment and spread of new invasive species, the spread of species already present into new ranges, and increased abundances of invasive species due to changed competitive interactions seem likely. With respect to competition, two different response levels to climate change will probably be most important, the individual response of the invasive species (invasiveness) and the responses of native communities (invasibility).

However, different facets of climate change might act in concert or counteract each other on each of these two levels. Hence complicated interactions between species, ecosystem, and changing conditions lead to a multitude of possible effects.

Many of the expectations on invasive plant responses are based on theoretical considerations or generalisations of hypotheses in invasion biology. For example, based on three recent reviews on this topic (Walther *et al.*, 2009; Bradley *et al.*, 2010; Diez *et al.*, 2012), only roughly one third of the references cite studies explicitly considering invasive species and climate change, while most of the references relate to studies on general processes during invasion, general traits of invasive species, or general studies on climate change impacts. Of these, only a few studies have an experimental basis, and experiments on invasive species with a climate change focus remain scarce. While many hypotheses in invasion research have only little empirical support (Moles *et al.*, 2012; Jeschke, 2014), knowledge on climate change impacts on plant invasions is highly theoretical and untested.

Given that high numbers of present invasive species and unknown numbers of future invasive species that will interact and compete with native biodiversity, there is little alternative to search for general, or at least transferable patterns. Therefore, this thesis aims to fill some of the research gaps regarding the response of native and invasive species to different facets of climate change.

1.3.2   Research questions

The objectives of this thesis are to assess climate-sensitive responses of invasive and native species, with a special focus on the influence of competition, seasonal, and temporal aspects of native and invasive plant performances. The studies contribute to the following main questions:

- How will invasive plant species respond to changes in winter and spring temperatures and climatic variability?

The studies in Chapters 3.1 and 3.2 assess how climate change will influence the spring phenology of native and invasive woody species. Chapter 3.1 studies how flexibly the species will respond to an expected shortening in chilling conditions and in day lengths with earlier springs. Chapter 3.3 explores whether invasive herb species tolerate climatic stress conditions better than related native species. The study in Chapter 3.4 analyses if and how climate change and climate variability might influence the elevational limits of native and invasive balsam species.

- Will changes in competitive ability influence invasion processes with climate change?

Chapter 3.3 investigates if competition changes the stress tolerance of species, and Chapter 3.4 analyses if the competitive ability of species changes along an elevational gradient. Whether the importance of competitive interactions in natural communities changes along that elevational gradient is assessed is Chapter 3.5. Furthermore, the question of how climate change might influence natural communities through changes in competitive abilities and functional traits is analysed (Chapter 3.5). The question of how the spring phenology of native and invasive woody species will react to climate change equally relates to the competitive ability of species (Chapter 3.1).

- Do the seasonal/temporal niches of native and invasive species differ, and is this relevant?

Two studies investigate the timing of the start of the vegetation period in spring for native and invasive woody (Chapter 3.1) and herb species (Chapter 3.4), and how these seasonal patterns will be affected by climate change. How the stress tolerance of native and invasive herb species changes with their life-cycle stage is further studied (Chapter 3.3). The study presented in Chapter 3.5 analyses functional traits related to life-cycle timing of native herb species with respect to elevation.

The rationale of this thesis is to compare the responses of invasive and related native species to different facets of climate change. More specifically, plant traits, with a special focus on timing, phenology, plasticity of traits, and the role of competition are the main focus.

1.3.3 Thesis outline

This cumulative thesis comprises five first-authored, peer-reviewed publications (Figure 2), three of them published (Chapters 3.1-3.3), and two in review stage (Chapters 3.4 and 3.5). Since all but one publication are based on my own experiments and field studies, the general introduction (Chapter 1) is followed by a short description of the general methodological approaches and considerations (Chapter 2). Chapter 3 compiles the publication abstracts. Chapter 4 summarises the key results and includes a general discussion with respect to other studies, and Chapter 5 provides an outlook. The references are listed in Chapter 6.
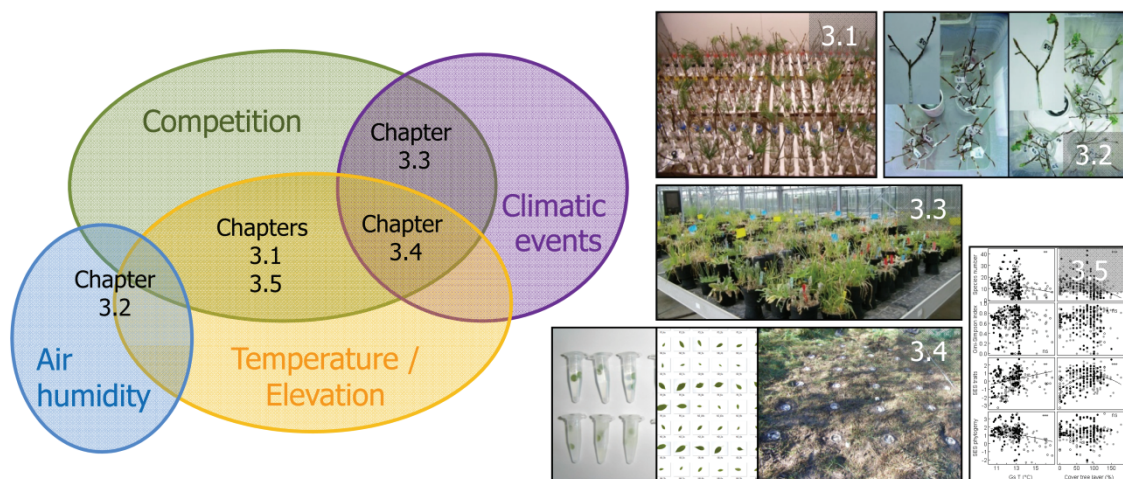

Figure 2: Main focus of the individual studies.

Abstracts of the individual publications are given in the respective chapters of this thesis (Chapters 3.1-3.5).

The first publication (Chapter 3.1) "Chilling outweighs photoperiod in preventing precocious spring development" (Laube *et al.*, 2014b) focuses on climate change effects on the timing of spring budburst dates of native and invasive tree and shrub species. The study questions how photoperiod and chilling influence the spring phenology of woody species, since both a reduction of chilling with warming winters, and a reduction of photoperiod with earlier springs are predicted with climate change. Upon publication, this was the first experimental study to work on a wide range of species (36 in total) in one single experimental setting. It was also the first publication that used a full factorial design to disentangle the separate effects of chilling and photoperiod. The high number of species investigated under identical conditions was possible due to the use of a newly re-discovered experimental method (twig method). It is based on using twigs as proxies for trees, and allows investigation of a broad variety of species and treatments under controlled conditions in climate chambers. Furthermore, the study introduced survival analysis as a useful statistical tool to analyse this type of data.

The second publication (Chapter 3.2) "Does humidity trigger tree phenology? Proposal for an air humidity based framework for bud development in spring" (Laube *et al.*, 2014a) resulted from unforeseen observations made during the experiment in Chapter 3.1. These observations

suggested that a possible driver of spring development dates, air humidity, was so far overlooked in phenological research. New experimental settings based on the twig method were used. The study questions if, how, and why air humidity might influence the spring phenology of trees, and hypothesises that not temperature itself, but the closely related absolute air humidity might be the main driver of phenological development in spring. While one experimental setting tested the influence of air humidity on the spring phenology of different woody species, another experiment was set up to test possible mechanisms. The study additionally uses long-term climate data to test if air humidity gives a reliable signal of spring.

The third publication (Chapter 3.3) "Tolerance of alien plant species to extreme events is comparable to that of their native relatives" (Laube *et al.*, 2015) examines if invasive herb species might profit from an increase in extreme events with climate change. The study analyses if three common invasive herb species, in comparison to closely related native species, show a higher homeostasis under temporally stressful climatic conditions. To address this question, a greenhouse experiment with five severity levels of multiple climatic stresses was conducted. Stress was applied at two different development stages of the plants, and at two differing settings (monoculture and competition), to assess differing responses with respect to the timing of the climatic stress events and the influence of competition.

The fourth publication (Chapter 3.4) "Small differences in seasonal and thermal niches influence elevational limits of native and invasive Balsams" (submitted to *Biological Conservation*) assesses possible climate change impacts on the current distribution limits of two invasive and the native balsam species at a mid-mountain range (Bavarian Forest). The study uses a combination of field study with measurements of plant functional traits and a field experiment on germination, establishment and reproduction patterns in relation to elevation and competition treatments. The focus was on trait plasticity, germination, and establishment patterns as well as competitive effects along the elevational gradient.

The fifth publication (Chapter 3.5) "Beyond thermal niches; the vulnerability of montane plant species to climate change" (submitted to *Journal of Vegetation Science*) examines possible climate change impacts on the native understorey flora in the Bavarian Forest. A comprehensive dataset of vegetation relevés was provided by the cooperation partner C. Bässler, National Park Bavarian Forest. The study examines this dataset using a combination of up-to-date methods in community ecology (including diversity indices, patterns of plant functional traits and phylogeny) and environmental niche analysis. This combination of analysis was used to assess the importance of competition along the gradient, to identify important plant functional traits, and to finally infer climate change effects on the species communities in the area.

2 Overview of methods

The research summarised in this thesis is mainly based on experimental studies, at times in combination with field observations (Figure 2 and Table 2). The studies used different approaches, experimental settings, and plant species, each with individual advantages and disadvantages, which are discussed in detail in the corresponding publications. However, the studies share several general considerations and methodological choices, which are summarised in the following chapters.

2.1 Terminology

- Invasive species

Invasive species are defined according to Richardson *et al.* (2000): Invasive species are species that occur outside their native range due to direct or indirect human influence, that persist and reproduce steadily over several generations also in natural and semi-natural habitats, and have spread considerably from their original point of introduction. Range shifts of native species due to climate change do not lead to invasive status (Webber & Scott, 2012). Invasive status is decoupled from negative impacts, although often used for political definitions (Richardson *et al.*, 2011), e.g. IUCN (2000), Hubo *et al.* (2007), Kettunen *et al.* (2009), since these are hardly practicable (type of impact, thresholds of impact size, currently unknown impacts, time-lag effects, etc.).

- Native species

Native species are species that evolved in, or spread into their current range without human assistance. I do not follow recent suggestions (van Kleunen *et al.*, 2010a) of dividing native species into native species that are and are not invasive elsewhere, which was supposed as valuable to distill "invasiveness" or "invasive traits". On the one hand, this distinction is not practicable, since for considerable parts of the world, reliable inventories of invasive species do not exist. On the other hand, not all species have (yet) been transported by humans to all possible destinations, and thus one cannot know whether a species would be invasive in regions they have not reached (yet).

- Competition

Throughout this thesis, competition is defined as the capture of essential and limited resources by plant individuals, at the same time restricting the availability of these resources to other individuals (Grime, 1979). Since resources are variable in space and time, competition does have spatial and temporal components (Gioria & Osborne, 2014). Plant individuals can compete for many different limited resources, and most prominent among them is competition for light, water, and nutrients, although many other competitive effects are known, e.g. competition for pollinators or seed-dispersing animals. In fact, only a very few resources are known to be unlimited, and thus are irrelevant for competition, such as atmospheric oxygen for dark-respiration in terrestrial ecosystems, or water in freshwater systems.

- Competitive ability

The competitive ability of individuals is the ability of species to compete and perform in a given environmental and biotic context. Phenotypic plasticity allows species to maintain fitness in unfavourable environments "jack of all trades", to increase fitness in favourable environments "master of some", or both (Richards *et al.*, 2006). Apart from the exploitation of limited resources, competitive ability is also influenced by other properties, e.g. allelopathic and facilitative effects, mycorrhizal networks, plant pathogens, and many other factors.

2.2 Methods in climate change research

A broad range of experimental settings is used to address questions on future climate change impacts on plants, from highly controlled climate chamber experiments, field studies controlling one or a few parameters, to uncontrolled experiments along natural climatic gradients and field observations.

Climate chamber experiments, as well as pot experiments in greenhouses allow the direct control of many environmental factors at a time, e.g. climate and soil conditions. Several designs are used to manipulate one or more climatic variables under field conditions, e.g. open top chambers or rain-out shelters. The least controlled experiments can be conducted along natural climatic gradients, for example with common garden or transplant experiments along latitudinal, elevational or precipitation gradients.

Generally, there is a trade-off between the level of control (and high reproducibility) and close-to-natural conditions with higher potential transferability to natural conditions (and low reproducibility) (Gibson *et al.*, 1999; Poorter *et al.*, 2012). While highly controlled settings usually are only available in highly artificial environments, the number and severity of unwanted side-effects increase. For example, pots in greenhouses or climate chambers restrict rooting volume, offer light quantities and qualities that differ from natural conditions, usually lack climatic variability, or are prone to unnatural insect infestations. On the other hand, highly controlled settings offer the possibility to disentangle confounding climatic effects, which is usually hard to attain under more close-to-natural conditions or when analysing field data. Close-to-natural conditions are advantageous with respect to more natural side-conditions, and thus are more likely to reproduce real-world climate change effects, but lack the possibility to clearly separate between influential parameters. Moreover, the lessened level of control also bears the risk of treatment failure, or the influence of unknown but important confounding factors.

Changes in mean values are often easier to apply than changes in variability. Many experimental facilities allow temperature manipulations, while for example soil water is more challenging to manipulate (Godfree *et al.*, 2013). Generally, experiments on large sized species are technically more challenging than experiments on small individuals, with respect to both treatment application and response measures.

Due to interactions among climatic variables, it is almost impossible to restrict experimental manipulations to one and only one climatic variable. For example, artificial temperature

increases are often associated with decreases in air and soil humidity, e.g. in open-top chambers or outdoor active warming systems (Marion *et al.*, 1997; Norby *et al.*, 1997). The use of rain-out shelters changes radiation and wind factors, while additional watering might lead to changes in soil nutrients due to washing-out or accidental addition of nutrients. Therefore, "hidden treatments" (Huston, 1997) are quite common, and need careful consideration.

Apart from the general experimental setting, a further choice with respect to the degree of change has to be made. Treatment conditions mimicking both climate change scenarios for a given site, or fixed changes (e.g. 2°C warming) are in use. Since the regionalisation of global climate change scenarios often only predict changes in mean values of a few climatic variables, their temporal resolution and variability often remain uncertain and vague (Beier *et al.*, 2012; Reyer *et al.*, 2013). While climatic conditions show a high inter- and intra-annual variability, experiments usually are restricted to a few differing treatments. Since non-linear responses to changed conditions are likely, the use of treatment gradients to assess quantitative differences per unit change are favourable (Cottingham *et al.*, 2005). Ideally, gradual manipulations are broad enough to obtain response-surfaces, and include tipping points to non-linear breakdown thresholds (Kreyling *et al.*, 2014).

Due to difficulties with climate change scenarios, and shortcomings of classical one-treatment-one-control ANOVA designs (Cottingham *et al.*, 2005; Beier *et al.*, 2012), the studies reported in this thesis used fixed treatment values, where possible with gradual changes (Table 2). In Chapter 3.1, three treatment conditions were chosen for both photoperiod and chilling length. Chapter 3.3 applied climatic stresses in increasing severity at five levels. Chapter 3.4 uses four different elevations for the experimental part, and two to three elevations for the field measurements. In Chapter 3.5, the complete elevational gradient was sampled.

2.2.1 Experiments

- Climate chamber experiment on winter and spring warming

So far much phenological research on tree species has been based on correlative studies, for example on data from long-term phenological ground observations, phenological gardens, or remote sensing (Primack *et al.*, 2015, in press). Since the phenology of seedlings differs from that of adult tree individuals (Vitasse, 2013), and experiments with adult individuals are difficult to conduct, so far only a few experimental studies have analysed the effects of controlled climatic treatments on the phenology of tree species.

Only recently, the use of twigs was re-discovered as a viable option to observe the spring phenology of tree species under manipulative treatments (Basler & Körner, 2012). In my thesis, twigs in climate chambers are used as proxies for trees (Vitasse & Basler, 2014). The influence of chilling, photoperiod and air humidity on the timing of budburst was assessed under controlled conditions (Chapter 3.1 and 3.2).

- Greenhouse experiment on climatic stress

In Chapter 3.3 the magnitude of several climatic events was manipulated directly within a greenhouse experiment. Spring frost, summer drought, and heavy autumn precipitation were

simulated. The main decision was to apply the events in the form of gradually increasing event intensity, and to include several different events at a time, which is widely anticipated to occur more often within one year and site in the future (Reyer *et al.*, 2013). In Chapter 3.4 natural frost events influenced the outcome of the experiments.

- Field study and field experiment at an elevational gradient

Elevational gradients offer a good option to study species performance under different, yet natural, climatic conditions. Nevertheless, elevational gradients of course comprise more than just climatic changes, and with special relevance to invasive species, they also subsume gradients with respect to decrease in infrastructure, decrease in land use intensity, or more general, decrease in human influence. Former studies on invasive species in mountain ecosystems focused on highly comparable, though rather strongly disturbed road-side communities, e.g. Alexander *et al.* (2009), Haider *et al.* (2010), Paiaro *et al.* (2011). On the one hand, this is a valid approach to minimise unwanted side-effects. On the other hand, results from road-side communities cannot easily be transferred to more natural habitats. In this thesis, an experiment at an elevational gradient was used to assess possible impacts of climate change on a pair of invasive species in rather natural conditions (Chapter 3.4).

2.2.2 Additional insights from field studies

While correlative studies on field data allow estimates of the influence of climatic factors, they do not permit the detection of causation. However, the transferability of experimental results to field conditions is often not possible, and the relevance of observed effects often remains unknown. Therefore, approaches that combine both correlative field studies and experimental approaches are highly valuable. The studies of this thesis try to combine both approaches wherever feasible (Table 2).

In Chapter 3.1, manipulated budburst dates were related to observed budburst dates in the field. The study in Chapter 3.2 used long-term climate data to assess the reliability of the air humidity spring signal. In Chapter 3.4, I used a dual approach of plant trait measurements and field experiment to study drivers of elevational range limits, and included long-term climatic data of the area to assess the possible importance of the observed patterns. Possible changes with respect to the native species pool in the area was analysed in Chapter 3.5.

Table 2: Approaches used in the individual studies

Chapter	Type experiment: *Treatments*	Number of treatment levels	Type field study	Additional data analysed
3.1	climate chamber experiment - twig method *photoperiod x chilling*	3 x 3 (each: short/inter-mediate/high)	phenological field observations	climate data (year of study), long-term climate data
3.2	climate chamber experiment - twig method box experiment - bare twigs *air humidity*	2 (each: low/high)	-	long-term climate data
3.3	greenhouse experiment *climatic stresses (frost, drought, water-logging)* *competition* *stress timing*	stress: 5 (none to high stress level) competition: 2 (low/high) stress timing: 2 (seedling/adult)	-	-
3.4	field experiment: *elevation*	4 (300m-1200m a.s.l.)	trait measurements at 3 elevations	climate data (year of study), long-term climate data
3.5	-	-	vegetation relevés (elevational gradient)	long-term climate and environmental data

2.3 Competition experiments

Since many competitive effects are dependent on plant size and density, a comparison of the competitive ability of different plant species is challenging. Plant species are different, and therefore a change in co-occurring species usually also changes the amount of competing biomass per experimental unit. Plants grown in competition are usually smaller then when grown alone, which is a mixture of effects of higher densities (per-capita competitive effects) or biomass (per biomass competitive effects) and differing competitive abilities of co-competing species. Maintaining equal numbers/amounts of individuals and biomass with changing species identity is generally very hard to attain (Lepš, 2005). Several experimental designs and indices to compare the performance of plant species in competition have been developed in the past (Weigelt & Jolliffe, 2003). There is a multitude of experimental designs that try to separate the effects of competing biomass or density from the effect of species identity, but these usually require an overly high number of control units and/or pilot studies, leaving few resources for the assessment of treatment effects. To give an example of this challenge, a recent study suggested the "opportunity to use groups of equivalent competitors, each one working at a different point of the gradient, but all in a comparable range of environmental suitability and potential size-asymmetry relative to neighbours. Once defined these equivalence conditions, … [the new index] is suited to measure how the relative weight of neighbour impact changes" (Mingo, 2014). Given these obstacles, problems in study designs reduce the interpretability of results (Connolly, 1988), and "a coherent approach to the difficulties posed by the study of competition" (Gibson *et al.*, 1999) is still not available (Damgaard & Fayolle, 2010; Mingo, 2014). This is especially true if, rather than competition, climate change impacts on competition,

not to mention effects of climate variability on competition, are the main focus of study. On the other hand, the basic attempt in parsing-out species identity versus biomass effects is still arguable, since higher amounts of competing biomass and density are likely to occur in competitive environments under natural conditions.

The competitive settings used in this thesis therefore used mildly competitive settings with monocultures of one target species in low densities, in contrast to highly competitive settings with mixtures of target species and competitors in total higher densities (Chapters 3.3 and 3.4). The species under comparison were chosen with care with respect to size (see Chapter 2.5).

Amongst other effects, climate change will change the timing and seasonality of climatic conditions. Therefore, temporal aspects of the competition treatments also need to be considered. On the one hand, it is known that different life-cycle phases of species vary with respect to competitive ability, e.g. seedlings generally show low competitive ability in comparison to adult individuals. Therefore, it has been supposed that ideal experimental settings use individuals in mixed life-history stages to simulate close to natural setting (Goldberg & Werner, 1983). However, the seasonality of most plant species is not random (for example timing of seedling emergence, sprouting, flowering), and shows distinct phenological patterns during the season. Moreover, a multiplication of several mixtures of development stages with other treatments is usually not operational. Therefore, it seems reasonable to restrict experiments to those phases expected to be most sensitive, such as early seedling stages (Chapter 3.3), or highly decisive, such as timing of reproduction (Chapter 3.4), germination (Chapter 3.4) or budburst (Chapter 3.1).

2.4   Measures of plant performance

In climate change research the main questions are often on the long-term outcome of plant performance, that is, long-term persistence and biomass development, long-term reproductive success, or changes in species' abundance and density. However, these responses are not obtainable via short-term experiments. Therefore, observed changes and patterns during short-term experiments can only be interpreted as proxies and tendencies that might translate into relevant long-term outcomes (Gibson *et al.*, 1999; Jolliffe, 2000).

The studies compiled in this thesis use different types of direct response measures. Biomass was measured as a proxy for vitality, growth and competitive ability (Chapters 3.3 and 3.4). Survival or death rates were analysed as a proxy for vitality and persistence (Chapters 3.3 and 3.4). Furthermore, the number of flowers or other reproductive organs were used as a proxy for seed output and thus reproductive success (Chapters 3.3 and 3.4).

It has been noted that fixed, often arbitrary points in time are bad predictors for long-term outcomes (Trinder *et al.*, 2013). In this thesis, biomass at the latest possible point during the vegetative period (peak biomass, (Trinder *et al.*, 2013)), death rates, and as far as possible measures on reproduction were included, to ensure that as many influential responses as possible were observed (Chapters 3.3 and 3.4).

Apart from these direct measures of plant performance, indirect methods were also used to assess possible competitive effects. The timing of budburst of woody species (Chapter 3.1 and

3.2) relates to growing season length, total carbon acquisition, and thus growth and competitive ability. The germination and flowering dates of herbs (Chapter 3.4) were analysed with respect to frost exposure and reproductive success. The abundance of species and functional traits were analysed in Chapter 3.5 as measures for species and traits performance along an elevational gradient.

2.5 Selection of model species

All studies summarised in this thesis use species as the main study subject. For many climate change related questions the use of entities below the species level are also of high interest and in use, and there is growing evidence that provenance differences can be decisive (Clements & Ditommaso, 2011; Alexander, 2013; Valladares *et al.*, 2014). However, knowledge on provenances, and the distribution limits of provenances are restricted to rather a few species (Valladares *et al.*, 2014). Comparably little is known on provenance differences, provenance limits and the relevance of provenance differences for most invasive species. Often even rough knowledge on source population range is missing (Moran & Alexander, 2014), and it remains unknown whether single or multiple introductions were involved.

As already discussed, many competitive interactions are known to be size-dependent (either size-symmetric or asymmetric), that is, larger individuals have competitive advantages over smaller individuals, since they are able to exploit linearly or over-linearly more resources per individual (Schwinning & Weiner, 1998; Bennett *et al.*, 2013). Nevertheless, many past competition experiments with invasive species tended to work with highly unequal pairs of species, often comparing highly competitive invasive, that is large, fast growing herbs, with threatened native species, thus often small species with low growth rates (Vilà & Weiner, 2004). Moreover, phylogenetic bias has to be considered (Pyšek & Richardson, 2007; van Kleunen *et al.*, 2010b). To avoid these confounding effects, the studies summarised in this thesis used native and invasive species of comparable size, and where possible with high taxonomic relatedness.

A further problem with artificially exposing species to climate change and/or competition treatments is a potential bias due to differing niches of the species. Moreover, if the main trigger for occurrence or abundance is neither limited by competition or climate, but human management, the usefulness of results for climate change predictions is highly limited. The studies used for native/invasive comparisons in this thesis therefore shared main habitat requirements, life form, and functional group.

With invasive species, further restrictions have to be considered with respect to the invasion stage. It is well known that the most influential parameters change during the different stages of the invasion process (Theoharides & Dukes, 2007; Hellmann *et al.*, 2008; Pyšek *et al.*, 2009a; Pyšek *et al.*, 2009b; Pyšek *et al.*, 2015). As stated, during earlier invasion stages other factors are more important, while competitive interactions gain importance only during the later stages of invasions, when spread into natural communities occurs (Figure 1). Since the actual stage is often not exactly known for each invasive species, the residence time can be used as a proxy for invasion stage (Pyšek & Jarošík, 2005; Williamson *et al.*, 2009). Therefore, the studies

compiled in this thesis used only invasive species in later stages of the invasion process, that is, with long residence time.

Concerning the experimental studies, further practical restrictions existed, e.g. availability of seed or samples, possibility to use the species in the desired way. For instance, the species used for the studies in Chapters 3.1 and 3.2 were more restricted by the necessity to obtain examples from highly comparable, and close-by sites. Additionally, the method used did not work out for invasive *Buddleja davidii* Franch., hence this species could not be studied. A table listing the focal invasive and native species used for the different studies is given in Appendix A.

3 Abstracts of individual publications

3.1 Chilling outweighs photoperiod in preventing precocious spring development.

It is well known that increased spring temperatures cause earlier onset dates of leaf unfolding and flowering. However, a temperature increase in winter may be associated with delayed development when species' chilling requirements are not fulfilled. Furthermore, photosensitivity is supposed to interfere with temperature triggers. To date, neither the relative importance nor possible interactions of these three factors have been elucidated. In this study, we present a multispecies climate chamber experiment to test the effects of chilling and photoperiod on the spring phenology of 36 woody species. Several hypotheses regarding their variation with species traits (successional strategy, floristic status, climate of their native range) were tested. Long photoperiods advanced budburst for one-third of the studied species, but magnitudes of these effects were generally minor. In contrast to prior hypotheses, photosensitive responses were not restricted to climax or oceanic species. Increased chilling length advanced budburst for almost all species; its effect greatly exceeding that of photoperiod. Moreover, we suggest that photosensitivity and chilling effects have to be rigorously disentangled, as the response to photoperiod was restricted to individuals that had not been fully chilled. The results indicate that temperature requirements and successional strategy are linked, with climax species having higher chilling and forcing requirements than pioneer species. Temperature requirements of invasive species closely matched those of native species, suggesting that high phenological concordance is a prerequisite for successful establishment. Lack of chilling not only led to a considerable delay in budburst but also caused substantial changes in the chronological order of species' budburst. The results reveal that increased winter temperatures might impact forest ecosystems more than formerly assumed. Species with lower chilling requirements, such as pioneer or invasive species, might profit from warming winters, if late spring frost events would in parallel occur earlier.

- *Contributions:*

Together with AM, THS, and NE, I developed the idea and experimental design for the study. Setting up the experiments and recording was done by myself, with considerable help of two students – Anja Thole and Clemens Kramer - who also assisted with data entry. The analysis was done by myself, with statistical guidance from JH and DPA. I wrote the manuscript, with contributions and revisions from all other authors. About 70% of the work was done by myself.

3.2 Does humidity trigger tree phenology? Proposal for an air humidity based framework for bud development in spring.

In temperate climates, temperature is considered the main driver of the spring development of plants. But our ability to predict onset dates remains imprecise, and our understanding of how plants sense temperature is vague.

From a climate chamber experiment on 9 tree species we present evidence that air humidity is an important, but previously overlooked, factor influencing spring phenology. A second experiment shows that water uptake by above-ground tissue is involved in the phenological development of trees. Analysis of climate data from several meteorological stations across Germany proves that the increase in air humidity after winter is a reliable signal of spring, i.e. less variable or susceptible to reversal compared to temperature. Finally, a third experiment suggests that winter dormancy and chilling might be linked to dehydration processes.

Taken together, our results suggest an alternative framework, which considers the dormancy and spring development of temperate trees as a response to air humidity, and not to temperature. The influence of air humidity on the spring phenology of temperate trees should improve phenological models, and help to design more realistic warming experiments. It should equally encourage physiological research to reappraise knowledge on temperature sensors in plants.

- *Contributions:*

I made the observation that air humidity influences bud development during the previous experiment, and developed the ideas and settings of the following experiments with AM and THS. Setting up the experiments and recording was done by myself, partly with the help of two students – especially Anja Thole, and also Clemens Kramer. The analysis was done by myself, with statistical advice of THS. NE provided climate data. I wrote the text, with revisions from all other authors. About 80% of the work was done by myself.

3.3 Tolerance of alien plant species to extreme events is comparable to that of their native relatives.

In addition to increases in temperature and CO_2, other features of climate change, such as extreme events and short-term variations in climate are thought to be important. Several factors indicate that invasive plant species might benefit from climate change via these features. However, apart from theory-based predictions, knowledge of the tolerance of invasive species to short-term climatic stress is very limited. We investigated whether three naturalized alien plant species in Central Europe, *Ambrosia artemisiifolia*, *Hieracium aurantiacum* and *Lysimachia punctata* perform better under stressful conditions than comparable native species. A greenhouse experiment with a fixed stress sequence of frost, drought and water logging was set up. We applied this stress treatment to two life history stages (seedling and adult plants), plants grown in monoculture (mild intraspecific competition) and in a highly competitive setting with intra- and interspecific competition. Whilst small differences in plant responses were detected the alien species overall were not more tolerant to stress. The responses of alien and native congeners/confamilials to stress in all treatments (monoculture, competition, adult, seedling) were similar, which indicates that stress thresholds are phylogenetically conserved. All species were more vulnerable to stress at the seedling stage and when subject to competition. Our data indicates that results obtained from experiments using only monocultures and one development stage are not appropriate for drawing generalisations about lethal thresholds. Moreover, rather abrupt species-specific thresholds exist, which indicates that a prediction of species responses based on just two stress levels, as is the case in most studies, is not sufficient.

- *Contributions:*

I developed the idea of the experimental design with contributions of AM, THS, KZ and NE. Setting up the experiments was done by KZ and me, recording and data entry was done by KZ and student assistance. Analysis was done by myself, with statistical advice from THS. I wrote the manuscript, with revisions from all other authors. About 70% of the work was done by myself.

3.4 Small differences in seasonal and thermal niches influence elevational limits of native and invasive Balsams.

Laube J, Sparks TH, Bässler C, Menzel A (submitted to *Biological Conservation*, 04/2015)

Recent studies suggest that invasive plant species have colonised mountains to previously unknown elevations, ongoing climate change being one possible driver. Thus, they might pose new threats to high-elevation ecosystems, which are often of high conservational value. Current range predictions are primarily based on climate niche models, while many other factors might also contribute.

We studied the species-specific elevational limits of one native (*Impatiens noli-tangere*) and two invasive balsams (*I. glandulifera* and *I. parviflora*) on a mid-mountain range in Germany. We used a combination of trait measurements and a field experiment to assess the relative importance of temperature, trait adaptations, and biotic interactions on elevational limits.

Results indicate that concurrent seedling emergence, low frost resistance and, for *I. glandulifera*, late flowering, are important contributors to elevational limits. Because of a lack of seed bank persistence, erratic spring and autumn frost events coinciding with the plants' annual life-cycles likely influence the upper limits of the invasive species strongly. The abundance of the species seems further limited by herbivory, mainly by molluscs.

Given that a highly nuanced interaction of phenological development and erratic frost events are important for range limits, predictions based solely on climatic mean values, such as mean temperatures, are unlikely to capture future invasion limits of balsam species.

Our results indicate that occasional occurrences of the species do not necessarily call for eradication actions, that management efforts might be most effective at intermediate elevations, and that any measure encouraging terrestrial molluscs will help to maintain biotic resistance.

- *Contributions:*

I developed the idea and setting of the study, with contributions of AM, THS and CB. Setting up the experiments, field measurements, and data entry was done by me with student help. I analysed the data, with statistical advice of THS. I wrote the manuscript, with revisions from all other authors. About 80% of the work was done by myself.

3.5 Beyond thermal niches; the vulnerability of montane plant species to climate change.

Laube J, Sparks TH, Menzel A, Heibl C, Müller J, Bässler C (submitted to *Journal of Vegetation Science*, 04/2015)

Climate change impact assessments for mountain ecosystems leave two important knowledge gaps. Firstly, most research focuses on the alpine belt, and thus a transferability of the results to isolated mid-mountain ranges remains questionable. Secondly, competitive exclusion is thought to be the main driver for range retractions at the lower elevational limits of species. However, to date studies of species changes in mountain ecosystems have not detected competitive exclusion, and predictions of species distribution models only include competitive processes very indirectly.

We analysed a comprehensive dataset of the understorey flora on a mid-mountain range in Central Europe to infer possible climate change impacts on plant species composition. We assessed species distributions and community assembly with respect to functional traits and phylogeny along the complete elevational gradient. Species vulnerabilities were derived from both their climatic and light niche (the whole mountain range is below the tree line), while community assembly and trait analysis were used to identify the main drivers in the area and to interpret results.

Overall, the regional species pool shows a high vulnerability to climate change, which is a result of expected range retractions at the lower elevational, competition-triggered limit of the species. The temperature gradient seems to select for several reproductive traits, and generally less complex reproduction patterns are found at colder sites. Changes in tree cover relate more strongly to many life-strategy traits, with larger plant sizes and more competitive leaf traits at sites with high tree cover.

Considering both their reproductive and life-strategy traits, montane species are expected to respond primarily to changes in tree cover, and probably less to diffuse and rather unpredictable changes in competition among understorey plants. While this might facilitate predictions for the understorey flora, our ability to predict future elevational limits of tree species remains limited. However, our estimates suggest that most of the suitable habitats of montane species will be limited to local refugia.

- *Contributions:*

The dataset was compiled by the National Park Bavarian Forest, especially by CB and JM. The idea for the analysis was developed by THS, CB and me. CH contributed the phylogenetic tree. I analysed the data, with advice from CB, THS and AM, and wrote the manuscript, with contributions and revisions from all other authors. About 70% of the work was done by myself.

4 Discussion

4.1 Key findings

4.1.1 Expected impacts of climate change on the spring phenology of native and invasive woody species

Climate change has already influenced the phenology of species (Menzel & Fabian, 1999; Schwartz & Reiter, 2000; Sparks & Menzel, 2002; Fitter & Fitter, 2002; Walther *et al.*, 2002; Peñuelas *et al.*, 2002; Menzel *et al.*, 2006b; Cleland *et al.*, 2007), and will continue to change species' phenology. Future spring onset dates are of high importance since they promise competitive advantages with early spring light gain and carbon assimilation (Picard *et al.*, 2005; Augspurger, 2008; Richardson *et al.*, 2010; Migliavacca *et al.*, 2011; Richardson *et al.*, 2012), but trade-off with increased risk of frost damage (Lechowicz, 1984; Inouye, 2008; Kreyling, 2010; Augspurger, 2013; Vitasse *et al.*, 2014b). Spring onset dates thus will influence individual fitness (Walther, 2004; Cleland *et al.*, 2012), future community structure (Willis *et al.*, 2008; Walther, 2010), and distribution of species (Chuine, 2010; Hulme, 2011).

The phenology of invasive species has been shown to differ from that of native species, and generally, a more flexible response of invasive species to changing temperatures has been suggested (Willis *et al.*, 2010) and refuted (Fridley, 2012). However, earlier leaf-out dates and later autumn leaf-fall probably contribute to the success of invasive species (Wolkovich & Cleland, 2011; Fridley, 2012; Wolkovich & Cleland, 2014).

> **Question 1:** What is the influence of photoperiod and chilling on budburst dates in spring? Do native and invasive species differ? (Chapter 3.1)

The spring phenology of tree species is known to be influenced mainly by high spring temperatures, "forcing" temperatures that trigger development (de Réaumur, 1735; Lechowicz, 1984; Chuine, 2010). Second, low winter temperatures are of influence, "chilling" temperatures that break dormancy (Murray *et al.*, 1989; Heide, 1993; Søgaard *et al.*, 2008). Third, photoperiod is relevant, with long day lengths starting or hastening spring development (Körner & Basler, 2010; Caffarra & Donnelly, 2011; Basler & Körner, 2012). Furthermore, other secondary factors are known, such as higher nutrient status (Jochner *et al.*, 2013c), autumn temperatures (Heide, 2003; Søgaard *et al.*, 2008; but see Chuine & Cour, 1999), reduced red to far red ratio of twilight (Linkosalo & Lechowicz, 2006), precipitation (Peñuelas *et al.*, 2002; Estiarte *et al.*, 2011; Fu *et al.*, 2014), or ontogenetic stage (Augspurger & Bartlett, 2003; Vitasse, 2013).

Yet, the relevance of species' chilling requirements and photosensitivity remain unclear, and both factors are, with differing effect sizes and parameterisations, input values in current phenological models. Contradictory results on the effects of both factors have been reported, and responses, especially at the species-level, remain largely vague (Körner & Basler, 2010; Chuine *et al.*, 2010; Polgar & Primack, 2011; Vitasse & Basler, 2013).

DISCUSSION

Thus, the first study (Chapter 3.1) addresses the question of how photoperiod and chilling influence budburst dates of native and invasive woody species in a full factorial climate chamber experiment (Table 2).

The results show that almost all woody species delayed development with reduced chilling length - on average by almost 3 weeks (200°Cdays). However, the magnitude of responses, and chilling requirements also differ considerably between species. Short photoperiods delay the spring development of one third of the species. However, effects of photoperiod are comparably small (on average 20°Cdays), and only detectable for not fully chilled individuals. Short chilling length leads to highly asynchronous spring development of the species. Thus, warming winters are anticipated to change the leaf-out chronology of communities, which might impact individual species fitness.

Overall, the flexibility of phenological responses is primarily triggered by species-specific chilling requirements and forcing needs. On average, invasive species show smaller chilling requirements than native species. On the other hand, forcing needs until budburst are highly comparable between invasive and native species, and as for native species, some invasive species react to photoperiod, and some do not. Non-native non-invasive species (exotic tree species grown for ornamental or other purposes) considerably differ in spring phenology from native and invasive species. This suggests that a high pre-adaptation of spring phenology might be a cue for invasion success.

Q 1.1: Is the flexibility of spring phenology related to life strategy or origin of species?

The results indicate that life strategy relates to phenological responses: Early successional species in general show lower chilling requirements, and also lower forcing requirements than climax species. Moreover, pioneer species tend to respond less to photoperiod than climax species, although this finding might be confounded with overall lower chilling requirements. The results show no relationship between the responses to chilling and photoperiod with respect to differing climatic conditions at the native range of the species.

Q 1.2: Will invasive woody species respond more flexibly to changing chilling and photoperiod conditions?

Since invasive species show a tendency towards less chilling requirements than native species, they might, on average, react more plastically to increasing winter and spring temperatures. This can, at least partly, be attributed to the fact that many invasive woody species are pioneer species (Rejmánek, 2000). As stated, effects of photoperiod are rather small, and thus photosensitivity of invasive species will probably not be decisive under current or future spring conditions.

In the meantime, a further study on a large set of woody species using the twig method was published (Polgar *et al.*, 2014). Although using a different experimental setting, and a different set of woody species (North American native and invasive species), the results highly mirror the results of Chapter 3.1. This study found no effect of photoperiod in 17 species, except for American beech (*Fagus grandifolia* Ehrh.), which is highly comparable to our results, where 1/3

of species responded significantly to photoperiod, but effects were rather marginal, except for European beech (*Fagus sylvatica* L.). The results of both studies are also comparable with respect to life strategy. Polgar *et al.* (2014) found both high chilling and forcing requirements for native tree species, native shrub species being intermediate, and invasive shrubs showing least chilling and forcing requirements.

A preceding study using the twig method showed that differences in photosensitivity exist between life-strategy types (Basler & Körner, 2012). Our study, based on a broader range of species, and with a full-factorial design of chilling and photoperiod treatments, supposes that these results were possibly biased towards not fully chilled climax species, and fully chilled early-successional species. We only found that individuals respond to photoperiod when not fully chilled. This suggests that woody species do not use day length to detect spring, as supposed earlier, e.g. Körner & Basler (2010), but rather to avoid an extraordinary delay in flushing due to lack of chilling after warm winter conditions.

Chapter 3.1 shows that, depending on an appropriate chilling length, the twig method mirrors the budburst sequence of species under natural conditions. According to Vitasse & Basler (2014), no significant difference in twig and tree spring development exists when kept under identical conditions. This reveals that the phenology of twigs under artificial conditions is a good proxy for the phenology of trees under natural conditions.

> **Question 2:** Are we on the right track to predict spring phenology with climate change? (Chapter 3.2)

While air humidity was proposed to influence the phenology of tree species in the tropics earlier (Do *et al.*, 2005; Jochner *et al.*, 2013a), this factor has been, so far, neglected for temperate woody species.

Phenological models, no matter how complex, are not able to predict budburst dates accurately (Fisher *et al.*, 2007; Richardson *et al.*, 2013), leave uncertainty with respect to model structure and parameterisation (Migliavacca *et al.*, 2012; Olsson & Jönsson, 2014), and predictions are usually biased (Blümel & Chmielewski, 2012). The knowledge on physiological processes during bud development are scarce, and process-based models are yet to be developed (Richardson *et al.*, 2013), although some phenological models are presented as such, e.g. DORMPHOT (Caffarra *et al.*, 2011) or Unified Model (Chuine, 2000). Furthermore, a recent study indicates that temperature responses obtained by experiments differ considerably from those of field observations (Wolkovich *et al.*, 2012). While phenological research assumes that temperature and day length are the main limiting factors during bud development, the question of how tree water uptake starts in spring is far from trivial, as several publications have shown (Cruiziat *et al.*, 2002; Zimmermann *et al.*, 2004; Zwieniecki & Holbrook, 2009; Brodersen & McElrone, 2013; Rockwell *et al.*, 2014). A growing body of literature shows that foliar water uptake is also a common water acquisition strategy for temperate trees (Boucher *et al.*, 1995; Zimmermann *et al.*, 2004; Burgess & Dawson, 2004; Limm *et al.*, 2009; Laur & Hacke, 2014).

Under natural conditions, absolute air humidity and temperature are highly correlated (Figure 3). It thus seemed possible that observed phenological responses of woody species to temperature were confounded with effects of air humidity. However, since an increase of temperatures with

climate change only partly is accompanied by corresponding changes in air humidity (Dai, 2006; Willett *et al.*, 2010), an identification and quantification of the individual effects of temperature and air humidity is of relevance for phenological predictions.

Therefore, the second study (Chapter 3.2) assesses if the spring phenology of trees responds to air humidity, and investigates possible mechanisms.

Based on two experiments using the twig method (Table 2), the study shows that high air humidity advances budburst of woody species considerably, and suggests that some kind of foliar water uptake process might be involved. Based on these results, an analysis of long-term climate data of six German weather stations reveals that instead of temperature, an increase in absolute air humidity also gives a highly reliable signal of spring. A re-calculation of the data obtained in Chapter 3.1 shows that forcing requirements obtained in the experiment were not in line with budburst dates from field observations when calculations are based on temperature, but this improves considerably when based on absolute air humidity. By revising literature on physiological, water-related changes during winter and spring, the study develops the idea of an alternative, humidity-triggered framework of the spring phenology of tree species. This considers the dormancy and chilling during winter (cold and dry air) as a desiccation process, while spring development is a response to increasing air humidity, possibly evoked by foliar uptake processes (Figure 3).

Overall, the study asks if a possible main driver of tree phenology in spring has been overlooked in the past, and if temperature indeed is the main limiting, and thus driving factor, for the spring phenology of temperate trees.

Recent studies showed that foliar water uptake at high air humidity occurs in drought-stressed spruce individuals, and supposed (Laur & Hacke, 2014) or showed (Mayr *et al.*, 2014) that foliar water uptake processes contribute to xylem embolism repair in spring. However, the authors do not suppose that an air humidity uptake, but rather that snow-melt water at the tree surface might contribute to xylem recovery. On the other hand, the fact that wood anatomy influences budburst dates (Lechowicz, 1984; Panchen *et al.*, 2014), with small-diameter vessels relating to early, and large vessel-diameters relating to late leaf-out dates, equally suppose that water availability is a factor for the spring development of trees. Results of a free-air-humidity manipulation facility in Estonia showed that leaf fall of birch (*Betula pendula* Roth) is delayed with moderately increased relative humidity (+7%), although no such effect was found for hybrid aspen (*Populus tremula* L. × *Populus tremuloides* Michx.) (Godbold *et al.*, 2014). However, the manipulations were restricted to the growing season, and thus possible effects of increased air humidity on the spring phenology of the species remain unclear. Probably the only study that investigated air humidity effects on spring development dates back to the 1970s, and reports a considerably advance in budburst for potted wine cultivars under increased air humidity (Düring, 1979).
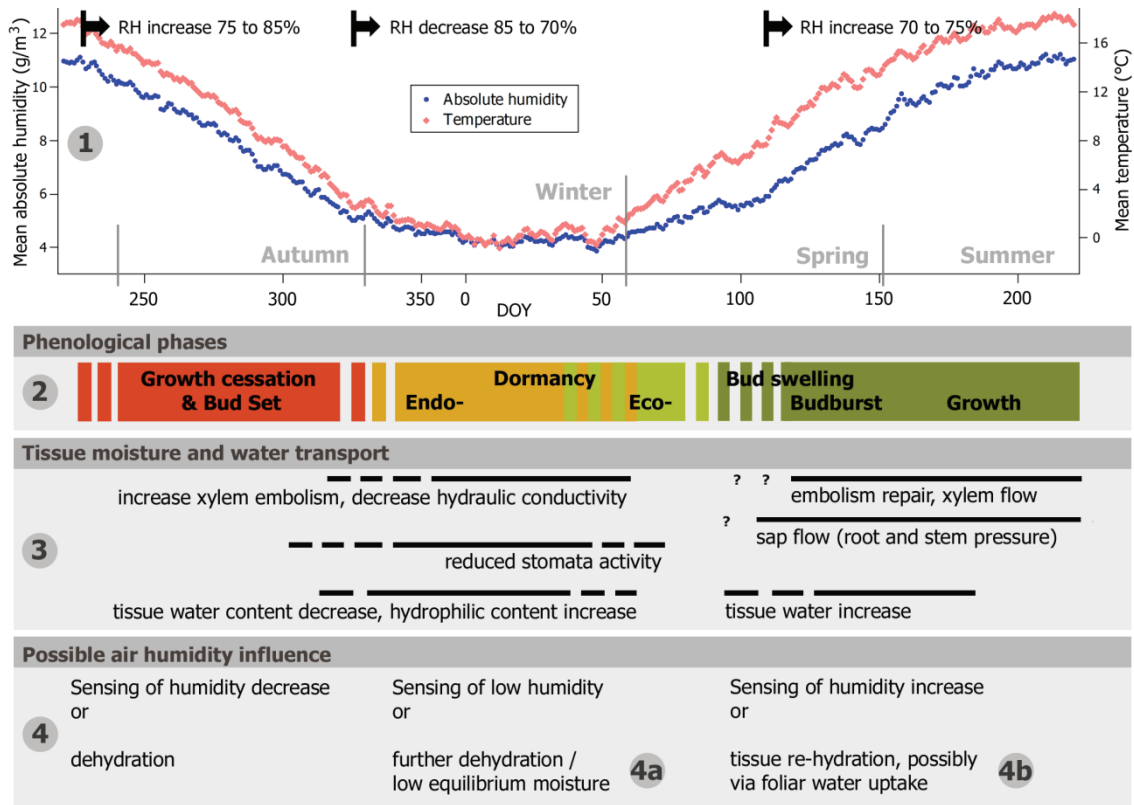
Figure 3: Scheme illustrating the air humidity based framework of spring phenology.

(1) Temperature and absolute humidity characteristics during the year, meteorological seasons, and trend for relative air humidity (RH) – based on mean daily values 1951-2006, DWD climate station Hohenpeißenberg, Germany. While temperature and absolute air humidity develop rather parallel, RH increases during autumn, and starts to increase during late spring. However, transpiration processes are not triggered by RH, but by the gradient of absolute values between cell space air and outside air (Peak & Mott, 2011). (**2**) Rough timing of main phenological phases. (**3**) Known physiological processes that relate to tissue moisture. *Winter*: Due to frost-thaw cycles, reduced ability to replace water losses due to frozen soils, and reduced stem conductivity with low temperatures (Cochard *et al.*, 2000), xylem embolisms increase during winter, and cavitation maxima occur shortly before budburst (de Fay *et al.*, 2000; Cochard *et al.*, 2001; Cruiziat *et al.*, 2002; Nardini *et al.*, 2011). The stomata activity is determined by an internal rhythm (Seidman & Riggan, 1968), and stomata are inactive during winter. Tissue water contents decrease, while cells accumulate highly hydrophilic substances (Lipavská *et al.*, 2000; Welling & Palva, 2006). *Spring*: Embolism repair takes place, but the exact timing with respect to budburst remains vague (often at or shortly after budburst) (Cochard *et al.*, 2001; Fonti *et al.*, 2007; Cufar *et al.*, 2008; Cuny *et al.*, 2012). The development of root and stem pressure contributes to xylem recovery (Cochard *et al.*, 2001; Westhoff *et al.*, 2008), but exact timing with respect to budburst equally remains vague. Stomata activity starts, which additionally is influenced by a sharp decrease in ABA concentrations shortly before budburst (Rinne *et al.*, 1994). Tissue and bud water content increase sharply, which is related to early bud development (Rinne *et al.*, 1994; de Fay *et al.*, 2000; Welling *et al.*, 2004; Yooyongwech *et al.*, 2008). **(4)** Proposed processes of an air humidity based framework of bud development in spring. A simple sensing of changes in air humidity might trigger phenological development, as both a decrease during autumn and winter, and an increase during spring might be sensed, and promote reactions in plants. The second possibility (4a and 4b) is that a dehydration/hydration process takes place, which triggers phenological development. **(4a)** The dormant, passive plant tissue desiccates during winter towards an equilibrium state with decreasing absolute air humidity. A reduced stomata activity prevents from lethal water loss, but cuticular losses as well as a "programmed dehydration" (Welling & Palva, 2006), which protects against frost damage, lead to a dehydration of tissue during winter. **(4b)** In early spring, a reversed humidity gradient might establish, with low absolute humidity in tissue space air, and sharply increasing absolute humidity of surrounding air. In combination with high concentrations of hydrophilic substances in cells, and reactivated stomata, this gradient might facilitate foliar water uptake. Thus, early stages of bud development might be influenced by air humidity changes, until the root- and stem bound water supply reaches a sufficient level.

4.1.2 Performance of native and invasive herb species with climatic stress events

Question 3: Do invasive species show a higher homeostasis, and thus higher performance than native species with climatic stress events? (Chapter 3.3)

Overall, the idea persists that invasive plant species will profit from several aspects of climate change (Dukes & Mooney, 1999; Thuiller *et al.*, 2007; Vilà *et al.*, 2007; Walther *et al.*, 2009; Bradley *et al.*, 2010). Several reviews have discussed possible effects of climatic extreme events on plant invasions, and concluded that an increase in the frequency of extreme events might have positive, negative or no net effects (Bradley *et al.*, 2010; Diez *et al.*, 2012). The reviews agree that, apart from theory-based considerations, knowledge on the stress tolerance of invasive species is too limited to allow reasonable predictions.

On the one hand, invasive plant species often show broad environmental niches (Vilà *et al.*, 2007; Hellmann *et al.*, 2008) and a high phenotypic plasticity (Davidson *et al.*, 2011). Moreover, invasive species often are superior to native species with respect to growth rates (Vilà & Weiner, 2004; Pyšek & Richardson, 2007; van Kleunen *et al.*, 2010b), and thus, a lessened response to stress, and a faster recovery after stress seem likely. Effects of competition are thought to interact with effects of climatic stress events, but only a few studies so far have examined possible interferences of both factors. Moreover, knowledge on the sensitivity of different development stages to climatic stress is scarce (Beier *et al.*, 2012).

Therefore, the third study (Chapter 3.3) assesses the responses of three invasive species and three closely related native species to climatic stresses, and includes differing plants' life-history stages and competitive settings (Table 2).

The results of this greenhouse experiment show that the stress tolerances of invasive species are highly comparable to that of the native congeners and confamilials. The results thus do not support the concern that an increase of climatic extreme events will facilitate plant invasions *per se*. However, the data indicate that species, irrespective of native or invasive status, are considerably more vulnerable to climatic stress at the seedling stage. Additionally, individuals perform worse with increasing stress when grown in competition. This indicates that the consideration of both factors is essential for the assessment of stress tolerances, which should be considered in future experimental settings. Moreover, rather abrupt species-specific thresholds exist, which shows that a prediction of species' responses based on just two modest stress levels, as usually applied (He *et al.*, 2013), is equivocal.

Q 3.1: Are invasive species more tolerant to climatic stress?

The results do not support the idea that invasive species are more stress tolerant than native species. However, the results suggest that the tolerance to climatic stress conditions might be phylogenetically conserved, since closely related species show very similar responses under all treatment conditions, i.e. five stress levels, two different development stages and two different competitive settings.

Q 3.2: How is the stress tolerance of invasive and native species modulated by competition and life-cycle stage?

Competition interacts strongly with climatic stress level. The biomass of individuals grown in strong interspecific competition decreases more strongly, and death rates increase more strongly, with stress level than for plants grown in mild intraspecific competition. However, there are only very slight to no effects of the invasive status. Thus, while competition strongly influences the effects of climatic stress, the effects of competition do not differ between invasive and native species under climatic stress.

The life-cycle stage at which stress was applied strongly influences the effects of stress level, with individuals in the seedling stage being more sensitive than adult individuals. But as for competition, there is no indication that the interaction of life-cycle stage and stress level is influenced by native or invasive status of the species.

Out of the few studies that compared the stress tolerance of native and invasive species, rather conflicting patterns were reported. Former studies showed that the invasive congener of dandelion (*Taraxacum officinale* agg.) was less drought resistant than the native species (*T. ceratophorum* (Ledeb.) DC.) (Brock & Galen, 2005), and a lower frost tolerance is known for invasive balsam species in comparison to the native congener (Skálová *et al.*, 2011). Invasive daisies were shown to perform worse than native ones under water stress (Garcia-Serrano *et al.*, 2007), and daisies of invasive populations worse than those of native populations under water and nutrient limited conditions (He *et al.*, 2010). On the other hand, some studies on non-related invasive and native species showed a higher homeostasis of the invasive species, and found that invasive species suffered less (Collinge *et al.*, 2011; Jimenez *et al.*, 2011), or profited more from release of competition (White *et al.*, 2001; Collinge *et al.*, 2011; Mason *et al.*, 2012) than native species under climatic stress.

Thus, it seems unlikely that invasive species *per se* will resist climatic stress events better than comparable native species. Most likely, highly species-specific responses have to be expected with an increase in extreme climatic events.

4.1.3 Expected impacts of climate change on elevational range limits of native and invasive species

Mountain ecosystems are anticipated to be strongly affected by climate change. Temperature increases in mountains have so far been much higher than in lowlands (Beniston & Rebetez, 1996; Beniston *et al.*, 1997; Wang *et al.*, 2014). Moreover, geospatial isolation (Körner, 2007) and disproportional decline in land surface with elevation (Rahbek, 1995) limit the area and reachability of high elevation refugia. Moreover, many species specialised to mountain habitats, as well as whole ecosystems of mountain ranges, depend on the exclusion of temperature-limited, more competitive species of the lowlands (Grabherr *et al.*, 1994; Theurillat & Guisan, 2001).

Much of past climate impact research focused on the alpine regions, such as GLORIA (Grabherr *et al.*, 2000; Pauli *et al.*, 2007), for which niche models predict very high species

losses with climate change (Thuiller *et al.*, 2005; Randin *et al.*, 2009; Engler *et al.*, 2011). Much less is known on possible impacts of climate change on mid-mountain ranges.

With respect to invasive species, an upward shift has been noticed during recent decades, which is at least partly attributed to climate change (Becker *et al.*, 2005; Pauchard *et al.*, 2009). Thus, a further upward shift of invasive species into vulnerable mountain ecosystems seems likely, which often host a considerable number of rare species.

Question 4: Will invasive species shift their elevational limits upwards with climate change? (Chapter 3.4)

The fourth study (Chapter 3.4) asks which factors currently influence the elevational range limits of two invasive and one native balsam species at a mid-mountain range, the Bavarian Forest (Table 2).

The results show that rather than mean temperatures, combinations of simultaneous germination pattern, missing seed bank, frost sensitivity of seedlings, and for himalayan balsam (*I. glandulifera*) the late start of the reproductive phase influence the current elevational limits of the species. Therefore, we expect changes in late spring and early autumn frosts, rather than increasing temperatures, to trigger future upward shifts of the species with climate change. However, an upward shift for invasive himalayan balsam with climate change seems likely, since this species might profit from higher mean temperatures during the growing season, and thus reach the reproductive phase earlier. A more regular, yearly reproductive success will thus also become more likely at higher elevations. However, both invasive species seem to be highly prone to spring frost, and an increased frequency will thus challenge existing populations and counteract possible positive effects of increasing mean temperatures.

Q 4.1: Which factors contribute to the current elevational limit of invasive and comparable native species?

A finely tuned interplay of phenology and recurrence of frost events seems to shape the upper distribution limits of this genus. While the measurements of functional traits in natural populations suggest that a decrease in plant size with elevation, and thus a possible decrease in per-capita competitive ability might be of additional influence, these results are not supported by the field experiment. Although the invasive congeners responded more plastically to elevation in some traits, e.g. size and phenology, these responses were not likely to increase fitness.

Q 4.2: Can we predict future elevational range limits?

The results reveal that the prediction of future upper range limits is far from trivial, even if the main driving factors can be identified. It seems clear that upward shifts will be smaller than predicted by mean temperature increases, since the spring frost risks are predicted to increase (Inouye, 2008; Kreyling, 2010), and autumn frost are expected to shift only slightly (Menzel *et al.*, 2003).

Our ability to predict the frequency and timing of erratic events, such as future timings of late spring frost or early autumn frost events is limited. Moreover, for most of the invasive species,

information on the full phenological patterns such as germination, flowering, and fruit ripening is unknown, and information on the frost sensitivity of species is usually not available. Therefore, the results warn against predictions based on climate envelope models, since for most invasive plant species and most regions, none of the mentioned factors are known.

For himalayan balsam, earlier studies assessed latitudinal range limits of the species (Beerling, 1993; Kollmann & Banuelos, 2004). These studies concluded that a reduction of plant and leaf size might reduce competitive superiority at high latitudes (Kollmann & Banuelos, 2004), and that growing season length limits the latitudinal range (Beerling, 1993; Kollmann & Banuelos, 2004). The results of Chapter 3.4 suggest that these findings also explain elevational range limits, at least in part. We also found a large reduction in plant size, and that overall growing season length plays a role. However, direct effects of competition were not detectable. Furthermore, growing season length does not seem to be the best climatic proxy, since the period between last spring and first autumn frost is of particular relevance. Laboratory assessments of frost sensitivity of all three congeners from Czech populations support our finding that invasive congeners are less frost resistant than the native touch-me-not balsam (Skálová *et al.*, 2011). Highly simultaneous germination patterns have also been previously reported for the genus (Beerling, 1993; Kollmann & Banuelos, 2004; Andrews *et al.*, 2009). The fact that a high trait plasticity does not necessarily translate into higher fitness was suggested earlier (Davidson *et al.*, 2011), which in the case of balsams supposedly applies for plant size and phenology.

Question 5: How vulnerable are current native mid-mountain ecosystems to climate change? (Chapter 3.5)

The fifth study (Chapter 3.5) analyses community patterns, plant functional traits, and environmental niches of native understorey flora along the same elevational gradient (Bavarian Forest) to give an estimate on vulnerabilities of the native flora to climate change (Table 2).

With respect to the current thermal and light niches of the species, functional traits, and community assembly, a rather high vulnerability of the montane species in the area has to be assumed. Over one third of all species occur at sites colder than the predicted future coldest sites, and/or at sites with low tree cover ("vulnerable species"). Plant functional traits show distinct responses to both temperature and tree cover. Functional traits of the vulnerable species lead to the conclusion that they will suffer from both an increase in competitive interactions, and increasing tree cover with climate change. Community traits related to low competitive abilities (rosette-type leaves, small plant size) are more common at high-elevation sites and with low tree cover. However, analysis revealed that the abundance or diversity of understorey species does not restrict the presence of vulnerable species. Thus, tree cover, and not diffuse competitive interactions within understorey species, seems to be important.

Trait adaptations to high elevation sites, such as simple reproduction patterns, will be of little advantage under future warmer and longer growing seasons. Thus, competition-driven range retractions at the lower elevational limits seem likely. The study suggests that, so far, the vulnerability of plant species at mid-mountain ranges has been underestimated.

Q 5.1: Are there plant functional traits that explain current elevational distributions?

Several changes in community weighted mean traits are identified, with communities of higher elevations showing traits that facilitate reproduction, and thus are favourable under short or unstable summer conditions. Communities at lower sites show more complex reproductive traits with higher levels of dicliny. On the other hand, traits that usually relate to a high competitive ability of species, such as large plant size or heavier seed, are more common at lower elevation sites with higher tree cover. However, the trait patterns in the area are rather complex, since both temperature and tree cover seem to be influential.

Q 5.2: Can we infer the vulnerability of species from community assembly and functional traits?

While we found clear changes with temperature and tree cover for some of the traits, overall most of the signals are rather weak, with low percentages of explained variance by temperature and tree cover. While trait diversity shows that communities at warm sites with high tree cover are mainly shaped by competitive interactions, the analysis of phylogenetic diversity resulted in contradictory results. Yet, the main pattern that both increasing temperatures and tree cover are linked to communities with considerable influence of competition, and the fact that many of the vulnerable montane species show traits related to rather low competitive abilities, increases the understanding of possible processes. Thus, the analysis of community assembly and plant functional traits allows deeper insights than vulnerability estimates based on climate envelopes alone.

Overall, a high percentage of species in the Bavarian Forest is vulnerable to climate change. The percentage of vulnerable species was indeed much higher than European-wide studies found for species of the mountain or high-mountain belt (Engler *et al.*, 2011). However, results are only partly comparable, since that study was based on climatic niche models, and included all refugia theoretically available, especially in the Alps. Our results indicate that tree cover changes rather than competition by any understorey species will threaten montane species. However, detailed predictions on tree species' range shifts with climate change are also not yet available, since an interplay of growing season length (Lenz *et al.*, 2013), absolute minimum and growing season mean temperatures (Körner, 2007), frost events during budburst (Kollas *et al.*, 2014), and climate variability (Zimmermann *et al.*, 2009) contribute. Furthermore, these results stress the need to include traits and biotic interactions into niche models (Laughlin & Laughlin, 2013), and to take the spatial isolation into account.

4.2   Summary with respect to the main research questions

- How will invasive plant species respond to changes in winter and spring temperatures and climatic variability?

The study on two very abundant invasive balsam species in the Bavarian Forest, himalayan and small balsam (Chapter 3.4), revealed that himalayan balsam might particularly profit from increased growing season length and growing season temperatures. On the other hand, both

invasive himalayan and small balsam will be challenged by increased spring frost risks. Thus, while changes in mean temperatures might favour invasive species, increasing climatic variability will likely hinder upward shifts.

Invasive herb species were not more resistant to climatic stress events than comparable native species (Chapter 3.3). Nevertheless, invasive species as a group might be able to profit indirectly from climatic extremes, since propagules might be able to reach disturbed native communities faster than native species due to high fecundity, short generation times, and thus high dispersal abilities.

It seems likely that invasive woody species might profit from climate change due to a more flexible spring phenology in comparison to native woody species (Chapter 3.1). This suggests that, dependent on their individual frost sensitivity, they might gain competitive advantages over native woody species.

Thus, we expect that species will profit or suffer from changes in winter and spring conditions, as well as respond to increases in climatic variability in a highly species- and context-specific way. While some results suggest that generalisations are possible, invasive status is not a good predictor for overall responses to climate change.

- Will changes in competitive ability influence invasion processes with climate change?

With respect to anticipated changes in competitive ability, the results indicate that invasive tree species might profit from changed winter and spring conditions, and thus take competitive advantage of early spring light gain (Chapter 3.1). On the other hand, invasive herb species showed no increased competitive ability under climatic stress conditions (Chapter 3.3). Along the elevational gradient in the Bavarian Forest, we found signs of decreased competitive ability of the invasive species with elevation (Chapter 3.4), which might translate into increased competitive ability with climate change. However, these results were obtained by trait measurements in existing populations, but not supported by results of the field experiment.

Thus, while changes in competitive ability will likely influence responses of species to climate change, individual changes in competitive ability will depend on species' identity, the facet of climate change under consideration, and context. The studies did not support the idea that invasive species as a group will profit from an overall increase in competitive ability, or an overall decrease in competitive ability of native species with climate change.

- Do the seasonal/temporal niches of native and invasive species differ, and is this relevant?

Differences in the seasonal niche seem to play an important role in the current upper range limits of balsam species (Chapter 3.4). Simultaneous germination patterns and a low frost tolerance expose both invasive species to high risk of spring frost damage, and a long development phase until flowering exposes himalayan balsam to reproduction failure with autumn frosts. A high overall similarity of the spring phenology of native and invasive woody species (Chapter 3.1) suggests that a timely start to the growing season might be a pre-requisite for successful establishment in a new range. However, slight differences were also revealed, hence invasive woody species might respond more flexibly to winter and spring

warming, and thus might take advantage of a prolonged growing season (Chapter 3.1). The experiment on climatic stresses showed that the timing of stress application, that is, the development stages of plant species, is of high importance for individual stress tolerance of species (Chapter 3.3).

While it seems that the phenological development of invasive species needs to be sufficiently similar to native species to survive, slight differences in phenology might either give advantage due to temporal release of competition, for example for invasive woody species leafing out earlier, or disadvantage, e.g. frost exposure of balsam species, under current and future conditions. The critical phenological stage might also be different depending on species and context, e.g. one balsam species being most prone to seedling establishment and spring frosts, the other balsam species being prone to reproduction failure in autumn.

Thus, invasive species might profit from a temporal niche that is similar, but not too similar to that of native species, which was recently supposed to also be advantageous for other traits and phylogenetic relatedness (Carboni *et al.*, 2013). Probably similarity is a necessary pre-requisite for establishment and reproduction in a new range, and slight variation on this offers competitive advantages.

4.3 Novelty, strengths, and shortcomings of the studies

The following points summarise the novelty and strengths of the studies. While a detailed discussion on shortcomings of the chosen approaches and methods is given in the individual publications, this chapter discusses some overall deficits.

It is impossible to design and conduct perfect ecological experiments. As a rule, the deliberate change of one treatment factor, is followed by known and unknown "hidden treatments" (Huston, 1997). Good planning and experimental design are able to remove some of these side-effects. Nevertheless, practical constraints as well as a lack of facilities usually result in non-removable side-effects, which can only be considered to a certain extent.

- Phenology of woody species

The studies in Chapter 3.1 and 3.2 used a newly re-discovered method to examine the spring phenology of woody species under experimental conditions (twig method).

In Chapter 3.1 an experimental design was used to disentangle the effects of photoperiod and chilling on spring development. The experiment examines the effects of both factors on a, so far, unprecedented number of different species at one time (Figure 4). The study furthermore introduced a statistical method to phenological research (Survival Analysis), which is appropriate to analyse this type of data. Parallel observations of the donor trees allowed backing-up of experimental results with real-world budburst chronology, and in the meantime further studies (Polgar *et al.*, 2014; Vitasse & Basler, 2014) have also supported the validity of the method.

In Chapter 3.2, the twig method was further developed to study the effects of other factors relevant for the spring phenology of woody species. The study used the original twig method (twigs in bottles with tap water) to assess effects of differences in air humidity in climate

chambers. Furthermore, an even more artificial setting was used (bare twigs without water supply from vascular tissue under high air humidity), which allowed to investigate the spring development of the buds.

Thus, both studies contributed to the advance of the twig method, which enables the assessment of the spring phenology of woody species in easy-to-use experimental settings, and led to ideas on further developments and possible usages of the twig method (Primack *et al.*, 2015, in press).

The study in Chapter 3.1 contributed to process-understanding on species-specific phenological responses, and showed that chilling, and not day length, is of primary importance for spring onset dates. Chapter 3.2 highlighted that air humidity is a neglected factor in current phenological research on temperate woody species. The study also stresses the shortcomings of correlative research based on phenological field observations, which is not able to parse the effects of correlated climatic factors.
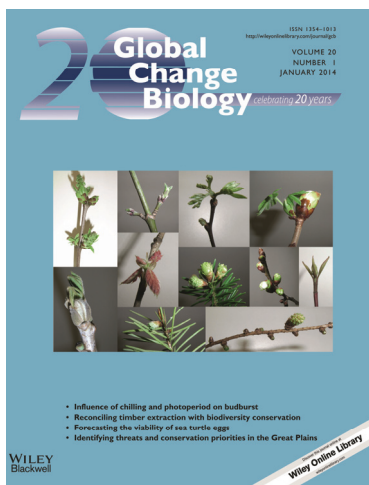

Figure 4: Global Change Biology cover page, Issue 20(1) - January 2014.

The cover picture corresponds to the publication in Chapter 3.1, based on own photographs.

Apart from the mentioned advancements with the twig method, some general problems with this experimental setting remain unsolved. The way in which variation of differing chilling lengths was applied (twigs cut earlier or later in winter) bears the risk of confounding effects with increasing natural day length. Although this problem might be minor, since twigs seem not to respond to photoperiod until shortly before the start of development (Zohner, pers. communication), the inclusion of artificial chilling seems to be a way forward. For example, recent studies in horticultural research (Jones *et al.*, 2013; Sønsteby & Heide, 2014) exposed twigs to controlled chilling conditions (e.g. in freezers or fridges) before applying forcing treatments. A further, yet unresolved problem with the twig method is that, so far, highly differing settings (with respect to temperature, e.g. increasing temperatures or fixed temperatures, night-day-temperature differences, but also observation frequency and so forth) are in use (Primack *et al.*, 2015, in press). It yet needs to be assessed how these treatment differences impact the

obtained results. Moreover, a major obstacle remains to be solved: Temperature thresholds above/below which temperatures result in forcing or chilling remain unknown. The analysis of the data used fixed, species-unspecific thresholds (0°C for forcing, 5°C for chilling) to calculate a temperature forcing requirement until budburst and chilling length, which is a gross over-simplification.

While there are broad similarities between twig and tree development, it also remains unclear how strong the effects of possibly missing root- and stem pressure during spring are. Thus, the response strengths of individuals under natural conditions might differ from that of twigs.

- Climatic stress

With respect to herb species, a large, gradient-type experiment with several climatic stresses was set up to assess effects of climatic stress events (Chapter 3.3). The study is one of the first to examine the influence of development stage on stress tolerance, to shed light on the effects of competition on stress tolerance, and to use a gradient-type approach surpassing mortality thresholds, which so far are understudied. The results show that stress experiments need to consider the timing or development stages of plants carefully. Moreover, the competitive setting is also of high importance for the responses to stress treatments. The results thus show that experiments using only mild stress settings, as often applied, are not sufficient to infer responses to more severe stress conditions.

While there is a plethora of problems related to greenhouse studies, which is discussed in more detail in the study of Chapter 3.3, the treatment severity levels, as well as the timing of treatments chosen might be criticised as arbitrary. The choice to apply a fixed sequence of climatic stress instead of single stress applications is closer to natural conditions, but on the other hand decreases the ability to assess effects of single stresses. As in most experiments, the use of a broader set of different species would have been favourable to obtain more general conclusions on the stress tolerance, but especially to assess if the stress tolerance indeed is phylogenetically conserved.

- Elevational limits

A combination of a field experiment, and trait measurements (Chapter 3.4) was used to study possible triggers of actual range limits of native and invasive balsam species. The experiment focused on germination, mortality of individuals, reproduction timing, and influence of competition. Trait measurements in the field were used to assess possible effects of trait plasticity. Furthermore, the analysis of long-term climate data of the region put the results into context. Overall, the combination of both field experiment and trait measurements allowed to identify the main factor triggering elevational limits of the species more clearly than each of the approaches alone.

Overall, the trait measurements resulted in a high variability of values, and thus, a higher number of sampled individuals or a higher number of sampled populations would have been preferable. However, these values were restricted by the number and size of known populations in the study area. Moreover, the choice of traits measured might have missed other relevant

traits. For the field experiment, a weekly observation would have allowed to distinguish more clearly the reasons of individuals' death.

- Analysis of relevés

The analysis of vegetation relevés from the same elevational gradient as in Chapter 3.4 allowed an assessment of the vulnerability of native plant species to climate change. A combination of analysis of current inhabited climatic niche, plant functional traits, and community assembly allowed to highlight the vulnerabilities of single species, as well as to shed light on influential traits and factors governing these vulnerabilities (Chapter 3.5). Overall, a broad range of current methods in community research was used to disentangle driving factors. Taken together, these allow better insights into the driving forces of plant communities under present conditions, and thus might contribute to qualitative improvements of future range predictions. The results obtained are based on a large dataset (330 relevés), with an exceptionally high number of site-specific environmental parameters available, and also used a very broad range of plant functional traits (N=24).

However, this does not ensure that the relevant environmental factors were adequately addressed, and the use of listed, mean trait values instead of direct trait measurements might have obscured trait responses along the elevational gradient. Moreover, some important traits might be missing. While the percentage of explained variance overall was in line with comparable studies, the low values reveal that either random processes are of high importance for community assembly, or that important factors (e.g. climatic extreme events in the past) need to be addressed. While some relationships were identified, and reasonable interpretations were found, other, even more important influences and relationships remain unknown.

5 Outlook

Overall, the studies compiled in this thesis delivered several novel insights into possible responses of invasive and native plant species to climate change. Nevertheless, studying a restricted number of species under a restricted set of conditions, many questions remain. The following outlook summarises some current shortcomings and missing links in invasion and phenological research, and suggests further research topics and approaches.

- Invasive species – the temporal niche as an understudied, yet highly important trait

Progress in the identification of simple "decisive" traits that allow prediction of future invasive and problematic species has been small (Moles *et al.*, 2012; Kueffer *et al.*, 2013) and slow (van Kleunen *et al.*, 2010b).

The use of large trait databases, which became available rather recently, e.g. TRY (Kattge *et al.*, 2011) and BIOLFLOR (Klotz *et al.*, 2002), might deliver further insights. However, traits with high species coverage are often rather easy to measure, and not necessarily ecologically important for a given site and question (van Kleunen *et al.*, 2010b). Of course, for subsets of species more detailed information on important traits, and ecological niches are available, such as for temperate trees (Niinemets & Valladares, 2006). Nevertheless, information on, and context for trait plasticity remain largely unknown, although of considerable importance (Albert *et al.*, 2010; Boucher *et al.*, 2013) under present and future conditions. However, there is only very scarce information on the temporal niches of species (apart from very cursory information, such as annual/perennial, winter-green/summer-green, etc.), and information on plant phenology, if given (for example in BIOLFLOR), usually only encompasses rough average values of one phenological stage, e.g. average month of flowering). Information on the temperature sensitivity or range of values remains unknown. Given that the phenological development and the temporal niche of species is of high importance under current conditions, and of utmost importance with respect to climate change impacts, this lack of knowledge is astounding.

Thus, clearly more research is needed with respect to the relevance of temporal niche for plant invasions, but also with respect to the broader question of how climate change will impact plant species (Wolkovich *et al.*, 2014). At least, it seems a highly valuable aim to identify the most critical development phase under current and future conditions. Temporal aspects so far remain to be uncovered, in invasion research as well as in many other fields, and to cite a recent review on competition experiments, the "critical point is that we just do not know how big an effect temporal dynamics have on apparent competitive outcomes" (Trinder *et al.*, 2013).

- Phenology – from observing changes to understanding processes

The value of former correlative research in phenology is undoubted, and phenology serves as an important, and easy to communicate line of evidence for climate change. Moreover, phenological studies clearly showed that species have already responded to temperature changes during recent decades. Thus, the field was amongst the first to not only hypothesise about the expected future, but to prove ongoing changes.

There is yet too little understanding of the relevant baseline processes in phenology. Due to the complexity and time-dependency of these processes, correlative studies cannot yet deliver concluding answers. We do not know when and which temperatures evoke responses during dormancy induction, chilling, or spring forcing. Nor do we know which time frame is of importance for which process. However, reliable predictions on future phenology, and especially on the start of the growing season, is of high importance for climate change impacts, adaptation, and climate predictions. While the following text refers to temperature as the main trigger of phenological development, the questions are equally valid for air humidity.

Experimental work is needed to prove or disprove hypotheses gained by large scale data analysis. Most obviously, we need to resolve which temperatures are relevant during forcing, and how long the forcing period lasts. Based on these fundamentals, effective chilling temperatures, chilling requirements, and responses to reduced chilling could be identified. Knowledge of these values would enable more informed analyses and interpretation of field observations, but would also help to develop and parameterise more process-based phenological models. Wolkovich *et al.* (2012) highlighted considerable discrepancies in temperature responses obtained by experiments and field observations. In contrast to the title ("Warming experiments underpredict plant phenological responses to climate change"), the study indeed argues that both types of studies are prone to interferences and artefacts, and thus true temperature responses remain unknown. Unfortunately, the study is cited as proof that experimental results are equivocal (Friedl *et al.*, 2014), and as an argument to conduct more correlative studies, e.g. Ellwood *et al.* (2013), Jochner *et al.* (2013b). However, as long as the mentioned baseline values, and thus the predictors remain unknown (effective temperatures and effective period), correlative studies are very unlikely to extract consistent temperature responses (Bolmgren *et al.*, 2013; Clark *et al.*, 2014). More likely, they will produce a multitude of possible temperature response estimates and patterns depending on often arbitrary choices of the predictor values. While predictions based on statistical relationships between temperature and phenological onset dates might be sufficient to predict the phenology of woody species in the near future, a shift into non-analog climates (Williams *et al.*, 2007) will drive current, correlative phenological models out of their calibration range (Richardson *et al.*, 2013; Olsson & Jönsson, 2014). A prediction of future spring phenology is impossible as long as the main drivers are not yet identified.

The twig method will contribute considerably in assessing these base values, most likely with experiments using different fixed temperature values during forcing, and different temperatures and treatment time for chilling.

- Why experiments?

For good reasons, both correlative research and modelling approaches flourish. The possibility to analyse large-area patterns, a multitude of environmental factors, and huge amounts of species at a time is highly valuable. Moreover, the increasing volume of available data on species distributions, traits, phylogenetic relatedness or environmental factors, together with

rapid evolvement of computational power and statistical, modelling, and geographical tools has led and will lead to new insights and hypotheses.

However, the pace of evolving hypotheses in data-rich science is to some extent decoupled from the pace that experimental ecologists are able to prove or dismiss. This is unfortunate, since in ecosystems an almost indefinite number of current and past drivers interact. It is clear that correlations do not imply causal relationships, e.g. Sparks & Tryjanowski (2005), and large datasets will not reveal more causation than small ones, except the analysis can fully control for confounding effects.

Experiments on the other hand are hard to design, highly troublesome to undertake, and restricted to few species, sites, and treatments. However, anticipating highly non-analog climates (Williams *et al.,* 2007), a need for process-orientated and predictive, rather than correlative and descriptive, studies is at hand. To conclude, while spurious relationships exist, "there are very few useless experiments" (Cousens (1996), cited in Gibson *et al.* (1999)).

6 References

Aitken SN, Yeaman S, Holliday JA, Wang T & Curtis-McLane S (2008): Adaptation, migration or extirpation: Climate change outcomes for tree populations. *Evolutionary Applications,* **1:** 95-111.

Albert CH, Thuiller W, Yoccoz NG, Soudant A, Boucher F, Saccone P & Lavorel S (2010): Intraspecific functional variability: Extent, structure and sources of variation. *Journal of Ecology,* **98:** 604-613.

Alexander JM, Naylor B, Poll M, Edwards PJ & Dietz H (2009): Plant invasions along mountain roads: The altitudinal amplitude of alien Asteraceae forbs in their native and introduced ranges. *Ecography,* **32:** 334-344.

Alexander JM (2013): Evolution under changing climates: Climatic niche stasis despite rapid evolution in a non-native plant. *Proceedings of the Royal Society B-Biological Sciences,* **280:** 20131446.

Andrews M, Maule HG, Hodge S, Cherrill A & Raven JA (2009): Seed dormancy, nitrogen nutrition and shade acclimation of Impatiens glandulifera: Implications for successful invasion of deciduous woodland. *Plant Ecology & Diversity,* **2:** 145-153.

Augspurger CK & Bartlett EA (2003): Differences in leaf phenology between juvenile and adult trees in a temperate deciduous forest. *Tree Physiology,* **23:** 517-525.

Augspurger CK (2008): Early spring leaf out enhances growth and survival of saplings in a temperate deciduous forest. *Oecologia,* **156:** 281-286.

Augspurger CK (2013): Reconstructing patterns of temperature, phenology, and frost damage over 124 years: Spring damage risk is increasing. *Ecology,* **94:** 41-50.

Basler D & Körner C (2012): Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology,* **165:** 73-81.

Becker T, Dietz H, Billeter R, Buschmann H & Edwards PJ (2005): Altitudinal distribution of alien plant species in the Swiss Alps. *Perspectives in Plant Ecology Evolution and Systematics,* **7:** 173-183.

Beerling DJ (1993): The impact of temperature on the northern distribution limits of the introduced species Fallopia japonica and Impatiens glandulifera in north-west Europe. *Journal of Biogeography,* **20:** 45-53.

Beier C, Beierkuhnlein C, Wohlgemuth T, *et al.* (2012): Precipitation manipulation experiments - challenges and recommendations for the future. *Ecology Letters,* **15:** 899-911.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W & Courchamp F (2012): Impacts of climate change on the future of biodiversity. *Ecology Letters,* **15:** 365-377.

Beniston M & Rebetez M (1996): Regional behavior of minimum temperatures in Switzerland for the period 1979-1993. *Theoretical and Applied Climatology,* **53:** 231-243.

Beniston M, Diaz HF & Bradley RS (1997): Climatic change at high elevation sites: An overview. *Climatic Change,* **36:** 233-251.

Bennett JA, Lamb EG, Hall JC, Cardinal-McTeague WM & Cahill JF (2013): Increased competition does not lead to increased phylogenetic overdispersion in a native grassland. *Ecology Letters,* **16:** 1168-1176.

Bertness MD & Callaway R (1994): Positive interactions in communities. *Trends in Ecology & Evolution,* **9:** 191-193.

REFERENCES

Blossey B & Nötzold R (1995): Evolution of increased competitive ability in invasive nonindigenous plants - a hypothesis. *Journal of Ecology,* **83:** 887-889.

Blümel K & Chmielewski FM (2012): Shortcomings of classical phenological forcing models and a way to overcome them. *Agricultural and Forest Meteorology,* **164:** 10-19.

Bock A, Sparks TH, Estrella N, *et al.* (2014): Changes in first flowering dates and flowering duration of 232 plant species on the island of Guernsey. *Global Change Biology,* **20:** 3508-3519.

Bolmgren K, Vanhoenacker D & Miller-Rushing A (2013): One man, 73 years, and 25 species. Evaluating phenological responses using a lifelong study of first flowering dates. *International Journal of Biometeorology,* **57:** 367-375.

Bolmgren K & Cowan PD (2008): Time - size tradeoffs: A phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora. *Oikos,* **117:** 424-429.

Boucher FC, Thuiller W, Arnoldi C, Albert CH & Lavergne S (2013): Unravelling the architecture of functional variability in wild populations of Polygonum viviparum L. *Functional Ecology,* **27:** 382-391.

Boucher JF, Munson AD & Bernier PY (1995): Foliar absorption of dew influences shoot water potential and root-growth in Pinus strobus seedlings. *Tree Physiology,* **15:** 819-823.

Bradley BA, Blumenthal DM, Wilcove DS & Ziska LH (2010): Predicting plant invasions in an era of global change. *Trends in Ecology & Evolution,* **25:** 310-318.

Brock MT & Galen C (2005): Drought tolerance in the alpine dandelion, Taraxacum ceratophorum (Asteraceae), its exotic congener T. officinale, and interspecific hybrids under natural and experimental conditions. *American Journal of Botany,* **92:** 1311-1321.

Brodersen CR & McElrone AJ (2013): Maintenance of xylem network transport capacity: A review of embolism repair in vascular plants. *Frontiers in Plant Science,* **4:** 108.

Broennimann O, Treier U, Mueller-Schaerer H, Thuiller W, Peterson A & Guisan A (2007): Evidence of climatic niche shift during biological invasion. *Ecology Letters,* **10:** 701-709.

Brooker RW (2006): Plant-plant interactions and environmental change. *New Phytologist,* **171:** 271-284.

Brooker RW, Callaway RM, Cavieres LA, *et al.* (2009): Don't diss integration: A comment on Ricklefs's disintegrating communities. *American Naturalist,* **174:** 919-927.

Burgess SSO & Dawson TE (2004): The contribution of fog to the water relations of Sequoia sempervirens (D. Don): Foliar uptake and prevention of dehydration. *Plant Cell and Environment,* **27:** 1023-1034.

Caffarra A & Donnelly A (2011): The ecological significance of phenology in four different tree species: Effects of light and temperature on bud burst. *International Journal of Biometeorology,* **55:** 711-721.

Caffarra A, Donnelly A & Chuine I (2011): Modelling the timing of Betula pubescens budburst. II. Integrating complex effects of photoperiod into process-based models. *Climate Research,* **46:** 159-170.

Cain ML, Milligan BG & Strand AE (2000): Long-distance seed dispersal in plant populations. *American Journal of Botany,* **87:** 1217-1227.

Callaway RM & Ridenour WM (2004): Novel weapons: Invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment,* **2:** 436-443.

REFERENCES

Carboni M, Münkemüller T, Gallien L, Lavergne S, Acosta A & Thuiller W (2013): Darwin's naturalization hypothesis: Scale matters in coastal plant communities. *Ecography,* **36:** 560-568.

Choler P, Michalet R & Callaway RM (2001): Facilitation and competition on gradients in alpine plant communities. *Ecology,* **82:** 3295-3308.

Chuine I (2010): Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B-Biological Sciences,* **365:** 3149-3160.

Chuine I & Cour P (1999): Climatic determinants of budburst seasonality in four temperate-zone tree species. *New Phytologist,* **143:** 339-349.

Chuine I (2000): A unified model for budburst of trees. *Journal of Theoretical Biology,* **207:** 337-347.

Chuine I, Morin X & Bugmann H (2010): Warming, photoperiods, and tree phenology. *Science,* **329:** 277-278.

Clark JS, Salk C, Melillo J & Mohan J (2014): Tree phenology responses to winter chilling, spring warming, at north and south range limits. *Functional Ecology,* **28:** 1344-1355.

Cleland EE, Chuine I, Menzel A, Mooney HA & Schwartz MD (2007): Shifting plant phenology in response to global change. *Trends in Ecology & Evolution,* **22:** 357-365.

Cleland EE, Allen JM, Crimmins TM, *et al.* (2012): Phenological tracking enables positive species responses to climate change. *Ecology,* **93:** 1765-1771.

Cleland EE, Esch E & McKinney J (2015): Priority effects vary with species identity and origin in an experiment varying the timing of seed arrival. *Oikos,* **124:** 33-40.

Clements D & Ditommaso A (2011): Climate change and weed adaptation: Can evolution of invasive plants lead to greater range expansion than forecasted? *Weed Research,* **51:** 227-240.

Cochard H, Martin R, Gross P & Bogeat-Triboulot MB (2000): Temperature effects on hydraulic conductance and water relations of Quercus robur L. *Journal of Experimental Botany,* **51:** 1255-1259.

Cochard H, Lemoine D, Ameglio T & Granier A (2001): Mechanisms of xylem recovery from winter embolism in Fagus sylvatica. *Tree Physiology,* **21:** 27-33.

Colautti RI, Ricciardi A, Grigorovich IA & MacIsaac HJ (2004): Is invasion success explained by the enemy release hypothesis? *Ecology Letters,* **7:** 721-733.

Colautti RI, Bailey SA, van Overdijk CDA, Amundsen K & MacIsaac HJ (2006a): Characterised and projected costs of nonindigenous species in Canada. *Biological Invasions,* **8:** 45-59.

Colautti RI, Grigorovich IA & MacIsaac HJ (2006b): Propagule pressure: A null model for biological invasions. *Biological Invasions,* **8:** 1023-1037.

Collinge SK, Ray C & Gerhardt F (2011): Long-term dynamics of biotic and abiotic resistance to exotic species invasion in restored vernal pool plant communities. *Ecological Applications,* **21:** 2105-2118.

Connolly J (1988): What is wrong with replacement series? *Trends in Ecology & Evolution,* **3:** 24-26.

Cottingham KL, Lennon JT & Brown BL (2005): Knowing when to draw the line: Designing more informative ecological experiments. *Frontiers in Ecology and the Environment,* **3:** 145-152.

REFERENCES

Cramer W, Bondeau A, Woodward FI, *et al.* (2001): Global response of terrestrial ecosystem structure and function to CO_2 and climate change: Results from six dynamic global vegetation models. *Global Change Biology,* **7:** 357-373.

Cruiziat P, Cochard H & Ameglio T (2002): Hydraulic architecture of trees: Main concepts and results. *Annals of Forest Science,* **59:** 723-752.

Cufar K, Prislan P, de Luis M & Gricar J (2008): Tree-ring variation, wood formation and phenology of beech (Fagus sylvatica) from a representative site in Slovenia, SE Central Europe. *Trees-Structure and Function,* **22:** 749-758.

Cuny HE, Rathgeber CB, Lebourgeois F, Fortin M & Fournier M (2012): Life strategies in intra-annual dynamics of wood formation: Example of three conifer species in a temperate forest in north-east France. *Tree Physiology,* **32:** 612-625.

Daehler CC (2003): Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology Evolution and Systematics,* **34:** 183-211.

Dai A (2006): Recent climatology, variability, and trends in global surface humidity. *Journal of Climate,* **19:** 3589-3606.

Damgaard C & Fayolle A (2010): Measuring the importance of competition: A new formulation of the problem. *Journal of Ecology,* **98:** 1-6.

Davidson AM, Jennions M & Nicotra AB (2011): Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters,* **14:** 419-431.

Davis MA, Grime JP & Thompson K (2000): Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology,* **88:** 528-534.

Davis MA, Pergl J, Truscott AM, *et al.* (2005): Vegetation change: A reunifying concept in plant ecology. *Perspectives in Plant Ecology Evolution and Systematics,* **7:** 69-76.

de Fay E, Vacher V & Humbert F (2000): Water-related phenomena in winter buds and twigs of Picea abies L. (Karst.) until bud-burst: A biological, histological and NMR study. *Annals of Botany,* **86:** 1097-1107.

de Réaumur R-AF (1735): Observations du thermomètre, faites à Paris pendant l´année 1735 comparées avec celles qui ont été faites sous la ligne, à l´Ile de France, à Alger et en quelques-unes de nos îles de l´Amérique. *Mémoire de l'Académie royale des sciences,* 545-576.

Diez JM, D'Antonio CM, Dukes JS, *et al.* (2012): Will extreme climatic events facilitate biological invasions? *Frontiers in Ecology and the Environment,* **10:** 249-257.

Do FC, Goudiaby VA, Gimenez O, Diagne AL, Diouf M, Rocheteau A & Akpo LE (2005): Environmental influence on canopy phenology in the dry tropics. *Forest Ecology and Management,* **215:** 319-328.

Dukes JS & Mooney HA (1999): Does global change increase the success of biological invaders? *Trends in Ecology & Evolution,* **14:** 135-139.

Düring H (1979): Wirkungen der Luft- und Bodenfeuchtigkeit auf das vegetative Wachstum und den Wasserhaushalt bei Reben. *Vitis,* **118:** 211-220.

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR & Mearns LO (2000): Climate extremes: Observations, modeling, and impacts. *Science,* **289:** 2068-2074.

REFERENCES

EEA (2012): *The impacts of invasive alien species in Europe*. European Environment Agency, Copenhagen, 118 pp.

Ehrlen J (2015): Selection on flowering time in a life-cycle context. *Oikos,* **124:** 92-101.

Ellenberg H (1953): Physiologisches und ökologisches Verhalten derselben Pflanzenarten. *Berichte der Deutschen Botanischen Gesellschaft,* **65:** 350-361.

Ellwood ER, Temple SA, Primack RB, Bradley NL & Davis CC (2013): Record-breaking early flowering in the eastern United States. *Plos One,* **8:** e53788*.*

Elton CS (1958): *The ecology of invasions by animals and plants*. Methuen & Co./Chapman & Hall, Kluwer Academic Publishers BV, Chicago, 181 pp.

Engler R, Randin CF, Thuiller W, *et al.* (2011): 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology,* **17:** 2330-2341.

Eppinga MB, Rietkerk M, Dekker SC, De Ruiter PC & Van der Putten WH (2006): Accumulation of local pathogens: A new hypothesis to explain exotic plant invasions. *Oikos,* **114:** 168-176.

Estiarte M, Puig G & Peñuelas J (2011): Large delay in flowering in continental versus coastal populations of a Mediterranean shrub, Globularia alypum. *International Journal of Biometeorology,* **55:** 855-865.

Fayolle A, Violle C & Navas ML (2009): Differential impacts of plant interactions on herbaceous species recruitment: Disentangling factors controlling emergence, survival and growth of seedlings. *Oecologia,* **159:** 817-825.

Fisher JI, Richardson AD & Mustard JF (2007): Phenology model from surface meteorology does not capture satellite-based greenup estimations. *Global Change Biology,* **13:** 707-721.

Fitter AH & Fitter RSR (2002): Rapid changes in flowering time in British plants. *Science,* **296:** 1689-1691.

Fonti P, Solomonoff N & Garcia-Gonzalez I (2007): Earlywood vessels of Castanea sativa record temperature before their formation. *New Phytologist,* **173:** 562-570.

Foster BL & Gross KL (1997): Partitioning the effects of plant biomass and litter on Andropogon gerardi in old-field vegetation. *Ecology,* **78:** 2091-2104.

Frenot Y, Chown SL, Whinam J, Selkirk PM, Convey P, Skotnicki M & Bergstrom DM (2005): Biological invasions in the Antarctic: Extent, impacts and implications. *Biological Reviews,* **80:** 45-72.

Fridley JD (2012): Extended leaf phenology and the autumn niche in deciduous forest invasions. *Nature,* **485:** 359-362.

Friedl MA, Gray JM, Melaas EK, *et al.* (2014): A tale of two springs: Using recent climate anomalies to characterize the sensitivity of temperate forest phenology to climate change. *Environmental Research Letters,* **9:** 054006.

Fu YH, Piao S, Zhao H, *et al.* (2014): Unexpected role of winter precipitation in determining heat requirement for spring vegetation green-up at northern middle and high latitudes. *Global Change Biology,* **20:** 3743-3755.

Gallinat AS, Primack RB & Wagner DL (2015): Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution,* **30:** 169-176.

Garcia-Serrano H, Sans F, X & Escarre J (2007): Interspecific competition between alien and native congeneric species. *Acta Oecologica,* **31:** 69-78.

REFERENCES

Garonna I, De Jong R, De Wit AJ, Mucher CA, Schmid B & Schaepman ME (2014): Strong contribution of autumn phenology to changes in satellite-derived growing season length estimates across Europe (1982-2011). *Global Change Biology,* **20:** 3457-3470.

Gaudet CL & Keddy PA (1988): A comparative approach to predicting competitive ability from plant traits. *Nature,* **334:** 242-243.

Gibson DJ, Connolly J, Hartnett DC & Weidenhamer JD (1999): Designs for greenhouse studies of interactions between plants. *Journal of Ecology,* **87:** 1-16.

Gilbert B & Levine JM (2013): Plant invasions and extinction debts. *Proceedings of the National Academy of Sciences of the United States of America,* **110:** 1744-1749.

Gioria M & Osborne BA (2014): Resource competition in plant invasions: Emerging patterns and research needs. *Frontiers in Plant Science,* **5:** 501.

Godbold D, Tullus A, Kupper P, *et al.* (2014): Elevated atmospheric CO_2 and humidity delay leaf fall in Betula pendula, but not in Alnus glutinosa or Populus tremula x tremuloides. *Annals of Forest Science,* **71:** 831-842.

Godfree RC, Robertson BC, Gapare WJ, Ivkovic M, Marshall DJ, Lepschi BJ & Zwart AB (2013): Nonindigenous plant advantage in native and exotic Australian grasses under experimental drought, warming, and atmospheric CO_2 enrichment. *Biology,* **2:** 481-513.

Godoy O, Valladares F & Castro-Diez P (2011): Multispecies comparison reveals that invasive and native plants differ in their traits but not in their plasticity. *Functional Ecology,* **25:** 1248-1259.

Goldberg DE & Werner PA (1983): Equivalence of competitors in plant communities - a null hypothesis and a field experimental approach. *American Journal of Botany,* **70:** 1098-1104.

Grabherr G, Gottfried M & Pauli H (1994): Climate effects on mountain plants. *Nature,* **369:** 448.

Grabherr G, Gottfried M & Paull H (2000): GLORIA: A global observation research initiative in alpine environments. *Mountain Research and Development,* **20:** 190-191.

Grime JP (1979): *Plant strategies and vegetation processes*. John Wiley & Son, Chichester, 222 pp.

Gurevitch J & Padilla DK (2004): Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution,* **19:** 470-474.

Haider S, Alexander J, Dietz H, Trepl L, Edwards PJ & Kueffer C (2010): The role of bioclimatic origin, residence time and habitat context in shaping non-native plant distributions along an altitudinal gradient. *Biological Invasions,* **12:** 4003-4018.

Harrington RA, Brown BJ & Reich PB (1989): Ecophysiology of exotic and native shrubs in southern Wisconsin. 1. Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. *Oecologia,* **80:** 356-367.

He Q, Bertness MD & Altieri AH (2013): Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters,* **16:** 695-706.

He WM, Thelen GC, Ridenour WM & Callaway RM (2010): Is there a risk to living large? Large size correlates with reduced growth when stressed for knapweed populations. *Biological Invasions,* **12:** 3591-3598.

Heide OM (1993): Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiologia Plantarum,* **88:** 531-540.

REFERENCES

Heide OM (2003): High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. *Tree Physiology,* **23:** 931-936.

Hellmann JJ, Byers JE, Bierwagen BG & Dukes JS (2008): Five potential consequences of climate change for invasive species. *Conservation Biology,* **22:** 534-543.

Hierro JL, Maron JL & Callaway RM (2005): A biogeographical approach to plant invasions: The importance of studying exotics in their introduced and native range. *Journal of Ecology,* **93:** 5-15.

Higgins SI & Richardson DM (1999): Predicting plant migration rates in a changing world: The role of long-distance dispersal. *American Naturalist,* **153:** 464-475.

Hobbs RJ, Higgs E & Harris JA (2009): Novel ecosystems: Implications for conservation and restoration. *Trends in Ecology & Evolution,* **24:** 599-605.

Holt RD (1990): The microevolutionary consequences of climate change. *Trends in Ecology & Evolution,* **5:** 311-315.

Hood WG & Naiman RJ (2000): Vulnerability of riparian zones to invasion by exotic vascular plants. *Plant Ecology,* **148:** 105-114.

Hubo C, Jumpertz E, Krott M, Nockemann L, Steinmann A & Bräuer I (2007): *Grundlage für die Entwicklung einer nationalen Strategie gegen invasive gebietsfremde Arten*. Bundesamt für Naturschutz, Bonn, 387 pp.

Hulme PE (2009): Relative roles of life-form, land use and climate in recent dynamics of alien plant distributions in the British Isles. *Weed Research,* **49:** 19-28.

Hulme PE (2011): Contrasting impacts of climate-driven flowering phenology on changes in alien and native plant species distributions. *New Phytologist,* **189:** 272-281.

Huntington TG (2006): Evidence for intensification of the global water cycle: Review and synthesis. *Journal of Hydrology,* **319:** 83-95.

Huston MA (1997): Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia,* **110:** 449-460.

Inouye DW (2008): Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology,* **89:** 353-362.

IPCC (2007): *Climate Change 2007: The physical science basis. Contribution of WG I to the fourth assessment report of the Intergovernmental Panel on Climate Change.* Cambridge Univ. Press, Cambridge, 996 pp.

IPCC (2013): *Climate Change 2013: The physical science basis. Contribution of WG I to the fifth assessment report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, 1552 pp.

IPCC (2014): *Climate Change 2014: Impacts, adaptation, and vulnerability. Contribution of WG II to the fifth assessment report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, New York, 1132 pp.

IUCN (2000): *IUCN Guidelines for the prevention of biodiversity loss caused by alien invasive species*. Gland, 24 pp.

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

REFERENCES

Jeschke JM (2014): General hypotheses in invasion ecology. *Diversity and Distributions,* **20:** 1229-1234.

Jimenez MA, Jaksic FM, Armesto JJ, Gaxiola A, Meserve PL, Kelt DA & Gutierrez JR (2011): Extreme climatic events change the dynamics and invasibility of semi-arid annual plant communities. *Ecology Letters,* **14:** 1227-1235.

Jochner S, Alves-Eigenheer M, Menzel A & Morellato LPC (2013a): Using phenology to assess urban heat islands in tropical and temperate regions. *International Journal of Climatology,* **33:** 3141-3151.

Jochner S, Caffarra A & Menzel A (2013b): Can spatial data substitute temporal data in phenological modelling? A survey using birch flowering. *Tree Physiology,* **33:** 1256-1268.

Jochner S, Höfler J, Beck I, Göttlein A, Ankerst DP, Traidl-Hoffmann C & Menzel A (2013c): Nutrient status: A missing factor in phenological and pollen research? *Journal of Experimental Botany,* **64:** 2081-2092.

Jolliffe PA (2000): The replacement series. *Journal of Ecology*, **88**: 371–385.

Jones H, Hillis R, Gordon S & Brennan R (2013): An approach to the determination of winter chill requirements for different Ribes cultivars. *Plant Biology,* **15:** 18-27.

Kattge J, Diaz S, Lavorel S, *et al.* (2011): TRY - a global database of plant traits. *Global Change Biology,* **17:** 2905-2935.

Keane RM & Crawley MJ (2002): Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution,* **17:** 164-170.

Keenan T, Baker I, Barr A, *et al.* (2012): Terrestrial biosphere model performance for inter-annual variability of land-atmosphere CO_2 exchange. *Global Change Biology,* **18:** 1971-1987.

Keenan TF & Richardson AD (2015): The timing of autumn senescence is affected by the time of spring phenology: Implications for predictive models. *Global Change Biology*, doi: 10.1111/gcb.12890 (in press).

Kettunen M, Genovesi P, Gollasch S, Pagad S, Starfinger U, ten Brink P & Shine C (2009): *Technical support to EU strategy on invasive alien species (IAS)*. Institute for Europen Environmental Policy, Brussels, 124 pp.

Klotz S, Kühn I & Durka W (2002): *BIOLFLOR - Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland*. Bundesamt für Naturschutz, Bonn, 333 pp.

Knapp S & Kühn I (2012): Origin matters: Widely distributed native and non-native species benefit from different functional traits. *Ecology Letters,* **15:** 696-703.

Kollas C, Koerner C & Randin CF (2014): Spring frost and growing season length co-control the cold range limits of broad-leaved trees. *Journal of Biogeography,* **41:** 773-783.

Kollmann J & Banuelos MJ (2004): Latitudinal trends in growth and phenology of the invasive alien plant Impatiens glandulifera (Balsaminaceae). *Diversity and Distributions,* **10:** 377-385.

Körner C & Basler D (2010): Phenology under global warming. *Science,* **327:** 1461-1462.

Körner C (2007): The use of 'altitude' in ecological research. *Trends in Ecology & Evolution,* **22:** 569-574.

Kovats RS, Valentini R, Bouwer LM, *et al.* (2014): Europe. In: *Climate Change 2014: Impacts, adaptation, and vulnerability. Part B: Regional aspects. Contribution of WG II to the fifth*

assessment report on the Intergovernmental Panel on Climate Change (eds. Barros VR, Field CB, Dokken DJ, et al.), pp. 1267-1326. Cambridge University Press, Cambridge, New York.

Kraft NJB, Cornwell WK, Webb CO & Ackerly DD (2007): Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist,* **170:** 271-283.

Kreyling J (2010): Winter climate change: A critical factor for temperate vegetation performance. *Ecology,* **91:** 1939-1948.

Kreyling J, Jentsch A & Beier C (2014): Beyond realism in climate change experiments: Gradient approaches identify thresholds and tipping points. *Ecology Letters,* **17:** 125-e1.

Kueffer C, Pyšek P & Richardson DM (2013): Integrative invasion science: Model systems, multi-site studies, focused meta-analysis and invasion syndromes. *New Phytologist,* **200:** 615-633.

Lambrinos JG (2004): How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology,* **85:** 2061-2070.

Laube J, Sparks TH, Estrella N & Menzel A (2014a): Does humidity trigger tree phenology? Proposal for an air humidity based framework for bud development in spring. *New Phytologist,* **202:** 350-355.

Laube J, Sparks TH, Estrella N, Höfler J, Ankerst DP & Menzel A (2014b): Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology,* **20:** 170-182.

Laube J, Ziegler K, Sparks TH, Estrella N & Menzel A (2015): Tolerance of alien plant species to extreme events is comparable to that of their native relatives. *Preslia,* **87:** 31-53.

Laughlin DC & Laughlin DE (2013): Advances in modeling trait-based plant community assembly. *Trends in Plant Science,* **18:** 584-593.

Laur J & Hacke U (2014): Exploring Picea glauca aquaporins in the context of needle water uptake and xylem refilling. *New Phytologist,* **203:** 388-400.

Lechowicz MJ (1984): Why do decidous temperate trees leaf out at different times? Adaptation and ecology of forest communities. *American Naturalist,* **124:** 821-842.

Lenz A, Hoch G, Vitasse Y & Körner C (2013): European deciduous trees exhibit similar safety margins against damage by spring freeze events along elevational gradients. *New Phytologist,* **200:** 1166-1175.

Lepš J (2005): Biodiversity and plant mixtures in agriculture and ecology. In: *Sward dynamics, N-flows and forage utilization in legume-based systems* (eds. Wachendorf M, Helgadóttir A, Parente G), pp. 13-20. ERSA, Gorizia.

Levine JM & D'Antonio CM (1999): Elton revisited: A review of evidence linking diversity and invasibility. *Oikos,* **87:** 15-26.

Levine JM, Adler PB & Yelenik SG (2004): A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters,* **7:** 975-989.

Limm EB, Simonin KA, Bothman AG & Dawson TE (2009): Foliar water uptake: A common water acquisition strategy for plants of the redwood forest. *Oecologia,* **161:** 449-459.

Lindner M, Maroschek M, Netherer S, *et al.* (2010): Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management,* **259:** 698-709.

REFERENCES

Linkosalo T & Lechowicz MJ (2006): Twilight far-red treatment advances leaf bud burst of silver birch (Betula pendula). *Tree Physiology,* **26:** 1249-1256.

Lipavská H, Svobodová H & Albrechtová J (2000): Annual dynamics of the content of non-structural saccharides in the context of structural development of vegetative buds of Norway spruce. *Journal of Plant Physiology,* **157:** 365-373.

Lockwood JL, Hoopes MF & Marchetti MP (2007): *Invasion Ecology.* Blackwell Publishing, Malden, 304 pp.

MacArthur R & Levins R (1967): Limiting similarity convergence and divergence of coexisting species. *American Naturalist,* **101:** 377-385.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M & Bazzaz FA (2000): Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications,* **10:** 689-710.

Maestre FT, Valladares F & Reynolds JF (2005): Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology,* **93:** 748-757.

Maestre FT, Callaway RM, Valladares F & Lortie CJ (2009): Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology,* **97:** 199-205.

Malcolm JR, Markham A, Neilson RP & Garaci M (2002): Estimated migration rates under scenarios of global climate change. *Journal of Biogeography,* **29:** 835-849.

Mangla S, Sheley RL, James JJ & Radosevich SR (2011): Intra and interspecific competition among invasive and native species during early stages of plant growth. *Plant Ecology,* **212:** 531-542.

Marini L, Bertolli A, Bona E, Federici G, Martini F, Prosser F & Bommarco R (2013): Beta-diversity patterns elucidate mechanisms of alien plant invasion in mountains. *Global Ecology and Biogeography,* **22:** 450-460.

Marion GM, Henry GHR, Freckman DW, *et al.* (1997): Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology,* **3:** 20-32.

Maron JL & Vilà M (2001): When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos,* **95:** 361-373.

Mason TJ, French K & Russell K (2012): Are competitive effects of native species on an invader mediated by water availability? *Journal of Vegetation Science,* **23:** 657-666.

Mayfield MM & Levine JM (2010): Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters,* **13:** 1085-1093.

Mayr S, Schmid P, Laur J, Rosner S, Charra-Vaskou K, Damon B & Hacke UG (2014): Uptake of water via branches helps timberline conifers refill embolized xylem in late winter. *Plant Physiology,* **164:** 1731-1740.

McDougall KL, Morgan JW, Walsh NG & Williams RJ (2005): Plant invasions in treeless vegetation of the Australian Alps. *Perspectives in Plant Ecology Evolution and Systematics,* **7:** 159-171.

McDougall KL, Alexander JM, Haider S, Pauchard A, Walsh NG & Kueffer C (2011): Alien flora of mountains: Global comparisons for the development of local preventive measures against plant invasions. *Diversity and Distributions,* **17:** 103-111.

REFERENCES

McGill BJ, Enquist BJ, Weiher E & Westoby M (2006): Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution,* **21:** 178-185.

Melaas EK, Richardson AD, Friedl MA, *et al.* (2013): Using FLUXNET data to improve models of springtime vegetation activity onset in forest ecosystems. *Agricultural and Forest Meteorology,* **171:** 46-56.

Menzel A & Fabian P (1999): Growing season extended in Europe. *Nature,* **397:** 659.

Menzel A, Estrella N & Fabian P (2001): Spatial and temporal variability of the phenological seasons in Germany from 1951 to 1996. *Global Change Biology,* **7:** 657-666.

Menzel A (2002): Phenology: Its importance to the global change community - an editorial comment. *Climatic Change,* **54:** 379-385.

Menzel A, Jakobi G, Ahas R, Scheifinger H & Estrella N (2003): Variations of the climatological growing season (1951-2000) in Germany compared with other countries. *International Journal of Climatology,* **23:** 793-812.

Menzel A, Sparks T, Estrella N & Roy D (2006a): Altered geographic and temporal variability in phenology in response to climate change. *Global Ecology and Biogeography,* **15:** 498-504.

Menzel A, Sparks TH, Estrella N, *et al.* (2006b): European phenological response to climate change matches the warming pattern. *Global Change Biology,* **12:** 1969-1976.

Migliavacca M, Sonnentag O, Keenan T, Cescatti A, O'Keefe J & Richardson A (2012): On the uncertainty of phenological responses to climate change, and implications for a terrestrial biosphere model. *Biogeosciences,* **9:** 2063-2083.

Migliavacca M, Reichstein M, Richardson AD, *et al.* (2011): Semiempirical modeling of abiotic and biotic factors controlling ecosystem respiration across eddy covariance sites. *Global Change Biology,* **17:** 390-409.

Min SK, Zhang X, Zwiers FW & Hegerl GC (2011): Human contribution to more-intense precipitation extremes. *Nature,* **470:** 378-381.

Mingo A (2014): Integrating importance and intensity: A novel approach to normalize measurement of neighbour effects. *Community Ecology,* **15:** 65-76.

Moles AT, Flores-Moreno H, Bonser SP, *et al.* (2012): Invasions: The trail behind, the path ahead, and a test of a disturbing idea. *Journal of Ecology,* **100:** 116-127.

Moran EV & Alexander JM (2014): Evolutionary responses to global change: Lessons from invasive species. *Ecology Letters,* **17:** 637-649.

Murray MB, Cannell MGR & Smith RI (1989): Date of budburst of 15 tree species in Britain following climatic warming. *Journal of Applied Ecology,* **26:** 693-700.

Nardini A, Lo Gullo MA & Salleo S (2011): Refilling embolized xylem conduits: Is it a matter of phloem unloading? *Plant Science,* **180:** 604-611.

Nathan R (2006): Long-distance dispersal of plants. *Science,* **313:** 786-788.

Niinemets U & Valladares F (2006): Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs,* **76:** 521-547.

Norby RJ, Edwards NT, Riggs JS, Abner CH, Wullschleger SD & Gunderson CA (1997): Temperature-controlled open-top chambers for global change research. *Global Change Biology,* **3:** 259-267.

REFERENCES

Olsson C & Jönsson AM (2014): Process-based models not always better than empirical models for simulating budburst of Norway spruce and birch in Europe. *Global Change Biology,* **20:** 3492-3507.

Paiaro V, Cabido M & Pucheta E (2011): Altitudinal distribution of native and alien plant species in roadside communities from central Argentina. *Austral Ecology,* **36:** 176-184.

Palacio-Lopez K & Gianoli E (2011): Invasive plants do not display greater phenotypic plasticity than their native or non-invasive counterparts: A meta-analysis. *Oikos,* **120:** 1393-1401.

Panchen ZA, Primack RB, Nordt B, *et al.* (2014): Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. *New Phytologist,* **203:** 1208-1219.

Parmesan C & Yohe G (2003): A globally coherent fingerprint of climate change impacts across natural systems. *Nature,* **421:** 37-42.

Pauchard A, Kueffer C, Dietz H, *et al.* (2009): Ain't no mountain high enough: Plant invasions reaching new elevations. *Frontiers in Ecology and the Environment,* **7:** 479-486.

Pauli H, Gottfried M, Reiter K, Klettner C & Grabherr G (2007): Signals of range expansions and contractions of vascular plants in the high Alps: Observations (1994-2004) at the GLORIA*master site Schrankogel, Tyrol, Austria. *Global Change Biology,* **13:** 147-156.

Peak D & Mott KA (2011): A new, vapour-phase mechanism for stomatal responses to humidity and temperature. *Plant Cell and Environment,* **34:** 162-178.

Pejchar L & Mooney HA (2009): Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution,* **24:** 497-504.

Peñuelas J, Filella I & Comas P (2002): Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology,* **8:** 531-544.

Peñuelas J, Rutishauser T & Filella I (2009): Phenology feedbacks on climate change. *Science,* **324:** 887-888.

Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C & Guisan A (2012): Climatic niche shifts are rare among terrestrial plant invaders. *Science,* **335:** 1344-1348.

Piao S, Ciais P, Friedlingstein P, *et al.* (2008): Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature,* **451:** 49-52.

Picard G, Quegan S, Delbart N, Lomas MR, Le Toan T & Woodward FI (2005): Bud-burst modelling in Siberia and its impact on quantifying the carbon budget. *Global Change Biology,* **11:** 2164-2176.

Pimentel D, McNair S, Janecka J, *et al.* (2001): Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture Ecosystems & Environment,* **84:** 1-20.

Pimentel D, Zuniga R & Morrison D (2005): Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics,* **52:** 273-288.

Polgar C, Gallinat A & Primack RB (2014): Drivers of leaf-out phenology and their implications for species invasions: Insights from Thoreau's Concord. *New Phytologist,* **202:** 106-115.

Polgar CA & Primack RB (2011): Leaf-out phenology of temperate woody plants: From trees to ecosystems. *New Phytologist,* **191:** 926-941.

Poorter H, Fiorani F, Stitt M, *et al.* (2012): The art of growing plants for experimental purposes: A practical guide for the plant biologist. *Functional Plant Biology,* **39:** 821-838.

REFERENCES

Primack RB, Laube J, Gallinat A & Menzel A (2015): From observations to experiments in phenology research: Investigating climate change impacts on trees and shrubs using dormant twigs. *Annals of Botany*, doi: 10.1093/aob/mcv032 (in press).

Pyšek P, Jarošík V & Kucera T (2002): Patterns of invasion in temperate nature reserves. *Biological Conservation,* **104:** 13-24.

Pyšek P & Jarošík V (2005): Residence time determines the distribution of alien plants. In: *Invasive Plants: Ecological and agricultural aspects* (ed. Inderjit M), pp. 77-96. Birkhäuser Verlag, Basel, Boston, Berlin.

Pyšek P & Richardson DM (2006): The biogeography of naturalization in alien plants. *Journal of Biogeography,* **33:** 2040-2050.

Pyšek P & Richardson DM (2007): Traits assiociated with invasiveness in alien plants. Where do we stand? In: *Biological Invasions* (ed. Nentwig W), pp. 97-125. Springer Verlag, Berlin, Heidelberg.

Pyšek P, Krivanek M & Jarošík V (2009a): Planting intensity, residence time, and species traits determine invasion success of alien woody species. *Ecology,* **90:** 2734-2744.

Pyšek P, Jarošík V, Pergl J, *et al.* (2009b): The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Diversity and Distributions,* **15:** 891-903.

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U & Vilà M (2012): A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. *Global Change Biology,* **18:** 1725-1737.

Pyšek P, Manceur AM, Alba C, *et al.* (2015): Naturalizations of central European plants in North America: Species traits, habitats, propagule pressure, residence time. *Ecology,* **96:** 762-774.

Rahbek C (1995): The elevational gradient of species richness - a uniform pattern. *Ecography,* **18:** 200-205.

Randin CF, Engler R, Normand S, *et al.* (2009): Climate change and plant distribution: Local models predict high-elevation persistence. *Global Change Biology,* **15:** 1557-1569.

Rejmánek M (1996): A theory of seed plant invasiveness: The first sketch. *Biological Conservation,* **78:** 171-181.

Rejmánek M & Richardson DM (1996): What attributes make some plant species more invasive? *Ecology,* **77:** 1655-1661.

Rejmánek M (2000): Invasive plants: Approaches and predictions. *Austral Ecology,* **25:** 497-506.

Reyer CP, Leuzinger S, Rammig A, *et al.* (2013): A plant's perspective of extremes: Terrestrial plant responses to changing climatic variability. *Global Change Biology,* **19:** 75-89.

Richards CL, Bossdorf O, Muth NZ, Gurevitch J & Pigliucci M (2006): Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters,* **9:** 981-993.

Richardson AD & O'Keefe J (2009): Phenological differences between understory and overstory: A case study using the long-term Harvard Forest records. In: *Phenology of Ecosystem Processes: Applications in Global Change Research* (ed. Noormets A), pp. 87-117. Springer, Dordrecht, Heidelberg, London, New York.

REFERENCES

Richardson AD, Black T, Ciais P, *et al.* (2010): Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Philosophical Transactions of the Royal Society B-Biological Sciences,* **365:** 3227-3246.

Richardson AD, Anderson RS, Arain MA, *et al.* (2012): Terrestrial biosphere models need better representation of vegetation phenology: Results from the North American Carbon Program Site Synthesis. *Global Change Biology,* **18:** 566-584.

Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O & Toomey M (2013): Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology,* **169:** 156-173.

Richardson DM & Bond WJ (1991): Determinants of plant distribution - evidence from Pine invasions. *American Naturalist,* **137:** 639-668.

Richardson DM, Pyšek P & Carlton JT (2011): A compendium of essential concepts and terminology in invasion ecology. In: *Fifty years of invasions ecology: The legacy of Charles Elton* (ed. Rieseberg LH), pp. 409-420. Wiley-Blackwell, Chichester.

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta F & West CJ (2000): Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions,* **6:** 93-107.

Richardson DM & Pyšek P (2008): Fifty years of invasion ecology - the legacy of Charles Elton. *Diversity and Distributions,* **14:** 161-168.

Ricklefs RE (2008): Disintegration of the ecological community. *American Naturalist,* **172:** 741-750.

Rinne P, Tuominen H & Junttila O (1994): Seasonal changes in bud dormancy in relation to bud morphology, water and starch content, and abscisic-acid concentration in adult trees of Betula pubescens. *Tree Physiology,* **14:** 549-561.

Rockwell FE, Wheeler JK & Holbrook NM (2014): Cavitation and its discontents: Opportunities for resolving current controversies. *Plant Physiology,* **164:** 1649-1660.

Rollinson CR & Kaye MW (2012): Experimental warming alters spring phenology of certain plant functional groups in an early successional forest community. *Global Change Biology,* **18:** 1108-1116.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C & Pounds JA (2003): Fingerprints of global warming on wild animals and plants. *Nature,* **421:** 57-60.

Rosenzweig C, Karoly D, Vicarelli M, *et al.* (2008): Attributing physical and biological impacts to anthropogenic climate change. *Nature,* **453:** 353-357.

Schelhaas MJ, Nabuurs GJ & Schuck A (2003): Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology,* **9:** 1620-1633.

Schwartz MD (1992): Phenology and springtime surface-layer change. *Monthly Weather Review,* **120:** 2570-2578.

Schwartz MD & Reiter BE (2000): Changes in North American spring. *International Journal of Climatology,* **20:** 929-932.

Schwinning S & Weiner J (1998): Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia,* **113:** 447-455.

Seidman G & Riggan WB (1968): Stomatal movements - a yearly rhythm. *Nature,* **217:** 684-685.

REFERENCES

Shea K & Chesson P (2002): Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution,* **17:** 170-176.

Sher AA & Hyatt LA (1999): The disturbed resource-flux invasion matrix: A new framework for patterns of plant invasion. *Biological Invasions,* **1:** 107-114.

Simberloff D (2006): Invasional meltdown 6 years later: Important phenomenon, unfortunate metaphor, or both? *Ecology Letters,* **9:** 912-919.

Skálová H, Moravcová L & Pyšek P (2011): Germination dynamics and seedling frost resistance of invasive and native Impatiens species reflect local climatic conditions. *Perspectives in Plant Ecology Evolution and Systematics,* **13:** 173-180.

Smith MD (2011): The ecological role of climate extremes: Current understanding and future prospects. *Journal of Ecology,* **99:** 651-655.

Søgaard G, Johnsen O, Nilsen J & Junttila O (2008): Climatic control of bud burst in young seedlings of nine provenances of Norway spruce. *Tree Physiology,* **28:** 311-320.

Sønsteby A & Heide OM (2014): Chilling requirements of contrasting black currant (Ribes nigrum L.) cultivars and the induction of secondary bud dormancy. *Scientia Horticulturae,* **179:** 256-265.

Sparks TH, Jeffree EP & Jeffree CE (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.

Sparks TH & Menzel A (2002): Observed changes in seasons: An overview. *International Journal of Climatology,* **22:** 1715-1725.

Sparks TH & Tryjanowski P (2005): The detection of climate impacts: Some methodological considerations. *International Journal of Climatology,* **25:** 271-277.

Strayer DL (2012): Eight questions about invasions and ecosystem functioning. *Ecology Letters,* **15:** 1199-1210.

Thackeray SJ, Sparks TH, Frederiksen M, *et al.* (2010): Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology,* **16:** 3304-3313.

Theoharides KA & Dukes JS (2007): Plant invasion across space and time: Factors affecting nonindigenous species success during four stages of invasion. *New Phytologist,* **176:** 256-273.

Theurillat JP & Guisan A (2001): Potential impact of climate change on vegetation in the European Alps: A review. *Climatic Change,* **50:** 77-109.

Thuiller W, Lavorel S, Araújo MB, Sykes MT & Prentice IC (2005): Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America,* **102:** 8245-8250.

Thuiller W, Richardson DM & Midgley GF (2007): Will climate change promote alien plant invasions? In: *Biological Invasions* (ed. Nentwig W), pp. 197-211. Springer, Berlin.

Thuiller W, Gallien L, Boulangeat I, de Bello F, Münkemüller T, Roquet C & Lavergne S (2010): Resolving Darwin's naturalization conundrum: A quest for evidence. *Diversity and Distributions,* **16:** 461-475.

Traveset A & Richardson DM (2006): Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution,* **21:** 208-216.

REFERENCES

Trinder CJ, Brooker RW & Robinson D (2013): Plant ecology's guilty little secret: Understanding the dynamics of plant competition. *Functional Ecology,* **27:** 918-929.

Valladares F, Matesanz S, Guilhaumon F, *et al.* (2014): The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters,* **17:** 1351-1364.

van Kleunen M, Dawson W, Schlaepfer D, Jeschke JM & Fischer M (2010a): Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters,* **13:** 947-958.

van Kleunen M, Weber E & Fischer M (2010b): A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters,* **13:** 235-245.

Verlinden M & Nijs I (2010): Alien plant species favoured over congeneric natives under experimental climate warming in temperate Belgian climate. *Biological Invasions,* **12:** 2777-2787.

Vilà M & Weiner J (2004): Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. *Oikos,* **105:** 229-238.

Vilà M, Corbin JD, Dukes JS, Pino J & Smith SD (2007): Linking plant invasions to global environmental change. In: *Terrestrial ecosystems in a changing world* (eds. Canadell J, Pataki D, Pitelka L), pp. 115-124. Springer, Berlin.

Vilà M, Basnou C, Pyšek P, *et al.* (2010): How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment,* **8:** 135-144.

Vilà M, Espinar JL, Hejda M, *et al.* (2011): Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters,* **14:** 702-708.

Vitasse Y, Delzon S, Dufrene E, Pontailler JY, Louvet JM, Kremer A & Michalet R (2009): Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? *Agricultural and Forest Meteorology,* **149:** 735-744.

Vitasse Y (2013): Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytologist,* **198:** 149-155.

Vitasse Y & Basler D (2013): What role for photoperiod in the bud burst phenology of European beech. *European Journal of Forest Research,* **132:** 1-8.

Vitasse Y & Basler D (2014): Is the use of twigs a good proxy to explore phenological responses of temperate forests in warming and photoperiod experiments? *Tree Physiology,* **34:** 174-183.

Vitasse Y, Lenz A & Körner C (2014a): The interaction between freezing tolerance and phenology in temperate deciduous trees. *Frontiers in Plant Science,* **5:** 541.

Vitasse Y, Lenz A, Hoch G & Körner C (2014b): Earlier leaf-out rather than difference in freezing resistance puts juvenile trees at greater risk of damage than adult trees. *Journal of Ecology,* **102:** 981-988.

Vitousek PM, Mooney HA, Lubchenco J & Melillo JM (1997): Human domination of Earth's ecosystems. *Science,* **277:** 494-499.

Walther GR, Post E, Convey P, *et al.* (2002): Ecological responses to recent climate change. *Nature,* **416:** 389-395.

REFERENCES

Walther GR (2004): Plants in a warmer world. *Perspectives in Plant Ecology Evolution and Systematics,* **6:** 169-185.

Walther GR, Roques A, Hulme PE, *et al.* (2009): Alien species in a warmer world: Risks and opportunities. *Trends in Ecology & Evolution,* **24:** 686-693.

Walther GR (2010): Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B-Biological Sciences,* **365:** 2019-2024.

Wang Q, Fan X & Wang M (2014): Recent warming amplification over high elevation regions across the globe. *Climate Dynamics,* **43:** 87-101.

Webb CO, Ackerly DD, McPeek MA & Donoghue MJ (2002): Phylogenies and community ecology. *Annual Review of Ecology and Systematics,* **33:** 475-505.

Webber BL & Scott JK (2012): Rapid global change: Implications for defining natives and aliens. *Global Ecology and Biogeography,* **21:** 305-311.

Webber BL, Le Maitre DC & Kriticos DJ (2012): Comment on "Climatic niche shifts are rare among terrestrial plant invaders". *Science,* **338:** 193.

Weigelt A & Jolliffe P (2003): Indices of plant competition. *Journal of Ecology,* **91:** 707-720.

Welling A, Rinne P, Vihera-Aarnio A, Kontunen-Soppela S, Heino P & Palva ET (2004): Photoperiod and temperature differentially regulate the expression of two dehydrin genes during overwintering of birch (Betula pubescens Ehrh.). *Journal of Experimental Botany,* **55:** 507-516.

Welling A & Palva ET (2006): Molecular control of cold acclimation in trees. *Physiologia Plantarum,* **127:** 167-181.

Westhoff M, Schneider H, Zimmermann D, *et al.* (2008): The mechanisms of refilling of xylem conduits and bleeding of tall birch during spring. *Plant Biology,* **10:** 604-623.

White TA, Campbell BD, Kemp PD & Hunt CL (2001): Impacts of extreme climatic events on competition during grassland invasions. *Global Change Biology,* **7:** 1-13.

Whitney KD & Gabler CA (2008): Rapid evolution in introduced species, 'invasive traits' and recipient communities: Challenges for predicting invasive potential. *Diversity and Distributions,* **14:** 569-580.

Wilcove DS, Rothstein D, Dubow J, Phillips A & Losos E (1998): Quantifying threats to imperiled species in the United States. *Bioscience,* **48:** 607-615.

Willett KM, Jones PD, Thorne PW & Gillett NP (2010): A comparison of large scale changes in surface humidity over land in observations and CMIP3 general circulation models. *Environmental Research Letters,* **5:** 1-13.

Williams JW, Jackson ST & Kutzbacht JE (2007): Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America,* **104:** 5738-5742.

Williamson M, Dehnen-Schmutz K, Kuehn I, *et al.* (2009): The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. *Diversity and Distributions,* **15:** 158-166.

Willis CG, Ruhfel B, Primack RB, Miller-Rushing AJ & Davis CC (2008): Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences of the United States of America,* **105:** 17029-17033.

REFERENCES

Willis CG, Ruhfel BR, Primack RB, Miller-Rushing AJ, Losos JB & Davis CC (2010): Favorable climate change response explains non-native species' success in Thoreau's woods. *Plos One,* **5:** e8878.

Willis SG & Hulme PE (2002): Does temperature limit the invasion of Impatiens glandulifera and Heracleum mantegazzianum in the UK? *Functional Ecology,* **16:** 530-539.

Wilsey BJ, Barber K & Martin LM (2015): Exotic grassland species have stronger priority effects than natives regardless of whether they are cultivated or wild genotypes. *New Phytologist,* **205:** 928-937.

Wolkovich E, Cook B, I, McLauchlan K & Davies T (2014): Temporal ecology in the Anthropocene. *Ecology Letters,* **17:** 1365-1379.

Wolkovich EM, Cook BI, Allen JM, *et al.* (2012): Warming experiments underpredict plant phenological responses to climate change. *Nature,* **485:** 494-497.

Wolkovich EM & Cleland EE (2014): Phenological niches and the future of invaded ecosystems with climate change. *Aob Plants,* **6:** plu013.

Wolkovich EM & Cleland EE (2011): The phenology of plant invasions: A community ecology perspective. *Frontiers in Ecology and the Environment,* **9:** 287-294.

Xu CY, Griffin KL & Schuster W (2007): Leaf phenology and seasonal variation of photosynthesis of invasive Berberis thunbergii (Japanese barberry) and two co-occurring native understory shrubs in a northeastern United States deciduous forest. *Oecologia,* **154:** 11-21.

Yooyongwech S, Horigane AK, Yoshida M, Yamaguchi M, Sekozawa Y, Sugaya S & Gemma H (2008): Changes in aquaporin gene expression and magnetic resonance imaging of water status in peach tree flower buds during dormancy. *Physiologia Plantarum,* **134:** 522-533.

Zimmermann NE, Yoccoz NG, Edwards TC, *et al.* (2009): Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences of the United States of America,* **106:** 19723-19728.

Zimmermann U, Schneider H, Wegner LH & Haase A (2004): Water ascent in tall trees: Does evolution of land plants rely on a highly metastable state? *New Phytologist,* **162:** 575-615.

Zohner CM & Renner SS (2014): Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. *Ecology Letters,* **17:** 1016-1025.

Zwieniecki MA & Holbrook N (2009): Confronting Maxwell's demon: Biophysics of xylem embolism repair. *Trends in Plant Science,* **14:** 530-534.

7 Acknowledgements

ACKNOWLEDGEMENTS

Christoph Schleip, Susanne Schnitzer, Christian Schunk, Dr. Christina Schuster, Hannes Seidel, Dr. Steffen Taeger, Dr. Clemens Wastl, Dr. Chiara Ziello, Nik Hofmann and Toni Knötig for the good working atmosphere and their helpfulness regarding technical and scientific questions. I thank Brigitte Fleischner for her help regarding administrative matters, and the team of TUM-IAS for their support, generosity and trust "Could you please add an explanation for what kind of analysis you need the wine?" (refers to an invoice for 1.300 bottles named Bordeaux).

Last but not least, I thank my family for supporting me throughout my thesis, listening to and discussing about twigs, invasive species, and climate change. Particularly, to Michael for his incredible patience, love, and maintaining a good mood no matter what.

Appendix

A List of focal species

Type	Status	Species	Chapter
Woody species	invasive	*Acer negundo* L.	3.1
		Aesculus hippocastanum L.	3.1
		Amorpha fruticosa L.	3.1
		Cornus alba L.	3.1
		Fraxinus pennsylvanica Marshall	3.1
		Juglans regia L.	3.1
		Pinus nigra subsp. nigra J. F. Arnold	3.1
		Pinus strobus L.	3.1
		Prunus serotina Ehrh.	3.1
		Pseudotsuga menziesii (Mirb.) Franco	3.1
		Quercus rubra L.	3.1
		Robinia pseudoacacia L.	3.1, 3.2
		Symphoricarpos albus (L.) S. F. Blake	3.1, 3.2
		Syringa vulgaris L.	3.1, 3.2
	native	*Abies alba* Mill.	3.1
		Acer pseudoplatanus L.	3.1, 3.2
		Betula pendula Roth	3.1, 3.2
		Carpinus betulus L.	3.1
		Cornus mas L.	3.1, 3.2
		Corylus avellana L.	3.1
		Fagus sylvatica L.	3.1, 3.2
		Fraxinus excelsior L.	3.1
		Larix decidua Mill.	3.1, 3.2
		Picea abies (L.) H. Karst.	3.1, 3.2
		Pinus sylvestris L.	3.1
		Populus tremula L.	3.1, 3.2
		Prunus avium L.	3.1
		Quercus robur L.	3.1, 3.2
	exotic, non-invasive	*Abies homolepis* Siebold & Zucc.	3.1
		Acer saccharum Marshall	3.1
		Acer tataricum L.	3.1
		Fraxinus chinensis Roxburgh	3.1
		Juglans ailantifolia Carrière	3.1
		Juglans cinerea L.	3.1
		Pinus wallichiana A.B. Jackson	3.1
		Quercus bicolor Willd.	3.1

APPENDIX

Type	Status	Species	Chapter
Herbs	invasive	*Ambrosia artemisiifolia* L	3.3
		Hieracium aurantiacum L.	3.3
		Lysimachia punctata L.	3.3
	native	*Achillea millefolium* L.	3.3
		Hieracium pilosella L.	3.3
		Lysimachia vulgaris L.	3.3
	invasive	*Impatiens glandulifera* Royle	3.4
		Impatiens parviflora DC.	3.4
	native	*Impatiens noli-tangere* L.	3.4

B List of publications, conference contributions, and teaching

B1 List of publications

Peer-Reviewed

Primack RB, **Laube J**, Gallinat A, Menzel A (2015): From observations to experiments in phenology research: Investigating climate change impacts on trees and shrubs using dormant twigs. *Annals of Botany* (Viewpoint article, in press).

Laube J, Ziegler K, Sparks TH, Estrella N, Menzel A (2015)*: Tolerance of alien plant species to extreme events is comparable to that of their native relatives. *Preslia,* 87(1): 31-53.

Laube J, Sparks TH, Estrella N, Menzel A (2014)*: Does humidity trigger tree phenology? Proposal for an air humidity based framework for bud development in spring. *New Phytologist,* 202(2): 350-355 (Letter).

Laube J, Sparks TH, Estrella N, Höfler J, Ankerst DP, Menzel A. (2014)*: Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology,* 20(1): 170-182.
With contribution of the issue's cover picture. ISI highly cited paper (top 1% in Environment/Ecology).

Submitted for Peer-Review

Laube J, Sparks TH, Bässler C, Menzel A (submitted to *Biological Conservation*)*: Small differences in seasonal and thermal niches influence elevational limits of native and invasive Balsams.

Laube J, Sparks TH, Menzel A, Heibl C, Müller J, Bässler C (submitted to *Journal of Vegetation Science*)*: Beyond thermal niches; the vulnerability of montane plant species to climate change.

In preparation

Jochner S, Sparks TH, **Laube J**, Menzel A: Can we detect a nonlinear response to temperature in European plant phenology?

 (* These five publications are part of this thesis.)

Other publications

Laube J, Thole A, Kramer C, Menzel A (2014): Es lenzt nicht, ehe es gewintert hat. *Phänologie-Journal des DWD*, Nr. 42, Juli 2014, pp. 6-8.

Schlumprecht H, **Laube J** (2012): Monitoring biodiversity of the Thuringian Green Belt. In: Marschall I, Gather M & Müller M (eds.): *Proceedings of the 1st GreenNet Conference*, 31st of January 2012, Erfurt, pp. 33-44.

Laube J (2011): Evaluating short-term effects of restoration using a chronosequence approach on bogs in northern Bavaria. *Aspects of Applied Biology,* 108: Vegetation Management, pp. 255-258.

Laube J (2009): Die Revitalisierung der Moore im Steinwald. *Ornithologischer Anzeiger* 48 (1), pp. 36-42.

Gerstberger P, **Laube J** (2007): Die Erstellung des Zwischenberichts zur Verbreitung der Gefäßpflanzenarten in Nordostbayern. In: Gerstberger P & Vollrath H (eds.): Flora Nordostbayerns. Verbreitungsatlas der Farn- und Blütenpflanzen. Zwischenbericht. Stand Dezember 2006. *Naturwissenschaftliche Gesellschaft Bayreuth, Beihefte zu den Berichtsbänden*, Heft 6/2007, pp. 3-9.

B2   Conference contributions

Talks

Laube J, Sparks TH, Menzel A, Bässler C (2014): Expected impacts of climate change on montane plant species in the National Park Bavarian Forest. 8. BIOMET-Tagung. Dresden, Germany. 02.12.-03.12.2014.

Laube J, Sparks TH, Estrella N, Menzel A (2014): Heat or humidity, which triggers tree phenology? EGU 2014. Vienna, Austria. 28.04.-02.05.2014.

Laube J (2013): Species diversity and climate change at mountain ranges. The Leichhardt Symposium on Biodiversity and Conservation. Brisbane, Australia. 23.-24.10.2013.

Laube J, Sparks TH, Estrella N, Höfler J, Ankerst DP, Menzel A (2013): Chilling × Photoperiod – a full factorial experiment on the spring phenology of trees. ClimTree 2013: International Conference on Climate Change and Tree Responses in Central European Forests. Zürich, Switzerland. 01.-05.09.2013.

Laube J, Sparks TH, Estrella N, Menzel A (2013): Air humidity: a missing factor in current research? 7th Annual Meeting of the Specialist Group for Macroecology of the Ecological Society of Germany, Austria and Switzerland (GfÖ). Göttingen, Germany. 13.-15.03.2013.

Laube J, Sparks TH, Menzel A** (2012): Does life-strategy matter in springtime? Phenology 2012. Wisconsin, USA. 10.-13.09.2012.

Laube J, Sparks TH**, Menzel A (2012): Moist and green? Phenology 2012. Wisconsin, USA. 10.-13.09.2012.

Laube J, Sparks TH, Bässler C, Menzel A (2012): How Balsams get to the top. A trade-off between adaptation and interaction. NEOBIOTA 2012 – Halting biological invasions in Europe: from data to decisions. Pontevedra, Spain. 12.-14.09.2012.

Laube J, Sparks TH, Menzel A (2012): Response of alien plant species to climatic trends. 6th Annual Meeting of the Specialist Group for Macroecology of the Ecological Society of Germany, Austria and Switzerland (GfÖ). Frankfurt a.M., Germany. 29.02.-02.03.2012.

Grebmayer T, **Laube J****, Birkel I, Moder F (2009): Strategisches Durchgängigkeitskonzept Bayern. 10. Bayerisches Wasserforum. München, Germany. 29.10.2009.

Laube J, Gerstberger P (2007): Die Revitalisierung der Moore im Steinwald. ANL-Fachtagung „Grenzüberschreitender Biotopverbund für Raufußhühner im Mittelgebirge". Friedenfels, Germany. 08.-09. 11.2007.

(** Speaker, if other than first author.)

Posters

Bock A, Jochner S, **Laube J**, Sparks TH, Menzel A (2014): Focus Group Global Change: Climate change impacts on spring phenology. TUM-IAS General Assembly 2014. TUM-IAS, Garching, Germany, 10.04.2014.

Laube J (2012): Alien plant species in habitats of conservational value. Student Conference on Conservation Science 2012. Cambridge, Great Britain. 20.03.-22.03.2012.

Laube J, Sparks TH, Menzel A (2011): Will alien species retain their competitive superiority following climate change? 11th International Conference on the Ecology and Managament of Alien Plant Invasions - EMAPI 2011. Szombathely, Hungary. 30.08.-03.09.2011.

Laube J (2011): Evaluating short-term effects of restoration using a chronosequence approach on bogs in northern Bavaria. Vegetation Managament, Association of Applied Biologists. Sheffield, Great Britain. 27.-28.04.2011.

Bertermann, D, **Laube J**, Roßner R, Schlumprecht H (2008): Optimierung der Abfluss-Regulation in Einzugsgebieten von Mittelgebirgen unter dem Aspekt des natürlichen Hochwasserrückhaltes. 5. Marktredwitzer Bodenschutztage. Marktredwitz, Germany. 08.-10.10.2008.

B3   Invited talks

Laube J (2014): Frühjahrsphänologie von Bäumen im Klimawandel - Faktoren, Prognosen, Experimente. Phänologie – Kolloquium, Bayerische Landesanstalt für Weinbau und Gartenbau (LWG). Veitshöchheim, Germany. 25.11.2014.

Laube J (2014): Invasive alien species in natural and semi-natural habitats in Bavaria. Seminar talk, Systematic Botany, LMU München. München, Germany. 12.11.2014.

Laube J (2014): Is moisture a limiting factor of spring phenology? Phenology meeting, Systematic Botany, LMU München. München, Germany. 16.09.2014.

Jochner S, **Laube J** (2014): Global Change: Advances in Phenological Research. TUM-IAS General Assembly 2014. TUM-IAS, Garching, Germany. 10.04.2014.

Laube J (2013): How climate change alters the timing of spring growth in forests. Scientists Meet Scientists – Wednesday Coffee Talk. TUM-IAS, Garching, Germany. 18.12.2013.

Laube J (2013): Invasive Springkräuter auf dem Weg zum Lusen? Wissenschaftliche Vortragsreihe des Nationalparks Bayerischer Wald. St. Oswald, Germany. 12.12.2013.

Laube J (2013): Some new ideas on chilling, photoperiod, and temperature influence on the spring phenology of trees. Seminar talk, Laboratoire d'Ecologie Alpine (LECA). CNRS Grenoble. France. 05.12.2013.

Laube J (2013): Invasive plant species, Competition, and Climate Change. Seminar talk, Working Group Invasion Ecology. TUM, Freising, Germany. 18.02.2013.

B4   Teaching

Supervision

Einfluss von Gewebefeuchte und Luftfeuchte auf die phänologische Frühjahrsentwicklung temperater Baumarten. Sarah Bauer, Master thesis in „Umweltplanung und Ingenieurökologie", Technische Universität München, in progress.

Frühjahrsphänologie und Spätfrostgefährdung der Stadtbaumarten „Stadtgrün 2021". Angela Funk, Bachelor thesis in „Agrar- und Gartenbauwissenschaften", Technische Universität München, in progress.

Die Verschiebung der phänologischen Phasen potentieller Nahrungspflanzen des Rehs (*Capreolus capreolus* L.), während der Setzzeit, als Folge des Klimawandels und die damit verbundene zeitliche Änderung der Nahrungsquantität und -qualität. Benjamin Stahl, Master thesis in „Forst- und Holzwissenschaft", Technische Universität München, in progress.

Simultaneous shifts in seasonal occurrences of eight butterfly species and their fodder plants in southern Germany. Hanna Weber, Master thesis in „Umweltplanung und Ingenieurökologie", Technische Universität München, 04/2015.

Do invasive species cope better with climatic stresses? Kathrin Ziegler, Master thesis in "Sustainable Resource Managament", Technische Universität München, 05/2013.

Experimentelle Analyse des Knospenaustriebsverhaltens ausgewählter Baumarten hinsichtlich ihres Ursprungs. Anja Thole, Bachelor thesis in „Forstwissenschaft und Ressourcenmanagement", Technische Universität München, 05/2012.

APPENDIX

Experimentelle Untersuchung der Frühjahrsphänologie von Pionier- und Klimaxbaumarten bei differierenden Photoperioden. Clemens Kramer, Bachelor thesis in „Forstwissenschaft und Ressourcenmanagement", Technische Universität München, 06/2012.

Lectures

Kurzeinführung in R für Master-Studenten. Ecoclimatology, Technische Universität München 2014.

Invasionsökologie. Vorlesung Landschaftsökologie. Katholische Universität Eichstätt 2012 & 2014. Invited lecturer.

Invasive Arten & Klimawandel. Ringvorlesung Ursachen & Auswirkungen des Klimawandels. Technische Universität München 2012-2015. Part of lecturer team, including statistical lecture and exam.